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VIII—On Diencephalic and Mesencephalic Nuclei and Fibre Paths in the Brains of Three Deep Sea Fish

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[Plate 28]

Contents

1—Introduction

Although a number of excellent papers have appeared on the brains of teleosts in general, very few studies have been reported on the brains of deep sea fish. A

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* Part of this work was performed while the author was a Fellow of the Rockefeller Foundation at Yale University.

paper by Trojan (1906) gives but a superficial survey, while that by Gierse (1904) deals primarily with the external form of the brain, the accessory organs of the brain, and the peripheral cranial nerves.

The purpose of this investigation is to present a somewhat detailed description of the cell areas and fibre pathways, especially of the diencephalon and mesencephalon, the object being to determine what modifications have taken place in connection with their unusual environment.

Very little is known about the natural history of these fish. In a personal communication concerning them, Professor Burr says, " The *Diaphus dumerili* were collected by the Bingham Oceanographic Expedition off the Cat Islands, the Bahamas, in 1927. Of these there are six specimens, Bingham Collection Nos. 9, 21, 36, 37, 38, and 39. The two *Saurida suspicio*, Bingham Collection Nos. 19 and 40, were collected also off Cat Island, the Bahamas. The *Bathypterois articolar phenox* is a very rare specimen ; it was collected at N. 20°—16′ W. 71°—18′, at a depth of from 900—945 fathoms, also in 1927."

The report concerns the brains of three deep sea fish, *Diaphus*, *Bathypterois*, and *Saurida*, all belonging to the order Iniomi. The *Diaphus* material consists of serial sections stained by the Weigert and the Weigert-Pal methods, four sets cut in the transverse plane, one in the sagittal and one in the horizontal plane. A single series of the *Bathypterois* brain, stained by iron hæmatoxylin and cut in the transverse plane, and two series of *Saurida*, one stained by the Weigert method and one by iron hæmatoxylin, both cut in the transverse plane, were available. Many series of other fish were used for comparative purposes, most of the latter belonging to the Central Institute for Brain Research.

The writer is particularly grateful to Professor Burr, of Yale University, for suggesting this problem, to Professor Kappers, the director, and to Dr. Addens, the assistant director of the Amsterdam Central Institute for Brain Research, for their interest and criticism.

This study was made possible through the co-operation of the Blossom Fund and the Bingham Oceanographic Collection of Yale University.

II—General Form

Although all three of these fish belong to the order Iniomi, the brain of each varies from the others in important respects. The *Diaphus* brain is relatively large and well developed in most of its parts, *i.e.*, olfactory (of which a description is not included in this paper), optic, auditory (especially the lateral line system, enormously hypertrophied), gustatory, and equilibratory. The brain of *Bathypterois* is smaller than those of the other two, though the fish itself is larger, because of the very poor development of the optic system, which is decidedly atrophic. The olfactory system is well developed, like that of *Diaphus* ; the auditory system is exceedingly large, and the gustatory system is not hypertrophied. The *Saurida* brain has a moderately well-developed olfactory system, a large optic system, and poorly developed auditory and gustatory systems.

An examination of the gross brain of *Diaphus*, fig. 1, Plate 28, shows its general form. The dorsal view shows the large cerebellum protruding forward, pushing the optic tecta laterally. The very large auditory tubercles extend forward and their rostral ends surround the caudal part of the cerebellum. The ventral surface shows the lobi inferiores and the conspicuous transverse commissure just caudal to the optic chiasm. The lateral view shows the auditory region especially well.

The epiphysis and also the paraphysis are identifiable in all three of the fish. The epiphysis in *Saurida* and *Bathypterois* extends far rostrally above the fore-brain. The paraphysis in *Bathypterois*, fig. 12, is especially large, very glandular, and also very vascular. In this figure the epiphysis is directly above the paraphysis.

Although DAMMERMAN (1910) has a paper entitled " Der Saccus vasculosus der Fische ein Tiefeorgan," nothing was observed in these deep sea fish to substantiate such a viewpoint. In fact, the saccus in these fish is rather small.

A description of the nucleus preopticus is not included in this paper, as nothing new was observed. CHARLTON (1932) has written an excellent paper on this region, including in his study some deep sea fish.

III—DIENCEPHALON

1 NUCLEUS HABENULARIS, figs. 2, 13, N.H.

The habenular nuclei are present in their usual places in the brains of *Diaphus*, *Saurida*, and *Bathypterois*, and are especially conspicuous in the *Bathypterois* brain due to the great reduction of the optic tectum. GIERSE (1904, p. 22) noted that the right habenular ganglion was larger than the left in the deep sea fish *Cyclothone*. HOLMGREN found marked asymmetry in the habenulæ of *Osmerus* and discusses its significance (1920, pp. 250-252). In the brains under consideration, asymmetry is most marked in *Bathypterois* (fig. 13) where the right nucleus is 25% larger than the left. KAPPERS (1906, p. 32) described the cells in the habenulæ of *Lophius* as consisting of an anterior group, more laterally placed, and a posterior group, located more medially. SHELDON (1912, p. 201, carp) found the cells in groups or islands. In the deep sea fish brains considered in this study, the cells of the habenulæ are round and uniformly small, very compact around the periphery, leaving a clear centre with a few islands of cells.

Connections

The brains used in this study are not especially good for unravelling the habenular complex. The tracts of the habenular system have been fully studied in teleosts by KAPPERS (1906), SHELDON (1912), and by TUGE (1929), and will not be described in this paper. The fasciculus retroflexus, which was found in its usual position, is labelled in figs. 3–8, 14.

2 *EMINENTIA THALAMI ANTERIOR*, figs. 2, 3, E.T.

The eminentia thalami of this description corresponds to that described by Kuhlenbeck (1929), Jeener (1930, *Idus idus*, *Clupea harengus*, *Osmerus eperlanus*, *Mormyrus caschive*). Jeener called attention to the fact that this is most probably the homologue of the eminentia thalami described by Herrick (1917) in the urodele amphibians. In a comparative study of this region, Jeener (1930) failed to find a differentiated eminentia thalami in the Crossopterygii, in the Dipnoi, in the Chondrostei, nor in the Holostei. In *Polypterus bichir* he found the subhabenular area occupied by a differentiated pars dorsalis, and a pars ventralis thalami. In the dipnoan *Protopterus annectens*, Jeener (1930, fig. 2) demonstrated what he considers as a greatly enlarged pars dorsalis thalami ; however, Kuhlenbeck (1929) and Gerlach (1933) appear not to agree with this interpretation.

The eminentia thalami of the *Diaphus* brain will be described, as it is very highly developed in this teleost, figs. 2–3. In Weigert preparations the eminentia is sharply differentiated from the relatively clear adjacent areas by its rich fibrocellular structure and deeply stained neuropil. Rostrally, the eminentia thalami protrudes from under the nucleus habenularis into the posterior pole of the cerebral hemisphere. The cephalic end of the eminentia is capped by the abundant fibres of the fasciculus medialis of the tractus opticus. The part of the fasciculus that goes to the eminentia thalami will be called " the fasciculus opticus ad eminentia."

The rostral end of the eminentia is separated from the ventricle by a broad area that is nearly free of cells or myelinated fibres. In passing caudally, the eminentia shifts medially and is only separated from the ventricle by a thin cellular area, the nucleus ventricularis diencephali. Ventrally, the eminentia is bounded by the medial and the lateral fore-brain bundles. The rostrolateral border is bounded by the optic tract fibres. From above it receives most of the pars ventralis of the posterior commissure. It is also in contact above with the rostral projection of the nucleus tegmenti motorius dorsalis. Caudally, a rostral wedge of the pars dorsalis thalami (segmentum internum of Brickner, 1929) projects between the eminentia and the nucleus tegmenti motorius dorsalis. This latter relationship is beautifully demonstrated in the paramedian sections. The posterior end of the eminentia is bounded above by the sulcus medius. Caudally, the eminentia is separated from the pars ventralis thalami by a long cell-free region. These two areas are, however, connected by the very large fasciculus descendens of Brickner (1929). Jeener (1930, p. 765) also observed an area separating the two that had very few cells.

The material (Weigert and Weigert-Pal) is unsuitable for studying the morphology of the cells or their arrangement. Jeener (1930, p. 10) found the cells of the eminentia thalami arranged in vertical strata. The cells in *Diaphus* are large and round, or oval, with no definite arrangement. Along the inner border there are some smaller round cells similar to the ventricular cells. Although the entire eminentia contains many myelinated fibres, they are more concentrated rostrally in the outer half, fig. 3. In the caudal region, the fibres become compact and form the fasciculus descendens. There is no histological evidence to indicate any functional differentiation in the eminentia, although on the basis of its fibre connections it might be suggested that the rostral part is primarily receptive and the caudal end effective.

An interesting feature noted in the eminentia thalami is the high degree of vascularization as compared with that of the adjacent areas.

In the brain of *Saurida* there is a poorly defined eminentia thalami. The rostral end receives some optic fibres, and, emerging from the caudal end, there is a feebly developed fasciculus descendens. In the brain of *Bathypterois* no optic fibres enter the subhabenular region ; also, there is no evidence of a differentiated eminentia thalami.

Connections

(1) *Fasciculus opticus ad eminentia*, fig. 2, F.O.-E.T.—Immediately after crossing, the optic tract splits into a broad lateral system of fibres that goes to the optic tectum, and a smaller, medial part, that courses dorsally into the subhabenular area. The bundle to the subhabenular region spreads out forming a dense area of medullated fibres that invade the anterior end of the eminentia thalami. Rostrally, these fibres are concentrated in the lateral half of the eminentia, but they gradually spread out in the more caudal sections. This optic fasciculus contributes most of the fibres seen in the rich fibrocellular area of the eminentia thalami. The fasciculus opticus ad eminentia appears to be only part of a broad system of fibres, the fasciculus medialis tractus optici of Jansen (1929). Some of these fibres reach the nucleus tegmenti motorius dorsalis of Brickner (1929), and the more caudal ones enter the optic tectum. This fasciculus clearly is not the fibræ ab optico in nucleum ventralem described by Brickner (1929, figs. 13–20, p. 263).

(2) *Olfactory connections*—The eminentia thalami is under the influence of olfactory impulses. Jeener (1930, p. 11) described connections between the stria medullaris and the eminentia, and between the nucleus habenularis and the eminentia. The *Diaphus* material confirms the findings of Jeener, and in addition it suggests that some of the fibres from the underlying fasciculus lateralis telencephali may also enter the lower part of the eminentia.

(3) *Fasciculus preopticus ad eminentia*, fig. 2, F.P.-E.T.—From the ventrolateral part of the nucleus preopticus, pars parvocellularis, there emerge thin myelinated fibres that join the fibres of the fasciculus opticus ad eminentia. These preoptic fibres, with those from the optic system, enter the rostral end of the eminentia.

(4) *Short connections*—These consist of short, poorly medullated fibres which pass between the medial border of the eminentia thalami and the cells of the nearby nucleus ventricularis diencephali. In reptiles the various periventricular diencephalic and mesencephalic centres are brought into relationship with each other and with the optic tectum by a highly elaborated system of periventricular fibres (Huber and Crosby, 1926, 1933, Cairney, 1926, Shanklin, 1930). However, a careful examination of the present material reveals no similar system in the fish brain.

(5) *Fibræ a nucleo dorsale in eminentiam thalami*—Many fibres pass between the dorsorostral part of the eminentia thalami and the ventrorostral part of the nucleus

tegmenti motorius dorsalis. These centres are also connected to each other by the pars ventralis of the posterior commissure, which is intimately associated with both centres. Nothing was observed that indicated the direction of conduction.

(6) *Fibræ a tecto in eminentiam thalami*—These fibres represent but part of a larger system of efferent tectal fibres, the fibræ tectales nervi optici of Jansen (1929) and of Charlton (1933), which are described under the connections of the optic tectum (11–2). This compact bundle of efferent tectal fibres splits (fig. 5) into two components: a dorsal that contributes to the nucleus tegmenti motorius dorsalis and to the pars ventralis of the posterior commissure, and a ventral that goes ventrally to mingle with the incoming optic fibres. Some of these ventrally coursing fibres enter the rich fibrillar mass of the lateral eminentia. These are designated as the fibræ a tecto in eminentiam thalami.

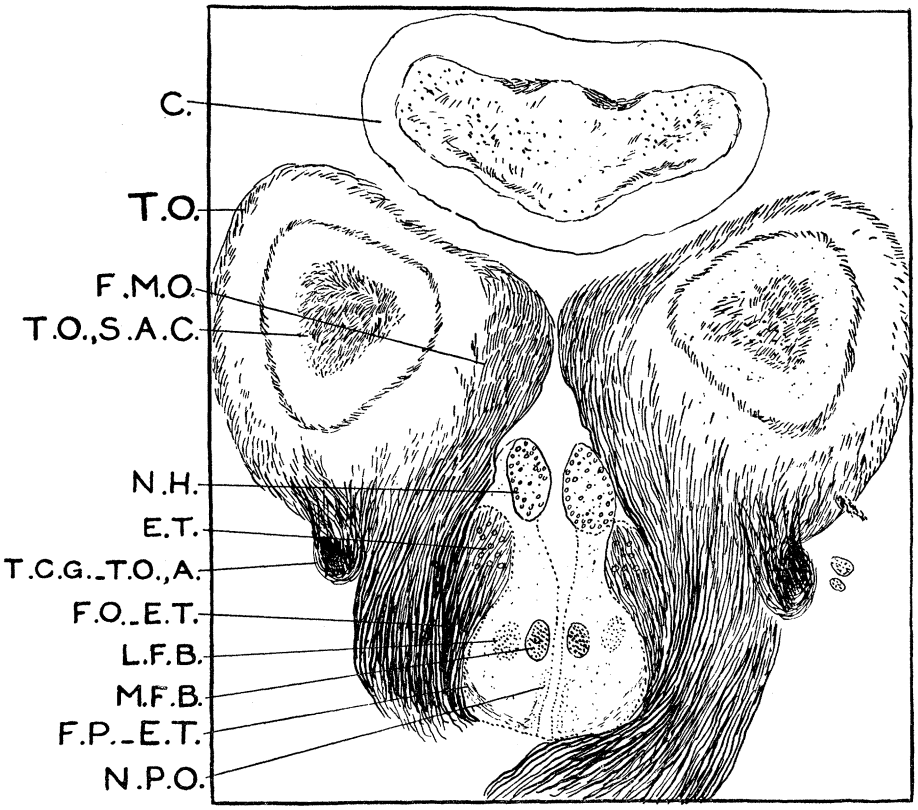

Fig. 2—Drawing of a transverse section from the *Diaphus* brain showing the rostral end of the eminentia thalami anterior and the entering primary optic fibres; Weigert-Pal stain, Bingham Collection (B.C. 9). × 50.

(7) *Fibræ ab eminentia thalami in commissuram posteriorem*, fig. 3—The most rostral sections of the eminentia thalami extend beyond the frontal limit of the commissura posterior, pars ventralis. As the frontal region of the posterior commissure is approached, the fibres of the eminentia become concentrated dorsally, and are

joined by fibres from the overlying nucleus tegmenti motorius dorsalis. Together these fibres arch over the ventricle forming the pars ventralis of the commissure. Extending caudally, the innermost fibres of the commissure are in intimate relation with the entire upper part of the eminentia.

The rostral and middle parts of the posterior commissure, pars ventralis, are almost entirely a mechanism to bring about, on the one hand, bilateral representation between the two parts of the eminentia, and, on the other, to bring into relationship to each other the nuclei tegmenti motorii dorsalis. In addition, the posterior commissure also brings the eminentia thalami and the dorsal motor tegmental nuclei into close functional relationship.

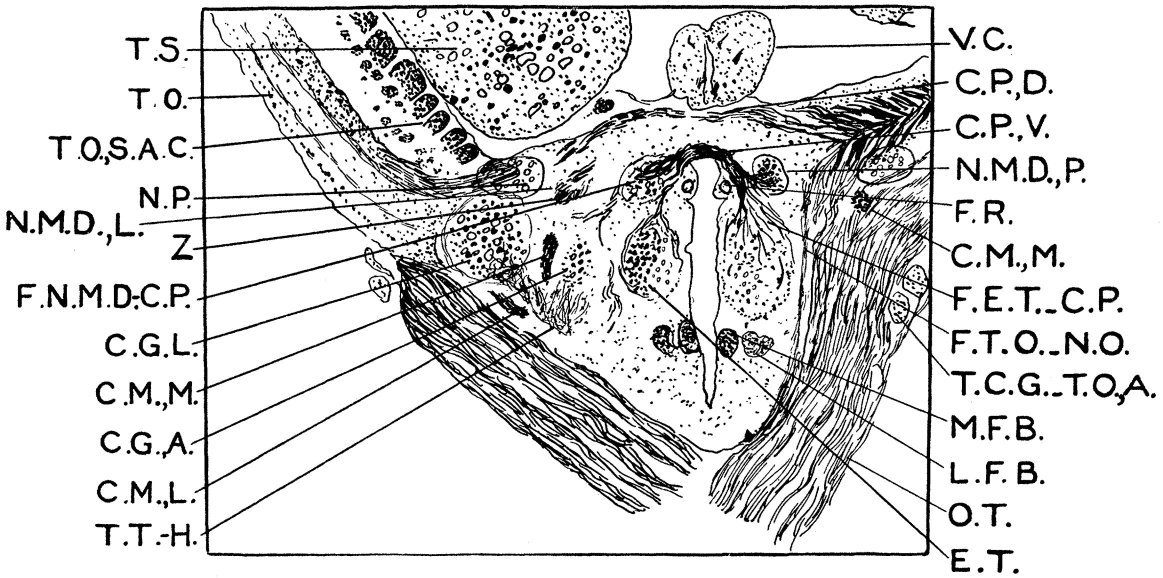

FIG. 3—A section through the caudal end of the eminentia thalami. This and the succeeding drawings including fig. 11 are from a *Diaphus* brain of the same set, B.C. 39; entire series stained by the WEIGERT method. × 50.

The pars ventralis of the posterior commissure is also connected with the optic tectum, the nucleus pretectalis and the corpus geniculatum. Hence it is very probable that the eminentia receives impulses from these centres through the posterior commissure.

(8) *Fasciculi ab eminentia thalami in partem dorsalem thalami*—This fasciculus is described with the connections of the pars dorsalis thalami (4–1).

(9) *Fasciculus descendens*, figs. 4, 5, 14–16, F.D., M.; F.D., L.—This large bundle representing the chief efferent pathway from the eminentia thalami is described under the pars ventralis thalami (3-1) where it terminates.

3 *PARS VENTRALIS THALAMI*, figs. 6, 15, 16, P.V.T.

The name "ventralis thalami" as used in this paper corresponds to the region described under this name in teleosts by JEENER (1930, p. 763). This investigator, as the result of his studies on the Teleostomes, concludes that the fish thalamus has a pars ventralis thalami and a pars dorsalis thalami homologous to the corresponding centres described in the amphibia by Herrick (1910, 1917).

The pars ventralis thalami of this description corresponds to the nucleus tegmenti motorius ventralis of Brickner (1929). The pars ventralis is a large and prominent area of medium-sized cells containing many myelinated fibres. The size and shape of this region is well seen in the transverse plane of the *Diaphus* brain, fig. 6. As previously noted when describing the eminentia thalami, the pars ventralis and the eminentia are separated from each other by a cell-free region. The rostral end of the pars ventralis thalami receives the two parts of the fasciculus descendens. Dorsally the pars ventralis is in apposition with the overlying pars dorsalis thalami, but the boundary between the two areas is easily determined, for the pars dorsalis contains rather small round cells, very few myelinated fibres, and clear intercellular substance. Another landmark found between these two areas is the sulcus medius. In *Saurida* the sulcus medius is a deep ventricular fissure, but in *Diaphus* and *Bathypterois* it is merely a shallow groove. Brickner (1929, p. 240) gives a list of teleosts in which he identified the sulcus medius. The two fore-brain bundles form a ventromedial relationship to the pars ventralis. Also ventromedially emerge fibres, some of which form the commissura ventralis, while others enter the hypothalamus.

Into the ventrolateral surface of the pars ventralis there enters a broad system of fine, lightly stained fibres that come from the caudal part of the transverse commissure, while dorsolaterally the large tractus thalamo-bulbaris is seen.

Connections

(1) *Fasciculus descendens*, figs. 4, 5, 14–16, F.D., M.; F.D., L.—This fasciculus was described by Brickner (1929) as a prominent bundle of fibres originating in the subhabenular area and passing along the dorsal edge of the nucleus tegmenti motorius ventralis. In *Diaphus* there are two large fasciculi, a medial and a lateral, passing between the subhabenular area, the eminentia thalami and the pars ventralis thalami. The medial bundle which corresponds to the fasciculus descendens of Brickner begins rostrally at the anterior limit of the posterior commissure, from the medial part of the eminentia thalami. The fasciculus passes along the upper border of the pars ventralis throughout its entire extent, becoming progressively smaller. The most caudally extending fibres turn dorsally, some to enter the medial longitudinal fasciculus, others to terminate among the large dorsal reticular cells. This caudal distribution substantiates the findings of Brickner (1929, p. 263).

The lateral component of the fasciculus descendens originates in the most rostral fibrocellular area of the eminentia thalami, figs. 4 and 5. Many fibres from the optic tract enter this fibrocellular mass and most probably (as discussed by Brickner, p. 263) some of them are fibres direct to the fasciculus descendens. The pars lateralis also has connections with the posterior commissure. Toward the caudal end of the pars ventralis thalami, fig. 6, the fasciculus descendens lateralis, joined especially by fibres from the large motor cells of this nucleus, turns abruptly dorsolaterally and forms the tractus thalamo-bulbaris et olivaris.

(2) *Fasciculi a commissura transversa in pars ventralem thalami*, fig. 6, F.C.T.-P.V.T.—Broad bundles of myelinated fibres pass between the transverse commissure and the nucleus ventralis thalami. One of these bundles passes between the ventromedial region of the nucleus and the transverse commissure, while the other passes between the ventrolateral part of the nucleus and the commissure.

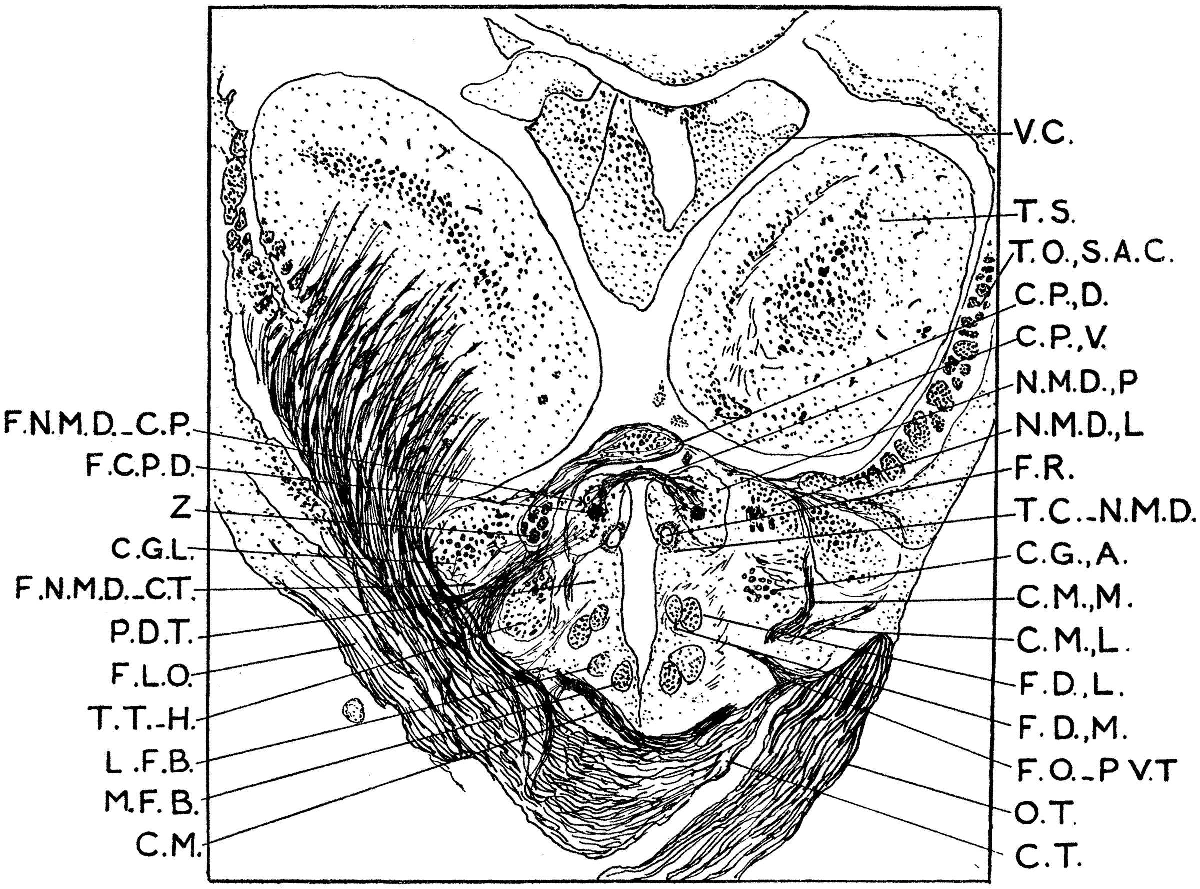

Fig 4—A section through the decussation of the transverse commissure of *Diaphus* showing the relationship of the commissure to the torus semicircularis. × 50.

(3) *Commissura ventralis*, figs. 6 and 15, C.V.—This is a system of scattered myelinated fibres connecting the lower parts of the pars ventralis thalami. Many of these fibres are intermingled with the fibræ ansulatæ.

(4) *Fibræ ansulatæ*—These fibres, best seen in *Diaphus*, come from the dorsolateral tegmental area (exact centres not determined) and pass as large, well-medullated scattered fibres ventromedially. Many of their fibres are lost in the pars ventralis thalami, and others cross in intimate contact with fibres of the most caudal

decussation of the transverse commissure. Brickner (1929, pp. 266 and 267) thinks these fibres are derived from the tecto-cerebellar tract.

(5) *Fibræ a parte ventrali in hypothalamum*—This is a system of poorly myelinated scattered fibres that leaves the lower border of the pars ventralis thalami and enters the inferior lobes. The more rostral of these fibres go to the region of the nucleus tuberis anterior. The more caudal ones go to the nucleus subrotundus.

(6) *Fasciculi a commissura posteriore in partem ventralem*—These consist of some fibres from the caudal end of the commissura posterior, pars ventralis that enter the upper and rostral part of the pars ventralis thalami.

(7) *Fibræ a parte dorsali thalami in partem ventralem*—Many short poorly myelinated fibres pass between the internal segment and the pars ventralis thalami.

(8) *Fibræ a nucleo dorsali in partem ventralem*—A well-defined bundle of fibres passes from the dorsal border of the pars ventralis thalami, arches around the outer edge of the segmentum internum of Brickner, and is lost in the inferior part of the dorsal motor tegmental nucleus.

(9) *Fibræ a commissura minore in partem ventralem*—A few very coarse varicose fibres pass between the commissura minor and the ventrolateral region of the pars ventralis thalami.

(10) *Fibræ ab optico in partem ventralem*, figs. 4 and 5, F.O.-P.V.T.—These fibres, which were described by Brickner (1929) emerge from the optic tract as a compact bundle of well-medullated fibres, figs. 4 and 5, at the level of the crossing of the commissura minor. The fibres extend toward the ventrolateral edge of the fasciculus descendens and the pars ventralis thalami. However, before reaching the above structures, most of the fibres lose their myelin. Their direction and proximity suggest they enter the fasciculus and nucleus as found by Brickner.

(11) *Fasciculi a parte ventrali in fasciculum longitudinalem medialem*—Part of the fasciculus descendens pars medialis, augmented by fibres from the pars ventralis thalami, pass dorsally along the ventricular wall to a position dorsomedial to the medial longitudinal fasciculus. From this position it turns caudally and after coursing for a considerable distance becomes intermingled with the fibres of the fasciculus itself.

(12) *Tractus thalamo-bulbaris et olivaris*, figs. 6–11, T.T.-B—This is probably the tractus a nucleo ventrali in bulbum of Brickner (1929). It is one of the most conspicuous and interesting tracts in the *Diaphus* brain. The tractus thalamo-bulbaris consists of fibres from the fasciculus descendens pars lateralis and the ventrally placed large stellate cells of the pars ventralis thalami. The tract emerges from the dorsolateral border of the nucleus and projects dorsolaterally between the medial longitudinal fasciculus and the fibres of the horizontal commissure and tractus mesencephalo-cerebellaris anterior, fig. 6. From this position it turns caudally lying near the lower border of the tractus tecto-bulbaris rectus, figs. 7–11. At the level of the dorsal tegmental motor nucleus a large fasciculus is added from the nucleus to this tract. It was not determined whether this latter component descended with the tract or passed through it to the pars ventralis thalami.

Caudal to the level of the commissura ansulata, the tractus thalamo-bulbaris is bounded dorsolaterally by the tractus tecto-bulbaris rectus, and medially by the tractus hypothalamo-bulbaris, figs. 10 and 11. As the tract passes caudally it is gradually reduced in size, terminating primarily in relation with the dendrites of the large reticular cells, most of the remaining fibres, about one-fourth of the original number, terminating in the well-developed inferior olive, and a few descending to the upper levels of the spinal cord.

4 *PARS DORSALIS THALAMI*, figs. 4–6, 15, 16, P.D.T.

This is the pars dorsalis thalami of Jeener (1930), or the inner segment of the pars dorsalis thalami of Brickner (1929). This area is sharply separated, in the brains of all three of the fish studied, from the adjacent areas, in Weigert preparations, because it has relatively few cells and very few myelinated fibres, whereas the nucleus tegmenti motorius dorsalis above, and the pars ventralis thalami below, are rich fibrocellular areas. Especially is this true in *Diaphus* (fig. 6). As

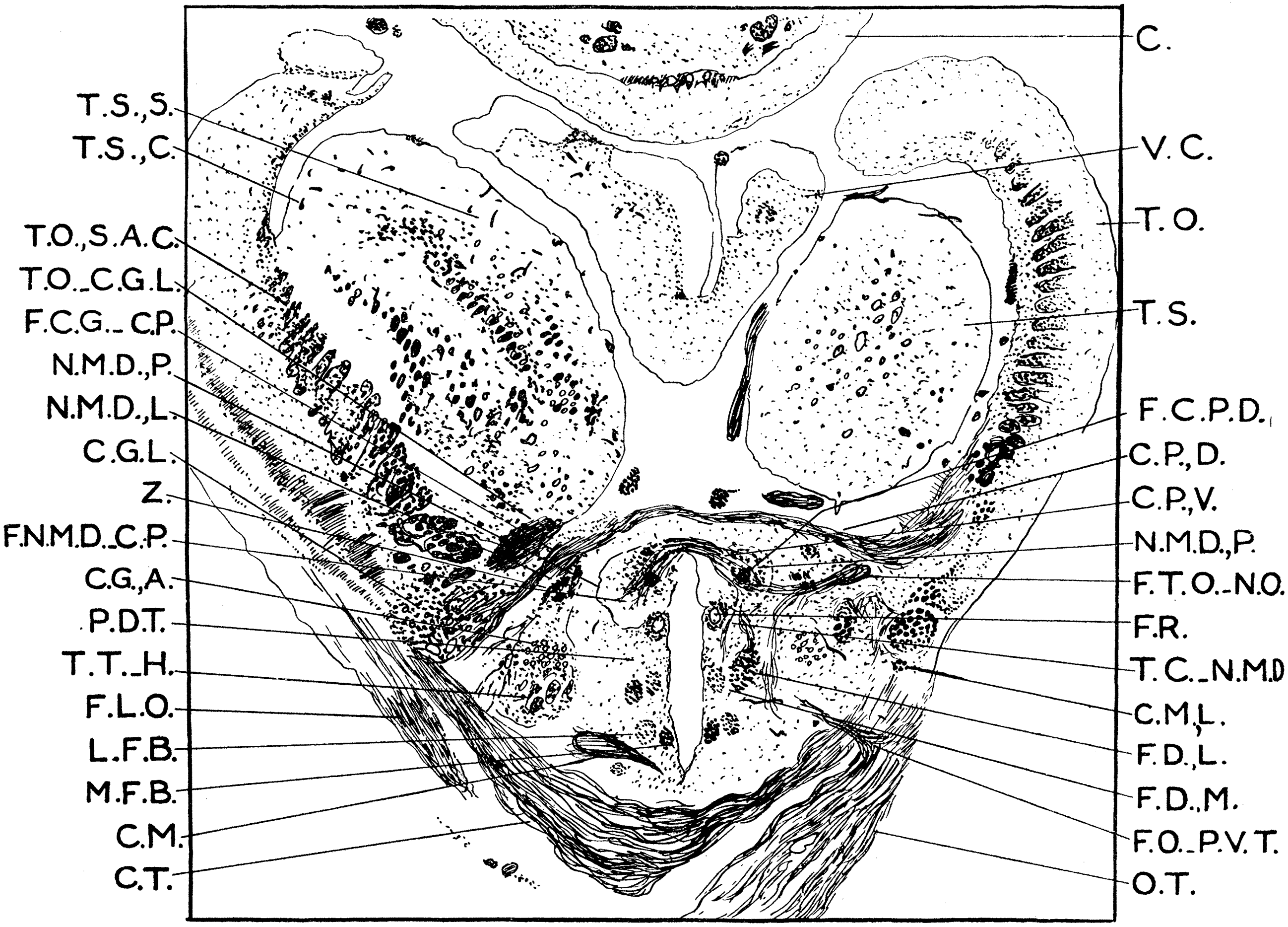

Fig. 5—A section through the caudal end of the posterior commissure of *Diaphus*. × 50.

previously stated, the rostral end of the nucleus dorsalis projects as a wedge between the eminentia thalami and the nucleus tegmenti motorius dorsalis. The upper edge of the pars dorsalis thalami is bounded by the fasciculus retroflexus, which is an important landmark for it separates the pars dorsalis from the overlying nucleus tegmenti motorius dorsalis; moreover, a similar relationship exists in amphibians, reptiles, and mammals (CRAIGIE and BRICKNER, 1927). The fasciculus retroflexus also arches over its posterior border, indicating the caudal limit. JEENER found the dorsal border in *Idus idus* marked off by a sulcus dorsalis. The dorsal sulcus is well developed in *Saurida*, but not in *Diaphus* or *Bathypterois*. The sulcus medius, indicating the ventral border of the pars dorsalis thalami has been referred to. Laterally there is no sharp line of demarkation.

In all three of the fish the cells of the pars dorsalis thalami are small and round. For the most part, they tend to be concentrated along the ventricle and along the upper border. The concentrated area of densely packed cells along the upper border is very conspicuous in the brain of *Bathypterois* (figs. 15 and 16) and *Saurida*, where it extends ventrolaterally and its cells are in continuity with the cells of the nucleus anterior thalami of SHELDON (1912), HOLMGREN (1920), and of BERGQUIST (1932), the corpus glomerosum, pars anterior of FRANZ (1912), and of BRICKNER (1929).

Both the cells of the pars dorsalis thalami and those of the nucleus anterior thalami are of the same size and shape. The intimate continuity of the cells between the two areas and their similar morphology make one suspect the existence of some functional interrelation. The cells of the lower part of the pars dorsalis are slightly larger and more deeply stained than those of the other parts. The central and lateral regions of the pars dorsalis tend to be relatively free of cells and are suggestive of a molecular layer.

Connections

Any description of the connections of the pars dorsalis thalami based entirely on WEIGERT and WEIGERT-PAL material must of necessity be incomplete as many of the fibres are poorly medullated.

(1) *Fasciculi ab eminentia thalami in partem dorsalem thalami*—These fasciculi are well seen in those parasagittal sections of the *Diaphus* brain which include the fasciculus retroflexus. The medullated fibres gather in the ventral half of the eminentia and are added to as they pass dorsally. They emerge from the dorsal edge of the eminentia as a series of fasciculi of loosely arranged fibres. In the pars dorsalis all of the fibres pass caudally for a short distance and are lost. Most of the fibres do not terminate around the cells of this region but in the clear molecular layer.

(2) *Fasciculi a commissura posteriore in partem dorsalem thalami*—Some well-medullated fibres from the lower half of the pars dorsalis thalami pass rostrally through a number of sections, then turn dorsally. These fibres join others from both parts of the fasciculus descendens and together they cross through the caudal part of the commissura posterior, pars ventralis. BRICKNER (1929) makes no mention of any

connections between the pars dorsalis thalami and the posterior commissure in the fish he studied.

(3) *Fibræ a parte anteriore in partem dorsalem thalami*—The intimate relationship existing between the cells of the pars dorsalis thalami and those of the pars anterior thalami has been described. These centres are also connected to each other by poorly medullated fibres that pass from the small cells of the pars anterior among the similar cells in the upper pars dorsalis thalami. A few fibres pass directly from the pars anterior thalami into the cell-free central or molecular area of the pars dorsalis. These fibres were observed in all three fish.

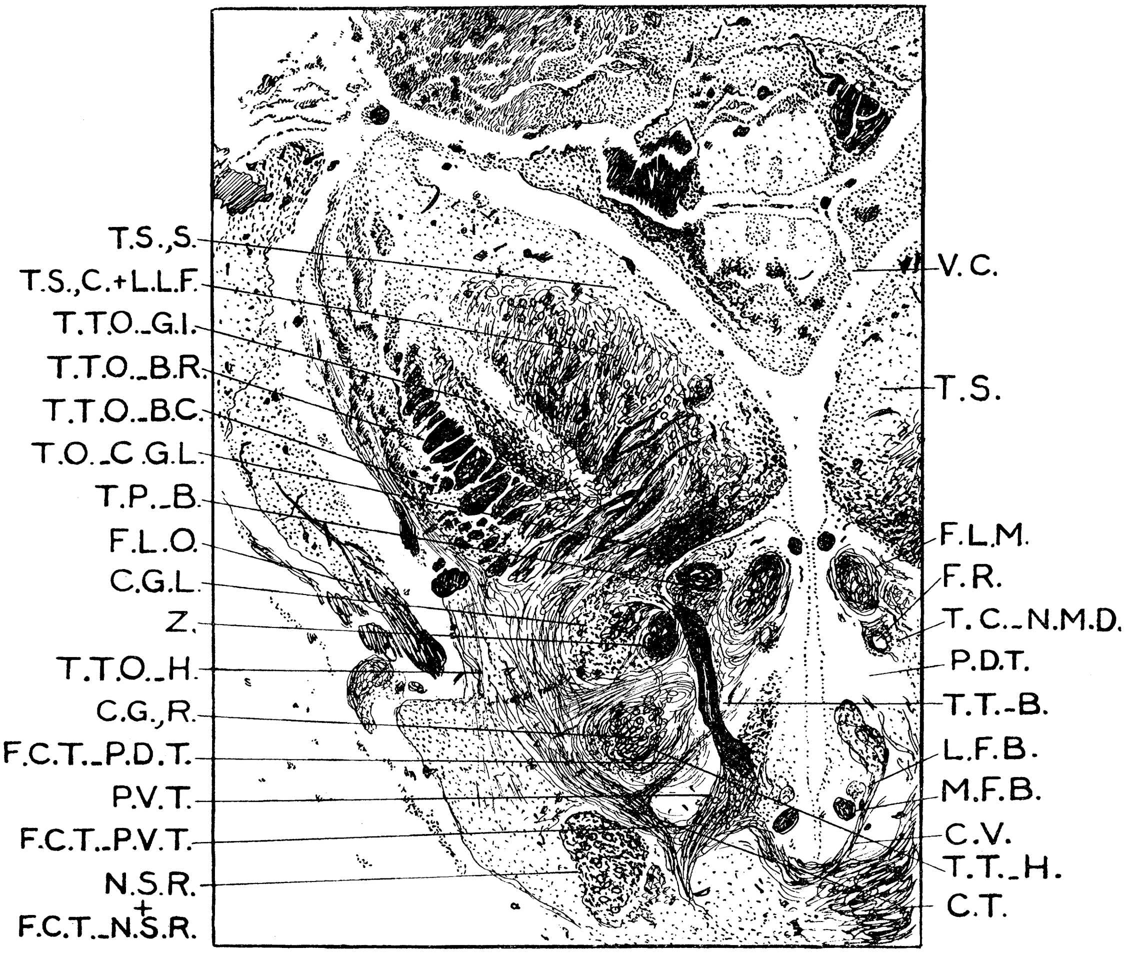

FIG. 6—A section showing the pars ventralis thalami, the origin of the tractus thalamo-bulbaris, and the pars dorsalis thalami of *Diaphus*. × 50.

(4) *Fasciculi a geniculo in partem dorsalem thalami*, fig. 15, F.C.G.-P.D.T.—A similar connection was described by BRICKNER (1929) as fasciculus a geniculato in segmentum internum. In the brain of *Bathypterois* a few fibres are clearly seen emerging from the medial border of the geniculate body. These fibres pass above the pars anterior

thalami and terminate chiefly in the cell area of the upper region of the pars dorsalis; a few, however, extend into the molecular layer.

(5) *Fasciculi a commissura transversa in partem dorsalem thalami*, fig. 6, F.C.T.-P.D.T.—This fasciculus is best seen in the *Diaphus* brain. Some very coarse, heavily medullated fibres emerge from the inner side of the transverse commissure and pass medially. Many of these fibres end among the cells of the inferior part of the pars dorsalis, while others enter the molecular layer. These findings are in agreement with those of Brickner (1929, p. 241).

(6) *Fasciculi a tecto in partem dorsalem thalami*—This is the fasciculus a tecto in segmentum internum of Brickner (1929, p. 241). Reference has previously been made to the fibræ tectales nervi optici, some of whose more medial fibres enter the rostral end of the pars dorsalis thalami. As these fibres come from the efferent layer of the optic tectum they undoubtedly carry optic impulses into the pars dorsalis thalami.

(7) *Tractus a parte dorsali thalami in hypothalamum*—A large bundle of fibres was described by Brickner in *Gasterosteus*, *Perca*, and *Pleuronectes* (1929, p. 242), passing between the segmentum internum (the pars dorsalis thalami of this paper) and the inferior lobes. The writer has been unable to find such a pathway in his preparations. Brickner failed to find this tract in *Gadus* and supposes it is unmedullated, and such may be the explanation in the present material. However, in these fish some fibres from the pars dorsalis thalami join the fibræ ansulatæ and cross with them. Some of these crossed and uncrossed fibres enter the rostral end of the inferior lobes in *Diaphus* and in *Bathypterois*, thereby putting the hypothalamus under the influence of the pars dorsalis thalami.

(8) *Fibræ a parte dorsali thalami in partem ventralem*—These fibres are described under the pars ventralis thalami (3 and 7).

5 *NUCLEUS TEGMENTI MOTORIUS DORSALIS*, figs. 3–5, N.M.D.P., N.M.D.L.

This is the nucleus tegmenti motorius dorsalis of Brickner (1929, p. 243). The dorsal region of the deep sea fish brain is divided into three distinct areas: an inner large fibrocellular mass with deep-stained neuropil, a middle relatively clear area, and a lateral area containing many large cells and large fibre bundles.

The medial fibrocellular area, the pars propia of this description, corresponds in part to the "ventral cell group" of Brickner (1929, p. 245), and the middle area, the pars lateralis of this paper, corresponds to his "lateral cell group." The outermost segment constitutes the pretectal and geniculate areas.

Pars propia—morphology—Rostrally, the pars propia is small and projects above the eminentia thalami and the pars ventralis of the posterior commissure, fig. 3, but passing caudally it rapidly increases in size. Ventrally, the pars propia is limited by a ventricular sulcus, the sulcus diencephalicus dorsalis of Kuhlenbeck (1929), by the fasciculus retroflexus and by the pars dorsalis thalami. Throughout, the pars propia is in intimate contact with the posterior commissure, pars ventralis, and ventrolaterally it extends towards the nucleus anterior thalami.

The rostral and middle parts of the pars propia contain large round cells that are very compactly arranged and evenly distributed. In the caudal third the cells are sparse, large, and stellate. There is no sharp line of demarcation caudally between the pars propia and the nucleus of the medial longitudinal fasciculus.

Pars lateralis—morphology—This area is sharply separated from the pars propia because its cells are much smaller and lighter stained, and the intercellular substance lacks the deep staining neuropil characteristic of the pars propia. In all of the deep sea fish brains four prominent bundles of fibres are projected into the pars lateralis : the commissura posterior, the commissura horizontalis, the tractus tecto-cerebellaris, and the tractus spino-tectalis et mesencephalicus, figs. 3–6 Z.

Connections

(1) *Fasciculus ab optico in nucleum dorsalem*—A broad system of incoming optic fibres has been described under the connections of the eminentia thalami. These fibres correspond to the fasciculus medialis tractus optici of Jansen (1929). Part of the rostral fibres of this fasciculus terminate in the eminentia thalami. Other fibres of this fasciculus after entering the eminentia do not terminate here but shift dorsally and form a conspicuous area of deeply stained fibres along the upper border of the eminentia. These latter fibres enter the rostral end of the nucleus tegmenti motorius dorsalis where it is in apposition with the eminentia. The fasciculus ab optico in nucleum dorsalem is very compact and conspicuous in rostral sections of the nucleus, but in passing caudally the fibres spread out and are lost. No direct optic fibres were found going to the dorsal tegmental nucleus in *Saurida*, nor in *Bathypterois*.

(2) *Fasciculi ab habenula in nucleum dorsalem*—Brickner (1929, p. 255) described fasciculi connecting the habenulæ and the dorsal tegmental nuclei. In the *Diaphus* brain, fibres from the rostral end of the dorsal tegmental nucleus approach the habenula, but none were actually traced into that nucleus. In *Bathypterois* the area between the habenula and the dorsal tegmental nucleus is almost free of myelinated fibres. The writer is sure that no myelinated fibres pass in this brain between the nucleus habenularis and the dorsal tegmental nucleus.

(3) *Fibræ a nucleo dorsali in commissuram posteriorem*, figs. 3–5, F.N.M.D.-C.P.—Rostrally, the nucleus tegmenti dorsalis and the commissura posterior, pars ventralis start at the same level. Caudally, the nucleus extends beyond the commissure. The commissure throughout is in very intimate relationship with the nucleus. Rostrally, where the nucleus overlies the commissure, the outer commissural fibres enter the ventral part of the nucleus. More caudally, the commissural fibres are associated especially with the ventral and medial parts of the nucleus.

At the level where the commissure terminates, some of its fibres turn caudally to form a compact bundle that descends in the nucleus tegmenti dorsalis. This fasciculus, which is called "fasciculus commissura posterior descendens," passes beyond the nucleus and goes caudally with fibres of the medial longitudinal fasciculus figs. 4 and 5, F.C.P.D.

(4) *Fasciculus a nucleo dorsali in commissuram transversam*, fig. 4, F.N.M.D.-C.T.—This fasciculus was described by Brickner (1929, p. 249). These fibres first make their appearance in *Diaphus* at the level of the middle part of the commissura posterior, pars ventralis and in reality are a broad system of fibres that are seen in many sections. These fibres, relatively small in calibre and well medullated, pass between the ventrolateral cell area of the dorsal tegmental nucleus and the inner border of the caudal part of the commissura transversa. Brickner (1929, p. 249) says of the above fasciculus, "This bundle evidently arises, for the most part, in the nucleus tegmenti motorius dorsalis." The most caudal cells, with which these fibres are associated, are very clearly motor, since they are very large and multipolar. Therefore the writer agrees with Brickner that, in part at least, conduction is away from the nucleus.

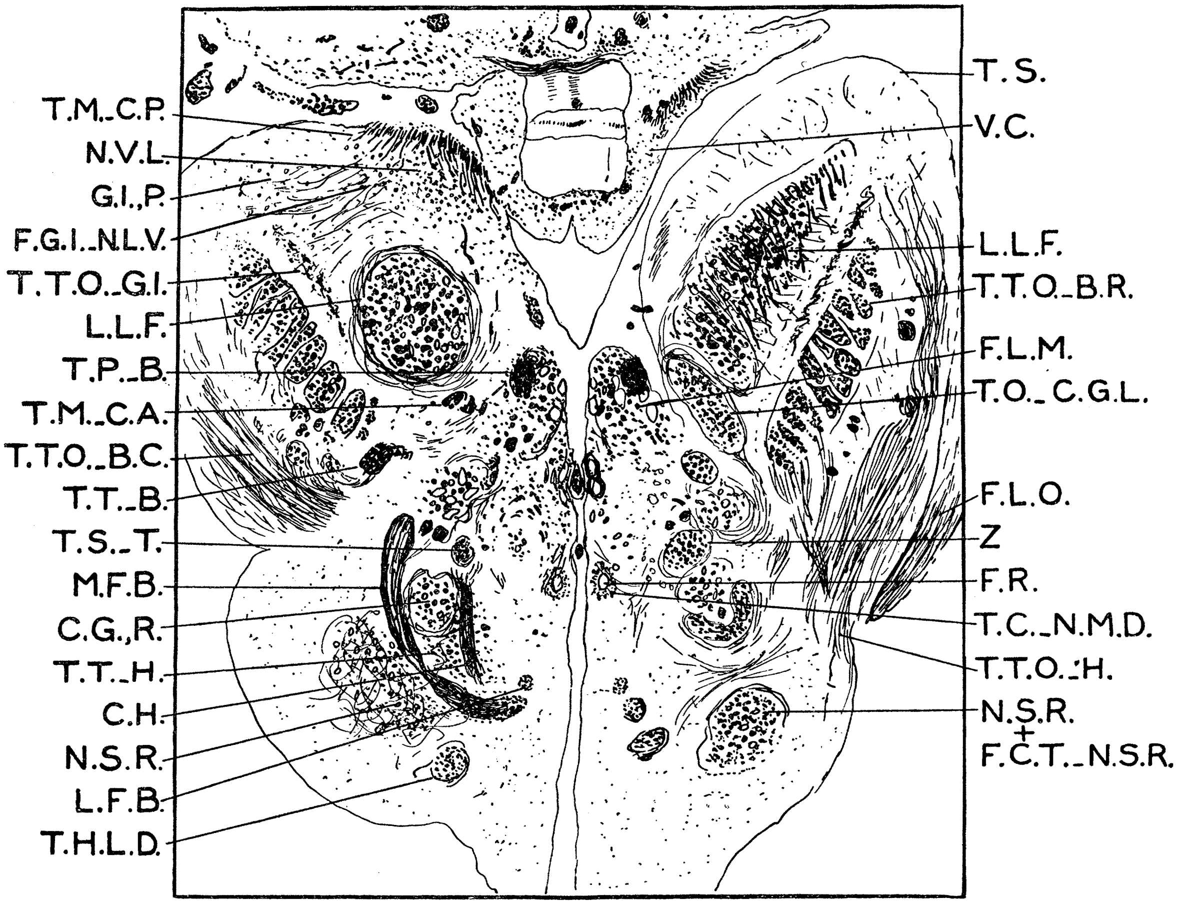

Fig. 7—A section caudal to the pars ventralis thalami and the pars dorsalis thalami of *Diaphus*. × 50.

(5) *Fasciculi a tecto in nucleum dorsalem*—This fasciculus is part of the system of fibres described under the connections of the eminentia thalami as "the fibræ tectales nervi optici." Some of the dorsally arching fibres of this fasciculus enter the commissura posterior; others enter the nucleus tegmenti motorius dorsalis, and

terminate chiefly in the ventrolateral part of the pars propia. None of these optic fibres go into the pars lateralis. It is very probable that some of the optic fibres that cross in the posterior commissure enter the dorsal tegmental nucleus of the opposite side.

(6) *Fibræ a geniculo in nucleum dorsalem*—In the *Bathypterois* brain the entire lateral part of the poorly defined nucleus tegmenti motorius dorsalis receives (or sends) fibres to the medial border of the large lateral geniculate body. Although many fibres pass in the *Diaphus* brain from the geniculate body towards the dorsal tegmental nucleus, none were actually followed into that structure.

(7) *Fibræ a parte anteriore in nucleum dorsalem*—These fibres are best seen in the *Saurida* brain. The poorly medullated fibres pass between the medial side of the pars anterior thalami and the ventrolateral part of the nucleus tegmenti motorius dorsalis. Similar fibres are present in *Diaphus* and *Bathypterois*.

(8) *Tractus a cerebello in nucleum dorsalem*—figs. 4–8, T.C.-N.M.D.—The very large, well-medullated fibres of this tract surround the fasciculus retroflexus. In WEIGERT preparations there is a striking contrast between the deep blue stained fibres of the tract and the pale stained unmedullated fibres of the fasciculus. SHELDON (1912, p. 217) says of these fibres, "These originate from the nucleus posthabenularis and pass caudal to the commissura ansulata, which they appear to enter, turning laterad." HOLMGREN (1920, p. 258) calls this the tractus eminentia-mesencephalicus. BRICKNER (1929, p. 251) succeeded in tracing these fibres from the brachium conjunctivum to the fasciculus retroflexus and followed them into his nucleus tegmenti motorius dorsalis and his nucleus tegmenti motorius ventralis.

This pathway is present in all of the deep sea fish brains in this description, but can best be followed in *Diaphus*. Where the brachium conjunctivum emerges from the cerebellum as a large, compact bundle, fig. 9, and decussates along the lower border of the medial longitudinal fasciculus some of the crossed fibres pass ventrally and join the fasciculus retroflexus at the laterorostral border of the interpeduncular ganglion. From this region they accompany the fasciculus retroflexus to the nucleus tegmenti motorius dorsalis. In sagittal series the fibres are seen leaving the upper border of the retroflexus and entering the ventral part of the dorsal tegmental nucleus. None of these fibres pass into the pars ventralis thalami, nor the pars dorsalis thalami.

(9) *Fibræ a rotundo in nucleum dorsalem*—These fibres pass from the rostral end of the pars rotunda of the corpus glomerulosum and from large multipolar cells lying immediately above rotundus to the ventral part of the nucleus tegmenti motorius dorsalis. Although many fibres pass between these two regions the direction of conduction has not been determined.

(10) *Tractus a nucleo dorsali in tractum tecto-cerebellarem*—This tract was described by BRICKNER (1929, p. 253). Caudal to the posterior limit of the posterior commissure, the combined fibres of the commissura horizontalis, the tractus tecto-cerebellaris and the tractus spino-tectalis form a compact bundle of fibres along the medial border of the geniculate body, fig. 6, Z. In passing rostrally these fibres shift dorsomedially and spread out in the pars lateralis of the dorsal tegmental nucleus, figs. 3–5.

These fibres are the most conspicuous elements in the pars lateralis, and many of them have their origin (or terminus) among the cells of this region. Others of these fibres are distributed to the pretectal area, the optic tectum, and the commissura posterior, pars dorsalis. There is no reason for assuming that all of these fibres are associated with the tractus tecto-cerebellaris, since it is most probable that many enter the commissura horizontalis.

(11) *Tractus thalamo-bulbaris et olivaris*—This tract is described under the pars ventralis thalami (31—3).

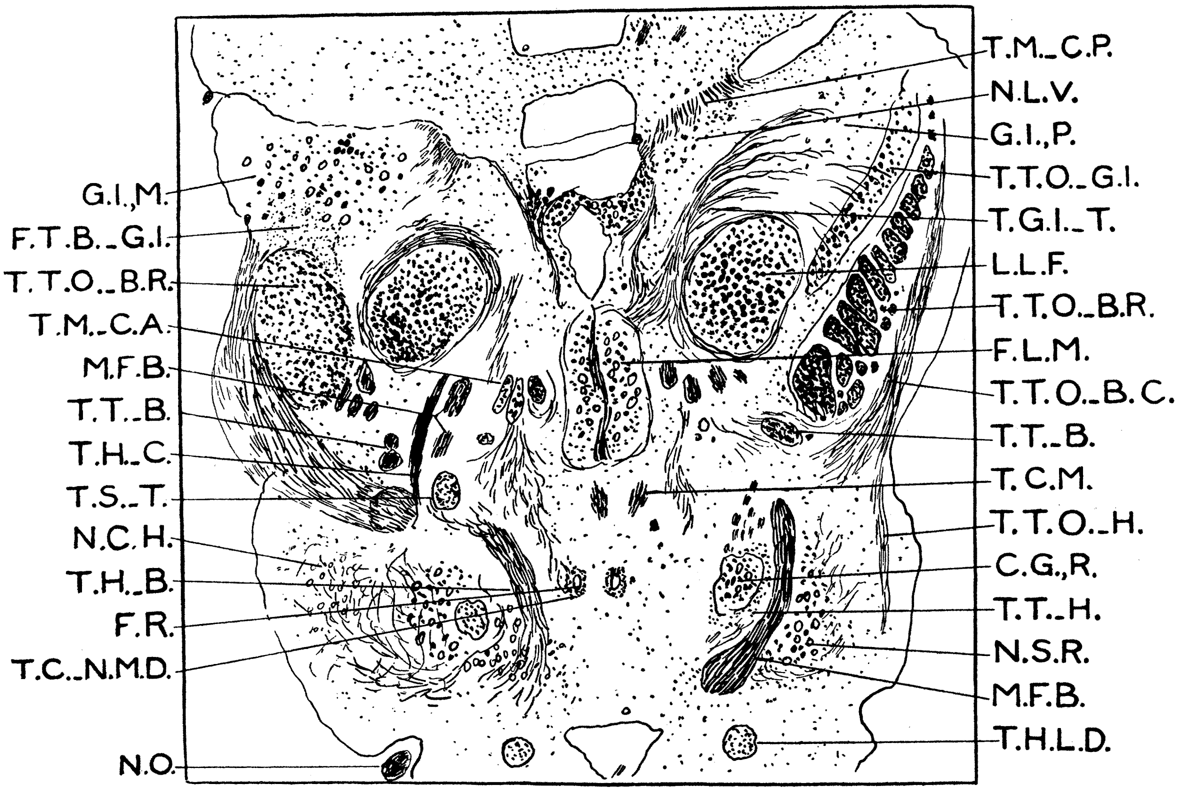

Fig. 8—A section through the nucleus subrotundus of *Diaphus* showing the origin of the tractus hypothalamobulbaris. × 50.

(12) *Fibræ a nucleo dorsali in partem ventralem*—These fibres are described under the pars ventralis thalami (3—8).

(13) *Fibræ a nucleo dorsale in eminentiam thalami*—These are described under the eminentia thalami (2—5).

6 *CORPUS GENICULATUM LATERALE*, figs. 3–6, 15, 16, C.G.L.

Franz (1912, p. 410) demonstrated in a series of figures many of the various forms of the lateral geniculate body in teleosts. In his study on the carp, Sheldon (1912, fig. 81) showed the relation of the geniculate body to the nucleus anterior thalami.

Burr (1928, p. 51) described a tripartite geniculate in *Orthagoriscus mola*. It seems assured that the geniculate is not simply a relay station for the optic pathway because Charlton (1933, p. 311) described its presence in blind fish. He considers it atrophied there, however. Jansen (1929, p. 1109) had previously noted atrophy of the right geniculate in a fish (*Idus idus*) that was blind in the left eye.

The geniculate body of the nearly blind fish *Bathypterois* is most conspicuous because of the greatly reduced tectal areas (figs. 15 and 16). Here the geniculate is a large, round structure situated at the outer inferior tectal border. The geniculate in *Bathypterois* contains very large cells that are represented by clear round spaces among the well-medullated fibres. The large size of the geniculate in *Bathypterois* indicates that there has been no atrophy of that body corresponding to the atrophy of the optic nerve, the optic tracts, and the optic tectum. In the *Saurida* brain the geniculate appears in its usual place at the rostromedial and inferior pole of the optic tectum. More caudally, the geniculate is adjacent to the outer border of the nucleus thalami anterior, and above it are the large, compact cells of the nucleus pretectalis. In *Diaphus* the geniculate is characterized by a large dense fibrillar mass in which there are scattered large multangular cells. The geniculate in this fish extends far caudally and occupies the angle between the torus semicircularis and the commissura transversa, figs. 3–6.

Connections

(1) *Optic tract*—The primary optic connections of the corpus geniculatum laterale will not be discussed as the present material adds nothing new to the excellent descriptions of Catois (1901), Holmgren (1920), Kappers (1921), and Jansen (1929).

(2) *Tractus geniculo-tectalis*, figs. 2 and 3, T.C.G.-T.O.', A; 15 and 16, T.C.G.-T.O., L—Catois (1901, p. 94) showed in silver impregnations that axons pass from the cells of the lateral geniculate (corps genouillé thalamique of Catois) to the optic lobes. This, he says, is the fasciculo geniculado-lobularis of P. Ramon Cajal. Kappers (1906, p. 27; 1921, pp. 815, 817) refers to these fibres as the brachium laterale tecti and the brachium mediale tecti. Holmgren (1920, p. 267) followed neurites from the tripolar cells of the geniculate to the optic tectum. Charlton (1933, p. 312) described the tractus geniculo-tectalis in blind fish, showing thereby that it is not dependent on primary optic influences.

In the present material the tractus geniculo-tectalis is described as consisting of three brachia: medial, lateral, and anterior. The first two have been referred to; the latter was described and figured by Kudo, 1923*a*, fig. 1, Br. tecti ant. The fibres of the anterior brachium, well developed in all three fish, pass from the more caudal part of the lateral geniculate rostrally as a compact bundle, and spread out in the superficial layers of the frontal pole of the optic tectum, fig. 2.

The brachium laterale has a long caudal extent. In *Bathypterois* this brachium forms a very distinct superficial bundle of fibres along the outer edge of the geniculate, figs. 15 and 16. As the brachium passes caudally these very deeply myelinated fibres enter the most superficial tectal layer.

The brachium mediale is best developed in *Saurida* where it is a small but distinct fasciculus passing across the base of the optic tectum. A fasciculus of fibres, probably homologous to the brachium tecti mediale, has also been observed in reptiles, Shanklin (1930, p. 438, *Chameleon*), Huber and Crosby (1933, p. 87, *Varanus*).

(3) *Fibræ a geniculo in nucleum anteriorem*—These are scattered but well-medullated fibres that pass between the medial border of the lateral geniculate and the ventro-lateral part of the anterior thalamic nucleus. Although not so many fibres are seen in any one section, they extend over many sections. These fibres were observed in the brains of *Saurida*, *Diaphus*, and *Bathypterois*.

Fig. 9—A section through the region of the emergence of the oculomotor roots of *Diaphus*, showing the anterior secondary gustatory nucleus. × 50.

(4) *Tractus thalamo-hypothalamicus*, figs. 3–8, T.T.-H.—A tractus geniculo-hypothalamicus was described by Franz (1912, p. 437) and a tractus preoptico-geniculo-hypothalamicus was found by Holmgren (1920, p. 224). The tract of the present description, which includes many fibres from the lateral geniculate but none from the nucleus preopticus, is described under the corpus glomerulosum (8—7).

(5) *Fasciculus geniculo-cerebellaris*—From the caudal end of the lateral geniculate a number of fibres are contributed to the tractus tecto-cerebellaris. This tract is described under the connections of the optic tectum as part of the tractus mesencephalo-cerebellaris anterior (11—8). Geniculate fibres to the cerebellum were described by Catois (1901, p. 151).

(6) *Fasciculus a geniculo in commissuram posteriorem*, fig. 5, F.C.G.-C.P.—This fasciculus, which is described with the posterior commissure, contributes crossed descending fibres to the medial longitudinal fasciculus (10—5).

(7) *Fasciculus a geniculo in partem dorsalem thalami*—The fibres of this fasciculus are described with the connections of the pars dorsalis thalami (4—4).

(8) *Tractus pretecto (et geniculo)—bulbaris*—This tract is described with the nucleus pretectalis (7—3)

(9) *Fibræ a geniculo in nucleum dorsalem*—These fibres are described under the nucleus tegmenti motorius dorsalis (5—6).

(10) *Tractus octavo-geniculatus*, figs. 5–7, T.O.-C.G.L.—Caudal to the enormous torus semicircularis, in *Diaphus*, the lateral longitudinal fasciculus consists of a large, round, compact area of well-medullated fibres. More rostrally, most of these fibres terminate in the torus semicircularis, but where the fasciculus begins to spread out into the torus a large, compact bundle splits off from the lower part, figs. 6 and 7. These fibres pass rostrally and ventrolaterally, terminating in the caudal end of the lateral geniculate body.

It should be stated that this large fasciculus may represent a descending pathway to the bulbar centres among the ascending octavus fibres. If this is to be considered a descending pathway, then it might correspond to the tractus pretecto-lateralis described by Holmgren (1920, pp. 262, 263). Holmgren described neurites from the pretectal cells that left his tractus pretecto-spinalis and entered the fasciculus lateralis longitudinalis ; these latter fibres he calls tractus pretecto-lateralis.

(11) *Fibræ a commissura transversa in geniculatum lateralem*—This is a system of very fine fibres that pass between the medial border of the transverse commissure and the lateral border of the caudal end of the lateral geniculate. The writer interprets these fibres as collaterals of the neurites forming the transverse commissure, since they appear to come from them at right angles and are of much smaller calibre. Fibres from the transverse commissure to the lateral geniculate were described by Burr (1928, p. 93, *Orthagoriscus*). However, it should be clearly stated that the connection of the transverse commissure with the geniculate body in *Diaphus* is a minor one, whereas, in *Orthagoriscus* it appears to be one of the chief end stations.

(12) *Commissura minor*—This commissure is well developed in the deep sea fish, but it is primarily a tectal commissure and not a commissura intergeniculata.

7 *NUCLEUS PRETECTALIS*, fig. 3, N.P.

The terms pretectal nucleus, pretectal nuclei, pretectal area, have been used to include so many various centres that the term has lost much of its value. Catois (1901), Goldstein (1905), and Holmgren (1920) have included in their descriptions not only the dorsolateral but also the dorsomedial centres corresponding, at least in part, to the nucleus tegmenti motorius dorsalis of this paper.

The nucleus pretectalis of the present description is restricted to the group of large multipolar cells, located in the pretectal region at the posterior level of the habenular ganglion. These cells are bounded ventrally by the upper border of the lateral geniculate, dorsally and laterally by the inferior and medial border of the optic tectum, especially the stratum profundum. A medial relationship is the pars lateralis of the nucleus tegmenti motorius dorsalis. The pretectal nucleus of Burr (1928, figs. 4–7 ptn.) appears to correspond to that of this description.

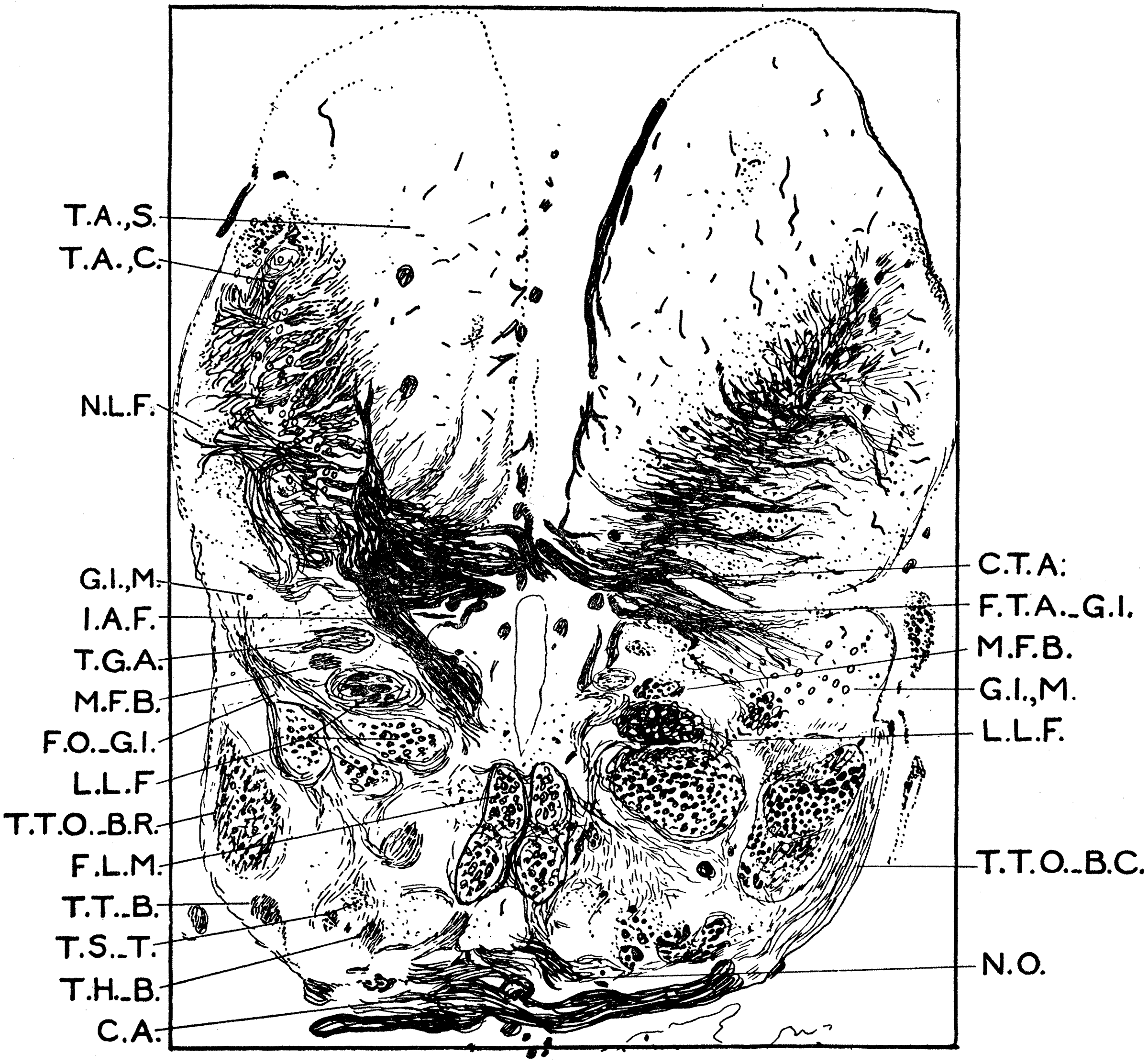

Fig. 10—A section through the caudal end of the commissura ansulata of *Diaphus* showing the connections of the ganglion isthmi with the tuberculum acusticum and with the lateral longitudinal fasciculus. × 50.

When used in the restricted sense, the term nucleus pretectalis has considerable comparative value, since it is present in many animals (Kappers, 1921, p. 818, teleosts ; p. 859, reptiles ; and p. 873, birds). In a recent paper Le Gros Clark (1932, pp. 444-449) gives an excellent discussion of the phylogenetic evolution of the nucleus pretectalis, expressing the opinion that the nucleus pretectalis and the pars intercalaris diencephali (HERRICK) of amphibia are probably homologous. He states that it is present in reptiles and birds, and a corresponding functional centre also occurs in mammals.

Connections

(1) *Commissura pretectalis*—This commissure is described with the commissura posterior through which pretectal fibres cross and then descend in the medial longitudinal fasciculus (10—5).

(2) *Tractus pretecto-cerebellaris*—This tract is also a tectal pathway and is described under the connections of the optic tectum as tractus mesencephalo-cerebellaris anterior (11—8)

(3) *Tractus pretecto* (*et geniculo*)—*bulbaris*, figs. 6 and 7, T.P.-B.—KAPPERS (1921, p. 811, figs. 431*a*, 439) described and figured a tractus pretecto-bulbaris whose fibres descended with the medial longitudinal fasciculus. These findings were confirmed by CHARLTON (1933, p. 315), who, moreover, succeeded in differentiating these fibres from those of the fasciculus and found their terminals related especially to the trigeminal motor nuclei. In *Diaphus*, fibres from the medial border of the nucleus pretectalis are joined by a much larger contingent from the caudal end of the lateral geniculate body. Together these fibres pass medially, fig. 6, and turn caudally to occupy a position along the dorsolateral border of the medial longitudinal fasciculus, fig. 7. More caudally, the tract shifts ventral to the fasciculus where for some distance it can be clearly differentiated, but is finally lost among the fasciculus fibres. The fibres of this tract are characterized by their exceedingly large calibre and deeply stained myelin.

The large calibre of these fibres strongly suggests a descending system. This is confirmed by the experimental work of WALLENBERG (1931) who destroyed a region of the brain in the gold fish that he calls (p. 257) the nuc. corticalis (lentiformis ?). A study of his figure (Abb. 11) shows that the region corresponding to the pretectal and geniculate areas of this paper is also destroyed ; hence the writer interprets the tr. metathal. bulb. of his figures (Abb. 12–21) as the equivalent of the tractus pretecto (et geniculo)—bulbaris of this paper. WALLENBERG found the degenerated fibres descending along the inner half of the fasciculus longitudinalis dorsalis and predorsalis as far as the middle of the medulla oblongata.

(4) *Tractus pretecto-lateralis*—This tract, described by HOLMGREN (1920, pp. 262 and 263) has been discussed with the tractus octavo-geniculatus (6—10).

(5) *Fibræ a nucleo pretectali in commissuram horizontalem*—Many fibres are contributed by the nucleus pretectalis to the horizontal commissure. This connection is described with the horizontal commissure under the diencephalic commissures (10—3).

8 *CORPUS GLOMERULOSUM*, figs. 3–8, 15, 16, C.G., A. ; C.G., R.

This description follows the suggestion of BRICKNER (1929, p. 229) based upon the relations discovered by FRANZ (1912, p. 423) that the nucleus anterior thalami of SHELDON (1912), HOLMGREN (1920), KAPPERS (1921), and BERGQUIST (1932), and the old nucleus rotundus be included under the term corpus glomerulosum, the nucleus anterior thalami being termed by him "pars anterior" and the nucleus rotundus "pars rotunda" of the corpus glomerulosum.

Pars anterior—The intimate relationship existing between the pars anterior and the pars rotunda and the connections of the pars anterior are well illustrated by FRANZ (1912, figs. 18–20).

In *Bathypterois* and in *Saurida* the small cells of the dorsal cell layer of the pars dorsalis thalami extend ventrolaterally and intermingle with the small cells forming the rostral end of the pars anterior, fig. 16. This cellular arrangement is similar to that figured in the carp by SHELDON (1912, fig. 81). Other relationships are smilar to those described previously and will not be discussed here.

Pars rotunda—The pars rotunda of these fish is not very highly developed, and a study of this centre adds very little to our previous knowledge from the descriptions by KAPPERS (1906), FRANZ (1912), and HOLMGREN (1920). Recently SUZUKI (1932) has made a comparative study of the adult and developmental appearance of the nucleus rotundus.

In this paper a discussion of the nucleus prerotundus has been deliberately omitted, as its identification in this material is uncertain.

Connections

(1) *Fibræ a geniculo in nucleum anteriorem*—These fibres are described under the lateral geniculate body (6—3).

(2) *Fibræ a parte anteriore in nucleum dorsalem*—This is a fine bundle of fibres described under the nucleus tegmenti motorius dorsalis (5—7).

(3) *Fibræ a parte anteriore in partem dorsalem thalami*—These fibres are described with the pars dorsalis thalami (4—3).

(4) *Scattered fibres*—Certain scattered fibres were found passing between the pars anterior and the transverse commissure.

(5) *Connection with commissura horizontalis*—The horizontal commissure was found passing through the substance of the medial part of the pars rotunda (fig. 7). On the basis of the present material the writer can add nothing new to the descriptions of FRANZ (1912) and HOLMGREN (1920).

(6) *Tractus thalamo-hypothalamicus*, figs. 3–8, T.T.-H.—This tract was described by KAPPERS (1906, p. 33) as extending from the small cells of the nucleus thalami anterior into the lobi anteriores. This is the tractus thalamo-mammillaris of FRANZ (1912, p. 427), by some others wrongly compared with the tract of VICQ D'AZYR.

In the deep sea fish this tract is much larger than that described by KAPPERS and contains many more components. In sections rostral to the decussation of the commissura minor there are a number of well-medullated fasciculi, figs. 3 and 4, that spread out among the cells of the pars anterior of the corpus glomerosum. These fasciculi occupy most of the area roughly bounded ventrally and ventrolaterally by the transverse commissure, dorsolaterally by the lateral geniculate, dorsomedially by the nucleus tegmenti motorius dorsalis, and medially by the eminentia thalami.

These fibres come from the inner border of the lateral geniculate and from the pars anterior. Very few if any appear to be contributed by the eminentia thalami.

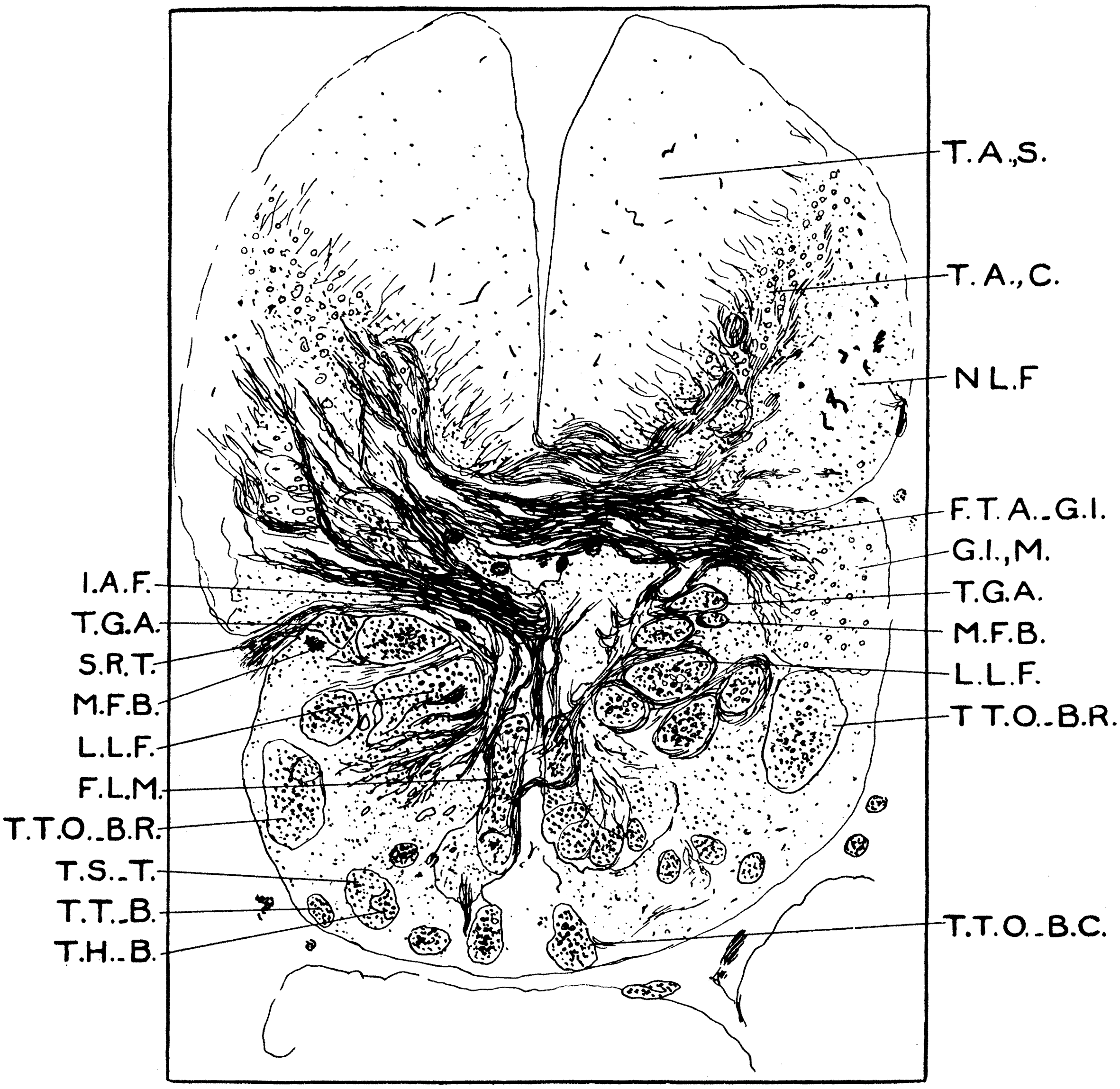

Fig. 11—A section through the region of the entrance of the sensory root of the trigeminal of *Diaphus*. × 50.

The descending tract is a very conspicuous bundle surrounding the under side of the rostral projection and main part of the pars rotundus, figs. 4–8. Also lying above the tract are large multipolar cells, the axons of which increase its size noticeably. A broad system of fibres, extending through many sections, connects this tract with the ventrolateral edge of the nucleus tegmenti motorius dorsalis.

Scattered fibres are also added from the pars dorsalis thalami. As the tract passes adjacent to the entire corpus glomerulosum, abundant fibres are added from the glomerosal cells.

Near the caudal end of the pars rotunda the fibres of the tractus thalamo-hypothalamicus begin to spread out in the nucleus subrotundus where their arborization forms a large area of fine felt-like fibres.

(7) *Tractus rotundo-lobaris*—Kappers (1906, p. 38) used this term to designate a broad system of short fibres passing from the caudal and inferior border of the nucleus rotundus into the adjacent underlying hypothalamic cells. Though in *Diaphus* the tractus rotundo-lobaris fibres were identified, here the tractus thalamo-hypothalamicus appears to be the major outlet for rotundal impulses to the hypothalamic centres.

(8) *Tractus tecto-rotundus*—This tract is described with the optic tectum (11—4).

(9) *Fibræ a rotundo in nucleum dorsalem*—These fibres are described under the nucleus tegmenti motorius dorsalis (5—9).

9 LOBI INFERIORES

The lobi inferiores of the deep sea fish brains are divided into the three typical parts: lobus medius, lobi laterales, and tori laterales. These three divisions are especially clear in *Saurida*. Most of the hypothalamic centres of these fish show no marked variations from the generalized teleostean plan and will not be described. An exception to the other centres is the very highly developed nucleus subrotundus, a description of which follows.

Nucleus subrotundus—The nucleus subrotundus of this description, figs. 6–8 and 16, N.S.R., may correspond only in part to that of previous investigators, Kappers (1906, p. 39; 1921, p. 823), Sheldon (1912, p. 203), and Holmgren (1920, p. 243). In *Diaphus* this nucleus reaches a very high degree of development and for descriptive purposes its parts in this fish will be described as anterior, middle, and posterior.

The anterior part is a frontal projection that is in apposition with the caudalmost, decussating commissura transversa fibres. The cells of this part are medium sized. Between them are fibres from the transverse commissure running lengthwise with the nucleus, fig. 6.

Passing caudally the nucleus spreads out and occupies a large area beneath the main portion of the pars rotundus, figs. 7 and 8. This region is the middle part which is characterized by medium sized cells enmeshed in a dense arborisation of fine myelinated fibres. The caudal and lateral projection of this area is designated as the nucleus cerebellaris hypothalami, fig. 8, N.C.H.

From the inner and caudal edge of this middle region there projects another large cellular area, the posterior part, the place of origin of the tractus hypothalamo-bulbaris.

Connections

(1) *Fibræ a commissura transversa in nucleum subrotundum*, figs. 6 and 7, F.C.T.-N.S.R.—Among the cells of the pars anterior there are many poorly medullated

fibres that run lengthwise through the nucleus. These fibres enter the rostral end of the nucleus from the transverse commissure and some of them descend to the most caudal limit of the hypothalamus. The fibres from the transverse commissure appear to be the only important ones received by this part, and the marked size and frontal projection of the nucleus is probably associated with the high development of the commissure itself. This is very obviously a mechanism whereby octavus impulses are transmitted to hypothalamic centres.

(2) *Tractus tecto-hypothalamicus*, figs. 6–8, T.T.O.-H.—From the caudalmost tectal regions there emerges a broad system of fine lightly coloured fibres that pass superficially along the outer border of the accumulating fibres of the commissura ansulata. Some of these fibres turn medially as the tractus tecto-tegmentalis ; the majority, however, continue ventrally and terminate in the outer half of the middle part of the nucleus subrotundus. The fibres of this tract come from the same area out of which those of the tecto-bulbar systems emerge ; hence this would suggest that it is a hypothalamic centripetal conducting system, whereby the inferior lobes are subjected to optic influences. Holmgren (1920, p. 296) described a tractus lobo-mesencephalicus connecting the caudal part of the lobi laterales with the optic tectum.

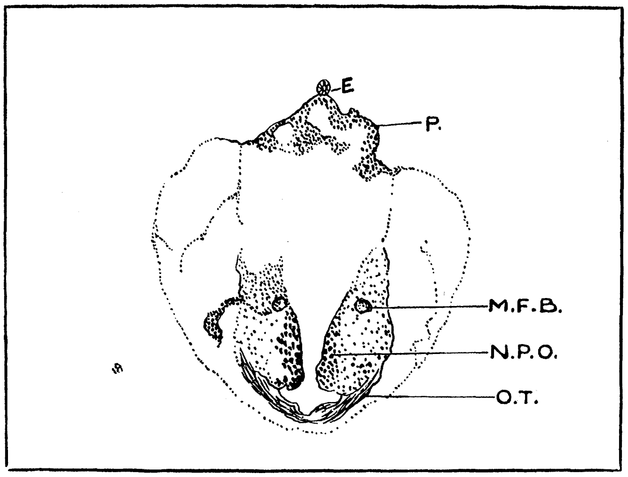

Fig. 12—A section through the preoptic region. This and the seven succeeding figures, including fig. 19, are from transverse sections from the same *Bathypterois* brain (B.C. 13) ; iron hematoxylin stain. × 50.

(3) *Tractus thalamo-hypothalamicus*—The middle part of the nucleus subrotundus lies under the pars rotundus from which it is separated by the large tractus thalamo-hypothalamicus. At the level of the caudal end of the pars rotundus the fibres of the tract spread out among the cells of the nucleus subrotundus forming the dense arborization characteristic of this part. (Also see section 8—7).

(4) *Tractus rotundo-lobaris*—This tract is described under the connections of the corpus glomerulosum (8—8). Suffice, here, to say that neurites from the tractus

rotundo-lobaris add to the rich arborization of the middle part of the nucleus subrotundus.

(5) *Commissura horizontalis*—The dorsomedial part of the nucleus subrotundus is traversed by the commissura horizontalis, from which a ventral component splits off to enter the medial border of the nucleus. This component is very clearly seen in *Diaphus*, *Bathypterois* and in *Saurida*. The horizontal commissure is described under the diencephalic commissures (10—3).

(6) *Tractus hypothalamicus longus descendens*, figs. 7 and 8, T.H.L.D.—It has been noted that fibres pass from the transverse commissure and descend through the anterior part of the nucleus subrotundus. Many of these fibres terminate in the middle region, but many new ones are added from the surrounding cells, and together they pass backward to the most caudal end of the hypothalamus. This is a large, compact tract of poorly medullated fibres.

(7) *Fibræ a hypothalamo in tegmentum*—This is a broad system of fibres, seen in a number of transverse sections, that passes between the fibrillar mass of the nucleus subrotundus, arches rostrally over the commissura ansulata, and distributes to a large part of the inferior tegmental areas.

(8) *Tractus hypothalamo-cerebellaris*, figs. 8 and 9, T.H.-C.—There is no sharp line of demarcation between the fibrocellular area of the middle subrotundus and the nucleus cerebellaris hypothalami. In the dorsal part of this latter nucleus, fibres concentrate and emerge to form a large compact tract that passes dorsally in front of the commissura ansulata. The tract ascends rapidly, passes along the medial border of the lateral longitudinal fasciculus, and enters the anterior secondary gustatory nucleus. From here some of the fibres enter the valvula cerebelli. Others, however, do not reach the cerebellum but remain in the gustatory nucleus. These fibres constitute the tractus gustatorius tertius described with the connections of the secondary gustatory nucleus (14—6).

(9) *Fibræ a parte ventrali in hypothalamum*—These fibres are described under the pars ventralis thalami (3—5).

(10) *Tractus hypothalamo-bulbaris*, figs. 8–11, T.H.-B.—A number of descending and ascending pathways have been described in teleosts connecting the hypothalamic areas with the bulb and the spinal cord. Among the descending bundles are the tractus hypothalamo-bulbaris, HOLMGREN (1920, p. 296), tractus lobo-bulbaris, KAPPERS (1921, p. 807), tractus mammillo-peduncularis, HOLMGREN (1920, p. 297), while the ascending are the tractus spino-hypothalamicus and tractus spino-subrotundus, HOLMGREN (1920, p. 285).

In *Diaphus* the tractus hypothalamo-bulbaris emerges from the caudal part of the nucleus subrotundus, arches over the rostral border of the commissura ansulata, and turns caudally, fig. 8. This large tract of coarse, well-medullated fibres descends as a separate bundle as far as the level of the sensory trigeminal root, fig. 11, where it is joined by the tractus spino-tectalis et menencephalicus. The neurites of this tract terminate about the dendrites of the large reticular cells of the bulb.

(11) *Fore-brain connections with the lobi inferiores*—In order to interpret the fore-brain pathways, a brief survey of this region in *Diaphus* is given. A section through the fore-brain at the level of the anterior commissure indicates that the cellular arrangement is very similar to that of the carp as described by Sheldon (1912, figs. 35 and 36). Centrally placed are the parts of the precommissural body; next is the palæostriatum, and outermost, dorsally to ventrally, appear the nucleus olfactorius lateralis, the nucleus pyriformis, and the nucleus tæniæ.

The commissures in *Diaphus* consist of the commissura interbulbaris and commissura anterior. The interbulbar commissure is rather large, consisting of fine, but well-medullated fibres that cross some sections rostral to the commissura anterior. The anterior commissure has distinct dorsal and ventral components.

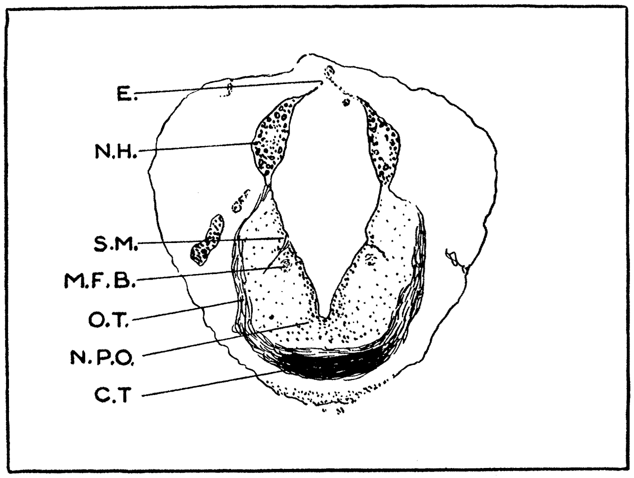

Fig. 13—A section at the level of the habenular nuclei of *Bathypterois*. × 50.

The dorsal component consists of fibres that are associated with the medial fore-brain bundle, and the ventral of fibres from the lateral olfactory region.

(11*a*) *Lateral fore-brain bundle*, figs. 2–7, L.F.B.—This fasciculus consists of a number of ascending and descending tracts that have been analysed by Catois (1901), Kappers (1906), Johnston (1911), Sheldon (1912), Holmgren (1920), and Tuge (1929).

In the *Diaphus* material many myelinated fibres (the tractus strio-thalamicus) appear rostrally in the paleostriatum, but shift ventrally and become concentrated in the region internal to the fissura endorhinalis. To these fibres are added others from the nucleus olfactorius lateralis, from the nucleus pyriformis, and from the upper part of the basal lobes and the ventral part of the anterior commissure. These descend (and ascend) as a broad bundle of feebly medullated fibres into the pedunculi thalami. In the region of the optic chiasm some of these fibres appear to go to the adjacent areas. Especially noted were fibres that spread out dorsolaterally toward the eminentia thalami anterior. Caudal to the optic chiasm a small fasciculus of fibres passes ventrally to enter the nucleus anterior tuberis. Throughout most of its course the lateral fore-brain bundle lies lateral to the medial fore-brain bundle, but at the level of the commissura minor it shifts dorsal to the medial bundle. When the medial fore-brain bundle shifts laterally it is followed by the lateral fore-brain bundle, whose fibres end chiefly in the medial side of the nucleus subrotundus.

(11*b*) *Medial fore-brain bundle*, figs. 2–16, M.F.B.—Kappers (1906, pp. 10 and 22) describes this bundle as originating in the epistriatum and ending in the nucleus rotundus and the adjacent areas. Sheldon (1912, pp. 219-222) divides this complex into six fibre bundles as follows : (1) Tractus hypothalamo-olfactorius medialis which originates in the nucleus posterior tuberis and crosses in the anterior commissure to terminate in the corpus precommissurale ; (2) Tractus olfacto-thalamicus, pars ventralis, originating from the corpus precommissurale and terminating in the nucleus rotundus, and the nucleus posterior thalami ; (3) Tractus olfacto-thalamicus, pars dorsalis, originating in the precommissural body and ending in the nucleus subrotundus. The remaining bundles are short fibre tracts connecting the different parts of the precommissural body to the nucleus preopticus and to the diencephalon.

This review of the tracts as described by Sheldon shows that these form a fibre system connecting the precommissural body, which is an olfactory centre, with various diencephalic centres in the region of the rotundus complex.

In *Diaphus* the medial fore-brain bundle is composed, for the most part, of fibres from the dorsal part of the anterior commissure and the precommissural body. This fasciculus descends as a large round compact bundle of well-medullated fibres. There is no marked change in size, though it is most probable that unmyelinated fibres are exchanged with the adjacent areas rostral to the level of the commissure horizontalis. No large component was found splitting off and passing dorsally to the region of the nucleus of the posterior commissure as described for *Orthagoriscus* by Burr (1928, p. 83).

The writer was surprised to find that only very few fibres were distributed to the nucleus rotundus and subrotundus. Instead of spreading out in this region the bundle remains compact as it arches under the pars rotundus and ascends along the lateral rotundal border, figs. 7 and 8. From the level of the pars rotundus the medial fore-brain bundle passes caudally and slowly ascends along the medial border of the lateral longitudinal fasciculus. It is possible that some fibres are added to the fore-brain bundle in this region. The bundle next arches over the dorsal surface of the lateral longitudinal fasciculus where it is accompanied by the ascending gustatory tract, fig. 9. These two sets of fibres are easily differentiated from each other, for those of the fore-brain bundle are thin, compact, and darkly stained, whereas the gustatory tract fibres are large, loosely arranged, and lightly stained. These two tracts pass side by side, figs. 10 and 11, under the incoming sensory trigeminal fibres. The medial fore-brain bundle fibres remain in the lateral position until they are lost at the level of the facial nerve.

After writing the above description the writer saw that an examination of Wallenberg's figures 12 and 13 in his 1931 paper on the gold fish indicates very clearly that the region of the lesion adjacent to the lateral edge of the pars rotundus corresponds to the position of the medial fore-brain bundle described in *Diaphus* in this paper, figs. 7 and 8. Wallenberg names these degenerated fibres the tractus basoquintalis. According to his description these fibres pass along the inner edge of the lateral longitudinal fasciculus and arch over its dorsal surface, whence some of them go to the ganglion isthmi and others to the anterior secondary gustatory nucleus. From the gustatory nucleus region the remaining fibres accompany those of the ascending gustatory tract. (See Wallenberg's figs. 11–21.) Very obviously this tract corresponds to the fibres described in this paper as representing the caudal course of the medial fore-brain bundle.

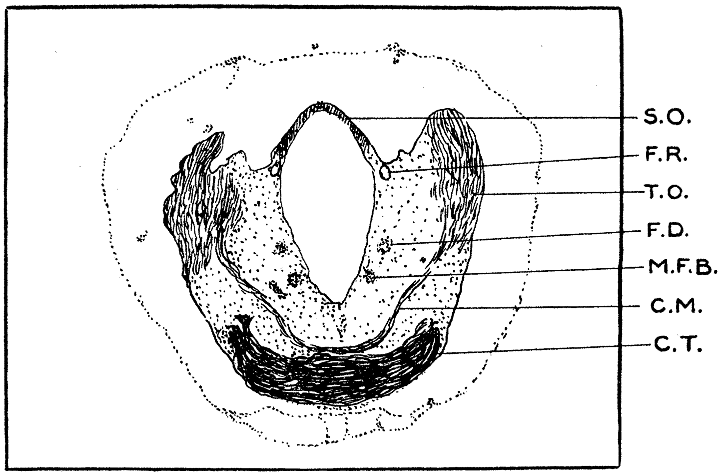

Fig. 14—A section through the decussation of the commissura minor and the commissura transversa of *Bathypterois*. × 50.

Hence, in *Diaphus* at least, the medial fore-brain bundle appears to be a mechanism through which the lower cranial nerve centres are placed under the influence of olfactory impulses.

10 DIENCEPHALIC COMMISSURES

(1) *Commissura transversa*, figs. 4–6, 13–17, C.T.—This commissure is the most conspicuous bundle of fibres in the tween-brain of *Diaphus*. The large size of this commissure is due to its intimate relationship with the enormously developed octavus system, especially the hypertrophy of the torus semicircularis. The transverse commissure lies immediately caudal to the optic chiasm, but the fibres of the transverse commissure are easily identified for they are lightly stained and loosely arranged, whereas those of the chiasm are very compact and darkly stained. The middle part of the commissure is bounded above by the commissura minor of Herrick, and the fibres of the most caudal part of the crossing are intermingled

with the fibræ ansulatæ. After crossing, the fibres of the commissura transversa arch superficially around the ventrolateral part of the diencephalon, then go dorsally to spread out fanlike into the equally hypertrophied torus semicircularis, fig. 4. Although no ventral component was identified (commissura ventralis of HERRICK) the fibres of the caudal part are distinctly finer and lighter stained. These lighter stained fibres are more intimately associated with the optic tectum than with the torus semicircularis, for as the commissure approaches the optic tectum the lighter stained component splits off and enters the deep tectal layers.

KAPPERS (1906, p. 26) says it is generally accepted that the commissure transversa contains no fibres from the optic nerve. KRAUSE (1898) determined by experimental methods that this commissure did not contain direct optic fibres in the carp. At no time is the commissural component to the optic tectum a part of the direct optic system and it probably represents a connection between the two optic tecta or between the torus semicircularis and the optic tectum of the opposite side. BURR (1928) also found fibres of the transverse commissure ending in the stratum profundum tecti.

In the *Diaphus* brain the anterior end of the nucleus subrotundus is surrounded by fibres of the transverse commissure, many of which enter this nucleus and descend to the caudalmost parts of the hypothalamus. Where the transverse commissure forms the outer boundary of the lateral geniculate, many thin fibres enter that structure. These are described with the connections of the lateral geniculate body. KAPPERS (1921, p. 807) suggests that in teleosts the ganglion isthmi is one of the end stations for the transverse commissure. LARSELL (1924, fig. 3) found the transverse commissure the largest isthmal connection in the frog. Both of the above structures are highly developed in *Diaphus*, but none of the commissural fibres could be traced as far caudally as the ganglion isthmi.

In *Bathypterois* the decussation of the commissura transversa is found in its usual location, figs. 13 and 14. After crossing, the fibres form a large conspicuous bundle on the lateral diencephalic wall. This bundle is especially well seen, figs. 15 and 16, as the optic fibres are very scanty. The reason for the large commissura transversa of this poorly developed brain finds its explanation in the large lateral longitudinal fasciculus, figs. 17 and 18, and the highly developed torus semicircularis, with which it is associated. Although considerably smaller in the brain of *Saurida*, the transverse commissure has the same location and is associated primarily with the torus semicircularis.

The commissura transversa, in addition to being a large commissural system between the tori semicirculares, has minor connections with the following centres: pars dorsalis thalami, pars ventralis thalami, geniculatum laterale, corpus glomerulosom, pars anterior, and nucleus subrotundus. The minor connections are described with the cell areas with which they are in relationship.

(2) *Commissura minor* of HERRICK, figs. 3–5 and 14, C.M., M.; C.M., L.—The commissura minor was identified in all three brains decussating in the usual place above the transverse commissure. In *Diaphus* the fibres form a large, compact

bundle that splits into medial and lateral parts as it approaches the lateral geniculate body. A small part of the lateral fibres spread out and are lost among the cells of the lateral geniculate. However, most of the lateral fibres form a very compact bundle that goes rostrally along the ventrolateral border of the geniculate body, figs. 3–5, and enters the optic tectum with the afferent optic tract fibres. The medial arm, figs. 3 and 4, ascends along the inner border of the lateral geniculate where a few fibres may terminate, but most of these also pass as a compact deep-stained bundle to the optic tectum.

In *Bathypterois* the commissura minor is thin but very distinctly (fig. 14) a tectal commissure. The same is true of *Saurida*. Kappers (1906, 1921) considers the commissura minor a tectal connection. Burr (1928) was unable to trace fibres beyond the lateral geniculate bodies. Goldstein (1905) found the commissura minor connecting the two lateral geniculate bodies and called it the commissura intergeniculata. In *Diaphus* this is primarily an optic commissure, and although in all three fish fibres terminate among the geniculate cells, the majority enter the tectum.

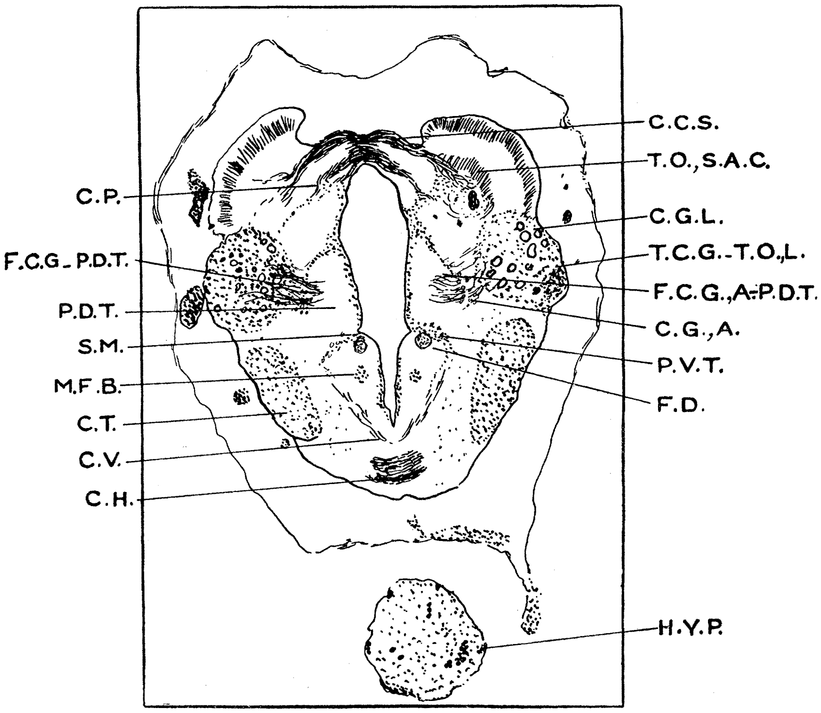

Fig. 15—A section through the level of the decussation of the commissura horizontalis. × 50.

It is the opinion of the writer that the commissura minor is primarily an optic commissure for it is especially well developed in fish with a large optic tectum (*i.e.*, *Diaphus*) and it is poorly developed in fish with a small optic tectum (*i.e.*, *Bathypterois*).

This viewpoint is corroborated by the recent study of Charlton (1933, pp. 312 and 313), who failed to find a commissura minor in some blind fish.

(3) *Commissura horizontalis of Fritsch*, figs. 7, 15, and 16, C.H.—This commissure is a well-medullated conspicuous bundle that decussates caudal to the commissura transversa. In all three of the brains the horizontal commissure has a larger dorsal part that consists of coarser and more heavily medullated fibres and a smaller, ventral part with thinner and lighter stained fibres. Both parts are in contact with each other except in *Diaphus* where after decussating they separate from each other. In *Diaphus* the ventral component is lost in the nucleus subrotundus. The dorsal bundle of coarse fibres sweeps dorsolaterally and enters the inferior and medial border of the pars rotunda. These coarser fibres pass through the medial part of the pars rotunda, fig. 7, and make their exit dorsally as a compact bundle practically as large as before entering. Above the pars rotunda the horizontal commissure joins the tractus mesencephalo-cerebellaris anterior and the tractus spino-tectalis et mesencephalicus whereon they pass together rostrally and dorsally as a large, compact, deeply stained bundle.

These combined bundles are bounded laterally by the lateral geniculate body, fig. 6. Rostrally this fibre bundle splits into three fascicles of nearly equal size. The fibres of the outermost fascicle end in the geniculate body. The remaining bundles ascend in the relatively clear area, figs. 3 and 4, Z., of the pars lateralis of the dorsal motor tegmental nucleus. From this region some of the fibres enter the dorsal part of the posterior commissure. However, most of the fibres spread out and terminate in the nucleus pretectalis, the nucleus tegmenti motorius dorsalis, pars propia, and the optic tectum.

In *Saurida* the coarse fibres of the horizontal commissure pass through the pars rotunda practically intact, join the tractus mesencephalo-cerebellaris anterior and course rostrally. Part of the fibres enter the posterior commissure, some terminating in the nucleus pretectalis and others entering the optic tectum. The commissura horizontalis of *Bathypterois*, figs. 15 and 16, could not be followed beyond the pars rotunda. It is most probable that these fibres also have the same endings in this brain but were lost due to defective staining.

(4) *Commissura habenularis*—This is the more rostral of the two dorsal diencephalic commissures. The commissure habenularis is present in all three brains, but it is best developed in *Bathypterois*. This commissure consists for the most part of non-medullated fibres that connect the dorsal surface of the two habenular nuclei. The fibres of the commissure rest on the bases of the tall columnar cells of the sub-commissural organ. A number of investigators (Kappers, 1906, Sheldon, 1912, Holmgren, 1920, Tuge, 1929) have discussed many tracts that decussate through the so-called habenular commissure. The writer is unable to report any additional information on these components.

(5) *Commissura posterior*, figs. 3–5, 15 and 16, C.P.; C.P., D.; C.P., V.—This large commissure marks the dorsal boundary between the diencephalon and the mesencephalon (Kappers, 1906, Burr, 1928).

The posterior commissure of *Diaphus* consists of two main parts, a dorsal and a ventral, that are entirely separated from each other, figs. 3–5. The rostral part of pars ventralis consists of rather fine but well-medullated fibres that are intimately associated with the eminentia thalami anterior and with the nucleus tegmenti motorius dorsalis, figs. 3–5. More caudally, the pars ventralis is primarily associated with the pars propia of the dorsal motor tegmental nuclei and the pars dorsalis thalami. However, the pars ventralis also receives fibres from the optic tectum through a fasciculus which is described with the connections of the optic tectum. Other fibres of the pars ventralis enter the fasciculus descendens pars lateralis. The most caudal part of the pars ventralis turns backward and enters the rostral end of the medial longitudinal fasciculus. This is called "fasciculus commissura posterior descendens," figs. 4 and 5, F.C.P.D.

The pars dorsalis of the posterior commissure is a system of coarser fibres than those of the pars ventralis. These fibres emerge from the inferior edge of the deep tectal layers and from the nucleus pretectalis. The relationship to the pretectal region has led Catois (1901) and Holmgren (1920) to call this component the commissura pretectalis. An unusual feature found in the *Diaphus* brain is the large connection between this pars dorsalis and the lateral geniculate body, fig. 5, F.C.G.-C.P. The pars dorsalis appears to give rise to two descending bundles of fibres. One of these is the fibre bundle to the tractus mesencephalo-cerebellaris anterior. The second descending component comes from the caudalmost fibres of the pars dorsalis that turn backward and form most of the more rostral bundles of the medial longitudinal fasciculus, fig. 6.

In *Bathypterois* the commissura posterior is undivided. The most rostral part is in contact with the commissura colliculi superioris, fig. 15. The rostral part of the commissure carries almost exclusively tectal fibres, whereas the caudal part, fig. 16, has a broad connection with the lateral geniculate body, with the pars dorsalis thalami and to a lesser degree with the nucleus pretectalis. The most posterior fibres turn caudally after crossing and form the largest constituent of the rostral end of the medial longitudinal fasciculus. Nothing new was observed in the commissura posterior, of *Saurida*.

IV—Mesencephalon

11 TECTUM OPTICUM, figs, 2–6, 14–17, 20, T.O.

It is not the purpose of the present investigation to include a detailed description of the histology of the optic tectum. For a histological analysis of the tectum the reader is referred to the work of Fusari (1887), Krause (1898), Cajal (1899, 1911), Kappers (1906, 1921), and Radl (1915).

For modifications of the tectum in teleosts having defective vision there are accounts by Ramsey (1901) and Charlton (1933).

An examination of the figures shows that the optic systems of *Diaphus* and *Saurida* are fairly well developed but that that of *Bathypterois* is decidedly atrophic. In fact, the optic nerves and optic tracts of *Bathypterois* are reduced to small fascicles of poorly medullated fibres, figs. 12 and 13, as are also the oculomotor, the trochlear, and the abducens nerves. *Bathypterois* is only found at great depths and always near the ocean bottom ; hence the atrophied optic system is probably correlated with the absence of light.

An examination of the figures of the brains of deep sea fish by TROJAN (1906) also suggests that some of these have poorly developed optic systems.

KAPPERS (1921, pp. 812 and 813, fig. 432) divides the optic tectum into three layers : a superficial fibre layer, a middle cellular layer, and an inner layer or stratum medullare profundum. These three chief layers of KAPPERS are present even in the brain of *Bathypterois*. The result of the diminished primary optic fibres in *Bathypterois* is reflected in a small gross optic tectum and a marked thinning of the superficial layers, figs. 15 and 16.

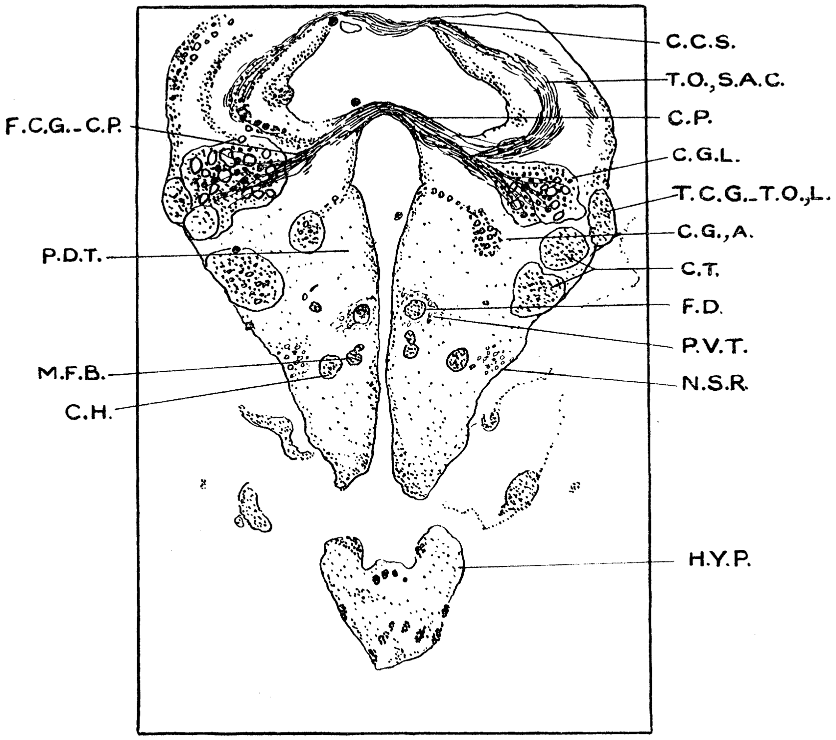

FIG. 16—A section through the caudal end of the posterior commissure of *Bathypterois*. × 50.

In most fish the optic tecta extend far frontally over the habenular nuclei. This is true of *Diaphus* and *Saurida*. It is also true of a number of other fish examined, such as *Irachinus draco*, *Periopthalmus*, *Idus idus*, *Gadus morrhua*, *Tetrodon fluviatilis*, *Pleuronectes limanda*, *Osmerus eperlanus*, and *Gasterosteus aculeatus*. In the *Bathypterois* brain, due to the marked decrease in size, the rostral limit of the tectum is caudal to the habenular nucleus, fig. 13 ; hence the habenulæ are very conspicuous. In *Diaphus* the enormous development of the tori semicirculares and the frontal projection of the cerebellum has displaced the middle and caudal parts of the teotum far laterally, figs. 4 and 5, so that the lamina commissuralis tecti is limited to the most rostral end.

The characteristic large cells of the mesencephalic nucleus of the trigeminal nerve are seen in their usual place in the deep tectal layers. However, concerning these cells the writer has nothing to add to the extensive descriptions of JOHNSTON (1909) and WEINBERG (1928).

Connections

(1) *Optic Tracts*—The optic tracts of teleosts have been described by various observers. Among the investigators of this fibre system may be included BELLONCI, (1879), KRAUSE (1898), KAPPERS (1906, 1921), FRANZ (1912), WALLENBERG (1913), HOLMGREN (1920), KUDO (1923*a*), and JANSEN (1929). The literature has been recently surveyed by JANSEN (1929, pp. 1104-1107) so will not be repeated here. JANSEN as a result of his studies, especially on sections of an *Idus idus* that was blind in one eye, concludes (pp. 1115 and 1116) that the optic tract consists of the following components: (1) Fasciculus dorsalis, (2) Fasciculus lateralis, (3) Fasciculus medialis, (4) Fasciculus dorsomedialis, (5) Tr. preoptico-opticus. JANSEN also concludes that the tractus isthmo-opticus (FRANZ) and the fibræ tectales n. optici (KRAUSE), formerly held to represent an efferent tecto-retinal component of the primary optic system, do not enter the optic nerve.

The complete decussation of the optic nerves takes place in their usual place in *Diaphus* and *Saurida*. In *Bathypterois* the small optic nerves cross rostral to the habenular nuclei, fig. 12, ascend dorsocaudally and without splitting into the usual components spread out in the superficial layers of the rostral part of the optic tectum. Although no collaterals were observed between these optic fibres and the relatively large lateral geniculate body, it is probable that such exist.

(1*a*) *Fasciculus dorsalis*—In *Diaphus* and *Saurida* the fasciculus dorsalis comes from the most rostral fibres of the decussation. These fibres sweep rostrally and dorsally to occupy the entire area between the outer border of the eminentia thalami and the inner border of the lateral geniculate body. These fibres are distributed to the superficial layers of the ventral and medial surfaces of the optic tectum. Numerous fine fibres pass between the optic tract and the lateral geniculate body; whether these are collaterals or terminal fibres was not determined.

Practically all of the fibres from the fasciculus dorsalis are distributed rostrally; this results in the absence of the large area of well-medullated fibres usually found occupying the dorsomedial area of the tectum. Compare the fasciculus dorsalis of the normal side of *Idus* (JANSEN, 1929, figs. 3–5) with the figures of *Diaphus*.

(1*b*) *Fasciculus lateralis tractus optici*, figs. 4–7, 20, F.L.O.—The fibres of the middle and caudal parts of the chiasm turn dorsolaterally to form the fasciculus lateralis, part of which lies along the outer border of the decussation of the commissura transversa. Caudal to the crossing of the transverse commissure, a large part of the fasciculus lateralis fibres continue caudally along the lateral border of the commissure immediately ventrally to the lower border of the tectum. These fibres continue to the most caudal end of the tectum distributing fibres to the superficial tectal layers, fig. 7.

(1*c*) *Fasciculus medialis tractus optici*—This fasciculus, which is only in part comparable with the fasciculus medialis described by Jansen (1929) is a very large conspicuous bundle of well-medullated fibres that split off from the medial edge of the optic fibres immediately following their decussation.

A few of the outermost fibres pass dorsally and enter the rostral part of the optic tectum; these are similar to those described by Jansen as the fasciculus medialis tractus optici.

The bulk of these fibres, however, spread out over the rostral end of the eminentia thalami anterior and for the most part are lost. This component, which is described as the fasciculus opticus ad eminentia, fig. 2, is discussed under the connections of the eminentia thalami (2—1). Holmgren (1920, p. 261) described optic collaterals to the eminentia thalami and called them tractus optico-eminentialis. It would appear to the writer that the fasciculus of the present description is merely a more highly elaborated system, associated with a very highly developed eminentia thalami, of which the tractus optico-eminentialis is the forerunner.

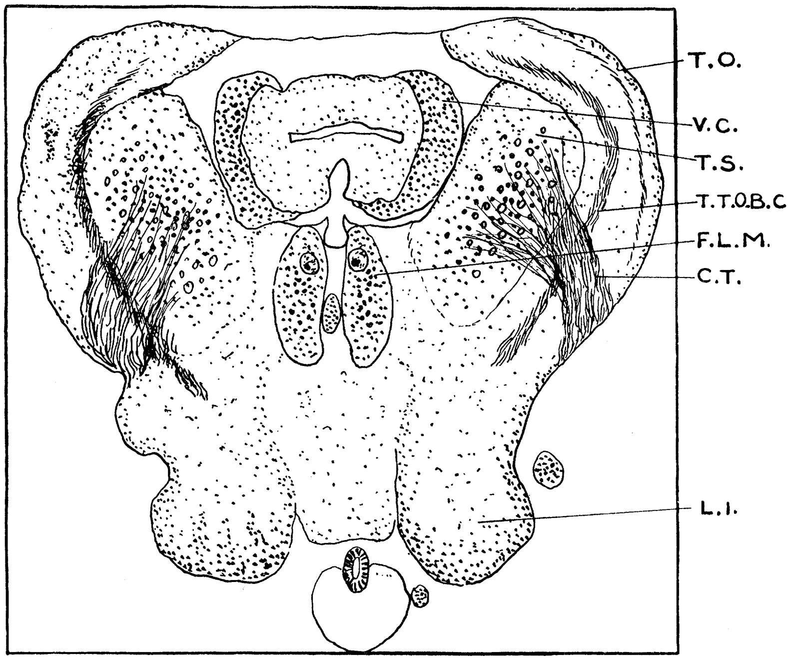

Fig. 17—A section showing the tori semicirculares and the entering transverse commissure fibres of *Bathypterois*. × 50.

Many of the optic tract fibres that enter the eminentia thalami do not end there but course dorsally to penetrate into the rostral end of the nucleus tegmenti motorius dorsalis. This is the fasciculus ab optico in nucleum dorsalem described under the connections of the nucleus tegmenti motorius dorsalis (5—1).

Jansen (1929, figs. 3–5) described and figured a fasciculus dorso-medialis that courses lateral to the posterior commissure and disappears in the dorsal part of the tegmentum mesencephali. It seems most probable that the fasciculus ab optico in nucleum dorsalem of this description corresponds to the fasciculus dorsomedialis of Jansen.

(1*d*) *Fibræ ab optico in partem ventralem*, figs. 4 and 5, F.O.-P.V.T.—This is a small optic fasciculus described under the connections of pars ventralis thalami (3—11).

(2) *Fibræ tectales nervi optici*, figs. 3–5, F.T.O.-N.O.—This is a system of fibres that emerges from the outer edge of the inferior border of the stratum profundum. Located above these fibres are optic fibres to the commissura posterior, pars dorsalis (commissura tecti). The fibræ tectales are intimately associated with the nucleus pretectalis ; very likely some fibres are contributed by the cells of this nucleus. As the bundle passes ventromedially it splits into dorsal and ventral fasciculi, fig. 5. From the dorsal fasciculus fibres go to the commissura posterior, pars ventralis, and others enter the ventrolateral part of the nucleus tegmenti motorius dorsalis ; these are the fasciculi a tecto in nucleum dorsalem described under Section 5. Some fibres also are traced to the upper part of the pars dorsalis thalami under which they are described as the fasciculi a tecto in partem dorsalem thalami (4—6).

The ventral fasciculus spreads out into a loosely arranged system of fibres that course ventrally to decussate along the inner border of the optic chiasm. These constitute in part, at least, the “ innermost commissural fibres ” of Charlton (1933, p. 310). A large fasciculus of these fibres, after crossing, passes along the inner edge of the optic tract fibres and distributes to the lateral border of the eminentia thalami. These are the fibræ a tecto in eminentiam thalami referred to under the eminentia (2—6).

The history of these fibres has recently been reviewed and discussed by Jansen (1929, p. 1112), and by Jeener (1930, pp. 765 and 766) and will not be repeated here. The studies of Jansen on a fish blind in one eye leads him to the conclusion that these are a component of the postoptic commissural complex.

(3) *Tractus tecto-toralis*—This tract is described under the torus longitudinalis (12—1).

(4) *Tractus tecto-rotundus*—Holmgren (1920, p. 276, fig. 84) in his silver preparations described fibres from the optic tectum that arborise in the nucleus rotundus. That such a tract is present in *Diaphus* is most probable, as the commissura horizontalis in this fish receives tectal fibres, and in turn passes through the nucleus rotundus.

(5) *Tractus olfactorio-opticus*—This tract was first described by Holmgren (1920, p. 188) in Cajal preparations, and confirmed by Kudo (1923*a*, pp. 65·68) in Weigert material. This tract is not evident in the deep sea fish material.

(6) *Tractus strio-tectalis*—A tract was described by Franz (1912, p. 412) that passed from the corpus striatum to the mid-brain roof. This tract was not identified in the deep sea fish.

(7) *Tractus recesso-tectalis*—This is a tract that was first described by Holmgren (1920, p. 222). Many very fine lightly stained fibres pass from the nucleus preopticus

pars parvocellularis of the chiasmal region and join the ascending optic tract fibres. These fibres appear to correspond to those forming the tractus recesso-tectalis.

(8) *Tractus mesencephalo-cerebellaris anterior*, figs. 7 and 8, T.M.-C.A.—This is the tractus mesencephalo-cerebellaris anterior of Kappers (1921, pp. 809 and 810), Addison (1923, pp. 6-8), Charlton (1933, pp. 300-302) ; the tractus pretecto-cerebellaris or tecto-cerebellaris of Holmgren (1920, p. 263), Burr (1928, p. 99), Brickner (1929, p. 267), Hoogenboom (1929, pp. 348 and 349).

The writer agrees with Charlton (1933, p. 300) that the name " tractus mesencephalo-cerebellaris " is preferable, and that the other terminology is inadequate because the tract has a number of origins. I need only mention that Charlton found components from the optic tectum, the nucleus pretectalis and the corpus geniculatum laterale.

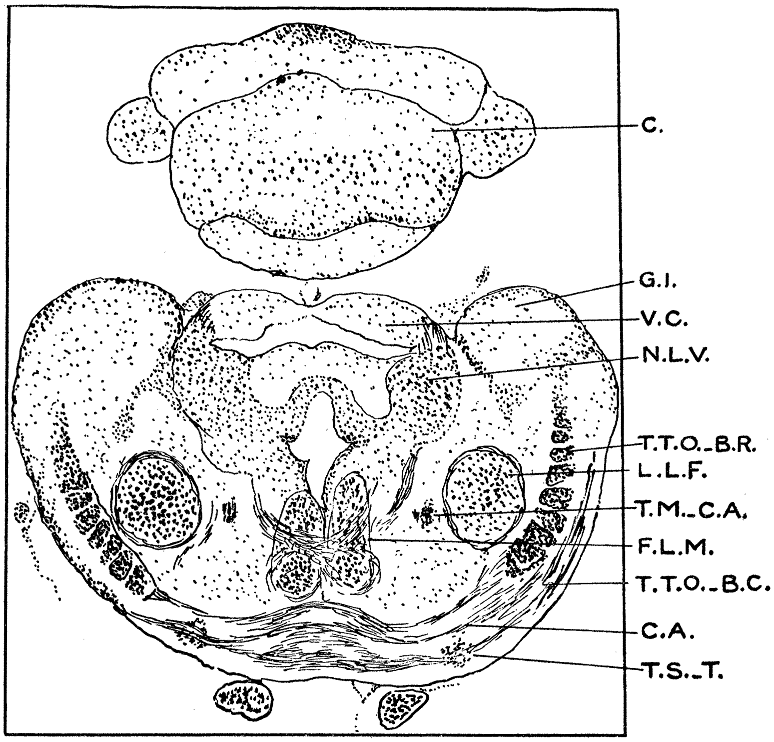

Fig. 18—A section through the commissura ansulata of *Bathypterois*. × 50.

This description is based on the findings in *Diaphus*, although the tract is also present in the other two fish.

The most rostral components to this tract come from the ventral border of the superficial layers of the optic tectum. Next are added the fibres from the pretectal nucleus. Caudally, two stout fasciculi of coarse well-medullated fibres are added from the posterior commissure, pars dorsalis. The geniculate component comes from the caudal end of that body, and is added as a large fasciculus where the tract passes along its medial border. Rostrally, many fibres of the tractus mesencephalo-cerebellaris anterior originate in the nucleus tegmenti motorius dorsalis, pars lateralis. It must be stated that the fibres of this tract are intermingled with those of the commissura horizontalis and the tractus spino-tectalis et mesencephalicus; therefore all of the origins may not be accurately determined.

The combined fibres of these tracts form a large, compact, well-medullated area of fibres embedded in the outer half of the caudal end of the lateral geniculate body, fig. 6, Z. Caudal to the geniculate body, the tractus mesencephalo-cerebellaris is the first to split off and shift dorsally, occupying a position ventromedial to the lateral longitudinal fasciculus, figs. 7 and 8, from which it turns abruptly and enters the valvula cerebelli. The relationship of this cerebellar tract to the commissure horizontalis is well demonstrated by figure 20 of HERRICK (1905).

(9) *Fasciculi a tecto optico in commissuram posteriorem*—Many tectal fibres enter the pars dorsalis of the posterior commissure; these are described with the commissure under the heading diencephalic commissures (10—5).

(10) *Fasciculus a tecto optico in commissuram transversam*—The commissura transversa receives (or sends) a distinct fasciculus of fibres from the stratum profundum, but the brain of *Diaphus* clearly reveals that the transverse commissure is primarily a commissural system for the tori semicirculares.

(11) *Fasciculus a tecto optico in commissuram minorem*—The deep sea fish material shows this to be primarily an optic commissure. This commissure and its connections are discussed under diencephalic commissures (10—1).

(12) *Tractus isthmo-tectalis and tractus tecto-isthmicus*—These tracts are described with the connections of the ganglion isthmi (16—1).

(13) *Tractus gustato-tectalis*—This tract, described by BRICKNER (1930, p. 155), is included under the gustatory centres of this paper (14—1).

(14) *Tractus tecto-hypothalamicus*—This tract is described under the lobi inferiores (9—2).

(15) *Tractus geniculo-tectalis*—This tract is described under the lateral geniculate body (6—2).

(16) *Tractus tecto-bulbaris*, figs. 6–11, 17–19, T.T.O.-B.R., T.T.O.-B.C.—The optic tectum is an optic correlation centre, the output of which is transferred by large descending pathways to the motor nuclei of the medulla and the cord. According to KAPPERS (1921, p. 817) the fibres of the tecto-bulbar system originate from the great pyramidal cells of the chief cell layer. Although the present material does not permit a statement regarding the exact cells of origin, these fibres very obviously come from the chief cell layer. From this layer, which consists of various cell types embedded in a very pale, fine, felt-like meshwork of fibres, there gather small but very deeply myelinated fasciculi which are in sharp contrast to the light stained meshwork of fibres. Beginning in the most frontal sections, these fasciculi gather along the inner border of the chief cell layer forming a thick region of myelinated fibres among the cells of the granular stratum adjacent to the optic ventricle. Caudally this thick fibre layer is bounded medially by the torus semicircularis.

Where the fibres of the transverse commissure enter (and leave) the torus semicircularis they penetrate between the tecto-bulbar fibres and split them into a number of large fasciculi. HUBER and CROSBY (1933) call the corresponding layer of the reptilian brain the stratum album centrale, a term that is used in this paper.

In *Diaphus* as additional tecto-bulbar fibres are added, in passing from the rostral to the caudal levels, the new additions push the older acquisitions medially. At the caudal tectal levels these more medial fibres are completely separated from the lateral fibres, figs. 5 and 6. The medially placed fibres descend as the tractus tecto-bulbaris rectus, whereas the more superficial layer decussates to descend as the tractus tecto-bulbaris cruciatus.

To summarize, fibres from the frontal and middle tectal regions descend uncrossed, for the most part, but those from the caudal level represent a crossed descending system to the bulbar centres. The experimental work of WALLENBERG (1907, 1913) and DE LANGE (1910) clearly demonstrates that this is a descending system.

(16*a*) *Tractus tecto-bulbaris rectus*—Caudal to the optic tectum these fibres occupy a large area bounded above by the ganglion isthmi and medially by the lateral longitudinal fasciculus. Many very fine fibres pass between the tractus tecto-bulbaris rectus and the adjacent ganglion isthmi. A comparison of the size of the rectus before and after the ganglion isthmi suggests a considerable part of the fibres are lost in this region. As the name implies, this is commonly accepted as a descending system; hence the inference is that these fibres conduct toward the ganglion isthmi.

From the inner edge of the rectus pathway there emerges a large system of fine fibres that pass ventrally and are lost among the centrally placed reticular cells. The uncrossed tract remains in the lateral position and becomes progressively smaller as it descends. It is the writer's impression that in the caudal levels very few of these fibres pass medially, for the material shows very large reticular cells and the outlines of their unstained dendrites passing ventrolaterally to the region of the tractus tecto-bulbaris cruciatus. The writer's suggestion is that these dendrites receive the descending optic impulses, and in turn the neurites of these cells convey the impulses to the various bulbar and spinal motor nuclei, the outlet to the cord being through a reticulo-spinal tract such as that described by BURR (1928, p. 118).

At the level of the inferior olive the remaining fibres of the tractus tecto-bulbaris rectus turn ventromedially and are lost in the substance of the inferior olive. None of the fibres have been followed into the spinal cord.

(16*b*) *Tractus tecto-bulbaris cruciatus*—This tract occupies the area lateral to the much larger region of the rectus fibres, figs. 6–8. As the crossed tecto-bulbar pathway goes caudally, it slowly shifts medially to form the commissura ansulata. From the ventromedial edge of these fibres a large component passes medially and is lost among the centrally placed large reticular cells.

The decussation of the tract takes place at the level of the emerging oculomotor fibres. It is difficult to determine to what extent the decussation is a complete one, but most of the fibres appear to cross. After crossing, these fibres form, in all three fish, two very well circumscribed ventrally placed bundles, one on each side of the midline, figs. 11, 17, 18.

Immediately following the decussation, fibres pass from the tractus cruciatus to the region of the reticular cells, lateral to the lower border of the medial longitudinal fasciculus. As the tract descends it becomes progressively smaller, and is lost in the lower bulbar regions.

(17) *Tractus spino-tectalis et mesencephalicus*, figs. 7–11, 18 and 19, T.S.-T.—In the most caudal levels of the medulla the fibres of the descending tractus hypothalamo-bulbaris and those of the ascending tractus spino-tectalis et mesencephalicus form a single large bundle, fig. 11. At the level of the inferior olive this large area of deeply medullated fibres is located dorsal to that body and medial to the tractus tecto-bulbaris rectus. More rostrally, these tracts begin to separate, and at the caudal border of the commissura ansulata the hypothalamic tract shifts more medially and arches over the commissure whence it can be traced to its origin, the nucleus subrotundus, whereas the ascending tract shifts more laterally and dorsally, figs. 8–10. Immediately above the pars rotunda of corpus glomerulosum the fibres of the tractus spino-tectalis are intermingled, figs. 3–6, Z, with those of the commissura horizontalis, and the tractus mesencephalo-cerebellaris anterior, hence the exact

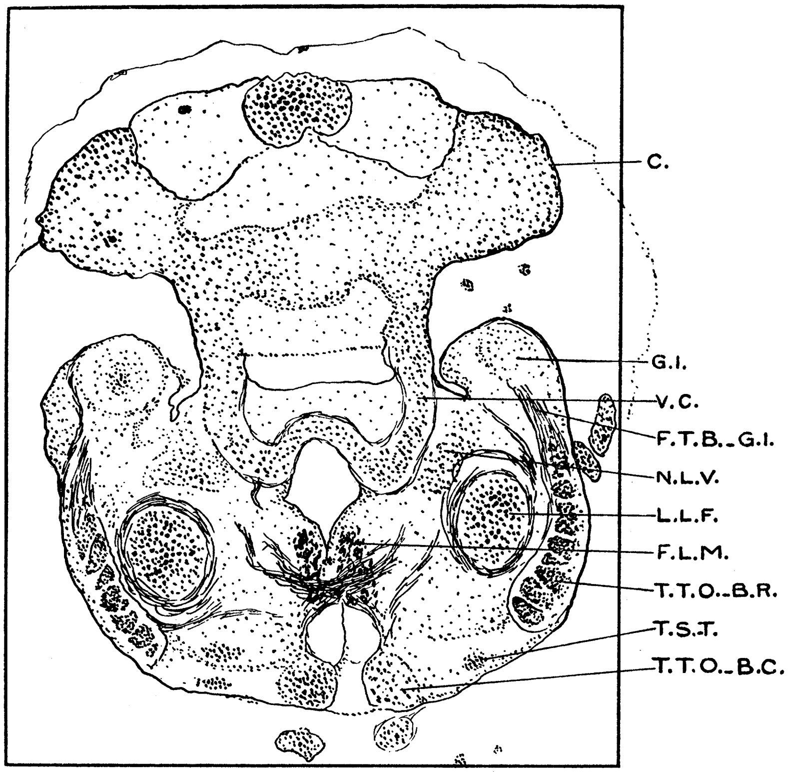

Fig. 19—A drawing of a few sections caudal to the commissura ansulata of *Bathypterois*. × 50.

terminations of the spino-tectal tract are not determined. The terminations of these intermingled fibres are discussed under the horizontal commissure (10—3). Suffice here to state that they terminate in the nucleus pretectalis, the dorsal motor tegmental nucleus, the lateral geniculate body, and the optic tectum.

12 *TORUS LONGITUDINALIS*, fig. 20, T.L.

In the brain of *Diaphus* the torus longitudinalis is fairly well developed, whereas in *Saurida* it is a relatively small structure suspended from the under surface of the mid-tectal roof, fig. 20. An interesting exception to the rule is the complete absence of a torus in the brain of *Bathypterois*. SARGENT (1903) studied the torus in a number of teleosts and found it poorly developed in the Siluridæ but well developed in the Cyprinidæ (*Notropis*), and in the Pœciliidæ (*Fundulus*), in the Salmonidæ, and others. Concerning the torus longitudinalis, SARGENT says (1903, p. 405), "In *Chologaster papilliferus*, which has degenerate eyes though still functional, the optic lobes are much smaller than in the closely related *Fundulus*, which has normal eyes. The tectum is thin and the torus lobes are but little developed. In three other genera which are totally blind, having only vestigial eyes, the torus is scarcely developed as an independent structure."

RAMSEY (1901) found the torus longitudinalis poorly developed in the cave dwelling fish *Amblyopsis*. CHARLTON (1933) also described the torus in the blind fish *Troglichthys rosea* and *Typhlichthys eigenmanni*. Judging by the figures of CHARLTON the torus is fairly well developed in these fish.

Concerning the deep sea fish *Cyclothone*, GIERSE (1904, p. 34) says, "Ein torus longitudinalis wird bei Cyclothone vollständig vermisst im Gegensatz zu andern Knochenfischen." TROJAN (1906) found a poorly developed torus in the deep sea fish *Leucicorus lusciosus*.

In conclusion, it appears that the size of the torus longitudinalis is very largely dependent on the development of the optic tectum with which it is so intimately associated.

Connections

(1) *Tractus tecto-toralis. Tractus toro-tectalis*—The connections of the torus have been fully described by SARGENT (1903).

A number of tracts have been described associated with the torus longitudinalis. Among these are (*a*) tractus tecto-toralis described by FRANZ (1912), RADL (1915), KUDO (1923*b*), CHARLTON (1933); (*b*) tractus toro-tectalis described by SARGENT (1903), FRANZ (1912), KUDO (1923*b*), CHARLTON (1933); (*c*) tractus toro-cerebellaris described by SARGENT (1903), and (*d*) tractus cerebello-toralis, described by KUDO (1923*b*).

In the brains of both *Diaphus* and *Saurida* the only connections found were myelinated fibres passing between the upper part of the torus and the overlying intertectal commissure. The direction of conduction was not determined.

13 NUCLEUS LATERALIS VALVULÆ, figs. 7, 8, 17, 18, N.L.V.

This nucleus is the "Übergangsganglion" of STIEDA (1868), MAYSER (1882), FRANZ (1911), or the nucleus lateralis valvulæ of HERRICK (1905), KAPPERS (1921), ADDISON (1923), and BURR (1928).

In *Diaphus* this nucleus is very large and appears caudal to the torus semicircularis, embedded in the cerebellar peduncle. Ventrolaterally it is bounded by the pars parvo-cellularis of the ganglion isthmi, and dorsomedially by the valvula cerebelli. This nucleus is more than a part of the granular cells of the valvula cerebellaris, for its cells, although round, are somewhat larger and yellow stained (in WEIGERT preparations), whereas those of the valvula are stained a deep orange colour.

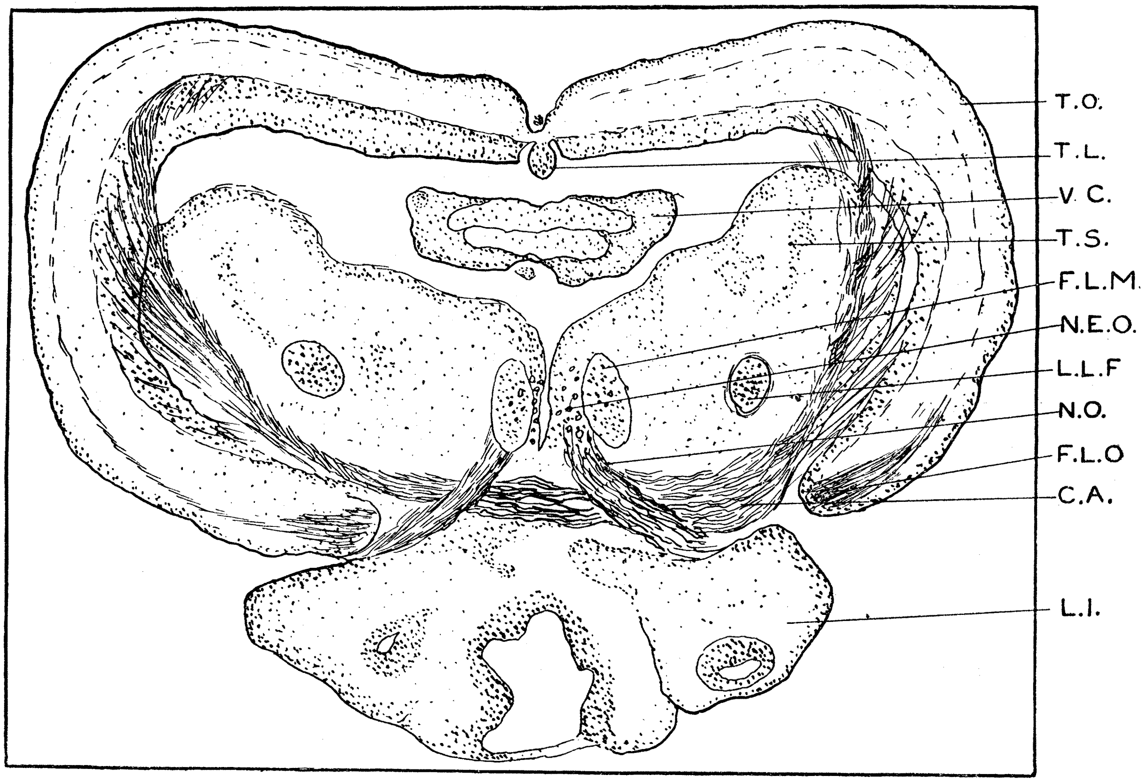

FIG. 20—A section from the *Saurida* brain (B.C. 40) through the region of the emergence of the oculomotor nerve; WEIGERT stain. × 50.

Into this cell area come fibres from the adjacent ventral areas. In the nucleus these fibres become compact and enter the valvula cerebelli as the large tractus mesencephalo-cerebellaris posterior (figs. 7 and 8, T.M.-C.P.).

The tractus mesencephalo-cerebellaris anterior also passes through the caudal end of this nucleus on its way to the valvula cerebelli.

Connections

(1) *Fibræ a ganglio isthmi in nucleum lateralem valvulæ*, fig. 7, F.G.I.-N.L.V.—Many fine but well-medullated fibres pass between both parts of the ganglion isthmi and the nucleus lateralis valvulæ. These do not constitute well-defined fasciculi, but pass between the two nuclei where they are in apposition with each other.

(2) *Tractus tegmento-nucleum lateralem valvulæ*—Many of the fibres to the nucleus lateralis valvulæ originate in the medial part of the tegmentum and ascend as a broad system of fibres passing between the ventricle and the lateral longitudinal fasciculus, while others course around the outer border of the fasciculus in order to reach the nucleus.

(3) *Fibræ a octavo in nucleum lateralem valvulæ*—Scattered fibres reach the anterior end of the nucleus lateralis valvulæ from the torus semicircularis, while other fibres emerge from the outer side of the lateral longitudinal fasciculus to turn dorsomedially and enter the caudal end of the nucleus. However, the number of fibres observed do not appear to be sufficient to explain the high development of this nucleus, if we assume that the nucleus lateralis valvulæ is dominated by octavus impulses.

(4) *Tractus gustato-nucleum lateralem valvulæ*—Herrick (1905, p. 419) noted a broad connection between the anterior secondary gustatory nucleus and the nucleus lateralis valvulæ. He found that these fibres are unmedullated in the brain of *Minytrema melanops*, but delicately medullated in *Catastomus*. In *Diaphus* some scattered thin medullated fibres pass from the cephalic end of the secondary gustatory nucleus to the caudal part of the nucleus lateralis valvulæ.

(5) *Tractus mesencephalo-cerebellaris posterior*, figs. 7 and 8, T.M.-C.P.—From the broad nucleus lateralis valvulæ the fibres pass dorsally to form the very large, compact tractus mesencephalo-cerebellaris posterior. The distribution of this tract in the cerebellum will not be presented in this paper. An excellent description of this tract is given by Addison (1923).

14 NUCLEUS GUSTATORIUS SECUNDARIUS ANTERIOR, fig. 9, N.G.

This is the well-known "Rindenknoten" of Mayser (1882). In *Diaphus* the rostral ends of the two gustatory nuclei are separated from each other, but caudally they are fused, their lower border forming the roof of the aqueduct of *Sylvius*. Two large fibre systems pass through this nucleus, the tractus cerebello-motorius and the tractus ascendens gustatorius, fig. 9.

Connections

(1) *Tractus gustatorius ascendens*, figs. 9–11, T.G.A.—This tract, which is relatively small as compared to Siluroids and Cyprinoids (Herrick, 1905), originates in *Diaphus* from the sensory centres of the seventh, ninth, and tenth cranial nerves and ascends in its usual position beneath the fibres of the descending root of the trigeminal, fig. 11. A comparison of the paper of Wallenberg (1931, figs. 19—21) also demonstrates the same relationship existing between the two tracts. The tract accompanying the

gustatory pathway is labelled in the figures by Wallenberg Tr. baso-quint. deg. and in the *Diaphus* figures M.F.B. This fasciculus is described as the medial fore-brain bundle with the connections of the inferior lobes (9—11*b*).

The gustatory fibres are easily differentiated for they are lightly stained and loosely arranged so that the nerve contains many open spaces. As the gustatory tract approaches the outer border of the secondary gustatory nucleus part of the fibres split from the main bundle and enter the nucleus without decussating. The main portion of the tract, however, crosses before terminating in the gustatory nucleus, fig. 9. This appears to be an exception, for in summarizing his findings on the gustatory system Herrick (1905, p. 443) states that most of the ascending gustatory fibres terminate in the nucleus of the same side.

None of the gustatory tract fibres were traced to the ganglion isthmi, neither were gustatory fibres followed to the optic tectum such as were found by Brickner (1930). However, it is to be noted that Brickner (p. 153) also found the tractus gustato-tectalis lacking in a number of teleosts.

(2) *Commissura gustatoria*, fig. 9, C.G.—Although the most conspicuous crossing fibres in the region of the gustatory nucleus are those of the gustatory tract, large numbers of scattered fibres pass between the two nuclei where they are fused across the midline. These latter are true commissural fibres.

(3) *Fibræ a nucleo gustatorio secundario in ganglion isthmi*—These are scattered fibres connecting the secondary gustatory nucleus with the ganglion isthmi.

(4) *Fibræ a nucleo gustatorio secundario in cerebellum*—Scattered fibres pass from the secondary gustatory nucleus to the granular cells of the valvula cerebellaris ; others probably reach the nucleus lateralis valvulæ. These fibres are so few that they cannot be interpreted as indicating any important functional significance.

(5) *Fasciculi a nucleo gustatorio secundario in tegmentum*, fig. 9, F.N.G.-T.—A very small but distinct fasciculus of medullated fibres leaves the lateral part of the nucleus and passes ventrolaterally around the dorsolateral border of the fasciculus lateralis longitudinalis. These fibres terminate in the region between the fasciculus and the tractus tecto-bulbaris rectus.

(6) *Tractus gustatorius tertius*—In studying the tractus lobo-cerebellaris it was obvious that many of the fibres did not enter the cerebellum but remained in the gustatory nucleus. The explanation for this is suggested by the paper of Herrick (1905, p. 420, figs. 23 and 25). This investigator found neurites from the cells of the superior secondary gustatory nucleus that formed a tertiary gustatory tract whose fibres joined those of the tractus lobo-cerebellaris and terminated in the lateral part of the hypothalamus. Hence, it is very probable that these fibres in *Diaphus* represent a descending pathway to the hypothalamus.

15 TORUS SEMICIRCULARIS, figs. 3–7, 17, 20, T.S.

Associated with the enormous development of the nervus lateralis anterior and lateralis posterior, there are corresponding increases in the size of the related central nervous structures, *i.e.*, the tuberculum acusticum, the fasciculus longitudinalis lateralis, the torus semicircularis, the commissura transversa, and the ganglion isthmi. A description of the primary nerve fibres to the tuberculum will not be included in this paper. Excellent accounts of these nerves are found in the papers of van der Sprenkel (1915) and Holmgren and van der Horst (1925).

The size and extent of the tuberculum acusticum are well shown in drawings of the dorsal and lateral aspects of the gross *Diaphus* brain, fig. 1. As seen in the figures of the gross relations, the rostral part of the tuberculum acusticum embraces the caudal and basal part of the cerebellum. Caudally the tuberculum acusticum is replaced by a rounded knoblike structure, the vagal lobe.

The drawings, figs. 9–11, of the tuberculum acusticum reveal three distinct broad areas. The first of these is the ventrolateral region, which consists almost entirely of the ascending lateralis fibres, figs. 9–11, N.L.F. The second or middle is a broad area containing large cells enmeshed among strongly myelinated neurites, figs. 10 and 11, T.A., C. These neurites form two large systems of crossing fibres. The first of these crosses dorsal to the ventricle and connects the two tubercula acustica to each other. This is the commissura acustica of Kappers (1906, figs. XCVII—XCIX) and of Herrick (1908, p. 415). The second system of neurites forms a series of large fibre bundles that arch ventromedially and cross under the ventricle. These are the so-called internal arcuate fibres, figs. 10 and 11, I.A.F.

The third area of the tuberculum acusticum is situated dorsomedially. This layer is practically cell free and is apparently a synaptic layer, figs. 10 and 11, T.A., S. The most conspicuous elements in this layer are the broad dendrites from the cells of the middle layer, whose dendrites are stained (in Weigert preparations) a deep yellow, and hence are in sharp contrast to the deep blue of the myelinated fibres. The lateralis neurites arborize in this synaptic layer, among the dendrites of the acoustic cells, whose neurites give rise to the octavo-motorius pathways.

The neurites from the tuberculum acusticum give rise both to descending and to ascending pathways. The descending tracts will not be described in this paper; it will suffice at present to state that Wallenberg (1907) has followed degenerated fibres in Marchi preparations to the lower bulbar and spinal centres.

The chief outlet above all others for octavus impulses is the large fasciculus longitudinalis lateralis. This fasciculus is formed from the internal arcuate fibres that turn rostral after crossing through the fibres of the medial longitudinal fasciculus. The caudalmost of these fasciculi appear at the lower bulbar levels. In passing rostrally there are a series of large bundles of internal arcuate fibres that give rise to other fasciculi until a total of four is reached. In the caudal levels these fasciculi are sharply demarcated from each other, figs. 9–11, L.L.F., but rostrally they lose their individual identity, figs. 7, 8, 17, 18 and 19.

In addition to its chief terminus in the torus semicircularis, fig. 6, the fasciculus longitudinalis lateralis contributes many terminal fibres to the ganglion isthmi, figs. 9–11, F.T.A.-G.I., which are described with the connections of this ganglion as fibræ a octavo in ganglion isthmi (16—4). In *Diaphus* there is also a large pathway of these fascicular fibres to the lateral geniculate body, the tractus octavo-geniculatus, which is described with the connections of the lateral geniculate (6—10). Another centre receiving octavus fibres, though in lesser numbers, is the nucleus lateralis valvulæ.

Other ascending octavus systems besides the lateral longitudinal fasciculus have been noted after degeneration experiments by WALLENBERG (1907). This investigator followed degenerated fibres in MARCHI material into the medial longitudinal fasciculus. These are labelled by WALLENBERG (figs. 21–23), tr. octavo-mot. octavo diencephalo. KAPPERS (1921, pp. 807–808) describes octavus fibres to the thalamus and to the hypothalamus.

It is very obvious that many fibres from the tuberculum acusticum enter the medial longitudinal fasciculus in *Diaphus* ; however, nothing was found to indicate if after entering these became ascending or descending fibres. KAPPERS supposes that these are motor reflex fibres ; hence the name tractus octavo-motorius. In the *Diaphus* brain many fibres pass from the tuberculum acusticum to the ganglion isthmi, figs. 9–11. These are described under the ganglion isthmi as fibræ a tuberculo acustico in ganglion isthmi (16—5).

The enormous size of the torus semicircularis is one of the most striking features in the *Diaphus* brain, figs. 3–7, T.S. Rostrally the torus consists of large cells embedded in a rich plexus of medullated fibres, but there is no evidence of stratification or differentiation. In passing caudally the central area is filled with longitudinally coursing fibres, figs. 4–6. These are mostly the terminal fibres of the lateral longitudinal fasciculus. At the level from which the large commissura transversa takes its origin, fig. 4, the torus has three differentiated areas. The ventrolateral area consists of the ascending lateral fasciculus fibres, and the transverse commissure fibres. The middle layer is a zone of large cells that are compactly arranged. The inner layer contains very few cells and the thin fibres are poorly medullated. This latter, apparently, is a synaptic layer in which the octavus neurites arborize among the dendrites from the cell layer, and in turn the neurites of these cells form the emerging fibres of the transverse commissure. The entire arrangement here is strikingly similar to the three layers of the tuberculum acusticum.

Intimately associated with the outer part of the torus semicircularis is the " tiefes Mark." In fact, RADL (1915, p. 529) considers the " tiefes Mark " as one of the four parts into which he divides the torus. In *Diaphus* the amount of exchange of fibres between this system and the torus is very difficult to determine.

The torus semicircularis, besides the large connections with the lateral longitudinal fasciculus and the commissura transversa, has lesser connections with the ganglion isthmi.

16 GANGLION ISTHMI, figs. 7–11, 18, 19, G.I., P ; G.I., M.

In many teleosts the ganglion isthmi consists of a pars magnocellularis and a pars parvocellularis (KAPPERS, 1921, figs. 429 and 430, Perca fluviatilis). BURR, however, (1928, p. 59) failed to find a bipartite nucleus in *Orthagoriscus*.

Like the torus semicircularis, the ganglion isthmi of *Diaphus* is very highly developed, and it will be described in detail. Next in order of size is the ganglion isthmi of *Bathypterois*, the least that of *Saurida*. It should be noted that the size of the ganglion isthmi in these fish as well as the torus semicircularis bears a direct ratio to the size of the lateral longitudinal fasciculus.

Immediately caudal to the torus semicircularis there appears a large, lightly stained area containing small round cells, many of which are arranged in layers, figs. 7 and 8, G.L., P. This area, which is the pars parvocellularis of the ganglion isthmi is bounded rostrally by the torus semicircularis, ventrolaterally by the tractus tecto-bulbaris, ventromedially by the lateral longitudinal fasciculus, and dorsomedially by the nucleus lateralis valvulæ. Caudally, the small-celled area is replaced by the pars magnocellularis, figs. 9–11, 17 and 18, G.I., M. This latter part is also bounded ventrally by the tractus tecto-bulbaris rectus and the lateral longitudinal fasciculus. A medial and caudal relation of the pars magnocellularis is the ascending gustatory tract. Dorsally and rostrally it is in intimate contact with the eminentia granularis of the cerebellum and dorsocaudally with the tuberculum acusticum, figs. 9–11.

While the pars parvocellularis has small cells embedded in a clear intercellular substance, the pars magnocellularis contains medium-sized round or oval cells enmeshed among fine fibres with the intercellular substance stained a dark brownish colour in WEIGERT preparations. FRANZ (1912, p. 413) noted in the ganglion this same staining peculiarity and refers to it as " dunkelgraue Farbe."

KAPPERS (1921, p. 807) refers to the ganglion isthmi as follows : " Die Ganglia Isthmi bilden offenbar ein Korrelationszentrum zwischen den photostatischen Reizen und den gravistatischen Reizen des Octavus." BURR (1928, p. 108) referring to the ganglion isthmi says it is " an important correlation centre between the optic and auditory systems." The analysis of the fibre connections to be described amply corroborates the above conclusions.

LE GROS CLARK (1933, p. 547) concludes on the basis of comparative studies that the nucleus isthmi of reptiles is represented in primitive mammals by a part of what has usually been called the dorsal nucleus of the lateral fillet, and is not the homologue of the medial geniculate body as previously stated by JOUSTRA (1918), KAPPERS (1921).

Connections

(1) *Tractus tecto-isthmicus*. *Tractus isthmo-tectalis*—figs. 6–8, T.T.O.-G.I.—Connections between the ganglion isthmi and the optic tectum were described in teleosts by FRANZ (1912, p. 415), KAPPERS (1921, p. 807), KUDO (1923*a*, p. 75), HOLMGREN and VAN DER HORST (1925, p. 128), BURR (1928, p. 108), and CHARLTON (1933, p. 302). In *Diaphus* many well-medullated fibres gather among the cells of the outer part of pars parvocellularis and ascend (or descend) to penetrate between the torus semicircularis and the tractus tecto-bulbaris rectus. These fibres are related primarily to the stratum profundum of the optic tectum and as this layer is primarily associated with efferent optic impulses it is most probable that this is the tractus tecto-isthmicus. In the reptile ANOLIS, HUBER and CROSBY (1933, p. 124)

consider the corresponding fibres as tecto-isthmal because of their association with the deep tectal layers.

The tractus isthmo-opticus was thought by FRANZ (1912, p. 414) to carry neurites from the ganglion isthmi to the eye. KUDO (1923*a*, p. 73) demonstrated that these fibres do not go to the eye but to the optic tectum. This finding was confirmed by JANSEN (1929).

(2) *Tractus isthmo-torus semicircularis*—Some of the fibres referred to under the tractus tecto-isthmicus turn medially into the torus semicircularis. The direction of conduction was not determined.

(3) *Tractus isthmo-tegmentalis*, fig. 8, T.G.I.-T.—This is a broad system of poorly medullated fibres that originates in the outer part of pars parvocellularis. Some of these fibres go to the tectum and to the torus semicircularis. The tegmental fibres turn medially and curve over the upper border of the lateral longitudinal fasciculus and are distributed to the central tegmental areas, fig. 8. Many other fibres emerge from the ventrolateral part of both pars parvocellularis and magnocellularis to pass between the lateral longitudinal fasciculus and the tractus tecto-bulbaris rectus. These fibres terminate in the ventrolateral tegmental areas.

(4) *Fibræ a octavo in ganglion isthmi*, figs. 9 and 10, F.O.-G.I.—As the lateral longitudinal fasciculus approaches the caudal end of the ganglion isthmi large bundles of well-medullated fibres extend from the fasciculus dorsolaterally, fig. 10, and turn rostrally to enter the caudal end of pars magnocellularis. This relationship between the fasciculus and the ganglion isthmi does not appear to be so striking in all fish, for although FRANZ (1912, pp. 412—418) studied a number of species, he failed to note such, while HOLMGREN and VAN DER HORST (1925, p. 127) found but a few fibres in *Ceratodus*. BURR (1928, p. 108) only suggests that in *Orthagoriscus* collaterals may reach the ganglion from the lemniscus lateralis.

That the connection between the ganglion isthmi and the fasciculus longitudinalis lateralis is a very important one is substantiated by its high development in fish, *Diaphus*; in amphibians, frog (LARSELL, 1924, p. 314); in reptiles, Chameleon (JOUSTRA, 1918, p. 364; SHANKLIN, 1930, p. 440); in birds, Kiwi (CRAIGIE, 1930, p. 322).

(5) *Fibræ a tuberculo acustico in ganglion isthmi*, figs. 9–11, F.T.A.-G.I.—In addition to the important octavus connection with the lateral lemniscus, there are broad areas of fibres (mostly crossed) from the tuberculum acusticum to the ganglion isthmi. These are neurites from the layer of large cells of the tubercle that cross above the ventricle and enter the dorsomedial part of pars magnocellularis. None of these fibres appear to reach the pars parvocellularis.

(6) *Commissura ganglii isthmi*—It is quite probable that some of the crossing fibres in the tuberculum acusticum are isthmal commissure fibres, but on this point I have no accurate information. HOLMGREN and VAN DER HORST (1925, p. 127, fig. 33) describe and figure a commissura ganglii isthmi in *Ceratodus* that crosses ventrally. In *Diaphus* there is clearly no corresponding ventrally placed commissure.

(7) *Fibræ a tracto tecto-bulbaris in ganglion isthmi*, figs. 8 and 9, F.T.B.-G.I.—In addition to the well-developed optic connections with the tectum, large areas of fibres pass from the upper edge of the tractus tecto-bulbaris rectus to penetrate the under surface of the adjacent pars magnocellularis. These fibres are extremely thin and give rise to much of the fibrillar mass with the brown staining quality peculiar to this area.

Due to the marked reduction in size in *Diaphus* (approximately one-third) of the tractus tecto-bulbaris as it traverses the isthmal region, and the nature of the fibres, the evidence strongly suggests conduction is toward the ganglion.

(8) *Tractus isthmo-bulbaris rectus. Tractus isthmo-bulbaris cruciatus*—HOLMGREN and VAN DER HORST (1925, pp. 127 and 128) described isthmic fibres to the tractus tecto-bulbaris cruciatus from their commissura ganglii isthmi, and direct fibres from the ganglion to the tractus tecto-bulbaris rectus.

From the pars parvocellularis of *Diaphus* fibres turn ventrolaterally and penetrate between the fasciculi of the direct tecto-bulbar pathway. Some of these may turn caudally and represent a tractus isthmo-bulbaris rectus; others join the tectal fibres contributing to the commissura ansulata and represent a tractus isthmo-bulbaris cruciatus.

(9) *Fibræ a nucleo gustatorio secundario in ganglion isthmi*—BURR (1928, p. 107) suggested that direct fibres or collaterals may pass from the ascending gustatory tract to the ganglion isthmi. No such connections were observed in *Diaphus*. However, many scattered fibres pass between the lateral part of the anterior secondary gustatory nucleus and the medial part of the pars magnocellularis of the ganglion isthmi. The myelin of these fibres is lightly stained, in contrast with the dark stained myelin of fibres in the ganglion, the inference being that these are neurites from the gustatory nucleus.

(10) *Fibræ a ganglio isthmi in nucleum lateralem valvulæ*—These scattered fibres are described with the connections of the nucleus lateralis valvulæ (13—1).

(11) *Tractus basio-isthmicus*—This tract was described by FRANZ (1912, p. 415, figs. 9 and 10), WALLENBERG (1931, fig. 16). Judging from the experimental work of WALLENBERG, this is evidently an ascending tract from the region of the commissura ansulata to the ganglion isthmi. No fibres were followed from the medial fore-brain bundle (the corresponding tract) of this description into the ganglion isthmi.

V—SUMMARY

The nuclei and fibre pathways of the diencephalon and mesencephalon are described in the brains of three deep sea fish, each of which differs from the others in important respects.

The large size of the eminentia thalami is very striking in the *Diaphus* brain, whereas in the brains of *Bathypterois* and *Saurida* it is scarcely discernible. The eminentia thalami is primarily an optic centre receiving many fibres from the optic tract. The chief pathway of discharge is through the large fasciculus descendens, the principal termination of which is the pars ventralis thalami.

In *Diaphus* the pars ventralis thalami is a very highly developed fibrocellular area located ventral to the sulcus medius and the pars dorsalis thalami. The chief afferent tract is the fasciculus descendens, although it has other connections with the transverse commissure, the posterior commissure, the pars dorsalis thalami, the dorsal motor tegmental nucleus, the optic tectum, and the hypothalamus. The chief efferent tract is the large tractus thalamo-bulbaris et olivaris.

The pars dorsalis thalami is clearly differentiated in all three of these fish and as Craigie and Brickner (1927) suggest, it appears to be one of the most primitive parts of the thalamus. No long ascending or descending systems appear to be associated with this area, but it has connections with the following centres: eminentia thalami, commissura posterior, corpus glomerulosum, commissura transversa, tectum opticum, nucleus tegmenti motorius dorsalis, and pars ventralis thalami.

The nucleus tegmenti motorius dorsalis consists of the pars propia, a fibrocellular area containing abundant neurpil, and the pars lateralis, a relatively clear area. The rostral end of this nucleus receives in *Diaphus* many direct optic fibres. Other connections are with the posterior commissure, the transverse commissure, the optic tectum, the lateral geniculate body, the corpus glomerulosum, the cerebellum, the pars ventralis thalami, and the eminentia thalami.

The lateral geniculate body is highly developed in all three of the fish. The geniculate of *Diaphus* is especially large, and is characterized by a long caudal extent. Although the optic tracts and the optic tectum of *Bathypterois* are decidedly atrophic, the lateral geniculate is very large, clearly indicating that in this fish, at least, the geniculate body is not dependent on optic connections for its size. The enlargement of the geniculate finds its explanation in the reception of the large tractus octavo-geniculatus, and fibres from the transverse commissure, both of which carry impulses from the lateral line system. The caudal extent of the geniculate may be due to neurobiotatic influences because of the tractus octavo-geniculatus.

A number of the lateral geniculate connections, in which the direction of conduction was not determined, were found with other centres, such as the pars anterior of the corpus glomerulosum, the cerebellum, the pars dorsalis thalami, and the nucleus tegmenti motorius dorsalis. The co-ordinated optic and octavus impulses find their outlets as follows: (1) to the optic tectum through the three parts of the tractus geniculo-tectalis; (2) to the hypothalamus through the tractus thalamo-hypothalamicus; (3) to the bulbar centres by way of the tractus pretecto (et geniculo)—bulbaris et olivaris, and by way of the posterior commissure that after crossing descends through the medial longitudinal fasciculus.

The nucleus pretectalis apparently is primarily an optic centre from which fibres go to the cerebellum through the tractus mesencephalo-cerebellaris anterior, and which also discharges optic impulses to the bulbar centres, chiefly through the tractus pretecto (et geniculo)—bulbaris.

The corpus glomerulosum consists of two parts: pars anterior and pars rotunda. Neither of these parts shows any deviation from the usual description. A highly developed fibre bundle, the tractus thalamo-hypothalamicus, is closely associated with the corpus glomerulosum. The tract receives impulses from the lateral geniculate body, the nucleus tegmenti motorius dorsalis and the pars dorsalis thalami, and terminates in the nucleus subrotundus of the hypothalamus.

Of the centres of the lobi inferiores only the nucleus subrotundus appears to be especially highly developed. The lobi inferiores receive (1) olfactory impulses by the fore-brain bundles; (2) optic impulses through the tractus tecto-hypothalamicus, and from the lateral geniculate body through the tractus thalamo-hypothalamicus; (3) gustatory impulses from the anterior secondary gustatory nucleus, and (4) octavus impulses through a large contingent of fibres from the transverse commissure. These diverse impulses are co-ordinated in the inferior lobes from which two efferent fibre systems emerge, the smaller, the tractus hypothalamo-cerebellaris which goes to the cerebellum, and the larger, the tractus hypothalamo-bulbaris, whose neurites terminate among the dendrites of the motor cranial nerve cells and the large bulbar reticular cells.

A new observation concerns the medial fore-brain bundle, which instead of terminating in the region of the inferior lobes passes around the outer edge of pars rotunda of the corpus glomerulosum, turns dorsally and passes adjacent to the ascending gustatory tract as far caudal as the level of the sensory root of the trigeminal nerve. This is apparently a mechanism whereby olfactory impulses of the second and third order are relayed direct from the fore-brain to the cranial nerve centres.

The usual diencephalic commissures are identified as commissura transversa, commissura minor, commissura horizontalis, commissura habenularis, commissura posterior. One of the most unusual findings, especially in the *Diaphus* and *Bathypterois* brains, is the exceedingly large transverse commissure. The hypertrophy of this finds its explanation in the fact that it is a commissural system between the highly developed tori semicirculares, which in turn are large because of the large tuberculum acusticum and the large system of connecting fibres, the lateral longitudinal fasciculus. The brains of *Diaphus* and *Bathypterois* clearly show that the transverse commissure is a commissural system for the torus semicircularis, and not an optic commissure. In the *Saurida* brain, on the other hand, where the optic tectum is fairly large and the torus small, the transverse commissure is equally small. In addition to being a commissural system, the transverse commissure has connections with the following centres: optic tectum, corpus glomerulosum, corpus geniculatum laterale, pars dorsalis thalami, pars ventralis thalami, and the lobi inferiores.

The commissura minor is developed best in *Diaphus*, where it is primarily a tectal commissural system having lesser connections with the lateral geniculate body. The commissura minor of *Bathypterois*, which has a small optic tectum, is the least developed.

The crossing of the commissura horizontalis is found in its usual place. In *Diaphus* this commissure receives fibres from the lateral geniculate body, the pretectal nucleus, the optic tectum, both parts of the dorsal motor tegmental nucleus, and the posterior commissure.

Nothing new was noted concerning the commissura habenularis.

The commissura posterior consists of a pars dorsalis and a pars ventralis in *Diaphus* and *Saurida*, whereas in *Bathypterois* a single component is present. The pars ventralis is associated primarily with the eminentia thalami and the dorsal motor tegmental nucleus. The pars dorsalis is associated chiefly with the optic tectum, the lateral geniculate and the pretectal nucleus. The large component from the lateral geniculate appears to be a new observation. Both parts of the posterior commissure have descending components that enter the medial longitudinal fasciculus.

The optic tectum of both *Diaphus* and *Saurida* are well developed, but that of *Bathypterois* is very small. The optic tectum of *Diaphus* does not meet across the midline except in the most rostral sections, due to the large tori semicirculares and to the large valvula of the cerebellum ; hence the commissura colliculi superioris is limited to a few rostral sections.

The optic tracts of *Diaphus* and *Saurida* are normal, whereas those of *Bathypterois* are greatly reduced. The fasciculus medialis of the optic tract in *Diaphus* contributes only to the rostral end of the optic tectum, but the fasciculus lateralis extends caudally in its usual position.

The writer found that the majority of the fibres of the fasciculus medialis tractus optici, in *Diaphus*, terminated in the eminentia thalami, though it is probable that some descend through the fasciculus descendens direct to the pars ventralis thalami, and others ascend to the dorsal motor tegmental nucleus. Some primary optic fibres were followed into the pars ventralis thalami.

The chief centres receiving fibres from the optic tectum are the bulbar centres through the large crossed and uncrossed tecto-bulbar pathways, and also the ganglion isthmi through these same tracts.

The tractus tecto-hypothalamicus places the hypothalamus under the influence of optic impulses, and the fibræ tectales nervi optici contribute fibres to the dorsal tegmental motor nucleus, the pars dorsalis thalami, and the eminentia thalami. Tectal impulses also reach the cerebellum through the tractus mesencephalo-cerebellaris anterior.

The only new finding concerning the torus longitudinalis is its complete absence in the brain of the nearly blind fish, *Bathypterois*, giving further evidence that the torus is closely associated with the optic tectum.

The nucleus lateralis valvulæ is present in all three fish in its usual position. It receives fibres from the ganglion isthmi, the tegmentum, the torus semicircularis, and the anterior secondary gustatory nucleus. The chief efferent tract is the tractus mesencephalo-cerebellaris posterior to the cerebellum.

The nucleus gustatorius secundarius anterior is developed best in *Diaphus*. However, none of these deep sea fish have highly developed taste mechanisms such as is found in the Siluroids and the Cyprinoids. The gustatory nucleus receives the ascending gustatory tract and in turn has other connections with the ganglion isthmi, the cerebellum, the tegmentum, and the hypothalamus.

All structures in *Diaphus* and in *Bathypterois* that are associated with impulses from the lateral line system are enormously developed, *i.e.*, nervus lateralis, tuberculum acusticum, lateral longitudinal fasciculus, torus semicircularis, commissura transversa, and the ganglion isthmi. Most of the fibres of the lateralis nerves occupy the outer layer of the auditory tubercle; from this layer their fibres turn medially and arborize in the molecular layer about the large dendrites from the cells of the middle or cellular layer. The efferent fibres from the tuberculum form a descending system that passes through the medial longitudinal fasciculus. However, the majority ascend forming the lateral longitudinal fasciculus whose chief ending is in the torus semicircularis, although other large components are contributed to the ganglion isthmi and to the lateral geniculate body.

The torus semicircularis is exceedingly large and highly differentiated. Like the tuberculum acusticum it is made up of three parts: an outer consisting mostly of fibres from the lateral longitudinal fasciculus, a middle cellular layer, and a medial synaptic layer. Neurites from the lateral longitudinal fasciculus and also from the opposite torus by way of the transverse commissure arborize in this synaptic layer about the large dendrites from the cells of the middle or cellular layer.

In *Saurida* the tuberculum acusticum is very small, as is also the lateral longitudinal fasciculus, the torus semicircularis, the commissura transversa, and the ganglion isthmi.

In *Diaphus* the ganglion isthmi consists of a large and a small celled part. In this fish it is clearly a co-ordinating centre for octavus and optic impulses, for it has broad connections on the one hand with the tuberculum acusticum and the lateral longitudinal fasciculus, and on the other with the optic tectum and the tractus tecto-bulbaris rectus.

In conclusion, this study shows that striking changes have occurred in the brains of each of these fish. However, it will be impossible to evaluate the full significance of these modifications until more is known concerning their natural history and until more extensive studies are made on other deep sea fish.

VI—List of Abbreviations

C., cerebellum.
C.A., commissura ansulata.
C.C.S., commissura colliculi superioris.
C.G., commissura gustatoria.
C.G., A., corpus glomerulosum, pars anterior.
C.G.L., corpus geniculatum laterale.
C.G., R., corpus glomerulosum, pars rotunda.
C.H., commissura horizontalis.
C.M., commissura minor.
C.M., L., commissura minor, pars lateralis.
C.M., M., commissura minor, pars medialis.
C.P., commissura posterior.
C.P., D., commissura posterior, pars dorsalis.
C.P., V., commissura posterior, pars ventralis.
C.T., commissura transerversa.
C.T.A., commissura tuberculum acusticum.
C.V., commissura ventralis.
E., epiphysis.
E.T., eminentia thalami anterior.
F.B., fore-brain.
F.C.G.-C.P., fasciculus a geniculo in commissuram posteriorem.
F.C.G.-P.D.T., fasciculi a geniculo in partem dorsalem thalami.
F.C.G., A.-P.D.T., fibræ a parte anteriore in partem dorsalem thalami.
F.C.P.D., fasciculus commissura posterior descendens.
F.C.T.-N.S.R., fibræ a commissura transversa in nucleum subrotundum.
F.C.T.-P.D.T., fasciculi a commissura transversa in partem dorsalem thalami.

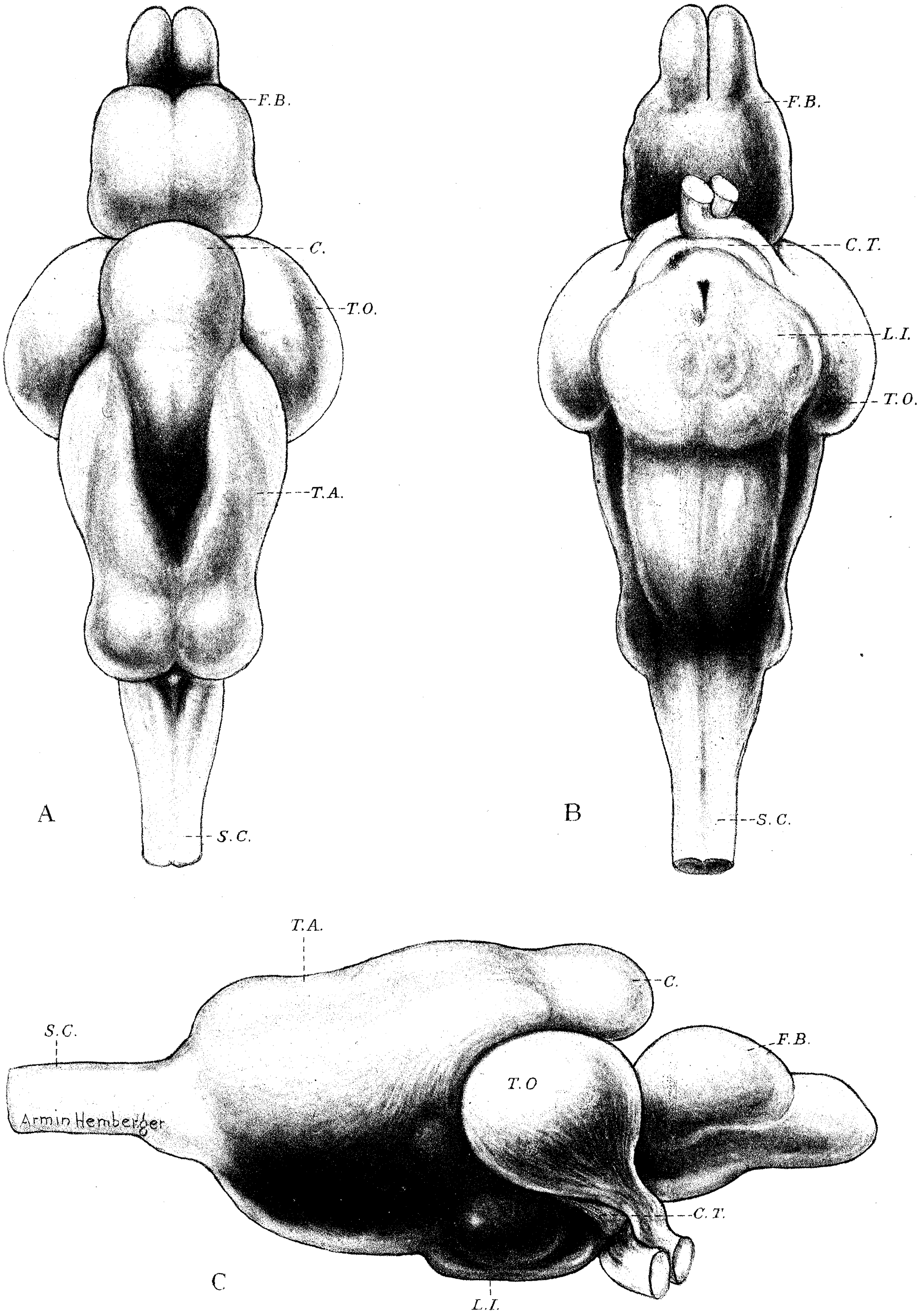

Fig. 1.

Brain of *Diaphus*

A, Dorsal View. B, Ventral View. C, Lateral View.

Huth coll.

F.C.T.-P.V.T., fasciculi a commissura transversa in pars ventralis thalami.
F.D., L., fasciculus descendens, pars lateralis.
F.D., M., fasciculus descendens, pars medialis.
F.E.T.-C.P., fibræ a eminentia thalami in commissuram posteriorem.
F.G.I.-N.L.V., fibræ a ganglion isthmi in nucleum lateralem valvulæ.
F.L.M., fasciculus longitudinalis medialis.
F.L.O., fasciculus lateralis tractus optici.
F.M.O., fasciculus medialis tractus optici.
F.N.G.-T., fibræ a nucleo gustatorio secundario in tegmentum.
F.N.M.D.-C.P., fibræ a nucleo dorsali in commissuram posteriorem.
F.N.M.D.-C.T., fasciculus a nucleo dorsali in commissuram transversam.
F.O.-E.T., fasciculus opticus ad eminentia thalami.
F.O.-G.I., fibræ a octavo in ganglion isthmi.
F.O.-P.V.T., fibræ ab optico in partem ventralem.
F.P.-E.T., fasciculus preopticus ad eminentia.
F.R., fasciculus retroflexus.
F.T.A.-G.I., fibræ a tuberculum acusticum in ganglion isthmi.
F.T.B.-G.I., fibræ a tracto tecto-bulbari in ganglion isthmi.
F.T.O.-N.O., fibræ tectales nervi optici.
G.I., ganglion isthmi.
G.I., M., ganglion isthmi, pars magnocellularis.
G.I., P., ganglion isthmi, pars parvo cellularis.
H.Y.P., hypophysis.
I.A.F., internal arcuate fibres.
L.F.B., lateral fore-brain bundle.
L.I., lobi inferiores.
L.L.F., lateral longitudinal fasciculus.
M.F.B., medial forebrain bundle.
N.C.H., nucleus cerebellaris hypothalami.
N.E.O., nucleus oculomotorius.
N.G., nucleus gustatorius secundarius anterior.
N.H., nucleus habenularis.
N.L.F., nervus lateralis fibres.
N.L.V., nucleus lateralis valvulæ.
N.M.D., L., nucleus tegmenti motorius dorsalis, pars lateralis.
N.M.D., P., nucleus tegmenti motorius dorsalis, pars propia.
N.O., nervus oculomotorius.
N.P., nucleus pretectalis.
N.P.O., nucleus preopticus.
N.S.R., nucleus subrotundus.
O.T., optic tract.
P., paraphysis.
P.D.T., pars dorsalis thalami.
P.V.T., pars ventralis thalami.
S.C., spinal cord.
S.M., sulcus medius.
S.O., subcommissural organ.
S.R.T., sensory root trigeminal nerve.
T.A., tuberculum acusticum.
T.A.,C., tuberculum acusticum, cellular layer.
T.A.,S., tuberculum acusticum, synaptic layer.
T.C.M., tractus cerebello-motorius.
T.C.-N.M.D., tractus a cerebello in nucleum dorsalem.
T.C.G.-T.O., A., tractus geniculo-tectalis, pars anterior.
T.C.G.-T.O., L., tractus geniculo-tectalis, pars lateralis.
T.G.A., tractus gustatorius ascendens.
T.G.I.-T., tractus isthmo-tegmentalis.
T.H.-B., tractus hypothalamo-bulbaris.
T.H.-C., tractus hypothalamo-cerebellaris.
T.H.L.D., tractus hypothalamicus longus descendens.
T.L., torus longitudinalis.
T.M.-C.A., tractus mesencephalo-cerebellaris anterior.
T.M.-C.P., tractus mesencephalo-cerebellaris posterior.
T.O., tectum opticum.
T.O.-C.G.L., tractus octavo-geniculatus.
T.O., S.A.C., tectum opticum, stratum album centrale.
T.P.-B., tractus pretecto (et geniculo)—bulbaris.
T.S., torus semicircularis.
T.S., C., torus semicircularis, cellular layer.
T.S.-S., torus semicircularis, synaptic layer.
T.S.-T., tractus spino-tectalis et mesencephalicus.
T.T.-B., tractus thalamo-bulbaris et olivaris.
T.T.-H., tractus thalamo-hypothalamicus.
T.T.O.-B.C., tractus tecto-bulbaris cruciatus.
T.T.O.-B.R., tractus tecto-bulbaris rectus.
T.T.O.-G.I., tractus tecto-isthmicus.
T.T.O.-H., tractus tecto-hypothalamicus.
V.C., valvulæ cerebelli.
Z., combined fibres of commissura horizontalis, tractus mesencephalo-cerebellaris anterior, and tractus spino-tectalis et mesencephalicus.

VII—References

Addison, W. H. F. (1923). 'J. Comp. Neurol.,' vol. **36**, p. 1.
Bellonci, G. (1879). 'Reale Acc. Lincei,' p. 1.
Bergquist, H. (1932). 'Acta Zool.,' vol. **13**, p. 57.
Brickner, R. M. (1929). 'J. Comp. Neurol.,' vol. **47**, p. 225.
—— (1930). 'J. Comp. Neurol.,' vol. **50**, p. 153.
Burr, H. S. (1928). 'J. Comp. Neurol.,' vol. **45**, p. 33.
Cairney, J. (1926). 'J. Comp. Neurol.,' vol. **42**, p. 255.
Cajal, P. Ramon (1899). Revista Trimestral Micrografica, vol. **4**, p. 87.
Cajal, S. Ramon y (1911). "Histologie du système nerveaux de l'homme et des vertébrés," vol. **2**. Paris.
Catois, E. H. (1901). 'Bull. Sci. Fr. Belg.,' vol. **36**, p. 1.
Charlton, H. W. (1932). 'J. Comp. Neurol.,' vol. **54**, p. 237.
—— (1933). 'J. Comp. Neurol.,' vol. **57**, p. 285.
Clark, W. E. Le Gros (1932). 'Brain,' vol. **55**, p. 406.
—— (1933). 'J. Anat.,' vol. **67**, p. 536.
Craigie, E. Horne (1930). 'J. Comp. Neurol.,' vol. **49**, p. 223.
Craigie, E. Horne, and Brickner, R. M. (1927). 'Proc. Acad. Sci. Amst.,' vol. **30**, p. 695.
Dammerman, K. W. (1910). 'Z. wiss. Zool.,' vol. **96**, p. 654.
Franz, V. (1911). 'Zool. Jahrb. Abt. Anat.,' vol. **32**, p. 401.
—— (1912). 'Folia Neuro-Biol.,' vol. **6**, p. 402.
Fusari, R. (1887). 'R. Accad. Lincei,' p. 151.
Gerlach, J. (1933). 'Anat. Anz.,' vol. **75**, p. 310.
Gierse, A. F. (1904). Inaugural Dissertation, Leipzig.
Goldstein, K. (1905). 'Arch. mikr. Anat.,' vol. **66**, p. 135.
Herrick, C. J. (1905). 'J. Comp. Neurol.,' vol. **15**, p. 375.
—— (1908). 'J. Comp. Neurol.,' vol. **18**, p. 409.
—— (1910). 'J. Comp. Neurol.,' vol. **20**, p. 413.
—— (1917). 'J. Comp. Neurol.,' vol. **28**, p. 215.
Holmgren, N. (1920). 'Acta Zool.,' vol. **1**, p. 137.
Holmgren, N., and Van der Horst, C. J. (1925). 'Acta Zool.,' vol. **6**, p. 59.
Hoogenboom, K. J. Hocke (1929). 'Z. mikr. Anat. Forsch.,' vol. **18**, p. 311.
Huber, G. C., and Crosby, E. C. (1926). 'J. Comp. Neurol.,' vol. **40**, p. 97.
—— (1933). 'J. Comp. Neurol.,' vol. **57**, p. 57.
Jansen, J. (1929). 'Proc. Acad. Sci. Amst.,' vol. **32**, p. 1104.
Jeener, R. (1930). 'Proc. Acad. Sci. Amst.,' vol. **33**, p. 755.
Johnston, J. B. (1909). 'J. Comp. Neurol.,' vol. **19**, p. 593.
—— (1911). 'J. Comp. Neurol.,' vol. **21**, p. 489.
Joustra, N. (1918). 'Psychiat. neurol. Bl. Amst. Winkler Feestbund.,' vol. **22**, p. 361.
Kappers, C. U. Ariens (1906). 'J. Comp. Neurol.,' vol. **16**, p. 1.

KAPPERS, C. J. A. (1921). "Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen," vol. **2**, Haarlem.

KRAUSE, K. (1898). 'Arch. mikr. Anat.,' vol. **51**, p. 820.

KUDO, K. (1923*a*). 'Proc. Acad. Sci. Amst.,' vol. **26**, p. 65.

—— (1923*b*). 'Anat. Anz.,' vol. **56**, p. 359.

KUHLENBECK, H. (1929). 'Morph. Jahrb.,' vol. **63**, p. 50.

LANGE, S. J. DE (1910). 'Folia neuro-biol.,' vol. **3**, p. 633.

LARSELL, O. (1924). 'J. Comp. Neur.,' vol. **36**, p. 309.

MAYSER, P. (1882). 'Z. wiss. Zool.,' vol. **36**, p. 259.

RADL, E. M. (1915). 'Morph. Jahrb.,' vol. **49**, p. 509.

RAMSEY, E. (1901). 'J. Comp. Neurol.,' vol. **11**, p. 40.

SARGENT, P. E. (1903). "The torus longitudinalis of the teleost brain." Mark anniversary volume. Henry Holt, New York. Art. 20, p. 399.

SHANKLIN, W. M. (1930). 'Acta Zool.,' vol. **11**, p. 425.

SHELDON, R. E. (1912). 'J. Comp. Neurol.,' vol. **22**, p. 177.

SPRENKEL, H. BERKELBACH V.D. (1915). 'J. Comp. Neurol.,' vol. **25**, p. 5.

STIEDA, L. (1868). 'Z. wiss. Zool.,' vol. **18**, p. 1.

SUZUKI, N. (1932). "The Saito Gratitude Foundation, Sendai, Japan," Ann. Rep., No. 8, p. 165.

TROJAN, E. (1906). 'Mem. Mus. Comp. Zool. Harvard,' vol. **30**, p. 219.

TUGE, H. (1929). Sci. Rep. Tôhoku Univ., Biol., vol. **4**, p. 481.

WALLENBERG, A. (1907). 'Anat. Anz.,' vol. **31**, p. 369.

—— (1913). 'Névraxe,' vol. **14**, p. 251.

—— (1931). 'Arch. Psychiat.,' vol. **94**, p. 246.

WEINBERG, ERNST (1928). 'J. Comp. Neurol., vol. **46**, p. 249.

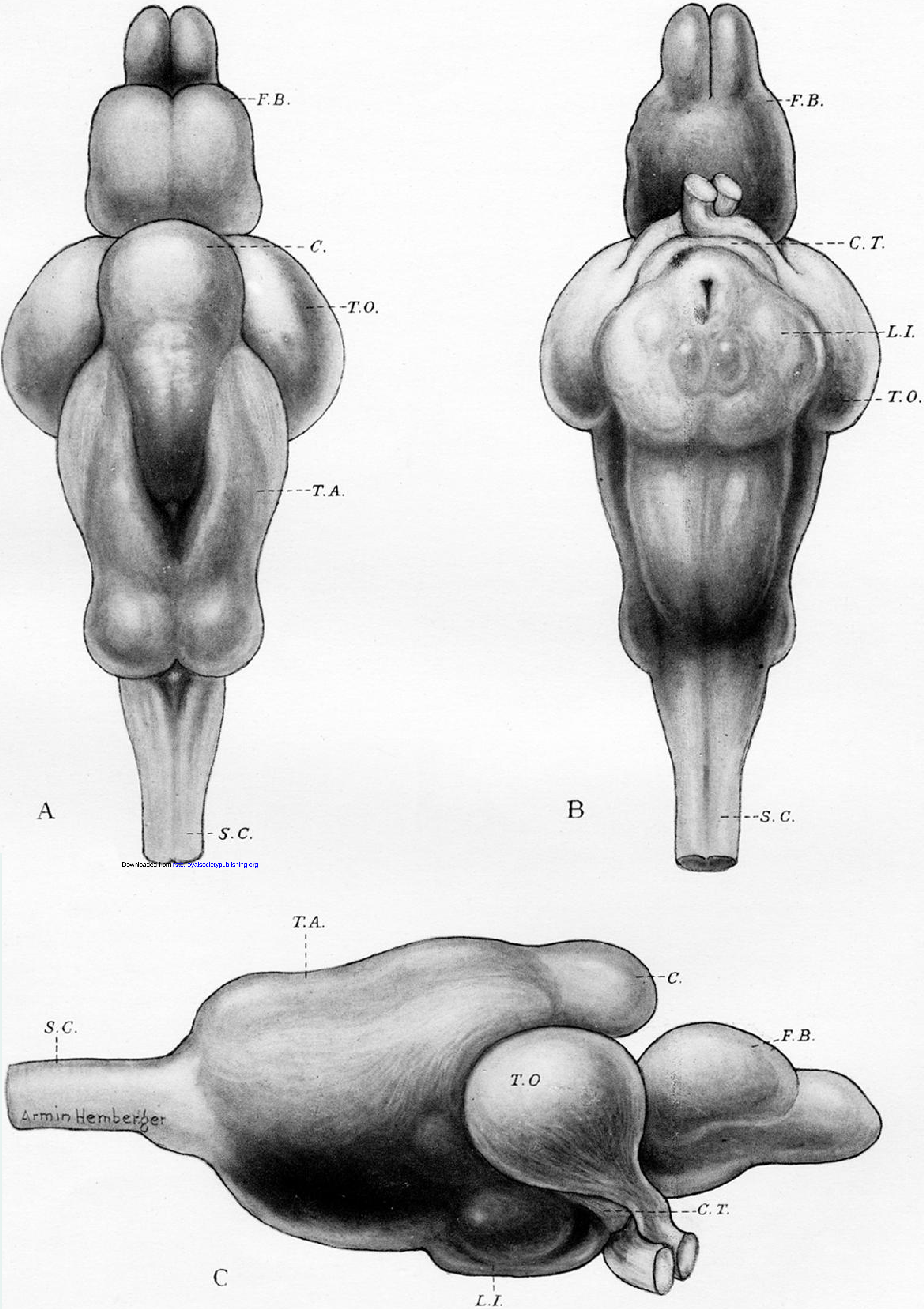

Fig. 1.

Brain of *Diaphus*

A, Dorsal View. B, Ventral View. C, Lateral View.