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THE MORPHOLOGY OF THE BRAIN OF SPHENODON

by

KERMIT CHRISTENSEN

PUBLISHED BY THE UNIVERSITY, IOWA CITY, IOWA

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HISTORICAL

A scarcity of Sphenodon material has not altogether limited the literature on the brain and pineal eye. Wiedersheim (1893) has not only referred to the brain of *Hatteria punctata* in his account of the reptilian brain, but also he has included illustrations of dorsal, ventral, and lateral views of the adult brain and a longitudinal section through the brain. Osawa (1898), working in Wiedersheim's laboratories, included in his anatomical studies of Hatteria a description of the brain and the cranial nerves. Developmental studies of the central nervous system of Sphenodon were begun by Dendy (1899) when he treated its embryology as a part of his outlines of the development of Tuatara. The most lengthy account of the brain of Hatteria has been presented by Gisi (1907), but her description of the microscopic structure is a small part of her thesis. Among the extensive studies Dendy continued to make, there appeared in 1909 his paper on the intracranial vascular system of Sphenodon. The crowning monograph of his work (Dendy, 1910) was "The structure, development, and morphological structure of the pineal organs and adjacent parts of the brain of Tuatara," in which he utilized among other materials seven adult brains. Unger (1914) in the third of his morphological studies on the reptilian brain describes the brain of Sphenodon. This paper has not been available, but is mentioned here to make the historical account complete. G. Eliot Smith (1919, 1909, 1902) on three different occasions has found the use of Sphenodon material valuable in his explanations of forebrain morphology. Hines (1923) having access to Dendy's preparations presented a worthy paper on the development of the telencephalon and its adult anatomy. The latest developmental study has been by Wyeth (1924) on the development of the forebrain.

Since the conclusion of my study there has appeared a detailed description of the forebrain by Cairney (1926).

In 1886, Baldwin Spencer announced the presence of the pineal eye in Hatteria by illustrations and descriptions in two different accounts, and four years later De Graaf (1890) figured the pineal eye and Hoffman described it in Bronn's "Thierreich." The embryology of the pineal eye was worked out by Dendy (1899) with brief mention in his outlines of the development of the Tuatara but with specific details in his "Development of the parietal eye and adjacent organs in Sphenodon." However his most sumptuous work was the monograph of 1910. The use of Spencer's drawing of the pineal eye has been made by Kingsley's "Text-book of Vertebrate Zoology" (1899, 1908), second American edition of Wiedersheim's "Comparative Anatomy of Vertebrates" (1897), and the third edition of Parker and Haswell's "Text-book of Zoology" (1921). A modified drawing from Dendy's (1899) paper on the development of the parietal eye is found in the third American edition of Wiedersheim's "Comparative Anatomy of Vertebrates."

The only paper on the hypophysis of Sphenodon is by Wyeth and Row (1923).

MATERIALS AND METHODS

Two preserved specimens of Sphenodon brought from New Zealand by the Fiji-New Zealand expedition were generously furnished to me by the late Professor C. C. Nutting.

The brain of the specimen preserved in formalin was embedded in celloidin and thick transverse sections were cut which were stained by the Weigert method. The brain of the specimen preserved in seventy per cent alcohol was sectioned in paraffin, ten micra in thickness through the medulla oblongata and fifteen micra in thickness through the remainder of the brain. These sections were stained with iron hæmatoxylin and Orange G. The technique of Houser (1901) was followed in both methods with the exception that in the iron hæmatoxylin method the time of mordanting in the iron-alum solution was shortened to thirty minutes and the time of staining was shortened to two hours.

Median longitudinal sections through the region of the pineal eye and both median longitudinal sections and transverse sections through the hypophysis were cut eight micra in thickness and were stained with hæmatoxylin and erythrosin.

Small pieces of brain and spinal cord were treated by the Golgi method but all attempts to get impregnation of the cells were unsuccessful, due probably to improper fixation. Consequently no Golgi material was used.

I wish to express my appreciation to Dr. Gilbert L. Houser for his direction and helpful criticisms throughout the progress of this work.

GENERAL

The removal of the dorsal surface of the skull leaves the dura mater, which has adhered closely, stretched over the top of the cranial cavity. Anteriorly it ends by overlapping the olfactory capsules; posteriorly it is continuous with the dura mater of the spinal cord. There remains with the dura mater an ovoid mass of connective tissue, the parietal plug, which has filled the interparietal foramen. Upon freeing the dorsal portion of the dura mater this membrane is found to be applied closely to the remainder of the cranium and leaving as a result a large subdural space.

The thin and transparent pia mater invests the brain loosely. From it strands of tissue radiate outward across the subdural space and join the dura mater (fig. A, s.). Seemingly a means of ballast for the brain is produced.

The adult Sphenodon brain is smaller than the cranial cavity, and since such a disparity exists, a cranial cast of the Sphenodon would in no wise indicate the external brain form. From this fact Dendy (1910) pointed out the futility of attempts to make cranial casts of some fossil reptiles.

Each division of the brain is separate and distinct, since, as a whole, the brain takes an extended form (fig. A, 1, 2, 3). There is a decided ventral flexure; and, although the medulla oblongata lies approximately on the level with the spinal cord, the remaining parts describe an arc, beginning with the metencephalon and curving upwards to the fore part of the cerebrum, and then slightly downwards to the olfactory bulbs.

The medulla oblongata (m. o., figs. A, 1, 2, 3,) is a much enlarged and broadened continuation of the spinal cord. An early emergence of the central canal gives an elongated, triangular fourth ventricle, which is bounded laterally by rather stout sidewalls. Covering the fourth ventricle is the choroid plexus which stretches from the edges of the cerebellum downwards to the medulla. Two median ridges in the floor of the ventricle mark the position of the median longitudinal fasciculi (f. l. m., fig. 2). With this exception no other markings of internal structures can be noted. On the sides of the medulla two nerve roots show prominently. Just ventral to the cerebellum is the large trunk of the fifth cranial nerve (v, figs. A, 1, 2, 3), and posterior to this are the combined trunks of seventh and eighth cranial nerves (vii & viii, figs. A, 1, 2, 3). The remaining nerve roots are small in size. The ninth nerve (ix, figs. 1, 2, 3) arises just posterior to the seventh-eighth root, and the tenth and eleventh (x, xi, figs. 1, 3) nerves have their small roots along the sides of the medulla posterior to the ninth. The small size and difficulty experienced in dissecting the smaller nerves have made it necessary to include only the approximate number and position of the tenth and the eleventh. The sixth (vi, fig. 3) arises as a pair of nerves in the ventral midline of the medulla at the level of the seventh-eighth root. The twelfth also originates ventrally, a little posterior to the level of the eleventh (xii, fig. 3).

The metencephalon (met., figs. 1, 3) includes the broadest part of the brain stem. The ventral portion externally shows no indication of fiber tracts. Dorsally there arises the cerebellum (c., figs. A, 1, 2) not unlike a hood in shape, since the posterior face is open and the anterior face, closed and sloping downwards to the isthmus. From the dorsal surface of the isthmus arises the fourth nerve (iv, figs. 1, 2), which curves outwardly around the optic lobes.

Two rounded optic lobes prominently make up the dorsal part of the mesencephalon (mes., figs. A, 1, 2, 3). The basal region of the mesencephalon is constricted, and continues, similarly to the metencephalon, as a part of the brain stem externally undifferentiated. The third cranial nerve (iii, figs. 1, 3) has its origin from the ventral midline.

Hidden by the overlying cerebral hemispheres anteriorly and by the optic lobes posteriorly, the diencephalon (d., figs. A, 1, 2, 3), becomes the most inconspicuous part of the Sphenodon brain. Dorsoventrally the diencephalon is ovoid in shape. A minute stalk, the pineal sac (p. s., figs. 1, 2), arises dorsally from it. On the ventral side is the optic chiasma (op. c., fig. 3), from which the optic nerves project forwards under the cerebrum. Posterior to the optic chiasma the infundibulum (inf., figs. 1, 3) runs obliquely downward and backward to join the hypophysis (h., figs. 1, 3).

The two large pyramidal lobes of the cerebral hemispheres compose the greater part of the telencephalon (t., figs. A, 1, 2, 3). From between the posterior parts of the hemispheres the small glandular stalk of the paraphysis (p., figs. 1, 2) rises vertically, parallel to the vertical portion of the pineal sac. The anterior continuations of the cerebral hemispheres are the much elongated olfactory tracts (o.t., figs. A, 1, 2, 3). These tracts terminate in slightly enlarged bulbar endings, the olfactory bulbs (o.b., figs. A, 1, 2, 3).

MEDULLA OBLONGATA

The Transition. Two factors, at least, have a part in the change from spinal cord to the medulla. The first of these is the relay of the two ascending tracts of the dorsal funiculus, the fasciculus gracilis and fasciculus cuneatus (f. g. and f. c., figs. 4, 5), to a ventral position. In a transitional level through the spinal cord (fig. 4) the central gray matter (c. g.) has pushed both medially and dorsally, and has established a connection with the nucleus gracilis and the nucleus cuneatus (n. g. and n. c.) which are being formed. These nuclei are not only terminals for the fasciculus gracilis and fasciculus cuneatus respectively, but also they are the nuclei of origin for fibers which cross downwards in arcs through the central gray matter to the raphe(r). From the raphe they cross to the opposite side and become localized in a median ventral position to form the medial lemniscus (m. l., fig. 6). The termination of the dorsal fasciculi clears a way for the merging of central canal into fourth ventricle. This termination is not complete at the level of the calamus scriptorius (fig. 5), however, and while the nucleus gracilis disappears not so far anteriorly, the nucleus cuneatus can be found well into the region of the tenth nerve.

A second factor in bringing about the transition is the reticular formation (r. f., figs. 4, 5). It springs up at the sides of the gray matter, and by persistent encroachment from ventral and lateral sides soon reduces the ventral cell column (v. c., fig. 4) as well as obliterating in part the dorsal cell column (d. c., fig. 4). The reticular formation continues into the mesencephalon.

Cranial Nerves and their Nuclei. The much reduced ventral cell column in the posterior medulla is the nucleus of the twelfth nerve (xii, figs. 3, 5). Here are large multipolar neurones which send their axones downward alongside the fasciculus longitudinalis medialis (f. l. m., figs. 4, 5), and in a bundle they leave the medulla ventrally as the root of the twelfth.

Eleventh, tenth, and ninth nerves are treated together, since their nuclei are so nearly confluent that they cannot be separated individually. The eleventh roots, visceral efferent, leave the sides of the medulla ventrolaterally. Visceral efferent fibers of the tenth nerve leave the medulla a little above those of the eleventh. The afferent fibers of the tenth (x, fig. 6) end in part in the terminal nucleus of this nerve, but some also end in the nucleus solitarius (n. and f. s., fig. 6). A similar termination of visceral afferent fibers of the ninth occurs. The visceral efferent fibers of the ninth apparently have their ultimate origin from the fasciculus longitudinalis medialis (see fig. 8, showing a similar origin for visceral efferent fibers of the seventh nerve). In its relation to cranial nerves the fasciculus longitudinalis medialis is not only closely associated with the somatic efferent fibers but also the visceral efferent fibers. The latter fibers originating on one side go into the fasciculus longitudinalis medialis; cross to the fasciculus of the side opposite; and from there emerge. This relationship, only slightly shown for the visceral efferent tenth, is brought out strongly in the ninth and in the seventh, and fifth as well.

The vestibular eighth nerve makes its appearance in the region of the anterior part of the ninth, and joined by the cochlear nerve takes over the whole lateral wall of the medulla (viii v. and viii c., fig. 7). The vestibular nucleus which is the larger is ventral; the cochlear nucleus is dorsal.

The seventh nerve, similarly to the ninth, has a visceral afferent portion whose fibers end in the terminal nucleus in part and another part in the nucleus solitarius, while the visceral efferent seventh has ultimate origin from the fasciculus longitudinalis medialis. The seventh nerve is closely associated with the eighth nerve morphologically for the eighth nerve has hardly reached its maximum in size when the efferent fibers of the seventh begin to run outward along the lower part of the eighth (vii a. and vii e., fig. 8).

The sixth nerve (n. vi and vi, figs. 7, 8) is formed by fibers from the somatic efferent cell column ventrolateral to the fasciculus longitudinalis medialis. These fibers follow a course ventrally and emerge on the ventral side of the medulla in the midline.

The fifth nerve has strong visceral efferent (v. e., fig. 9) and visceral afferent (v. a., fig. 9) roots. The visceral afferent fibers resemble those of the vestibular part of the eighth nerve, although only about half the size of the eighth root. Large pyramidal cells form the nuclei of the visceral efferent component of the fifth (n. v. e., figs. 9, 10). These fibers cross to the opposite side and emerge from the fasciculus longitudinalis medialis.

Secondary Tracts associated with the Cranial Nerves. Internal arcuate fibers are especially prominent in the region of the ninth, tenth, and eleventh nerves. These fibers (i. a. f., fig. 6) form secondary pathways whereby afferent impulses are brought to bear upon efferent nuclei.

From the cochlear nucleus, fibers of both myelinated and unmyelinated type, the striæ medullares acusticæ (s. m. a., fig. 7), stream obliquely downwards and end in the neighborhood of a small nuclear group, the superior olive (s. o., fig. 7). Some of the fibers may make synapse here; others may turn forwards, and with fibers originating in the superior olive form the lateral lemniscus (l. l., fig. 8). The lateral lemniscus is associated with the ventral spino-cerebellar tract until the latter tract moves laterally, and then the lateral lemniscus assumes its definitive position.

Fibers directly from the vestibular nucleus of the eighth nerve reach the cerebellum. This tract is the fasciculus vestibulo-cerebellaris (t. v. s., fig. 9). The vestibular nucleus in its anterior extension becomes medial to the dorsal spino-cerebellar tract at the level of the fifth nerve (fig. 9). Following the disappearance of the dorsal spino-cerebellar tract into the cerebellum, the vestibular tract becomes peripheral (fig. 10), from where it turns upward into the cerebellum.

Some of the afferent fibers of the seventh, ninth, and tenth nerves end in the nucleus solitarius. From this nucleus fibers are given off which form the fasciculus solitarius (n. and f. s., figs. 6, 7, 8) that goes posteriorly into the spinal cord. At the level of the seventh nerve (fig. 8) the fasciculus solitarius is a small circular bundle of fine fibers located in the lateral part of the central gray matter, and this position is retained until the fasciculus as a definite bundle is lost in transitional levels (fig. 4).

Ascending and Descending Fiber Tracts. The fasciculus gracilis (f. g., figs. 4, 5) has been mentioned in a preceding section. Entering the medulla as the most nearly medial of the two tracts of the dorsal funiculus, the fasciculus soon terminates in the nucleus gracilis (n. g., figs. 4, 5), the termination being practically complete at the calamus scriptorius level (fig. 5).

The fasciculus cuneatus (f. c., figs. 4, 5) already mentioned above, is the lateral fasciculus of the two dorsal tracts entering the medulla. It terminates in the nucleus cuneatus (n. c., figs. 4, 5) which continues well into the level of the tenth nerve (fig. 6).

Axones from the nucleus gracilis and nucleus cuneatus form the medial lemniscus (m. l., fig. 6). These axones, not in dense bundles but as scattered fibers, proceed down through the central gray matter, enter the raphe, and cross to the opposite side to take up a position ventrolateral to the tecto-spinal tract. The raphe (r., figs. 4, 5) is a dense tangle of fibers as long as the dorsal nuclei exist. In the posterior part of the medulla the medial lemniscus is not so sharply defined, but the position it has assumed is retained until it enters the mesencephalon.

In the posterior transitional levels of the medulla the fasciculus spino-cerebellaris dorsalis (t. s. c. d., figs. 4, 5, 6) has a dorsolateral position immediately ventral to the substantia gelatinosa, but as higher levels are reached it takes up a position dorsal to the substantia gelatinosa. The broadening out of the medulla and the incoming of the eighth fibers (fig. 7) push the tract to a ventral position in the medulla. Behind the fifth nerve it moves dorsally (fig. 9) from where it enters the cerebellum.

The ventral spino-cerebellar fasciculus (t. s. c. v., figs. 4, 5, 6) lies in the lateral funiculus ventral to the fasciculus spino-cerebellaris dorsalis. Between the levels of the tenth nerve (fig. 6) and the fifth nerve the ventral spino-cerebellar tract becomes ventrally placed, similar to the dorsal spino-cerebellar tract, but the former is medial to the latter (fig. 7, 8). At the root of the fifth nerve (fig. 9) the ventral tract assumes a ventrolateral position, and fibers of the fifth must traverse it in entering the medulla. The tract remains in this position until it swings into the anterior part of the cerebellum.

The fasciculus tecto-spinalis arises from the inner zone of the stratum medullare profundum (st. med., fig. 16), of the tectum mesencephali. In the medulla the fasciculus tecto-spinalis (t. t. s., figs. 4, 5, 6, 7, 8, 9) is located ventral to the fasciculus longitudinalis medialis.

The fasciculus longitudinalis medialis (f. l. m., figs. 4, 5, 6, 7, 8, 9), in transitional levels, is distinguishable as the dorsal part of the ventral funiculus, and in levels a little farther forward it becomes more clearly defined as a bundle.

METENCEPHALON

Cerebellum. The cerebellar cortex has well defined the three layers—molecular layer, layer of Purkinje cells, and the granular layer (fig. 33). The molecular and granular layers are about equally thick throughout. The molecular layer (mol.), which covers the cerebellum, shows little histological structure save for a few scattered nuclei. The granular layer (g. l.), which borders the fourth ventricle, is a mass of nuclei irregularly grouped into clustering masses which give an appearance not unlike the granular layer of the mammalian cerebellum. Between granular and molecular layers is the layer of Purkinje cells (p. c.). These cells are globular in shape and have large, prominent nuclei. Just beneath the Purkinje cells and intermingled somewhat with the cells of the granular layer are the fibers (f. t.) composing the white matter. In general, the incoming tracts are located on the upper side of the white matter while the outgoing tracts are below.

The Fiber Connections of the Cerebellum. The fasciculus spinocerebellaris dorsalis from its peripheral position on the sides of the medulla enters the most posterior part of the cerebellum. (t. s. c. d., fig. 9).

Following the dorsal spino-cerebellar tract into the cerebellum, the fasciculus vestibulo-cerebellaris (t. v. c., fig. 10) from the lateral walls of the medulla next moves into it.

The most anterior part of the cerebellum receives the fasciculus spino-cerebellaris ventralis (t. s. c. v., fig. 11).

The brachium conjunctivum, composed of outgoing fibers, begins to leave the cerebellum at the same level that the vestibulo-cerebellar tract enters (b. c., fig. 10). These fibers of the brachium conjunctivum, as they move forward, first decussate in the anterior part of the metencephalon (fig. 11). Here the fibers are scattered, and they make their crossing in the dorsal part of the raphe; but, in more anterior levels of the brain stem the decussation becomes broadened, and it is gradually shifted until it is ventral in the raphe, (see figs. 12, 13, 14, 15).

Basal Region of the Metencephalon. Except for the fiber paths which establish their connection with the cerebellum, as just noted in the previous section, the basal region through the metencephalon shows little change from that of the medulla. However, when the ventral spino-cerebellar tract turns dorsalwards from its ventrolateral position (figs. 10, 11) the lateral lemniscus moves laterally and dorsally until it is located medial to the new position of the ventral spino-cerebellar tract (see l. l., fig. 11). Following the disappearance of the latter tract, the lateral lemniscus becomes peripheral, and here below the nucleus isthmi (fig. 12) the fibers of the lemniscus concentrate.

ISTHMUS RHOMBENCEPHALI

Nucleus Isthmi. Between the metencephalon and the mesencephalon, that part of the brain called the isthmus contains a large prominent nuclear mass, the nucleus isthmi (n. i., fig. 12). The cells are large, spherical, and closely associated with fibers from the lateral lemniscus. Apparently these are the only fibers to enter the nucleus isthmi. Fibers leaving the nucleus can be traced to the inferior colliculi (i. c., fig. 13), and some may enter the tectum mesencephali.

Fourth Nerve. At the level of the nucleus isthmi the fourth nerve, somatic efferent, emerges dorsally from the brain (iv., fig. 12). The nucleus of nerve four (n. iv., figs. 12, 13) lies in the central gray matter dorsal to the fasciculus longitudinalis medialis; and fibers arising from this nucleus move upward through the central gray matter around the aqueductus cerebri; then dorsal to the aqueduct, they decussate (d. iv, fig. 12) to the opposite side before their emergence.

MESENCEPHALON

The Corpora Quadrigemina. The corpora quadrigemina are present in Sphenodon as represented by the large optic lobes or superior colliculi externally, and internally in the posterior part of the mesencephalon by a pair of cellular bodies, the inferior colliculi.

The Inferior Colliculi. The inferior colliculi (i. c., fig. 13) arise as two oval nuclear groups on each side of the dorsal midline just anterior to the level of the nucleus isthmi. In this position the inferior colliculi would be external were it not for the fiber tracts dorsally which outline the nuclei above. Anteriorly the inferior colliculus on each side is embedded in the central gray matter of the mesencephalon (figs. 14, 15) until the mesocœle is outlined, and then, since the inferior colliculus is reduced in size, it is accommodated in the central gray matter of the lateral wall of the tectum mesencephali (fig. 16).

Fiber Connections of the Inferior Colliculi. All fiber tracts associated with the posterior part of the inferior colliculi make their entrance from the dorsal side. The tract from the nucleus isthmi (t. n. i., fig. 13) moving medialward and forward to the inferior colliculus, is the first to enter. Closely following this tract is the lateral lemniscus (l. l., fig. 14), the majority of whose fibers end in the inferior colliculus. When the inferior colliculus becomes embedded in the central gray matter the fibers forming the dorsal boundary move upward as a part of the stratum medullare profundum of the superior colliculus (fig. 15). The fiber connections with the superior colliculus are then established along the lateral border of the inferior colliculus (figs. 15, 16).

The Superior Colliculi. Ramon (1896) described fourteen different layers in the tectum mesencephali of the reptile, but without Golgi material the designation of these layers in Sphenodon (fig. 34) could only be done arbitrarily. The nuclear groups are most conspicuous near the ventricular border. Aside from this prominence of cells there should be pointed out two fiber systems, the stratum opticum (st. op., fig. 34) which is nearly peripheral, and the stratum medullare profundum (st. med.) just above the mass of nuclei near the ventricle.

The Stratum Opticum. The tectum is the final termination of the optic tract which upon leaving the diencephalon divides into two parts, on each side, one to follow the ventrolateral line of the tectum, the other to follow the ventromedial line of the tectum (o. p., figs. 14, 15, 16, 17). From these two parts fibers enter the stratum opticum to spread upward, and to form as seen in cross-section the outermost arch of myelinated fibers of the tectum.

Associated with the stratum opticum there is a crossed tecto-thalamic tract whose fibers appear on the inside of the stratum. They form a bundle inside of the ventrolateral division of the optic tract, and in company with the optic tract can be traced to their decussation in the optic chiasma. In the diencephalon the tract becomes unmyelinated although in the mesencephalon it is myelinated. In Necturus, Herrick (1917) has designated this bundle as the tractus tecto-thalamicus et hypothalamicus cruciatus, pars posterior, and this tract is so named in Sphenodon (t. a., figs. 16, 17).

The Stratum Medullare Profundum. The stratum medullare profundum, the conspicuous arch of myelinated fibers in the deeper part of the tectum, is receptive to fibers from several tracts. Into the most posterior part of the stratum fibers of the lateral lemniscus are directed (fig. 14), and a little anteriorly it receives a broad band of fibers of the brachium conjunctivum (fig. 15). At the level of the third nerve a portion of the medial lemniscus enters by a gradual process of infiltration (fig. 16), while in the anterior part of the mesencephalon tecto-thalamic paths are relayed to the stratum medullare profundum through the nucleus pretectalis (n. p., fig. 17).

At the level of the third nerve (fig. 16) the innermost fibers of the stratum medullare stream downward in conspicuous bands, some to remain on the same side to enter the fasciculus tecto-spinalis (t. t. s), which is being formed ventral to the fasciculus longitudinalis medialis; others to cross to the opposite side in the tegmental decussation (teg. d.), and there enter the fasciculus tecto-spinalis of that side.

The outermost fibers of the stratum, ventrolaterally form the anterior part of the crossed tecto-thalamic tract (t. a., fig. 16). The small bundles of fibers become collected into a well defined tract that moves into the diencephalon, but in the diencephalon in continuing with the optic tract the former tract does not remain so sharply defined although the fibers remain myelinated. In the optic chiasma this tract, the tractus tecto-thalamicus et hypothalamicus, pars anterior, as named by Herrick, crosses dorsal to the anterior part of the same tract.

Fibers of the stratum medullare profundum, crossing between the two superior colliculi, form the decussation of the superior colliculi (d. s. c., fig. 16).

The Tegmentum. The basal region of the mesencephalon, the tegmentum, is the anterior extremity of the brain stem, and it provides a highway or relay for numerous fiber tracts, especially those related to the tectum.

The medial lemniscus (m. l.) has continued in a ventro-lateral position from the medulla, through the metencephalon and posterior tegmentum (figs. 13, 14, 15). Gradually it disappears from the tegmentum, some of its fibers running dorsally into the stratum medullare profundum (fig. 16), and some of them undoubtedly going forwards into the diencephalon, although they cannot be followed farther.

The Brachium Conjunctivum. As has been indicated in a previous section the decussation of the brachium conjunctivum occurs in the mesencephalon, and this is most distinct at a level as shown in fig. 15 (d. br. c.). Some of the fibers of the tract enter the small nuclear group, the primordium of the nucleus ruber (n. r., fig. 15), but the greater part of the tract goes into the tectum.

The third cranial nerve arises from the ventral median surface of the mesencephalon (iii, fig. 16). The nucleus (n. iii) of the third lies in the central gray matter of the tegmentum dorsal and medial to the fasciculus longitudinalis medialis, and fibers arising from it move ventrolaterally around the edge of the fasciculus longitudinalis medialis.

At the anterior part of the tegmentum two conspicuous structures which have been found throughout the brain stem have their ending. The first of these is the recticular formation, (r. f., fig. 17). The second, the fasciculus longitudinalis medialis, which gradually loses its distinctness as a bundle and ends in its nucleus (f. l. m., fig. 17).

DIENCEPHALON

The Epithalamus. The epithalamus in Sphenodon includes the dorsal part of the diencephalon; that is, the nucleus habenula and its fiber tracts, and the pineal structures.

The nucleus habenula (n. h., figs. 19, 20) is situated in the dorsally projecting ridge of the diencephalon. On the left side the ridge is slightly higher than on the right side. The largest cells in the habenular nucleus are toward the lateral and ventral portions.

By means of the small hebenular commissure (h. c., fig. 19), the two sides of the nucleus habenula are brought into relationship with each other. The fibers of the commissure, all of which are not myelinated, form for a short distance a bridge over the third ventricle.

Two tracts which connect the nucleus habenula with the telencephalon are collectively termed the striæ medullares (s. m., figs. 19, 20, 21, 22). The tractus olfacto-habenularis accompanies the basal forebrain bundles from which it is an offshoot into the diencephalon, and then extricates itself gradually to turn dorsally towards the nucleus habenula (s. m., fig. 22). The tractus corticohabenularis leaves the nucleus along side of the incoming tractus olfacto-habenularis. Posterior to the aberrant commissure the former tract runs into the cortex through a short union made between cortex and diencephalon (s. m., fig. 21). There is here a close association between the striæ medullares and the aberrant commissure.

The cells of the nucleus habenula give rise to a second tract, the tractus habenulo-peduncularis (t. h. p., figs. 18, 19, 20). This tract leaves the nucleus just before the final disappearance of the striæ medullares, and it follows a course downward and backward through the diencephalon, and finally ends in the tegmentum of the mesencephalon.

The Pineal Eye and Associated Structures. Above the diencephalon the pineal sac (p. s.) arises as a stalk-like structure bent at right angles (fig. 1). Two component parts are thus given to the pineal sac; one, a vertical component which connects at its lower extremity with the epithalamus (fig. 19); the other, a horizontal component which is much elongated (fig. 31, showing both components). The paraphysis, a glandular structure of the telencephalon, lies below the pineal sac (p., figs. 1 and 31).

The pineal eye (p. e., fig. 31) is anterior to the distal extremity of the pineal sac, and is found in the base of the interparietal foramen of the skull (in. f., fig. B). It is covered over by a plug of connective tissue which fills the interparietal foramen, the parietal plug (p. p., fig. 31). In shape the pineal eye is conical, the base of the cone being represented by the lens. The diameter of the eye from side to side is approximately 0.25 mm. From the posterior portion the nerve of the pineal eye is given off. It passes to the lower part of the pineal sac and follows the inner border around to the habenular region of the epithalamus.

Histologically the pineal sac presents the structure of a sensory organ rather than a glandular organ. Fig. 32 shows a section through the wall of the pineal sac. The innermost layer of cells which border the cavity of the pineal sac are an elongated type of sensory cells having rather large oval nuclei (s. c.). Processes of these cells project beyond the limiting membrane. A median layer of cells have very large spherical nuclei with cytoplasm not large in quantity. These are ganglion cells (g. c.). The outer layer of the wall proper is composed of elongated cells with small oval nuclei, and these cells are of a supporting type (su. c.). Their outer processes seem to fuse to form an external limiting membrane. A section through the pineal nerve is also shown in fig. 32. It is composed of nerve fibers (n. p. e.) with cells having elongated, oval nuclei situated between the fibers. Although the exact nature of these cells cannot be determined it is probable that they are neuroglia cells (ng. c.). Outside of the nerve are epithelial cells which line the cavity between paraphysis and pineal sac, called the dorsal sac. In the distal portion of the pineal sac, sensory cells alone do not make up the innermost layer for there is interposed between the sensory cells, pigment cells which are filled with brown pigmented granules. These pigment cells (pg. c.) greatly obscure the sensory cells as shown in the photomicrograph (fig. C). Dendy

(1910) similarly observed the presence of pigment cells in the pineal sac in one specimen.

The pineal eye (figs. D and 36), histologically, is composed of a cellular lens and a retina. The latter is homologous with the wall of the pineal sac, for it has the same cellular elements and a similar arrangement of them. The inner layer of the retina has the sensory cells (s. c.) with their oval nuclei and elongated cytoplasmic bodies, and they are so closely crowded with pigment cells (pi. c.) that on first appearance the layer appears only as a pigment layer. In the middle layer are the ganglion cells (g. c.) with large spherical nuclei, and the outer layer is composed of supporting cells (su. c.) with small oval nuclei. It is entirely possible that processes of these cells pass through the retina and fuse internally to form an internal limiting membrane. The lens of the pineal eye (l.) is biconvex. Above, it is covered by the connective tissue of the parietal plug. The inner lateral margins are closely applied to the retina, although retina and lens are sharply demarcated. The cellular structure of the lens is not uniform and consequently description will be limited to the statement that the nuclei are located marginally, and the central cells, which apparently are of large size, show little evidence of cell boundaries and an almost total absence of nuclei.

The Thalamus. The middle, much expanded portion of the diencephalon is the thalamus. This is the center for important nuclei which act as relays for tracts passing to and from the telencephalon and lower brain centers, as well as the pathway for tracts leading from the telencephalon. Along its lateral walls it serves as a highway for the optic tracts.

Nuclei. Among the nuclear groups present two are large, conspicuous, and their outline readily defined.

The nucleus dorsolateralis anterior is a large, somewhat wedge-shaped nuclear mass which arises in the anterior dorsal part of the thalamus (n. d. l. a., fig. 20). It continues backward to the middle of the diencephalon. Somewhat posterior to its origin a new nuclear mass, the nucleus rotundus, pushes laterally the dorsal and anterior nucleus, thus giving the last qualification to make the name of the nucleus applicable. The cells are fairly large in size, triangular in shape, and arranged in groups. In the nucleus a portion of the tractus strio-thalamicus (lateral forebrain bundle) terminates. Into this nucleus there is also sent the tractus mamillo-thalamicus.

The nucleus rotundus (n. r., figs. 19, 20) is a large oval nuclear mass extending from a position posterior to the origin of the nucleus dorso-lateralis anterior, to near the posterior part of the diencephalon. As mentioned before, it is the nucleus rotundus which pushes the nucleus dorso-lateralis anterior, laterally. The cells of the nucleus rotundus are small in size, and are closely surrounded by many fine fibers of tracts related to the nucleus. A portion of the tractus strio-thalamicus (lateral forebrain bundle) is given off to the nucleus rotundus as well as to the nucleus dorso-lateralis anterior. The tractus thalamo-tectalis has its origin in the nucleus rotundus. (t. t. t., fig. 19).

The forebrain bundles enter the thalamus from the telencephalon. The median forebrain bundle (m. f. b., figs. 19, 20, 21, 22, 23) is situated closely beside the lateral forebrain bundle (l. f. b., figs. 19, 20, 21, 22, 23). A strong component is given off by the median forebrain bundle to the hypothalamus (tractus septo-hypothalamicus) (fig. 21), and consequently when the bundle reaches the mesencephalon (tractus septo-mesencephalicus) it is much reduced in size. In the posterior part of the diencephalon and into the tegmentum of the mesencephalon the bundle can be followed only with difficulty.

The lateral forebrain bundle is larger than the median forebrain bundle. In the thalamus the lateral forebrain bundle gives off dorsally a most conspicuous system of fibers (tractus strio-thalamicus) which moves upward to the nucleus rotundus and the nucleus dorsolateralis anterior (fig. 20). The remainder of the lateral forebrain bundle runs into the tegmentum, giving off on the way fibers which accompany those from the median forebrain bundle to the hypothalamus. In the posterior part of the diencephalon the lateral forebrain bundle becomes unmyelinated.

The tractus thalamo-tectalis (t. t. t.) arising from the cells of the nucleus rotundus leaves the nucleus from the ventral and ventrolateral margins (fig. 19). The tract proceeds ventrolaterally, until in position with the tractus tecto-thalamicus cruciatus, pars anterior, it goes backward to enter the stratum medullare profundum of the tectum.

The tractus mammillo-thalamicus arises from the hypothalamus and moves dorsally and anteriorly to the nucleus dorsolateralis anterior (t. m. t., figs. 18, 19, 20).

The two crossed tecto-thalamic tracts (t. a. and t. p., figs. 18, 19, 20, 21, 22, 23), coming from the mesencephalon pass through the ventral part of the thalamus to the optic chiasma where, dorsally, they cross to the opposite side. The tractus tecto-thalamicus cruciatus, pars anterior is the more dorsal of the two tracts. As it passes through the thalamus its distinctness becomes more obscure, and nearing the optic chiasma it takes up a position along the dorso-medial side of the optic tract. In crossing the optic chiasma it is dorsal to the crossed tecto-thalamic tract, pars posterior. The tractus tecto-thalamicus cruciatus, pars posterior in the thalamus retains its close relationship to the optic tract as it does in the mesencephalon. Soon after entering the thalamus the fibers become unmyelinated. As just pointed out in this paragraph, this tract crosses in the chiasma ventral to the tractus tecto-thalamicus cruciatus, pars anterior.

The optic tract (o. p., figs. 18, 19, 20, 21) as a heavy mat of fibers bounds the two sides of the thalamus. The fibers cross in the optic chiasma (op. c., figs. 22, 23, 24, 25) and then turn obliquely backwards along the sides of the thalamus to gain the mesencephalon.

The Hypothalamus. The ventral projection of the diencephalon forms the hypothalamus which is much broader and deeper than the epithalamus. The nuclear structure of the hypothalamus is undifferentiated, and definite corpora mammillaria cannot be distinguished, but the infundibulum and hypophysis are prominent.

The nucleus hypothalamus (h. t., figs. 18, 19, 20, 21) is composed of small cells arranged medially in rows and concentrated especially next to the ventricle. Out to the sides the cells are scattered.

The fiber tracts to the hypothalamus are chiefly components from the forebrain bundles. The anterior part of the hypothalamus receives a strong component from the median forebrain bundle (m. f. b., fig. 21). This tract decussates just dorsal to the crossed tecto-thalamic tracts of the optic chiasma. A little posterior to the level at which the tract from the median forebrain bundle to the hypothalamus is given off, it receives fibers from the fornix which has become situated in the diencephalon medial to the median forebrain bundle (f., fig. 21). The lateral forebrain bundle also sends fibers into the hypothalamus (l. f. b., fig. 20). From the posterior part of the hypothalamus arises the tractus mammillo-thalamicus (t. m. t., fig. 20), which spreads dorsally to join the nucleus dorso-lateralis anterior. In the most posterior portion of the hypothalamus the two sides are correlated with each other by a short but conspicuous commissure of fibers, the decussation suprainfundibularis (d. s. i., fig. 18), whose fibers cross dorsal to the infundibulum.

Hypophysis. The hypophysis is easily divisible into two parts: a more dorsal and anterior part which joins the infundibulum, the pars nervosa (p. n., fig. 37), and the ventral and more posterior part, the pars buccalis (p. b., fig. 37). Between the pars nervosa and the pars buccalis is a third division the pars intermedia (p. i., fig. 37). The pars nervosa is very much convoluted, and so the pars intermedia, following the convolutions, can be found in various locations in sections through the hypophysis.

A section through the wall of the pars nervosa (fig. 38a) shows a conspicuous layer of epithelial cells (e. p. n.) along its inner border, which are continuous with the ependymal cells of the infundibulum. The remainder of the wall consists of a fibrous matrix, with a few cells, probably nerve cells (n. c.), scattered here and there. Some of the epithelial cells send out long processes which cross through the matrix in the plane of the section.

The pars intermedia is composed of several layers of elongated epithelial cells (e. p. i., fig. 38a) separated from the pars nervosa and the pars buccalis by connective tissue.

As distinguished by their staining reactions, the cells of the pars buccalis are of two types: eosinophiles (eos., fig. 38b), large cells with oval nuclei, which take a deep red cytoplasmic stain; and neutrophiles (neu., fig. 38b), smaller cells with spherical nuclei which have a very lightly stained cytoplasm. The eosinophiles are more numerous in the anterior part of the pars buccalis while the neutrophiles are more numerous in the posterior part. The structure of the pars buccalis follows the distribution of these two types of cells. Although typically glandular, this part of the hypophysis shows the alveolar and tubular arrangement of cells mostly in the case of the eosinophiles (as shown in fig. 38b), and the neutrophiles are arranged in columns of cells. Such groupings of neutrophiles thus predominate in the posterior part of the pars buccalis. The alveolar arrangement of the eosinophiles predominates in the anterior portion.

Pigment cells with black granules form pigmented areas in the pars nervosa as shown in fig. 37, pigm. These areas are also found in the walls of the lower infundibulum.

TELENCEPHALON

General Topography. Excepting the more basal regions, the telencephalon consists essentially of a definite cortex superimposed above a much enlarged corpus striatum, the cortex being separated from the corpus striatum by the lateral ventricle. The dorsomedial region of the cortex is the primordium hippocampus (p. h., figs. 22 to 28), and the dorsal cortex is the general pallium (g. p., figs. 22 to 28). Laterally the differentiation of the telencephalon is not advanced, and to the region as a whole the name lateral olfactory area will be given. The upper part of the corpus striatum is a much enlarged mass projecting into and nearly filling the lateral ventricle, the outline of the projecting mass varying with the level at which the section is taken (see n. s., figs. 22 to 28). Interestingly, the cell layer which follows the peripheral (ventricular) border of this part of the corpus striatum is continuous with the cortical cell layer of the general pallium. Following the nomenclature of G. Eliot Smith this is designated as the neostriatum (pl. s., figs. 24 to 27). Below the hippocampus primordium the portion of the telencephalon which is ventromedial is the septum (s., fig. 27), while the ventral, peripheral part of the telencephalon is the olfactory tuberculum (tu., fig. 28).

The Cortex. A section through the cortex in the region of the general pallium is shown in fig. 35. Three layers are evident: the outermost layer is the tangential fibers (t. f., figs. 35 and 21 to 28), in which fibers to the cortex are carried. The second layer consists of cells, sparsely distributed along the boundaries of the layer but massed in the median portion, and it is here that numerous typically pyramidal cells are found (py. c.). The third layer or alveus (a.) is innermost and lies just external to the ependymal cells (e. c.) which line the ventricular border. Myelinated fibers leaving the cortex compose the alveus.

Some Telencephalic Nuclei. The cortical layer of cells described for the general pallium is similar in the primordium hippocampus with the exceptions that more cells are concentrated into the layer and the pyramidal type of cells are not so prevalent in the latter. Laterally the cortical layer is continued around to form the nucleus olfactorius lateralis (n. o. l., fig. 26), a lateral grouping of cells not highly differentiated. From the lateral olfactory nucleus the cortical layer of cells goes into the neostriatum (n. s.). In the anterior part of the neostriatum the compactness of the cells is maintained, but in the posterior part the layer becomes broken up into small cellular masses (compare n. s., figs. 24 to 26 and figs. 21 to 23). The more posterior levels of the telencephalon (figs. 21 to 23) show in the ventromedial extremity a triangular grouping of cells to form the nucleus ventromedialis (n. v. m.). As a nucleus the degree of differentiation is slight. Such is the case in the last nucleus to be mentioned. In the septum the cells are not conspicuously grouped, and consequently the name, septal nucleus (s., fig. 26) is applied to the cellular group as a whole.

Fiber Tracts of the Telencephalon. The tangential fibers (t. f., figs. 21 to 28) contain fibers which interrelate different cortical areas besides bearing fibers which enter the cortex from other regions. Undoubtedly fibers from the olfactory tract go into this layer, and fibers arising from the olfactory tuberculum (tractus tuberculo-corticalis, fig. 27) and from the septum (tractus septo-corticalis, fig. 26) enter the cortex here. The system of tangential fibers could not be traced around to the lateral olfactory nucleus.

Alveus. The alveus (a., figs. 21 to 26) is a strongly myelinated layer of fibers leaving the cortex. Many of the fibers undoubtedly arise as axones of the pyramidal cells. In going downward from the cortex the fibers pass into the fimbria (fi., figs. 23 to 26), a fiber strip from which fibers lead to the septum (tractus cortico-septi, fig. 26) and fornix fibers (f., fig. 26) are given off. The alveus is concerned with two important commissures which will be described in the two following paragraphs, and it is also related to the striæ medullares (see fig. 21 and description of the habenular-cortical tract).

Hippocampal Commissure. The fibers of the hippocampal commissure (h. c., figs. 26, 25) arise from the hippocampus and come down to the septum by way of the alveus. The bundle which traverses the septum has a center composed entirely of unmyelinated fibers, around which is a margin of myelinated fibers (fig. 26). In a position anterior and dorsal to the anterior commissure, the crossing over of the hippocampal fibers takes place (fig. 25). The hippocampal commissure is also called the anterior pallial commissure.

Aberrant Commissure. The aberrant commissure (ab. c., fig. 22) or posterior pallial commissure is associated closely to the cortical areas since it crosses in a comparatively dorsal position. The commissure which is composed of myelinated fibers is relatively short.

Immediately behind it is the habenular-cortical tract with which the aberrant commissure must have some relationship.

Anterior Commissure. The anterior commissure (a. c., fig. 24) makes possible the crossing over of olfactory fibers. It is located just posterior to the hippocampal commissure, and is composed of unmyelinated fibers.

Fornix. Fornix fibers arise from the fimbria and pass through the septum lateral to the tract of the hippocampal commissure (f., figs. 21 to 26). Posterior to the anterior commissure they are associated with the medial forebrain bundle. At the beginning of the diencephalon they move around to the medial edge of the median forebrain bundle, and from there they go into the hypothalamus.

The Forebrain Bundles. The median forebrain bundle (m. f. b., figs. 23 to 26) has its origin from the cells of the septal nucleus. The fibers which are myelinated pass as a bundle downward, and in the posterior part of the telencephalon, in the basal region, they become closely approximated to the lateral forebrain bundle. The lateral forebrain bundle (l. f. b., figs. 23 to 26) arises in the corpus striatum, its myelinated fibers passing obliquely medialward where they concentrate as a bundle alongside of the medial forebrain bundle. Both medial and lateral forebrain bundles then go into the diencephalon.

The Olfactory Projection Tract. From the nucleus ventromedialis unmyelinated fibers are given off that enter the diencephalon laterally, and there curve over the forebrain bundles to join the fornix. This tract is the olfactory projection tract (ol. t., figs. 22, 23). With the fornix it goes to the hypothalamus.

It is difficult to trace any fiber connections for the lateral olfactory nucleus (n. o. l., fig. 26). A few scattered fibers seem to be given off which can be followed toward the lateral forebrain bundle; the tractus olfactorius lateralis (t. o. l., fig. 26).

The Olfactory Bulb. A section through the olfactory bulb (fig. 30) is ringlike, the thickness of the wall varying with the position from which the section is taken. Four layers excluding the inner ependymal layer compose the structural makeup of the wall. The outermost one is small bundles of interwoven fibers, the glomeruli (g.), where synapse between axones of olfactory sensory cells and dendrites of mitral cells occurs. A number of small cells strewn among the inner parts of the glomeruli compose the outer granular layer (o. g. l.). A circle of medium-sized pyramidal cells is the layer of mitral cells (m. c.), the most prominent cell group of the bulb. The wide layer of quite closely crowded cells is the inner granular layer (i. g. l.). The axones of the mitral cells which carry conduction towards the secondary olfactory centers are found internal to the mitral cells. Prolongations of these axones form the definitive olfactory tract.

The Olfactory Tract. The nuclear area of the olfactory tract (fig. 29) is apparently a continuation of the inner granular layer. The nuclear elements in the region above the ventricle join the lateral olfactory nucleus and hippocampus finally.

The definitive fiber system (o. t.) in the olfactory tract is peripheral and since it encircles a section it is difficult to determine the different bundles and their boundaries. The tract is distributed to the septum and the hippocampus, the olfactory tuberculum and the corpus striatum, and to the lateral olfactory area.

DISCUSSION AND SUMMARY

The brain of Sphenodon represents in a schematic way one of the steps in the evolutionary development of the mammalian brain. It has a generalized reptilian plan of structure, foreshadowing in one direction the avian brain and in the other, the mammalian brain.

The medulla oblongata has many primary reflex centers of the brain. All cranial nerves except the third and fourth arise from the medulla oblongata in almost a linear arrangement. Visceral components predominate, and somatic elements are relatively few as shown by the following table:

Somatic afferent VIII.
Visceral afferent V, VII ,IX, X.
Visceral efferent V, VII, IX, X, XI.
Somatic efferent VI, XII.

Of the proprioceptive paths, the fasciculus gracilis and fasciculus cuneatus terminate in their respective nuclei, and from these nuclei fibers which cross in the raphe form the medial lemniscus in the median ventral part of the medulla. The dorsal and ventral spinocerebellar tracts are prominent proprioceptive paths passing from the spinal cord through the medulla to the cerebellum.

The cochlear and vestibular eighth nerves are the chief somatic afferent divisions. From the cochlear eighth fibers arise which form the lateral lemniscus, a secondary auditory path to the inferior colliculus. The vestibulo-cerebellar tract from the terminal nucleus of the vestibular eighth is important because it is functionally proprioceptive.

The cerebellum is a special receptive center for proprioceptive conduction and for bringing about motor coördination. In Sphenodon the small size of the cerebellum indicates that relatively slight demands are placed upon it for equilibration. The cerebellar cortex has well defined the layers as found in mammals; namely, molecular layer, layer of Purkinje cells, and granular layer.

The vestibulo-cerebellar tract together with the dorsal spino-cerebellar tract, which enter the posterior part of the cerebellum, would form the inferior peduncle or corpus restiforme of mammals. The superior peduncle carries the ventral spino-cerebellar tract which enters the most anterior part of the cerebellum and the brachium conjunctivum which goes to the tectum mesencephali. The basal region of the metencephalon shows no acquisitions as yet, and although old phylogenetically it serves merely as a highway for conducting paths.

In the isthmus rhombencephali, the most conspicuous nucleus isthmi is present. It receives some fibers from the lateral lemniscus, and it sends fibers to the inferior colliculus. The function of this nucleus is, however, still a matter of conjecture.

In the posterior part of the mesencephalon the presence of the inferior colliculus marks the beginning of the important reflex center for auditory conduction. The lateral lemniscus ends in the inferior colliculus.

The tectum mesencephali as the center for visual reflexes nearly reaches its zenith in structural development, the optic tectum of the bird only surpassing it. The functioning as an association center is high, since the general pallium is lowly in development; but such is not the case in the mammal for with the rise of the neopallium the association function of the tectum is usurped, and the degenerated condition of the tectum mesencephali of the mammal, when compared with that of the reptile, stands as evidence.

The tracts which enter the tectum of the Sphenodon are the optic tracts and the crossed tecto-thalamic tracts from the eyes, the tecto-thalamic tract from the thalamus bringing olfactory conduction, the brachium conjunctivum from the cerebellum, and the proprioceptive fibers from the medial lemniscus. The associations of the various conducting paths bring about integrated responses that are conveyed to muscles by the tecto-spinal tract, the most conspicuous tract leaving the tectum.

The position of the nerves III, IV and VI, the two former especially close to the tectum, is advantageous since they control eye movements.

In the integrated responses from the mesencephalon, the tegmentum is important, for many fibers of different paths end here.

The parts of the diencephalon are the epithalamus, thalamus, and hypothalamus. The best known structure of the epithalamus is the pineal eye which has a cellular lens and a retina with cells that are sensory. The homologous structure of the retina of the pineal eye and the wall of the pineal sac give evidence that the pineal eye developed as a part constricted off from the distal extremity of the pineal sac (Dendy). The nucleus habenula with which the nerve of the pineal eye connects is a reflex center for conduction from the pineal eye and from the olfactory centers in the telencephalon. The striæ medullares bring olfactory conduction to the nucleus habenula. The tractus habenulo-peduncularis is an olfactory tract from the nucleus habenula to the tegmentum. The close association between the enlarged posterior commissure and fibers from the nucleus habenula provides for conduction from the pineal eye to the tegmentum where such conduction may be directed to efferent nuclei.

The thalamus provides a way station between the telencephalon and other brain centers. The nucleus rotundus and the nucleus dorsolateralis anterior both receive their strongest fiber connections with the tractus strio-thalamicus (lateral forebrain bundle). The nucleus dorso-lateralis anterior also receives the mammillo-thalamic tract which brings up visceral conduction. The nucleus rotundus sends out the tecto-thalamic tract to the tectum.

The hypothalamus functions mainly as a coördinating center for olfactory and gustatory stimuli. The median forebrain bundle, the fornix, and the olfactory projection tract are instrumental in bringing olfactory conduction.

The hypophysis consists of three parts: pars nervosa, pars intermedia, and pars buccalis. The pars buccalis is distinctly an internal secretory gland.

The telencephalon is an olfactory brain with olfactory tracts ending in the lateral olfactory area, the septum and the tuberculum, and from the septum and the tuberculum tracts are sent into the primordium hippocampus. The telencephalon includes a definite cortex divisible into the primordium hippocampus and the general pallium. The layer of the cortex are: tangential fibers by which conduction enters the cortex, a cell layer with pyramidal cells present, especially in the general pallium, and the alveus by which conduction leaves the cortex. The cortex is continuous laterally with the lateral olfactory area, and then it is continued into the corpus striatum as the newer part, the neostriatum. The paleostriatum is the older part of the corpus striatum. From the corpus striatum the lateral forebrain bundle is given off. The septum gives rise to the median forebrain bundle. Of the commissures present, the anterior commissure is an olfactory commissure, but the hippocampal and aberrant commissure are the anterior and posterior pallial commissures respectively. The striæ medullares are closely related to the aberrant commissure. The sending out of olfactory paths from the telencephalon to the epithalamus, thalamus, hypothalamus and tegmentum has already been noted.

It is quite evident that the brain, which probably arose as a servant to sense organs, a means of correlating different stimuli and in some cases of bringing certain stimuli to bear on muscles, has passed little beyond that stage in Sphenodon. A definite cortex however foreshadows the greatest of brain structures, the neopallium.

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PLATES

PLATE I

Fig. A. Photograph of the adult brain of Sphenodon *in situ,* dorsolateral view. The structures of the pineal region have been removed.

Fig. B. Photograph of the skull of the adult Sphenodon, dorsal view.

Fig. C. Photomicrograph of the distal part of the pineal sac under high power to show the presence of pigment in the layer of sensory cells.

Fig. D. Photomicrograph of the lens and a portion of the retina of the pineal eye under high power.

ABBREVIATIONS

c.	cerebellum
d.	diencephalon
inf.	infundibulum
int. for.	interparietal foramen
l.	lens of the pineal eye
mes.	mesencephalon
m. o.	medulla oblongata
o. b.	olfactory bulb
op. t.	optic tract
o. t.	olfactory tract
p. p.	parietal plug
pigm.	pigment
p. s.	pineal sac
r.	retina of the pineal eye
s.	strands of pia mater
t.	telencephalon
v.	root of the fifth nerve
vii & viii.	roots of the seventh and eighth nerves

PLATE I

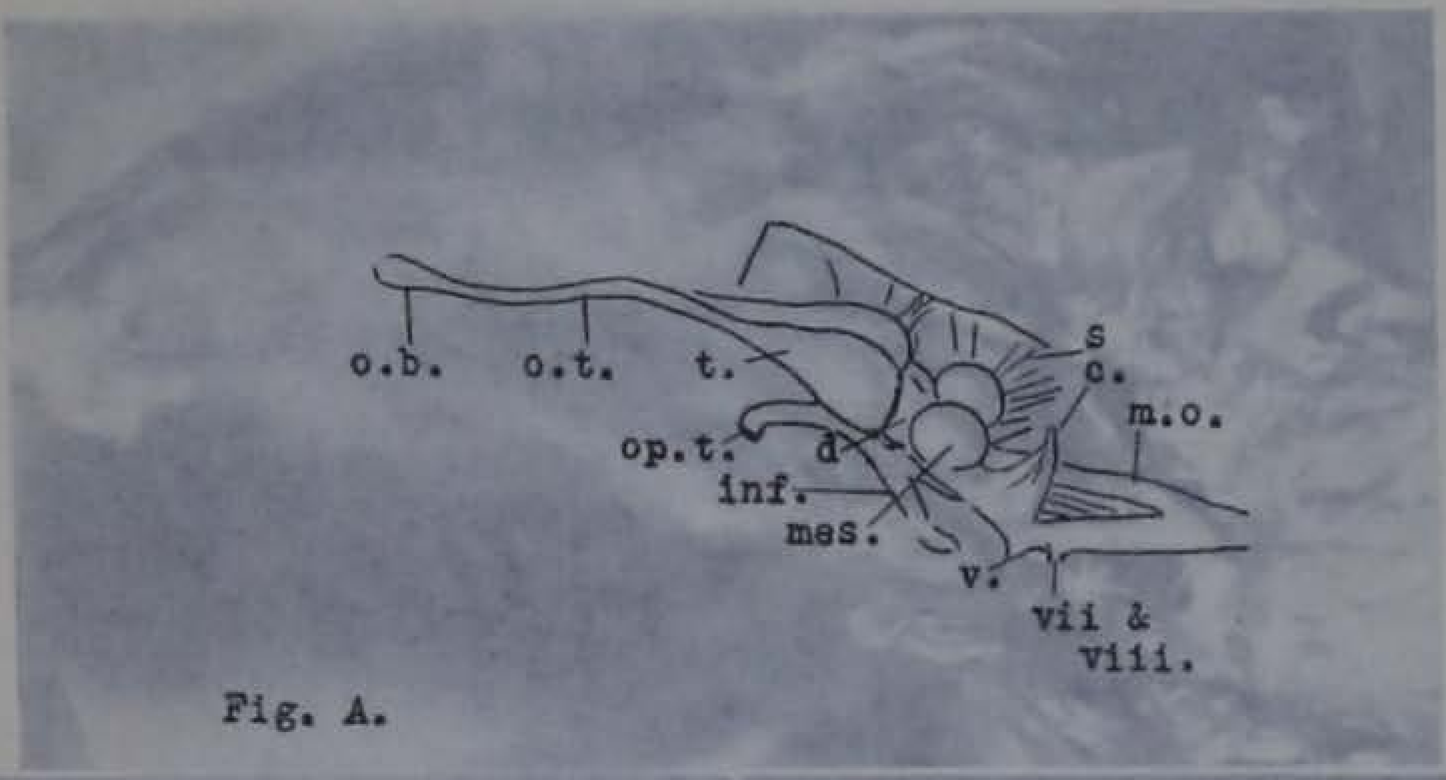


Fig. A.

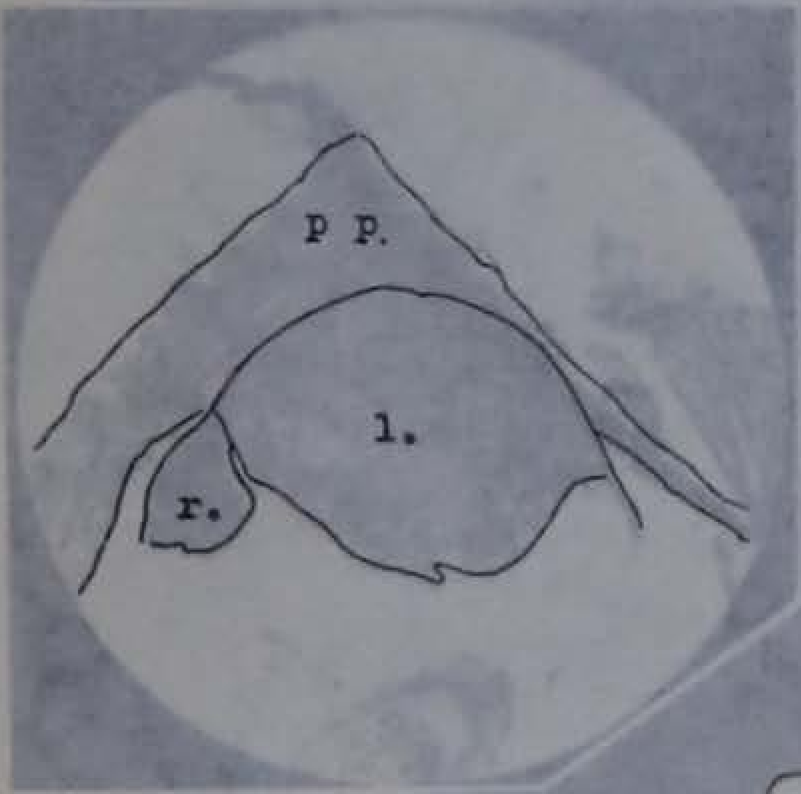


Fig. D.

Fig. C.

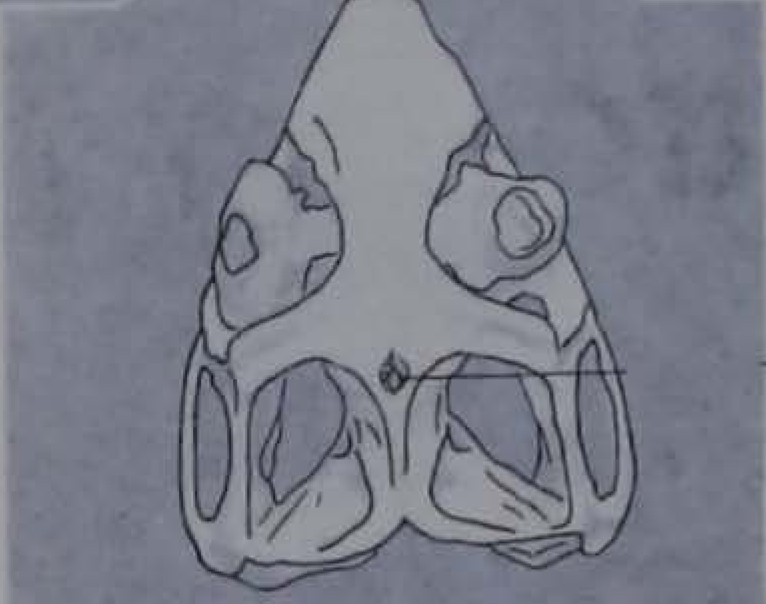


Fig. B.

PLATE I

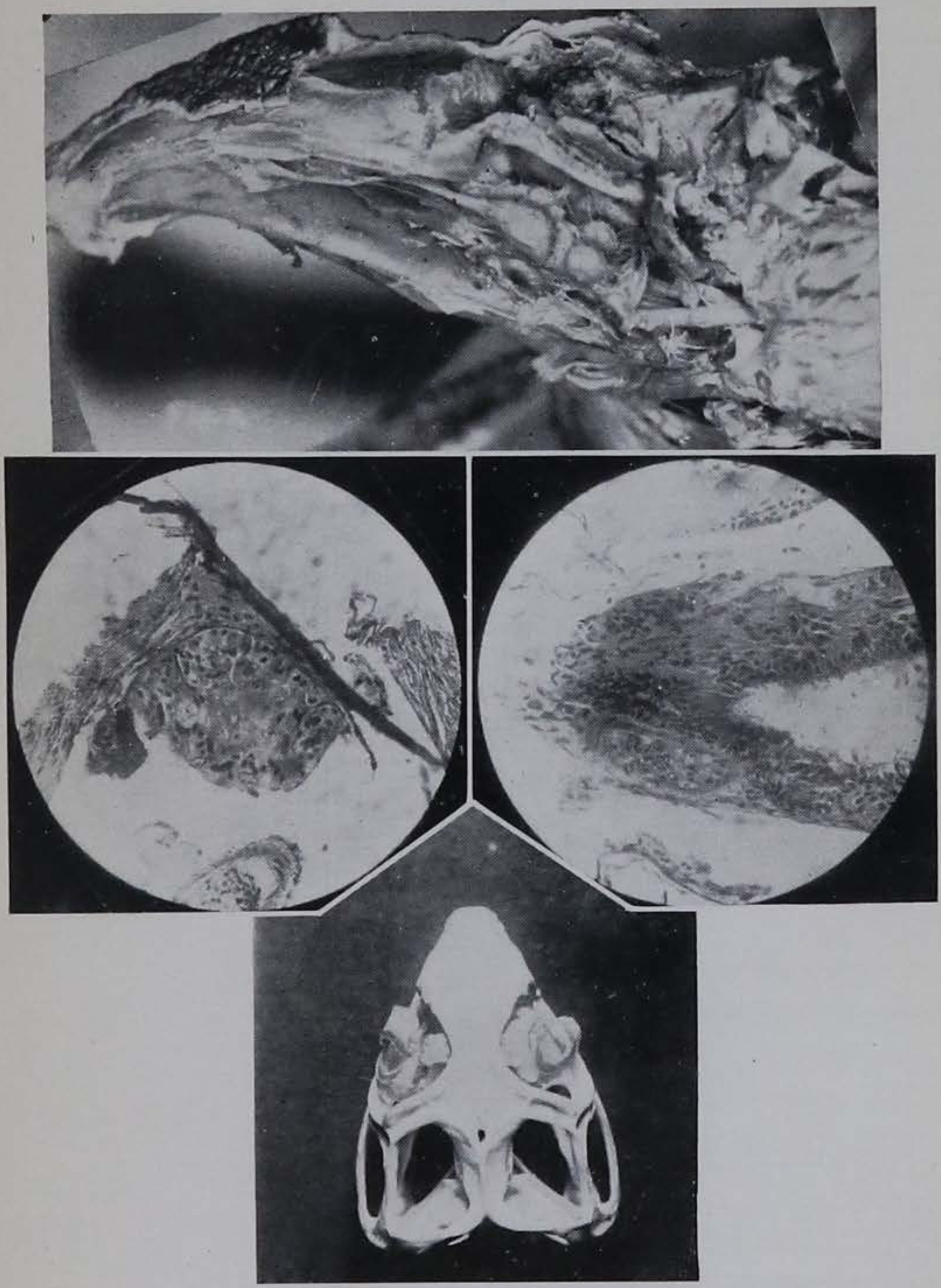


PLATE II

Fig. 1. Adult brain of Sphenodon, lateral view.

Fig. 2. Adult brain of Sphenodon, dorsal view.

Fig. 3. Adult brain of Sphenodon, ventral view.

ABBREVIATIONS

c.	cerebellum
d.	diencephalon
f. l. m.	fasciculus longitudinalis medialis
f. v.	fourth ventricle
h.	hypophysis
iii.	third nerve
iv.	fourth nerve
ix.	ninth nerve
inf.	infundibulum
mes.	mesencephalon
met.	metencephalon
m. o.	medulla oblongata
o. b.	olfactory bulb
op. c.	optic chiasma
op. t.	optic tract
o. t.	olfactory tract
p.	paraphysis
p. s.	pineal sac
t.	telencephalon
v.	fifth nerve
vi.	sixth nerve
vii.	seventh nerve
viii.	eighth nerve
xi.	eleventh nerve
xii.	twelfth nerve

PLATE II

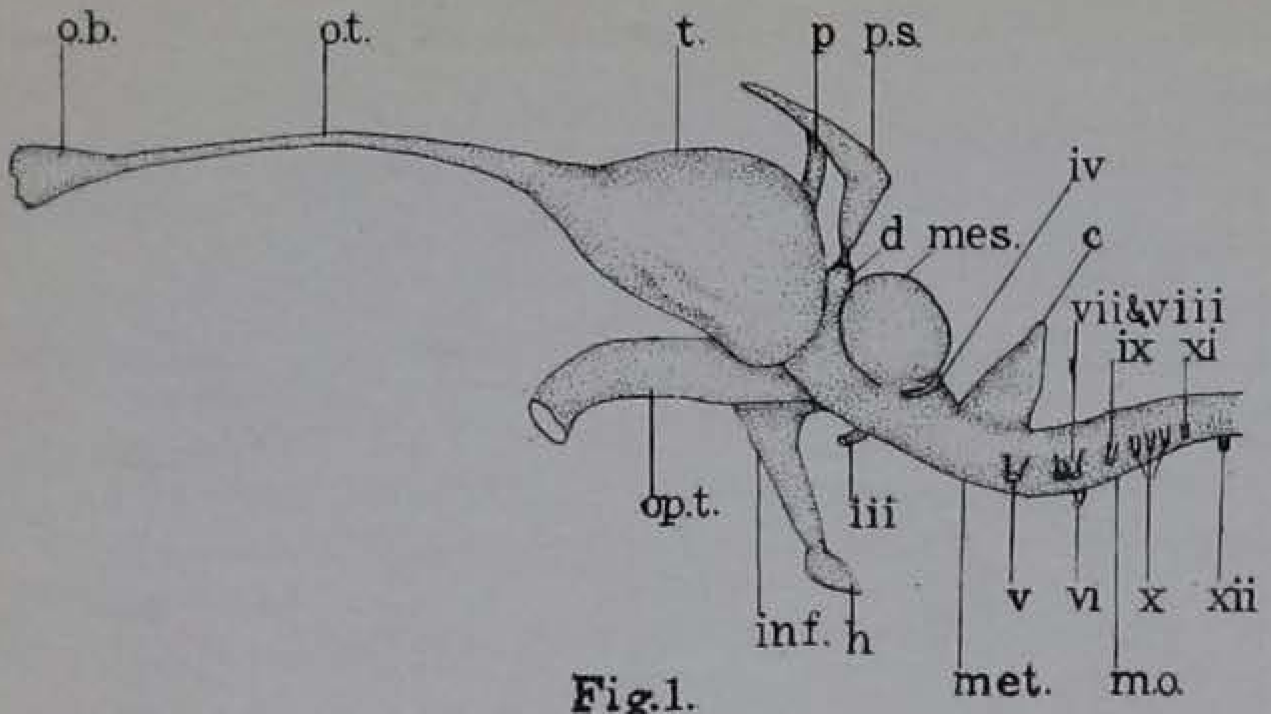
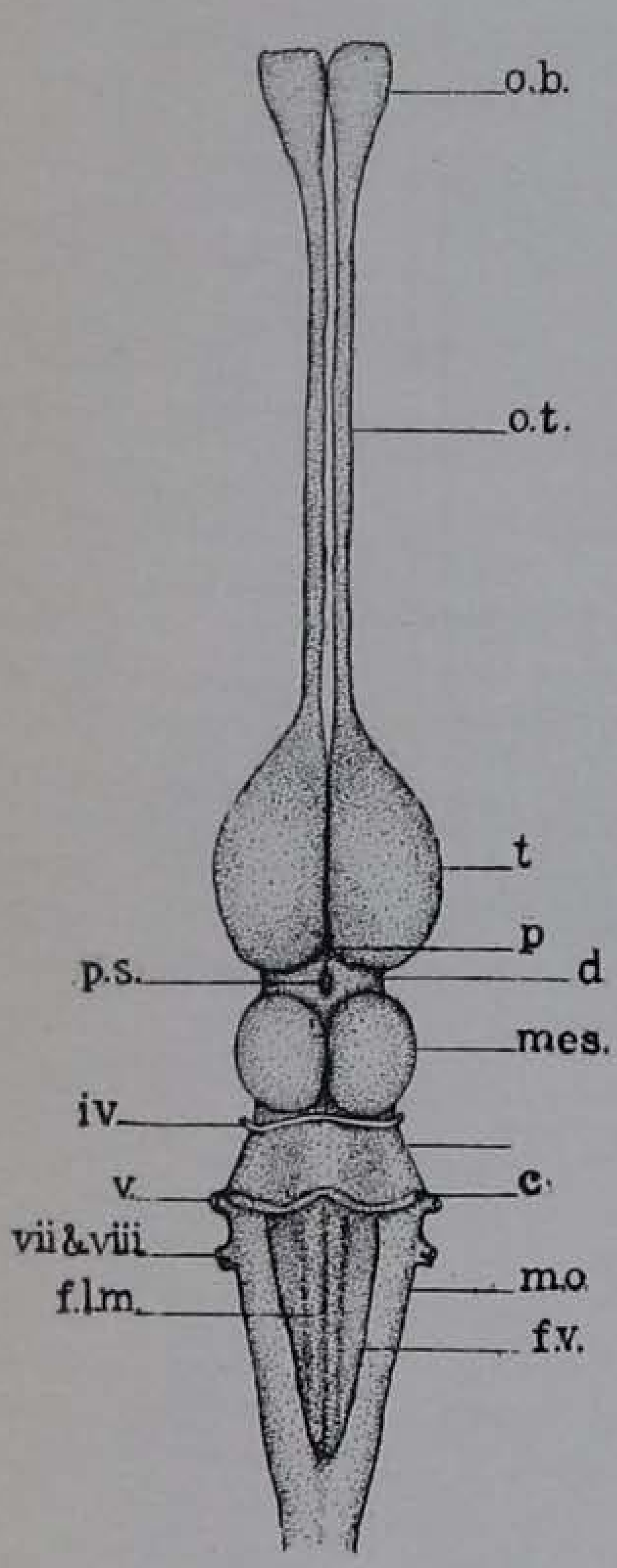


Fig. 1.



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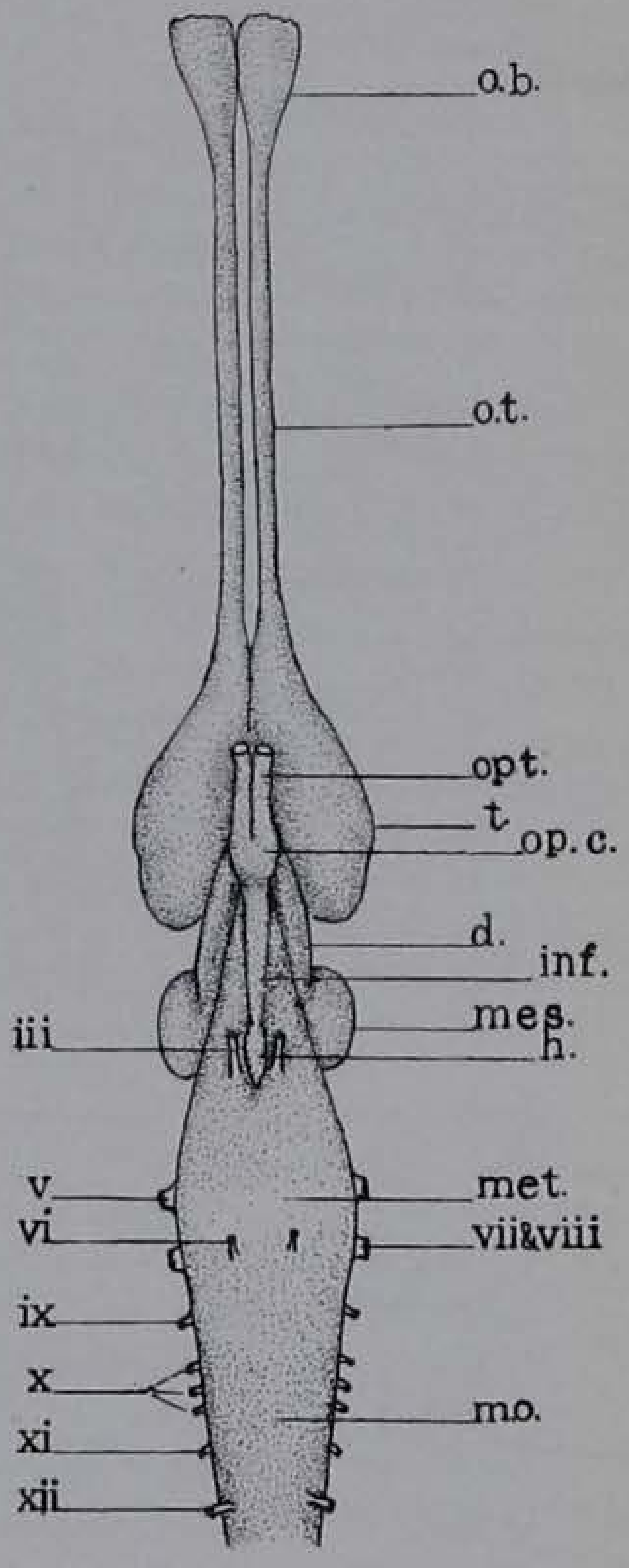


Fig. 3.

PLATE III

Fig. 4. Transverse section through a transitional level between spinal cord and medulla oblongata.

Fig. 5. Transverse section at the level of the calamus scriptorius, medulla oblongata.

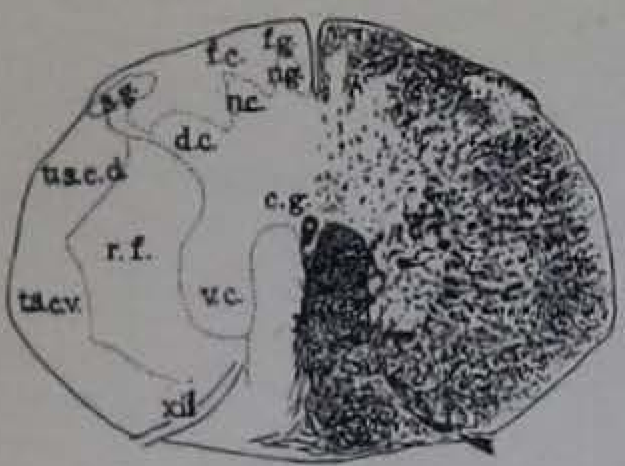
Fig. 6. Transverse section at the level of the tenth nerve, medulla oblongata.

Fig. 7. Transverse section at the level of the eighth nerve, medulla oblongata.

Fig. 8. Transverse section at the level of the seventh nerve, medulla oblongata.

ABBREVIATIONS

c. g.	central gray matter
d. c.	dorsal cell column
f. c.	fasciculus cuneatus
f. g.	fasciculus gracilis
f. l. m.	fasciculus longitudinalis medialis
i. a. f.	internal arcuate fibers
l. l.	lateral lemniscus
m. l.	medial lemniscus
n. c.	nucleus cuneatus
n. & f. s.	nucleus and fasciculus solitarius
n. g.	nucleus gracilis
n. vi.	nucleus of sixth nerve
r. f.	reticular formation
r.	raphe
s. g.	substantia gelatinosa
s. m. a.	striæ medullares acusticæ
s. o.	superior olive
t. s. c. d.	tractus spino-cerebellaris dorsalis
t. s. c. v.	tractus spino-cerebellaris ventralis
t. t. s.	tractus tecto-spinalis
v. c.	ventral cell column
vi.	sixth nerve
vii a.	afferent root of the seventh nerve
vii e.	efferent root of the seventh nerve
viii c.	cochlear part of the eighth nerve
viii v.	vestibular part of the eighth nerve
xii.	twelfth nerve



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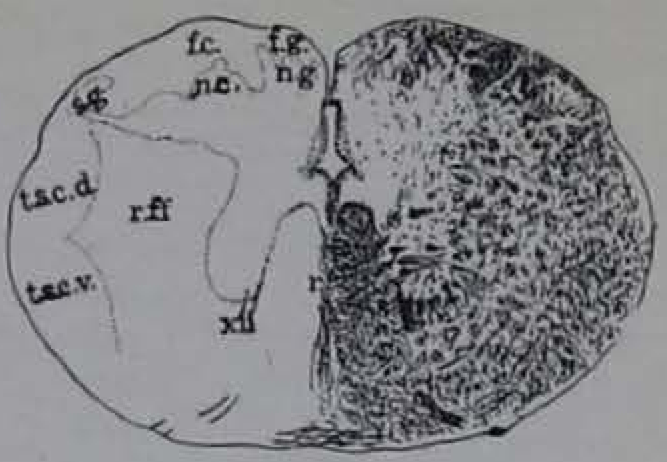

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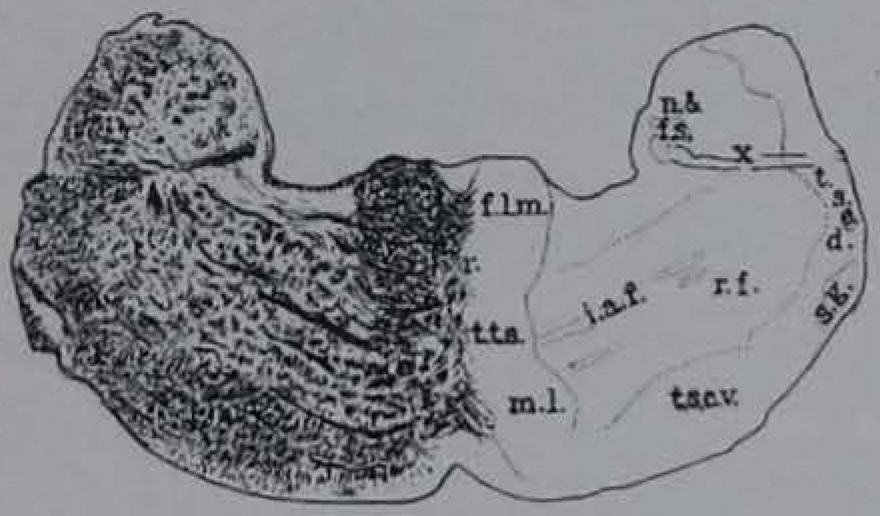

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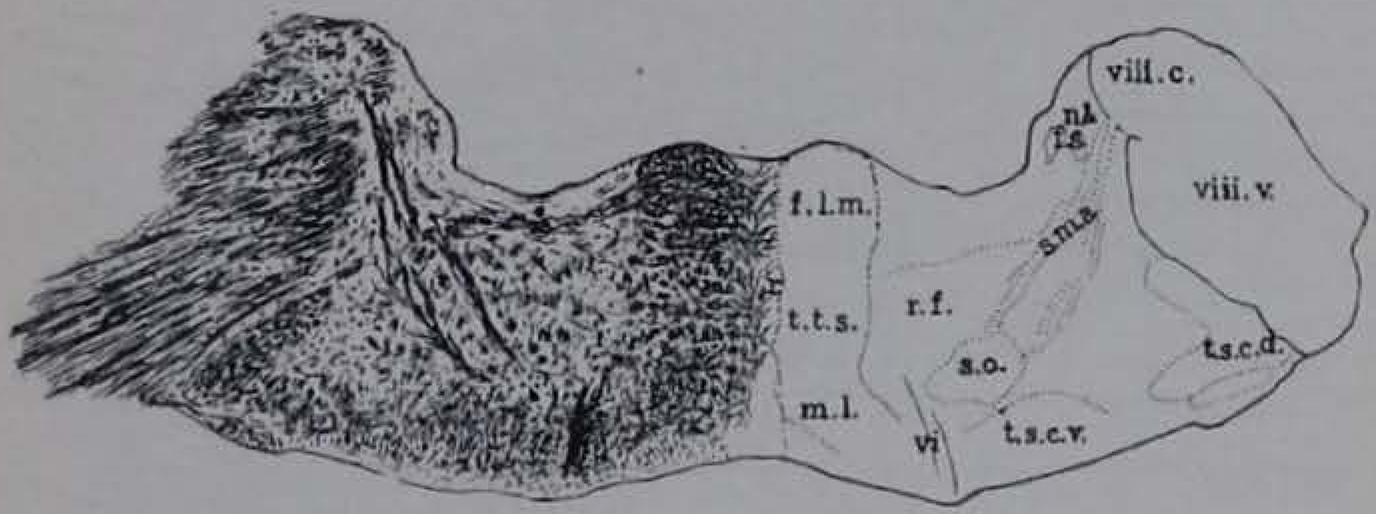

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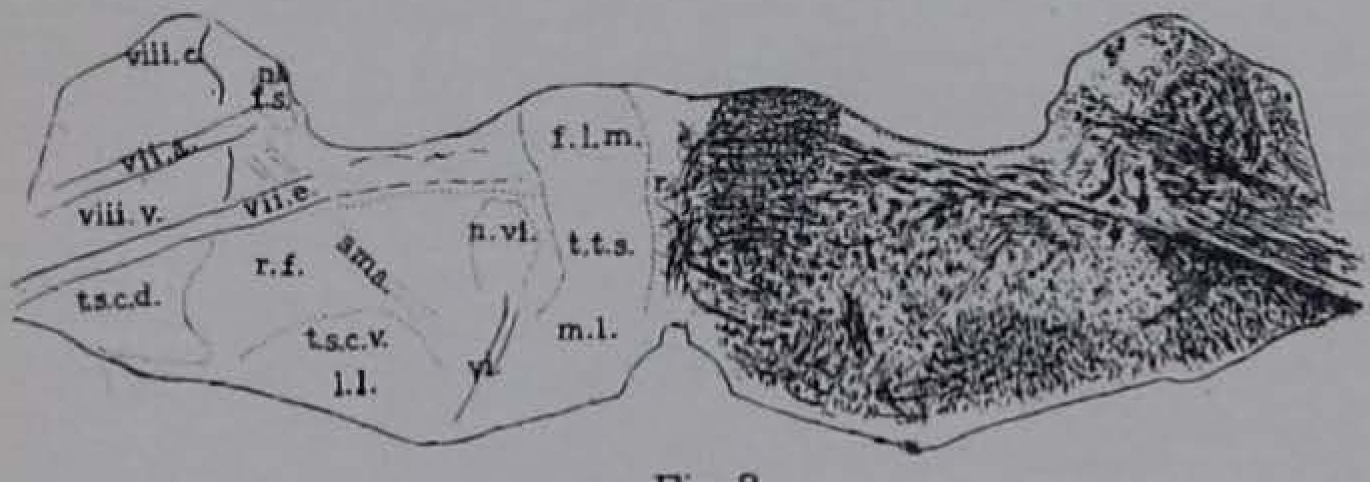


Fig. 8.

PLATE IV

Fig. 9. Transverse section through the medulla oblongata at the level of the fifth nerve.

Fig. 10. Transverse section through the posterior part of the metencephalon.

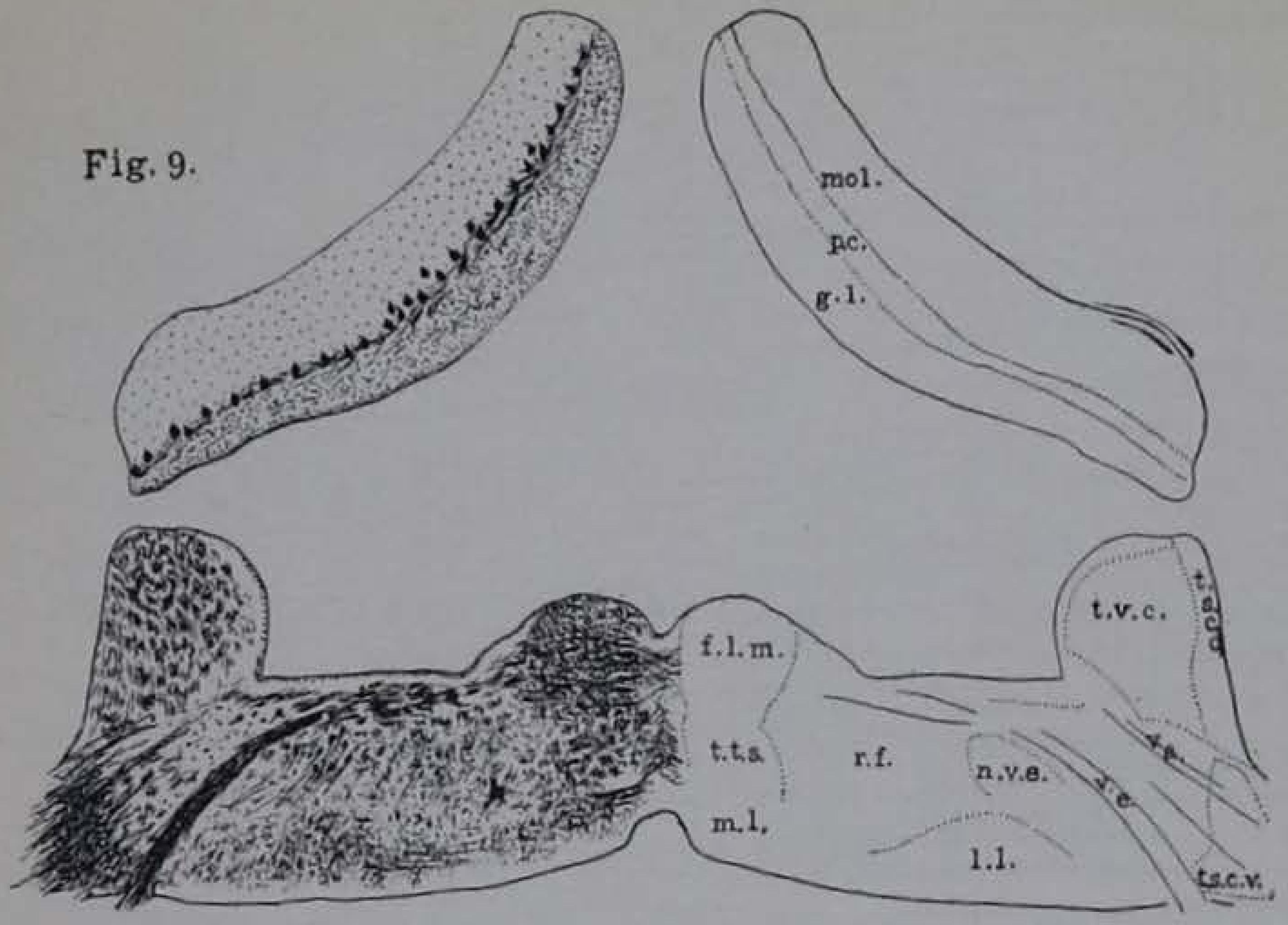
Fig. 11. Transverse section through the anterior part of the metencephalon.

ABBREVIATIONS

f. l. m.	fasciculus longitudinalis medialis
g. l.	granular layer
l. l.	lateral lemniscus
m. l.	medial lemniscus
mol.	molecular layer
n. v. e.	nucleus of the efferent root of the fifth nerve
p. c.	layer of Purkinje cells
r. f.	reticular formation
t. s. c. d.	tractus spino-cerebellaris dorsalis
t. s. c. v.	tractus spino-cerebellaris ventralis
t. t. s.	tractus tecto-spinalis
t. v. c.	tractus vestibulo-cerebellaris
v. a.	afferent root of the fifth nerve
v. e.	efferent root of the fifth nerve

PLATE IV

Fig. 9.



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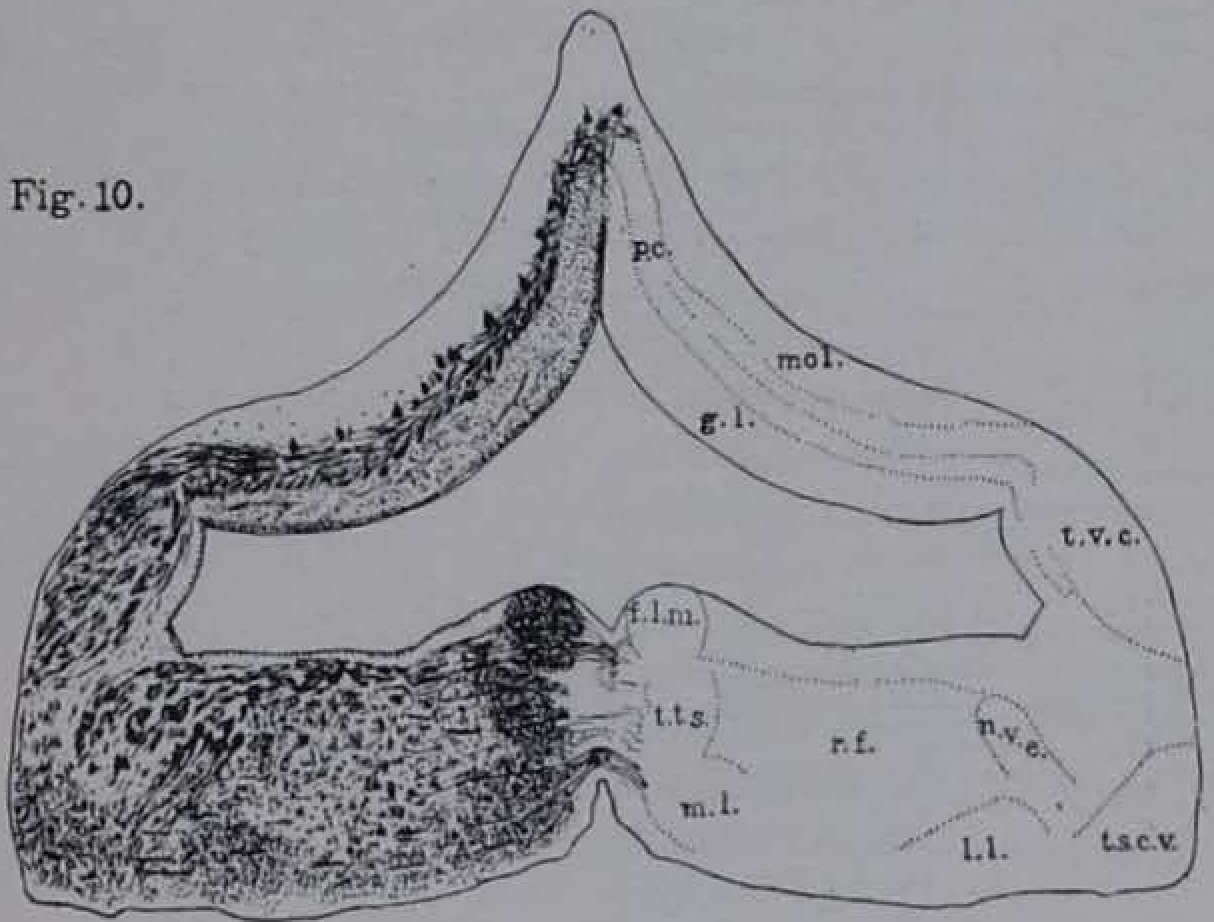

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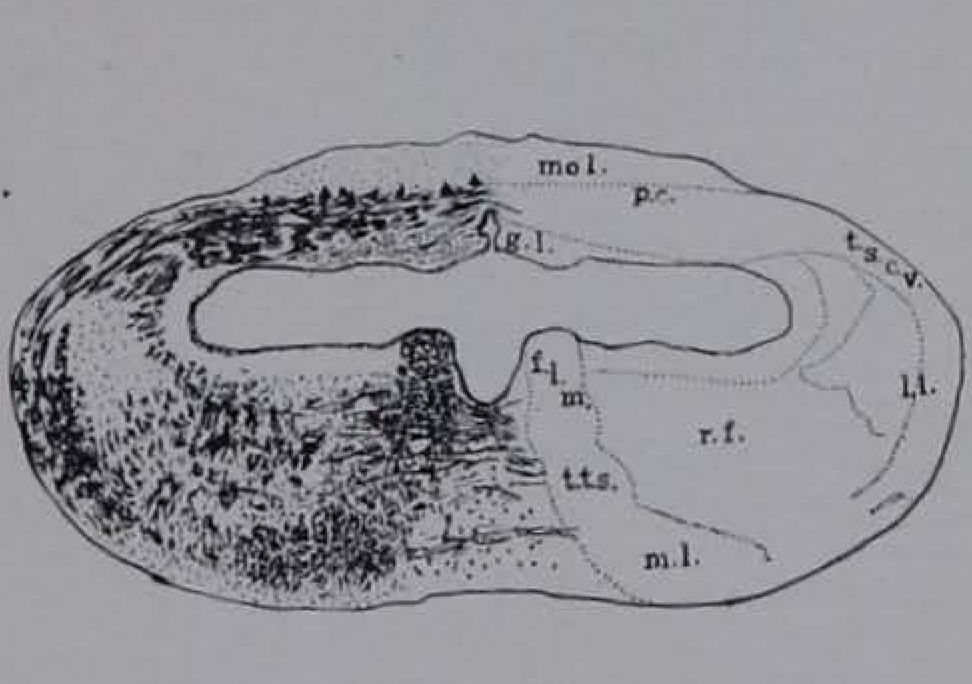


PLATE V

Fig. 12. Transverse section through the isthmus at the level of the fourth nerve and the nucleus isthmi.

Fig. 13. Transverse section at a transitional level between the isthmus and the mesencephalon.

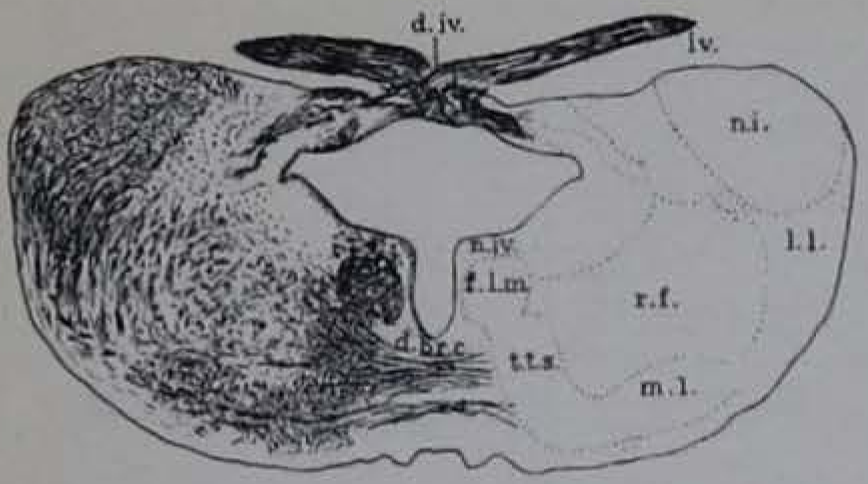
Fig. 14. Transverse section through the posterior part of the mesencephalon.

Fig. 15. Transverse section through the mesencephalon a little anterior to that shown in Fig. 14.

ABBREVIATIONS

br. c.	brachium conjunctivum
d. br. c.	decussation of brachium conjunctivum
d. iv.	decussation of the fourth nerve
f. l. m.	fasciculus longitudinalis medialis
i. c.	inferior colliculus
iv.	fourth nerve
l. l.	lateral lemniscus
m. l.	medial lemniscus
n. i.	nucleus isthmi
n. iv.	nucleus of fourth nerve
n. r.	nucleus ruber
op. t.	optic tract
r. f.	reticular formation
st. op.	stratum opticum
st. med.	stratum medullare profundum
t. n. i.	tract from the nucleus isthmi
t. t. s.	tractus tecto-spinalis

PLATE V



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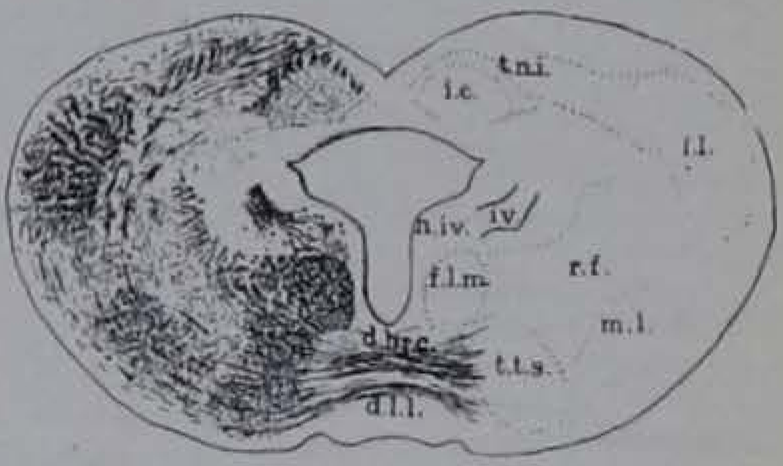

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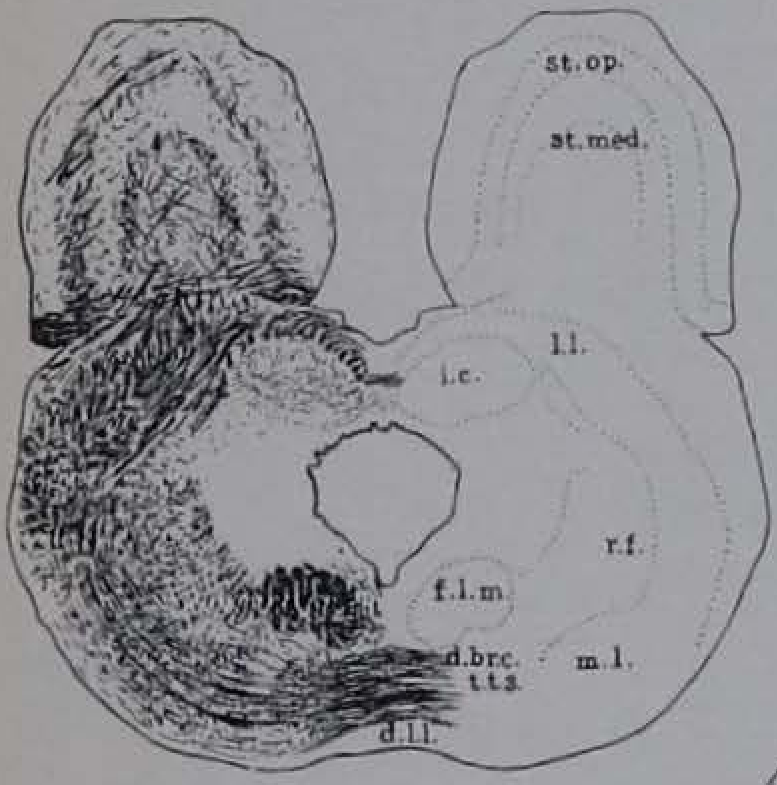

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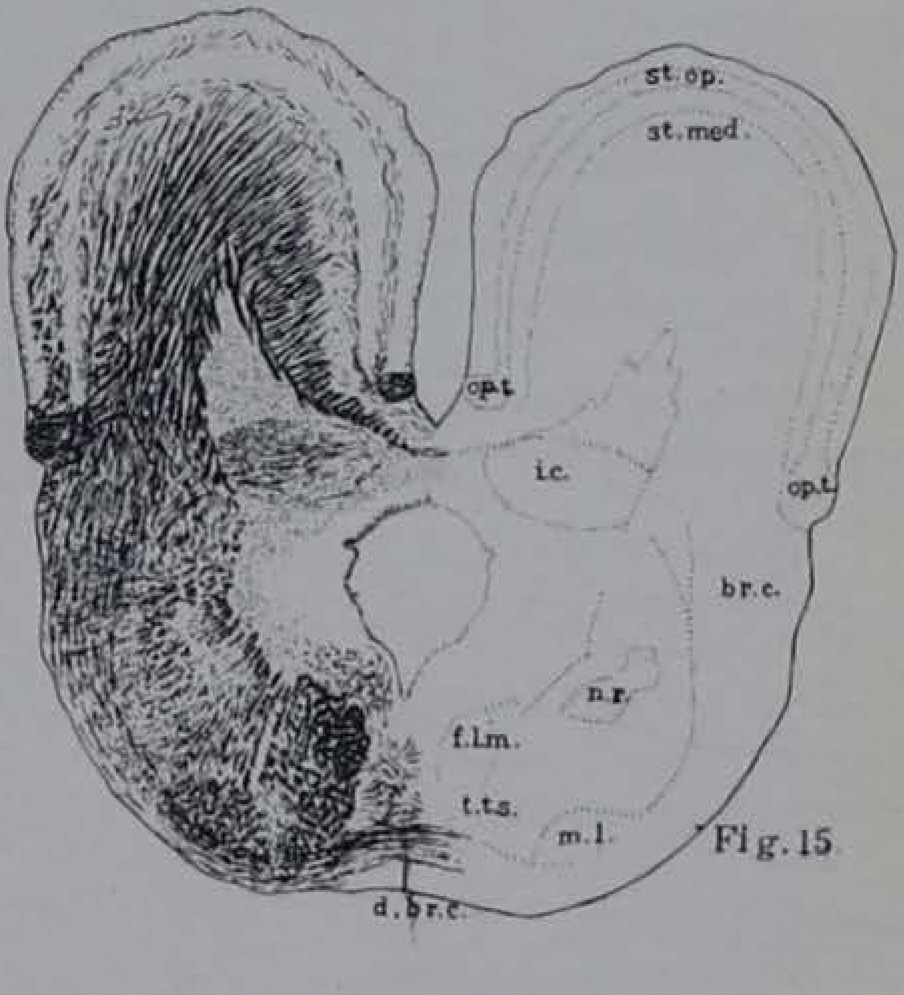


Fig. 15

PLATE VI

Fig. 16. Transverse section through the mesencephalon at the level of the third nerve.

Fig. 17. Transverse section at a transitional level between the mesencephalon and the diencephalon. The posterior commissure is most prominent.

Fig. 18. Transverse section through the posterior part of the diencephalon.

ABBREVIATIONS

d. c. c.	decussation of the superior colliculus
d. s. i.	decussation suprainfundibularis
f. l. m.	fasciculus longitudinalis medialis
i. c.	inferior colliculus
iii.	third nerve
inf.	infundibulum
l. f. b.	lateral forebrain bundle
m. l.	medial lemniscus
m. f. b.	median forebrain bundle
n. iii.	nucleus of the third nerve
n. p.	nucleus pretectalis
op. t.	optic tract
p. c.	posterior commissure
r. f.	reticular formation
st. op.	stratum opticum
st. med.	stratum medullare profundum
t. a.	tractus tecto-thalamicus cruciatus, pars anterior
teg. d.	tegmental decussation
t. h. p.	tractus habenulo-peduncularis
t. m. t.	tractus mammillo-thalamicus
t. p.	tractus tecto-thalamicus cruciatus, pars posterior
t. t. t.	tractus tecto-thalamicus

PLATE VI

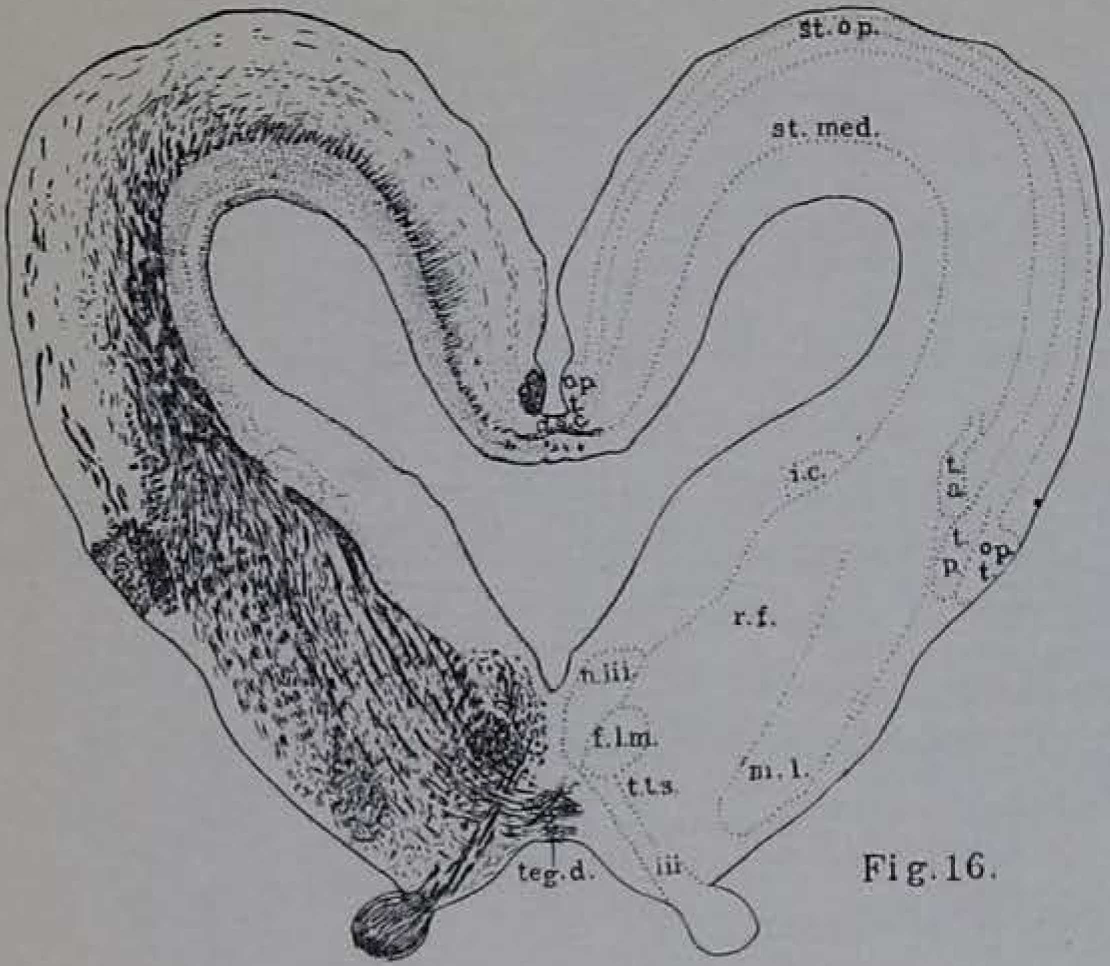
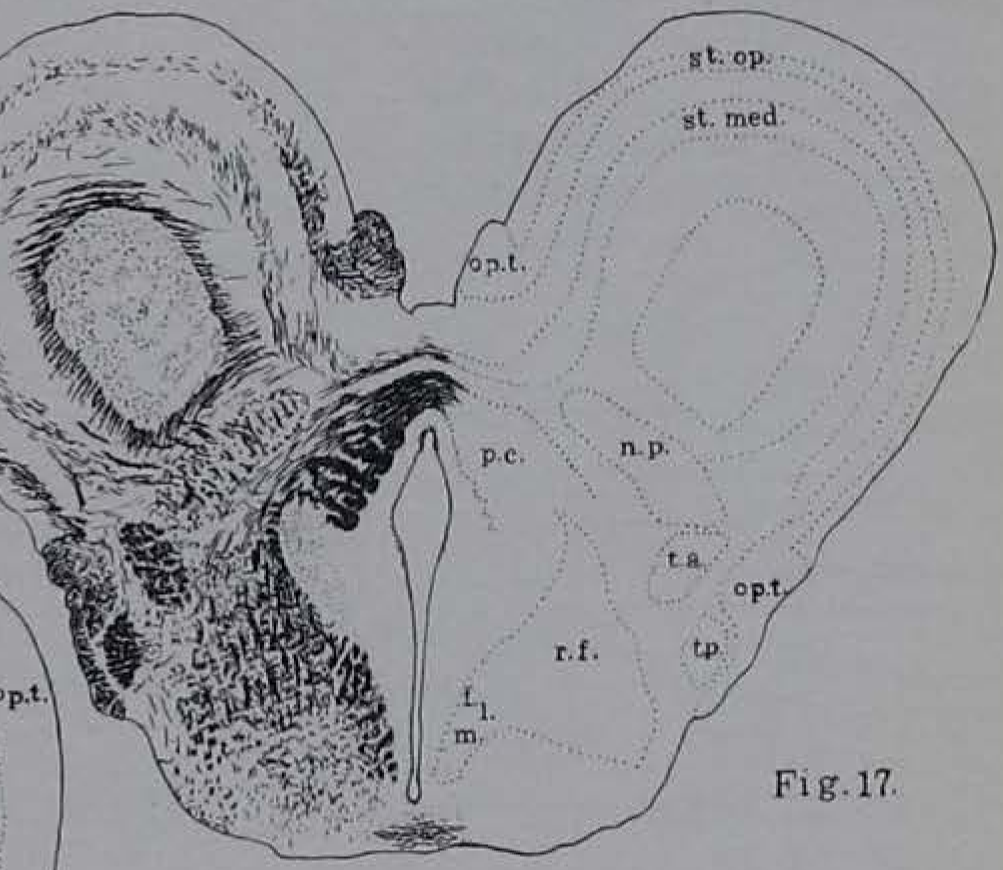


Fig.16.



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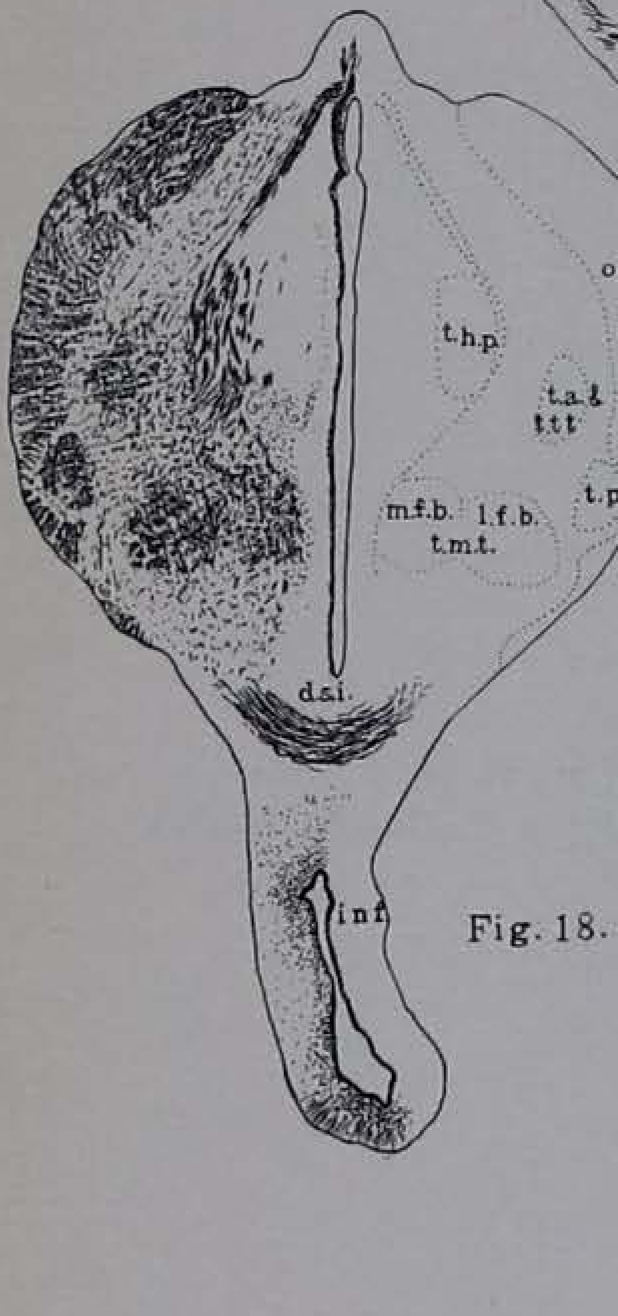


Fig. 18.

PLATE VII

Fig. 19. Transverse section through the diencephalon at the level of the habenular commissure.

Fig. 20. Transverse section through the diencephalon a little anterior to the section shown in Fig. 19. The tractus strio-thalamicus is very conspicuous in Fig. 20.

Fig. 21. Transverse section through the posterior part of the telencephalon and the anterior part of the diencephalon to show the close relationship of the cortex and the striæ medullares.

ABBREVIATIONS

a.	alveus
f.	fornix
g. p.	general pallium
h. c.	habenular commissure
ht.	nucleus of the hypothalamus
l. f. b.	lateral forebrain bundle
m. f. b.	median forebrain bundle
n. d. l. a.	nucleus dorsolateralis anterior
n. h.	nucleus habenula
n. r.	nucleus rotundus
n. v. m.	nucleus ventromedialis
n. s.	neostriatum
ol. t.	olfactory projection tract
op. t.	optic tract
p. h.	primordium hippocampus
p. s.	pineal sac
s. m.	striæ medullares
t. a.	tractus tecto-thalamicus cruciatus, pars anterior
t. f.	tangential fibers
t. h. p.	tractus habenulo-peduncularis
t. m. t.	tractus mammillo-thalamicus
t. p.	tractus tecto-thalamicus cruciatus, pars posterior
t. s. t.	tractus strio-thalamicus (lateral forebrain bundle)

PLATE VII

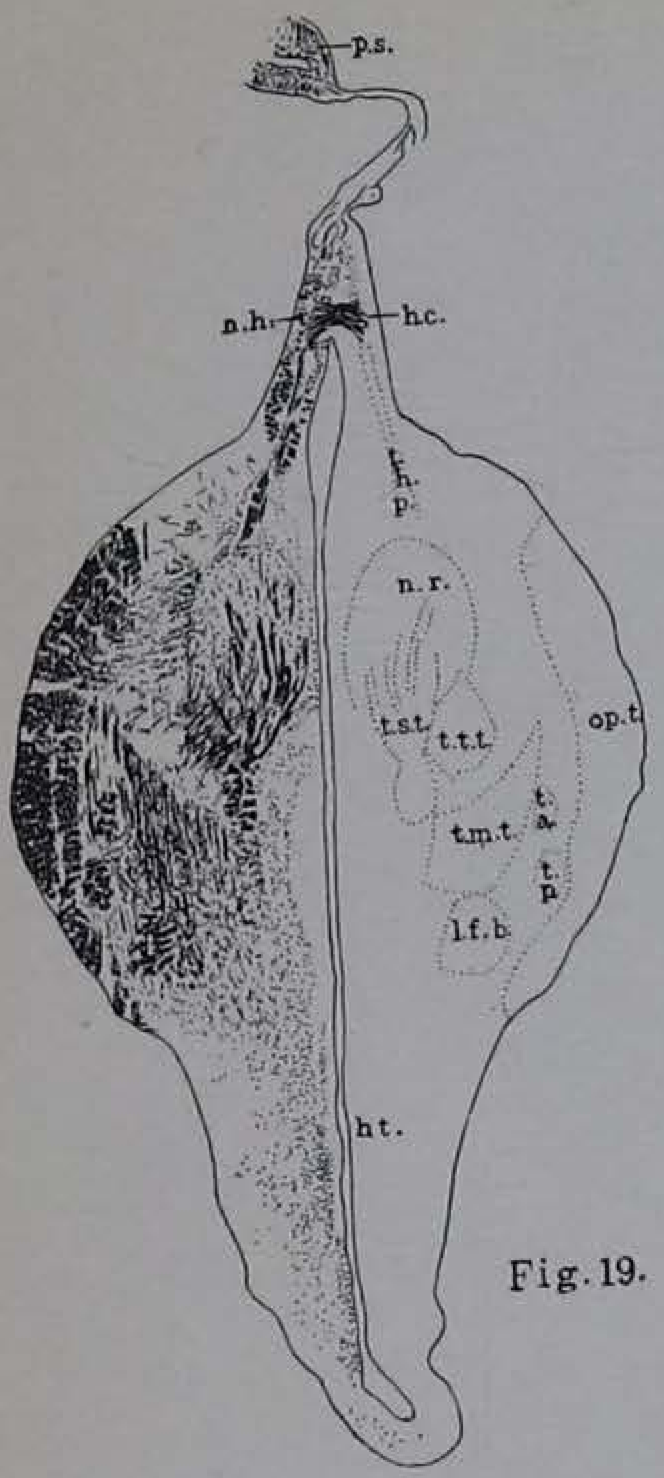
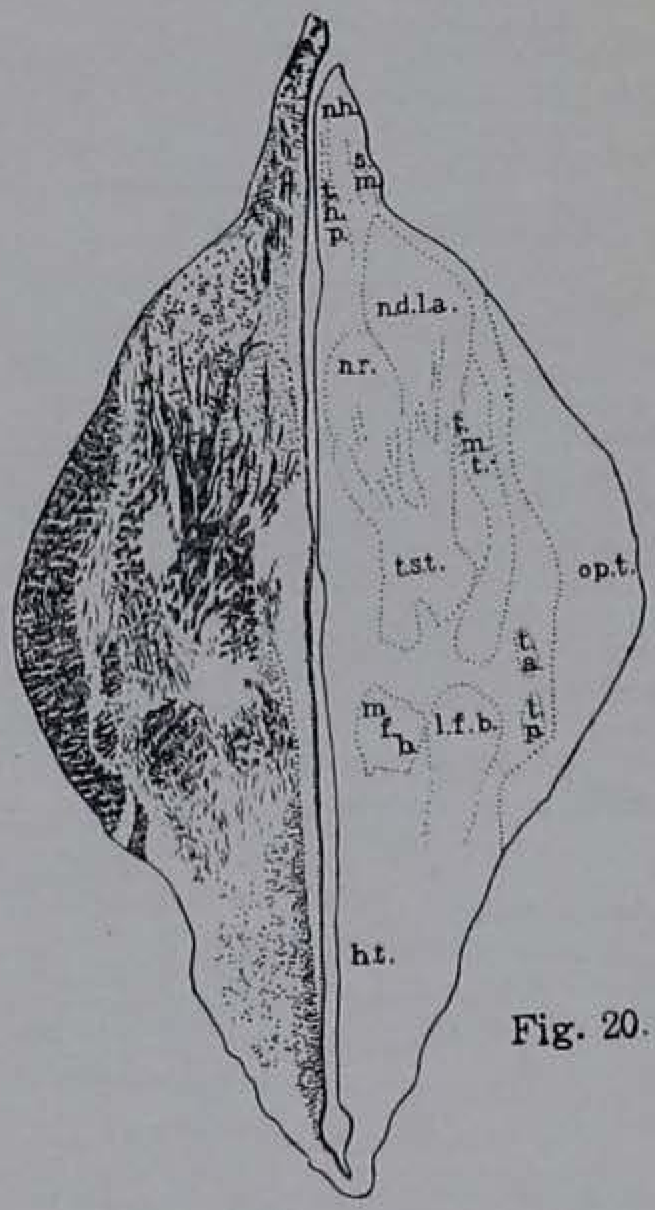


Fig. 19.



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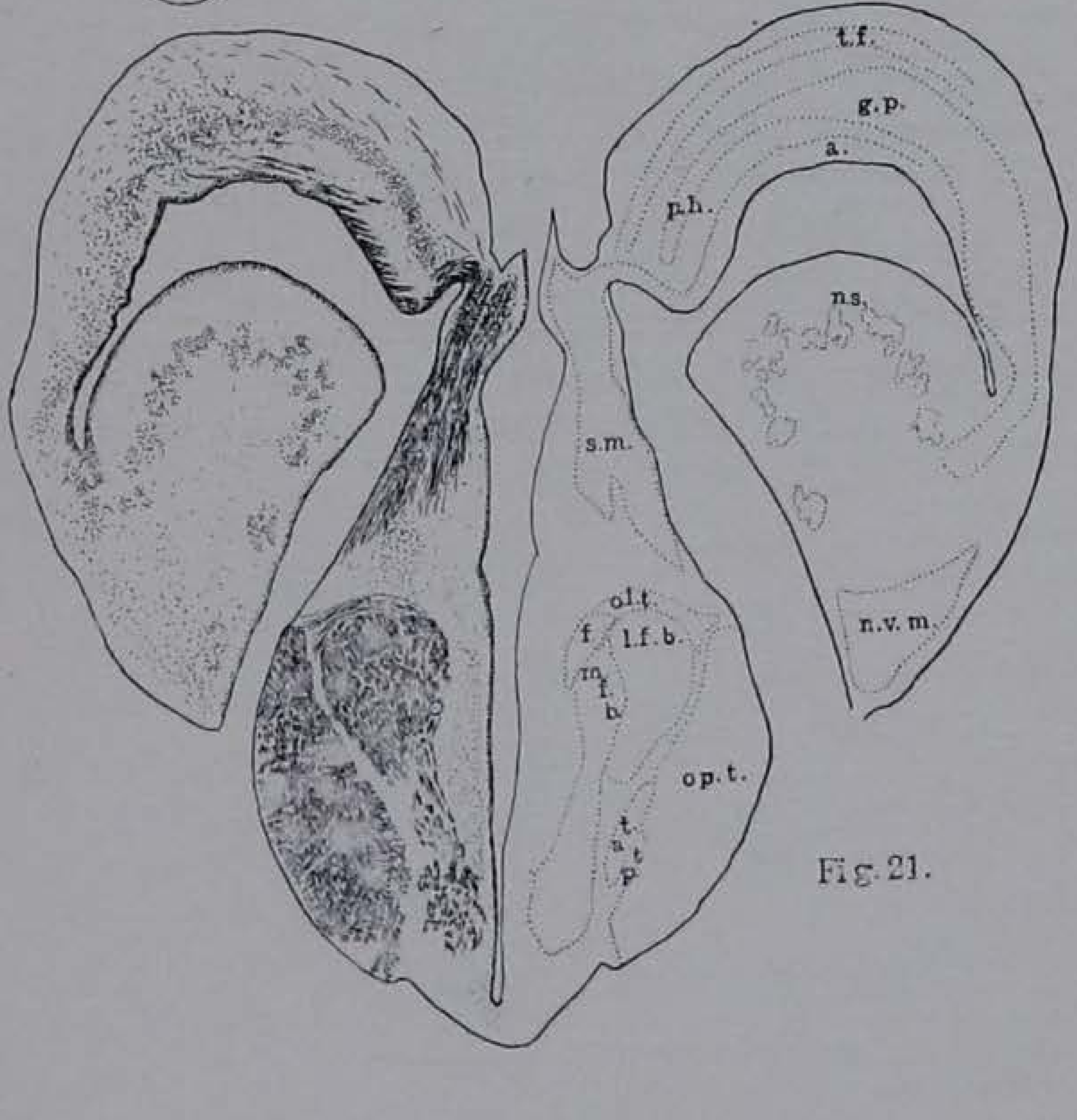


Fig. 21.

PLATE VIII

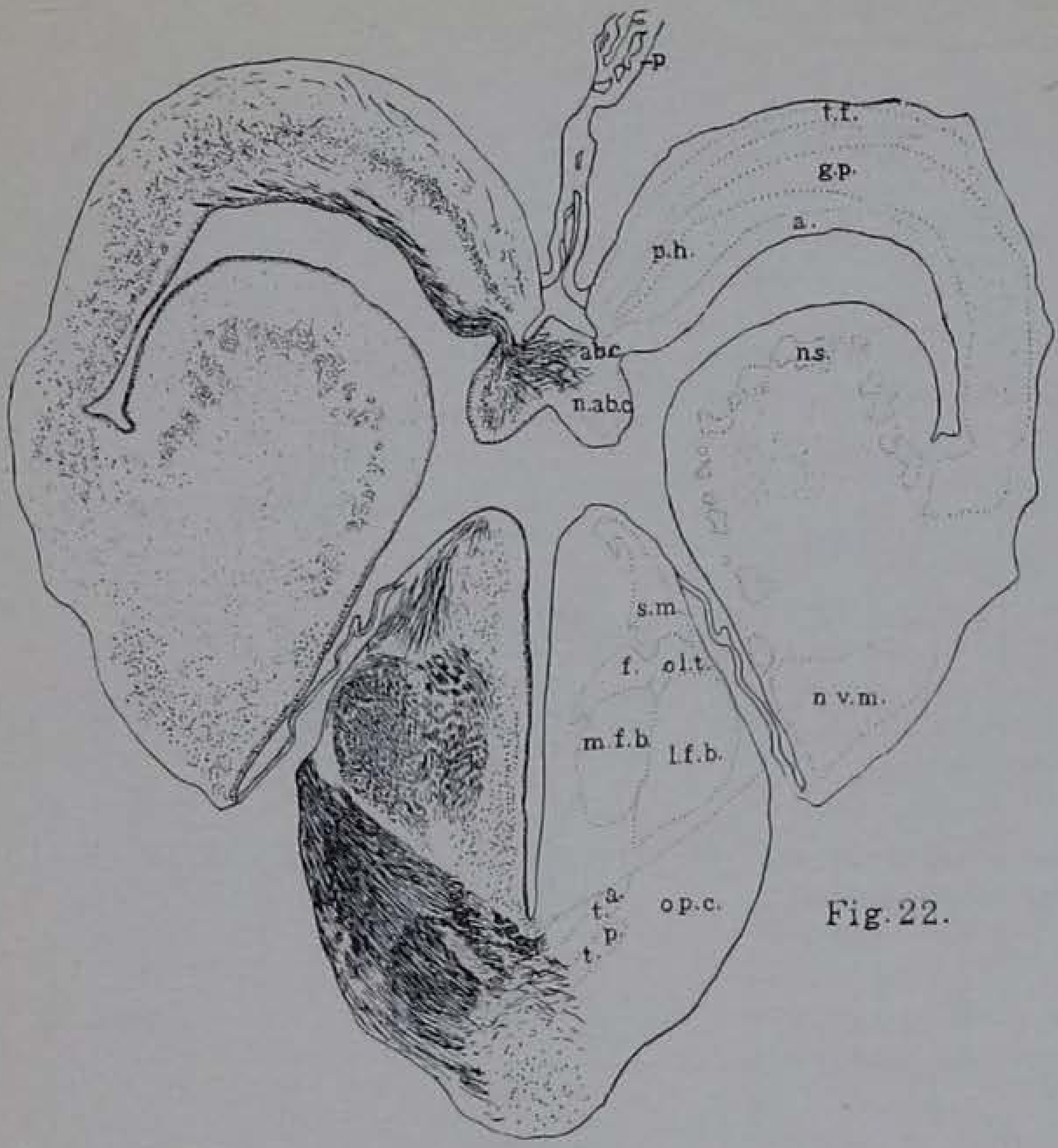
Fig. 22. Transverse section through the telencephalon and the diencephalon a little anterior to the section in Fig. 21. Fig. 22 shows a section at the level of the aberrant commissure.

Fig. 23. Transverse section through the telencephalon just anterior to the aberrant commissure, and the diencephalon, to show the olfactory projection tract.

ABBREVIATIONS

a.	alveus
ab. c.	aberrant commissure
f.	fornix
fi.	fimbria
g. p.	general pallium
l. f. b.	lateral forebrain bundle
m. f. b.	median forebrain bundle
n. ab. c.	nucleus of aberrant commissure
n. s.	neostriatum
n. v. m.	nucleus ventromedialis
ol. t.	olfactory projection tract
op. c.	optic chiasma
p. h.	primordium hippocampus
s. m.	striæ medullares
t. a.	tractus tecto-thalamicus cruciatus, pars anterior
t. f.	tangential fibers

PLATE VIII



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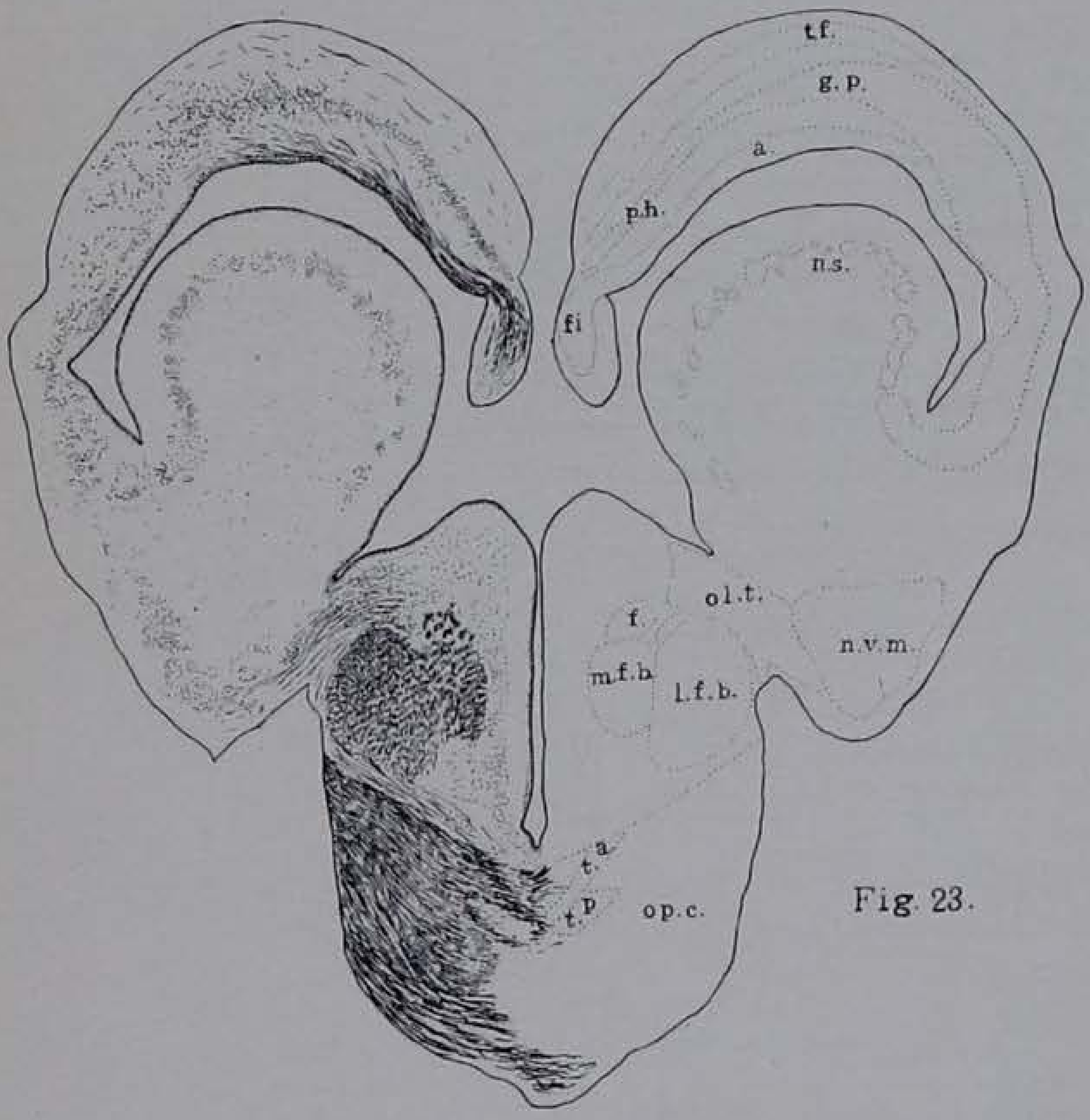


Fig. 23.

PLATE IX

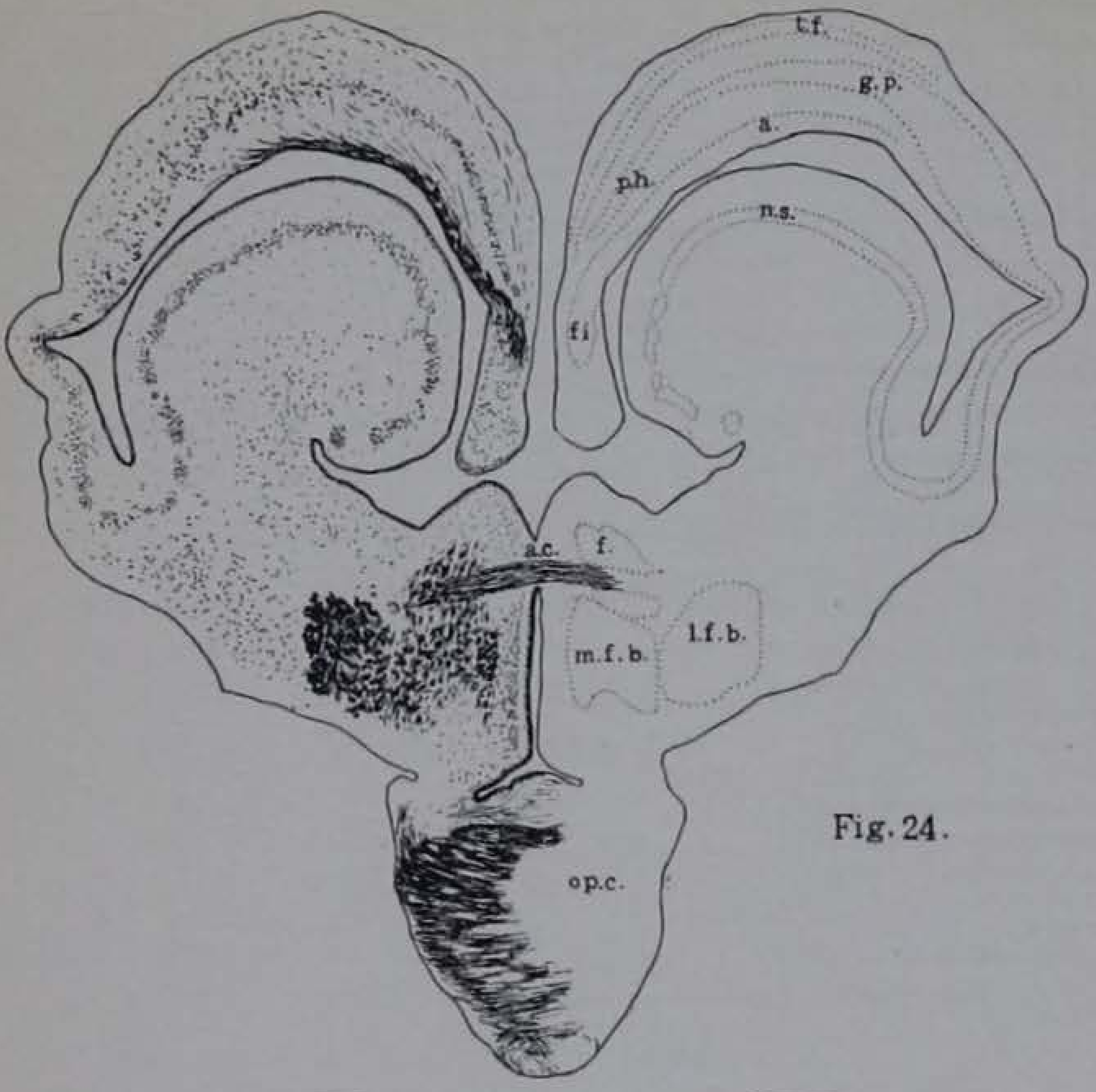
Fig. 24. Transverse section through the telencephalon at the level of the anterior commissure.

Fig. 25. Transverse section through the telencephalon at the level of the hippocampal commissure.

ABBREVIATIONS

a.	alveus
a. c.	anterior commissure
f.	fornix
fi.	fimbria
g. p.	general pallium
h. c.	hippocampal commissure
l. f. b.	lateral forebrain bundle
m. f. b.	median forebrain bundle
n. s.	neostriatum
op. c.	optic chiasma
p. h.	primordium hippocampus
t. f.	tangential fibers

PLATE IX



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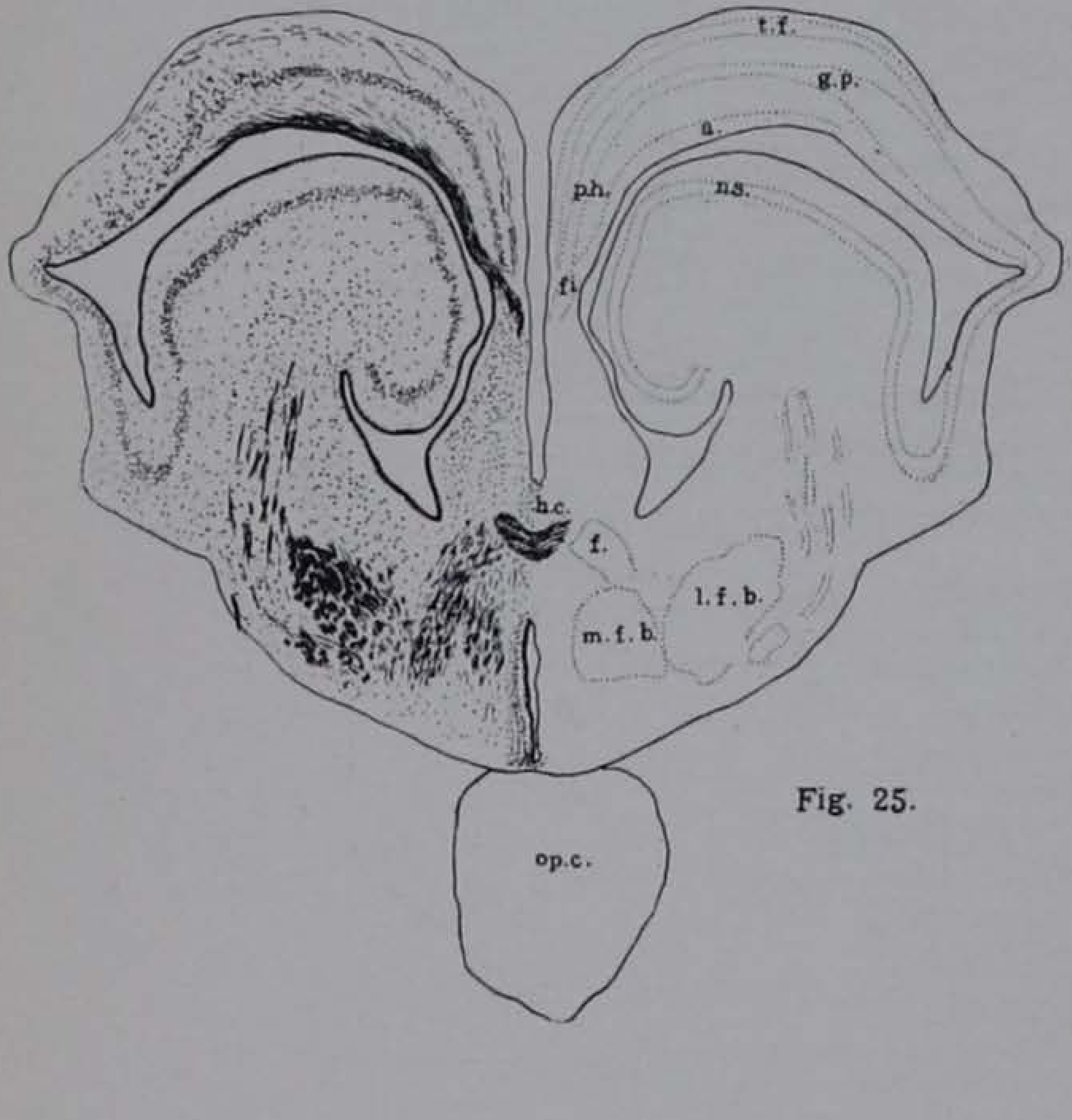


Fig. 25.

PLATE X

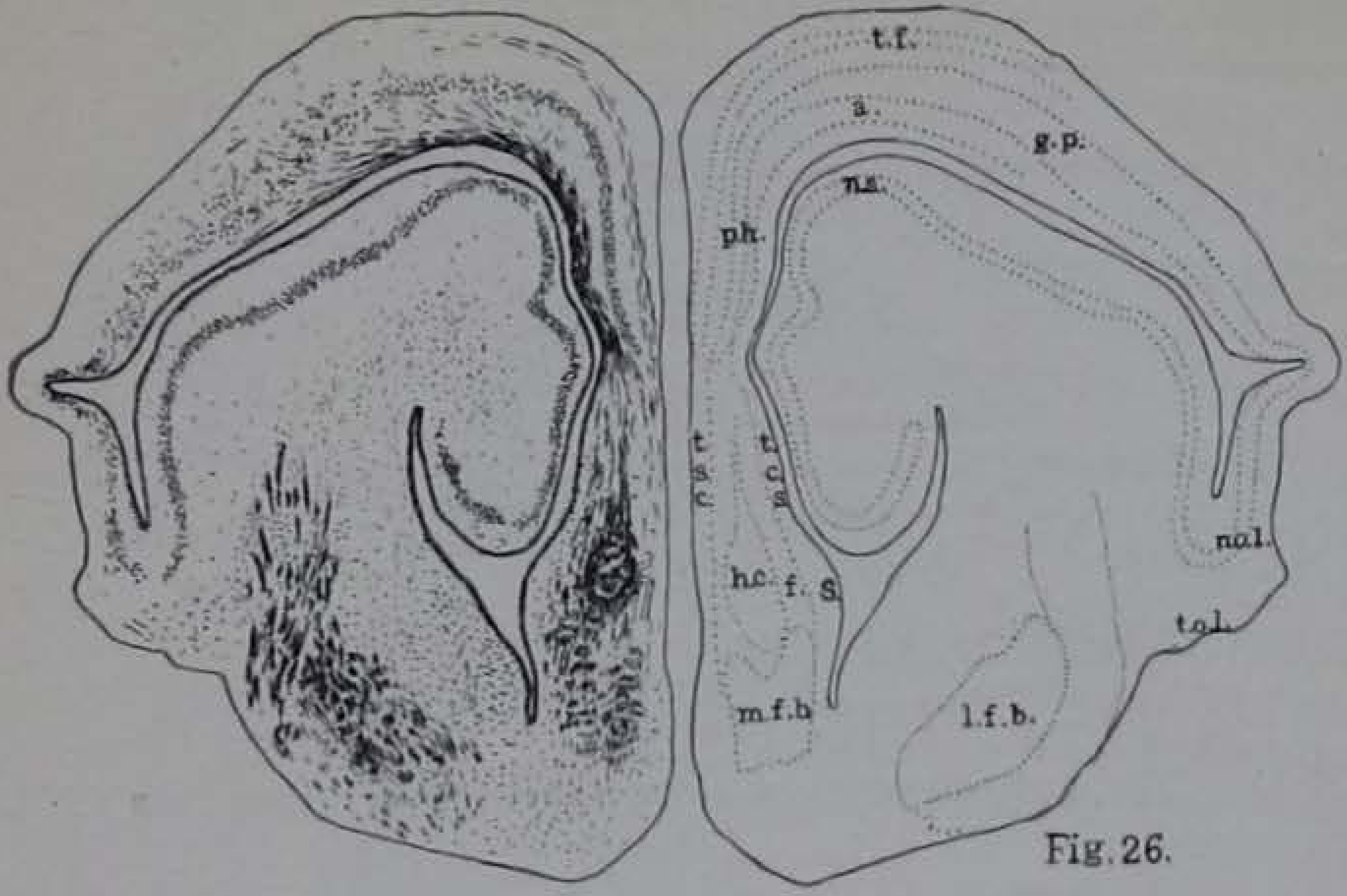
Fig. 26. Transverse section through the telencephalon anterior to the hippocampal commissure.

Fig. 27. Transverse section through the anterior part of the telencephalon.

Fig. 28. Transverse section through the telencephalon anterior to the section shown in Fig. 27.

ABBREVIATIONS

a.	alveus
f.	fornix
g.	glomeruli
g. p.	general pallium
h. c.	hippocampal commissure
i. g. l.	inner granular layer
l. f. b.	lateral forebrain bundle
l. o. a.	lateral olfactory area
m. f. b.	median forebrain bundle
m. c.	mitral cells
n. s.	neostriatum
n. o. l.	nucleus olfactorius lateralis
o. g. l.	outer granular layer
o. t.	olfactory tract
pal. s.	paleostriatum
p. h.	primordium hippocampus
s.	septum
t. c. s.	tractus cortico-septi
t. f.	tangential fibers
t. o. l.	tractus olfactorius lateralis
t. s. c.	tractus septo-corticalis
t. t. c.	tractus tuberculo-corticalis



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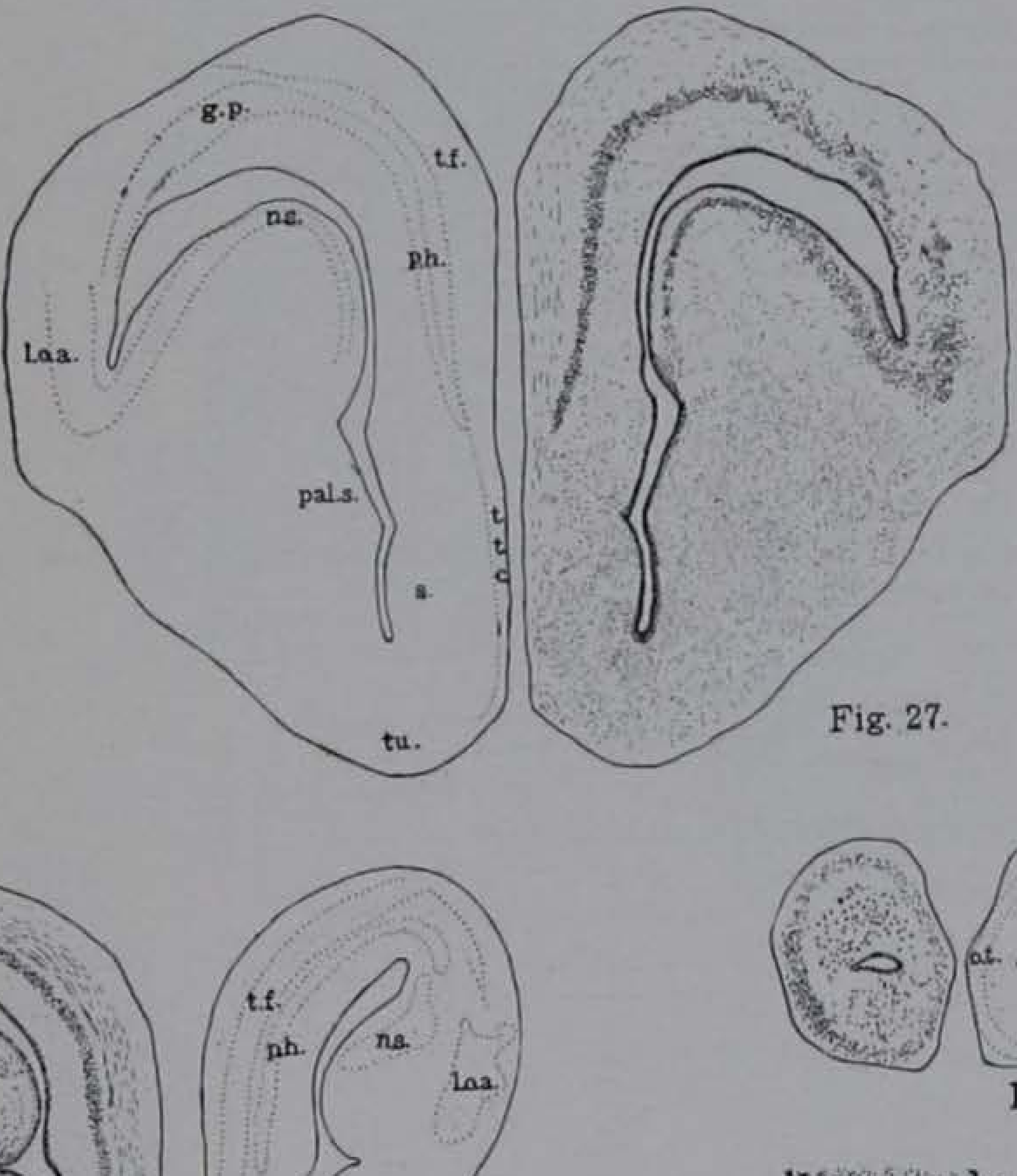

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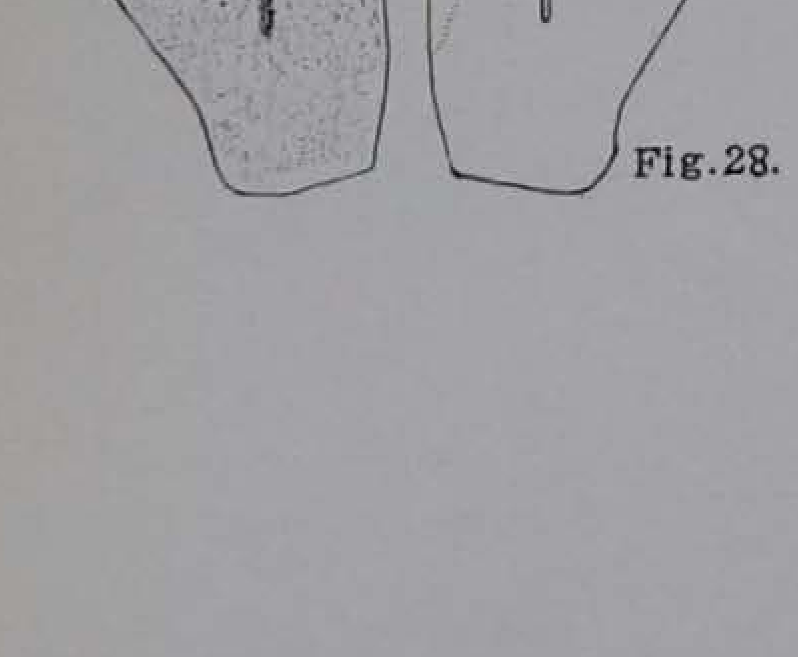

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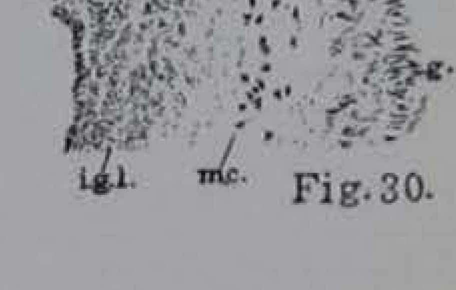


Fig. 29.

Fig. 30.

PLATE XI

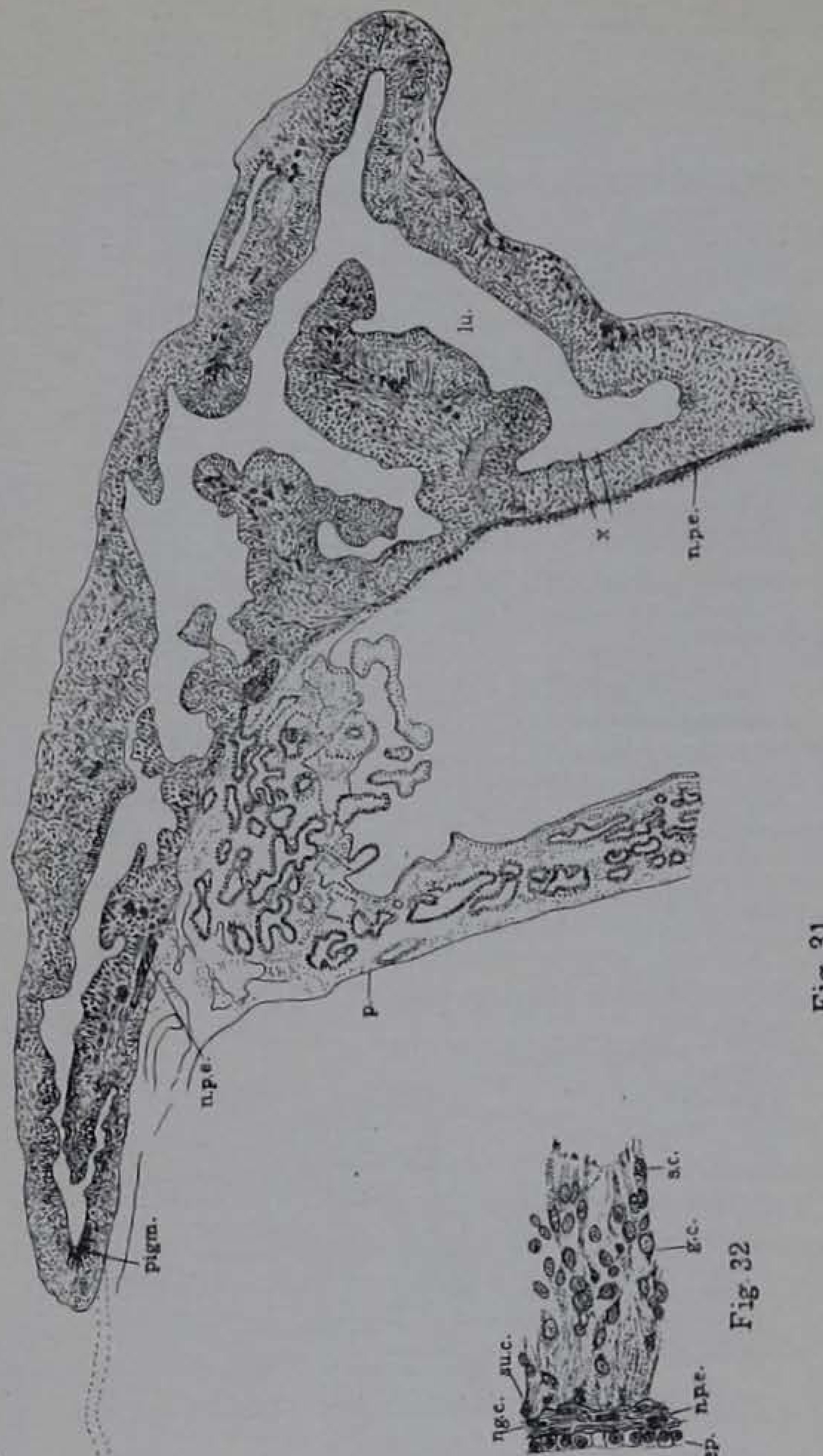
Fig. 31. Longitudinal, vertical section through the structures of the pineal region.

Fig. 32. A section through the wall of the pineal sac.

ABBREVIATIONS

x.	section drawn under high magnification in Fig. 32
ep.	epithelium
g. c.	ganglion cells
l.	lens of the pineal eye
lu.	lumen of the pineal sac
ng. c.	neuroglia cell
n. p. e.	nerve of the pineal eye
p.	paraphysis
pigm.	pigment cells at the distal extremity of the pineal sac
p. p.	parietal plug
r.	retina of the pineal eye
s. c.	sensory cell
su. c.	supporting cell

PLATE XI



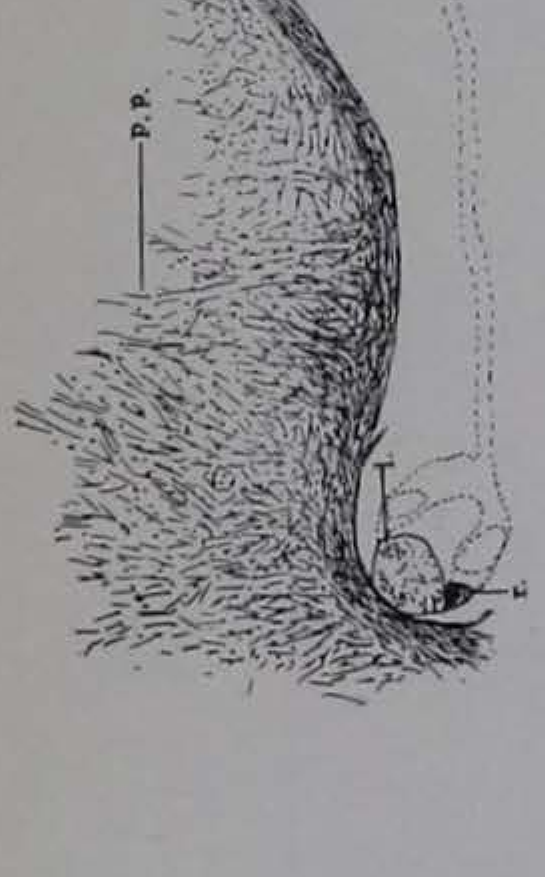


Fig 31.

Fig 32

PLATE XII

Fig. 33. Transverse section through the cerebellar cortex.

Fig. 34. Transverse section through the wall of the superior colliculus.

Fig. 35. Transverse section through the cortex of the general pallium.

Fig. 36. Longitudinal, vertical section through the lens and a part of the retina of the pineal eye.

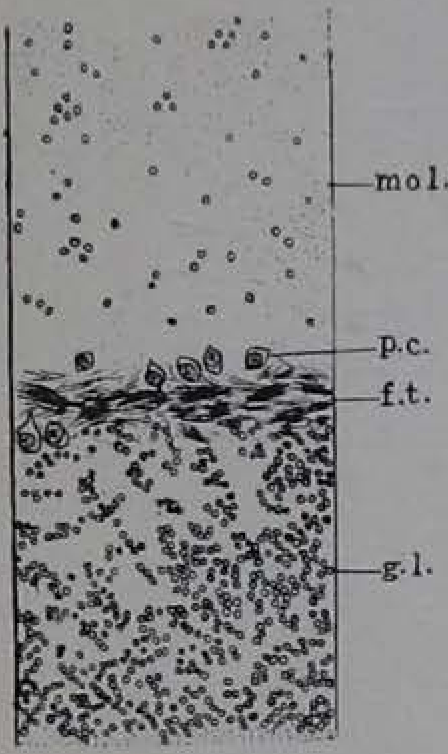
Fig. 38a. Transverse section through the pars nervosa and pars intermedia of the hypophysis.

Fig. 39b. Longitudinal, vertical section through the pars buccalis of the hypophysis.

ABBREVIATIONS

a.	alveus
e. l.	ependymal layer
e. p. i.	epithelium of the pars intermedia
e. p. n.	epithelium of the pars nervosa
eso.	eosinophiles of the pars buccalis
f. t.	fiber tracts
g. l.	granular layer
g. c.	ganglion cell
inf.	infundibulum
l.	lens of the pineal eye
mol.	molecular layer
n. c.	nerve cells
neu.	neutrophiles of the pars buccalis
p. c.	Purkinje cells
p. b.	pars buccalis
p. i.	pars intermedia
pigm.	pigment cells
p. n.	pars nervosa
py. c.	pyramidal cell
pi. c.	pigment cell
s. c.	sensory cell
st. op.	stratum opticum
st. med.	stratum medullare profundum
su. c.	supporting cell
t. f.	tangential fibers

PLATE XII



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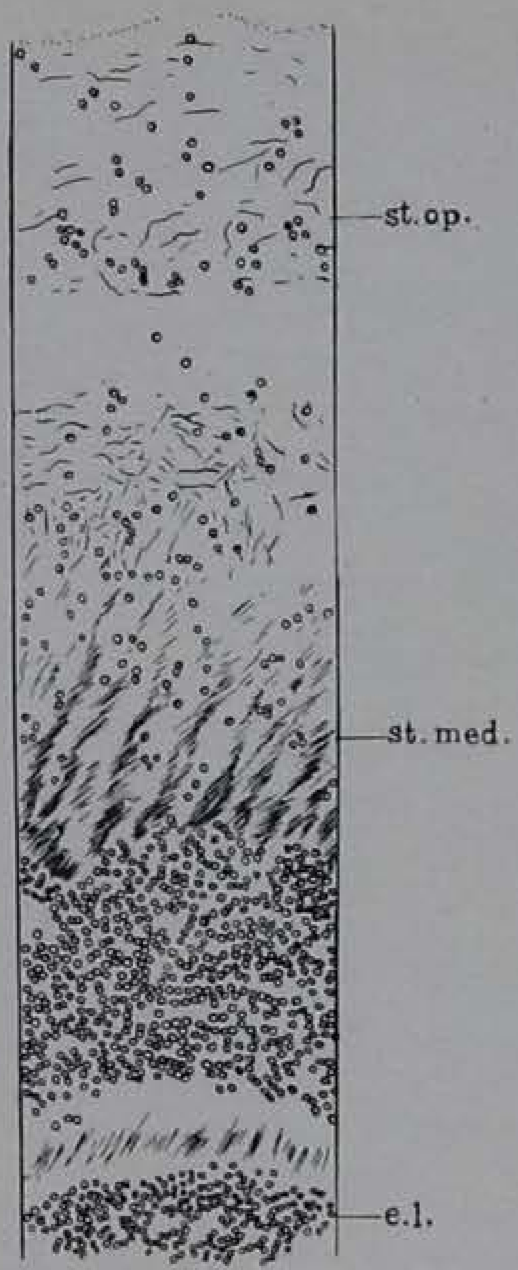

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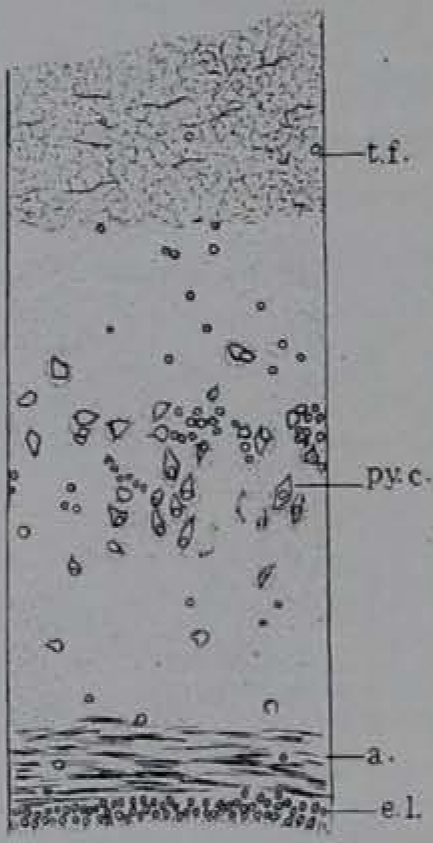

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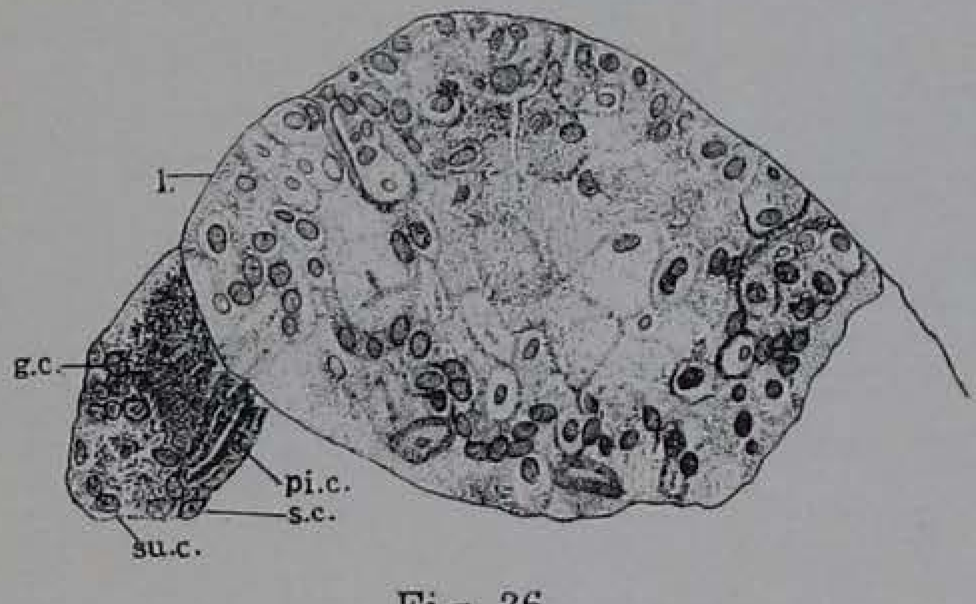

Fig. 36.

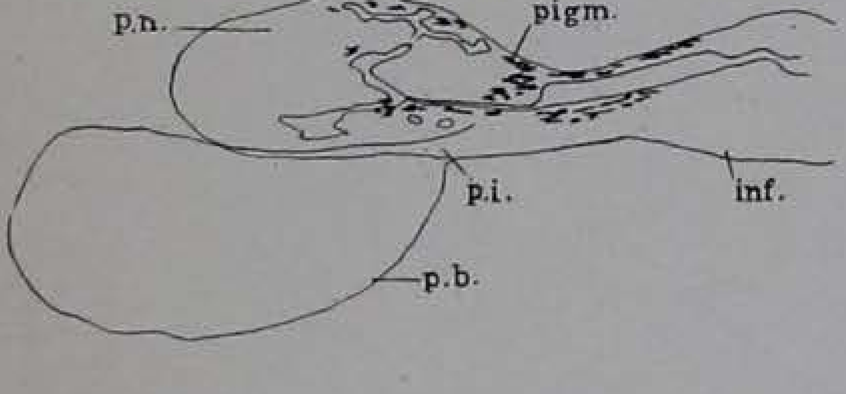

Fig. 37.

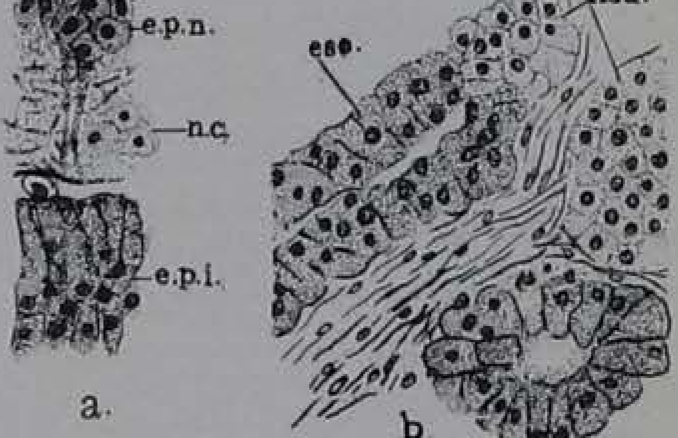

Fig. 38.

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