THE CEREBELLUM OF *SPHENODON PUNCTATUM*

By J. C. R. HINDENACH, M.B., Ch.B.
Department of Anatomy, University of Otago, New Zealand

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INTRODUCTION

The brain of *Sphenodon punctatum* has, for the past thirty years, held an important position in the field of comparative neurology, mainly due to the interest centering round the forebrain and pineal organ of this primitive reptile. Of recent years the cerebellum of man has been studied from a comparative anatomical view-point, and Dr W. P. Gowland suggested the study of the cerebellum of *Sphenodon* to me as an almost unexplored field. Up to the present no detailed account of its cerebellum has been given.

Gisi (1907) has published an exhaustive survey of certain aspects of its brain, confining herself chiefly to the external appearances and the relation of the brain to the skull. Her discussion of the internal structure of the cerebellum is incomplete. Apart from the work of Gisi, I know of no other detailed study of the cerebellum of *Sphenodon*. The greater portion of this account was therefore written on a basis of comparison with the brains of other vertebrates as described in available journals. In connection with the study of comparative neurology in New Zealand, one is hampered to some extent by the lack of some of the most important papers dealing with the reptilian brain.

At the present time, there is also a lack of suitably stained series of other reptilian brains for comparative purposes. For these reasons the following study has been made chiefly from a descriptive point of view, and a discussion of the possible homologies avoided where possible.

In addition, no detailed work has yet been done on the mesencephalon or the medulla oblongata of *Sphenodon*, and accordingly it has been difficult to link up completely the cerebellum by its connections, with the result that several of the cerebellar tracts still require further investigation.

The nomenclature used has been adopted from that in the works of Prof. C. Judson Herrick on the cerebellum of *Necturus* and other urodele amphibia, and of O. Larsell who has written on the cerebellum of *Amblystoma*, of the frog and of certain reptiles.

In connection with this study, I wish to express my thanks and indebtedness to Prof. W. P. Gowland, head of the Department of Anatomy of the University of Otago, at whose suggestion this work was commenced, and by whose efforts, serial sections of the brain of *Sphenodon*, suitably stained by modern neurological technique, have been made available for the detailed study of its internal structure.

MATERIAL AND TECHNIQUE

For this study, numerous series of sections of the brain of the adult *Sphenodon* were employed. Several foetal brains were available, stained by Huber's toluidin blue technique, but they were not sufficiently early to draw any conclusions concerning the development of the cerebellum.

For examination of the cell masses, the toluidin blue series were used. These were stained by the method suggested by Prof. G. Carl Huber, University of Michigan, Ann Arbor, and proved of the utmost value.

The fibre tracts were examined mainly in Weigert preparations, but use was also made of the material prepared by the silver impregnation method of Cajal which allowed of the recognition of non-medullated fibres.

Other series stained by the methods of Ranson, Gurdjian and Golgi-Cox also proved of use.

The following adult material was available for study:

Stained by Huber's toluidin method: six transverse series, four sagittal series, and one horizontal series;

Stained by the Weigert method: one transverse series, one sagittal series, and two horizontal series;

Stained by Cajal method: two transverse series, two sagittal series, and two horizontal series;

Stained by Ransom method: one transverse series;

Stained by Gurdjian III method: one sagittal series;

Stained by Golgi-Cox method: one transverse series.

GENERAL

The cerebellum of *Sphenodon* is of a most primitive type, being in the usual extroverted form characteristic of reptiles. Kappers (1921) has described the similarity between this reptilian type and the developing cerebellum of the human foetus. Larsell (1926) states that de Lange (1917) has called attention to the similarity between this extroverted form and that of the early foetus, and also between the alligator type and that of the 3 months' foetus. Larsell (1926), describing the cerebellum of *Gerrhonotus principis* and *Sceloporus biseriatus*, correlates the former with that organ in the human of about three months, and that of the latter with the 2 months' human foetal stage. The external appearance of the cerebellum of *Sphenodon* corresponds very closely to that seen in the 27 mm. (2 months) human foetus, as pictured by Kappers (1921, p. 706), and the similarity appears to be even more complete than that described above for *Sceloporus.*

It is of interest to note here the comparison made by Hines (1923), where she states that in the development of the telencephalon of *Sphenodon,* a stage is reached resembling point for point that of the 11·8 mm. (No. 1121) human embryo belonging to the Mall collection.

The degree of extroversion as seen in the series of brains of *Sphenodon* at my disposal, varies considerably. In one series (fig. 1) the cephalic surface, or molecular layer, is closely approximated to the convex surface of the optic tectum, and this is also demonstrable in longitudinal sections of the head of the embryo with the brain *in situ.* Other series show a considerable distance between the tectum and the cerebellum, the latter organ curving far caudally over the IVth ventricle from its attachment to the cephalic portion of the medulla. This variation is most probably explained by some loosening of the membraneous attachments of the cerebellum to the optic tectum during removal and fixation of the brain. I have had no opportunity of examining the brain *in situ* to determine the exact position, but I believe the former description, as present in the late embryo, is the more correct.

Another varying feature in the cerebellum is its size. The thickness of this organ and its lateral extent are comparatively constant, but its length varies to a considerable extent. In medial longitudinal sections, the length in one specimen is almost double the length in another. Whether this is due to a differentiation in type, or to a varying development of the musculature, it is impossible at present to offer any opinion.

The cerebellum can be described as being roughly of a triangular shape, the narrow base being the attached border, and the angles at the base being elongated laterally and rostrally to form the auricular lobes. This triangular sheet is concave anteriorly from base to apex, and also concave anteriorly from side to side, thus producing the typical extroverted form. In most specimens the cerebellum slopes caudally and dorsally from its attached base at about an angle of 70° with the horizontal, then passes dorsally, and finally curves rostrally to the tip. The rostral surface in these specimens is related to the optic tectum, the space between them being filled with pia-arachnoid. As I have previously mentioned, this relationship varies in different series. In sagittal sections the cerebellum is also triangular, tapering gradually from base to apex.

The bilateral origin is definitely shown by a longitudinal furrow in the midline of the caudal surface, dividing the cerebellum into two symmetrical halves. This sulcus is deepest at its commencement on the ventricular portion of the caudal surface, and gradually becomes less marked as it passes towards the tip, before reaching which, it disappears. This posterior median sulcus appears to invaginate the cerebellum, with the result that the cerebellum in horizontal cross section appears almost W-shaped (fig. 13 A), the two legs of the W being the auricular lobes, and the median portion being due to the pushing rostrally of the posterior sulcus. On either side of the midline, there is a thickening of the mass of the cerebellum which gradually tapers to the lateral rounded borders.

The rostral limit of the cerebellum is determined medially by the decussatio veli (fig. 1). Laterally, the rostral limit is more difficult to determine. It appears to be bounded by the nucleus isthmi which makes a definite projection on the dorso-lateral surface of the isthmial region, visible to the naked eye. The nucleus isthmi, though not actually a part of the cerebellum, is closely related to it, both anatomically and by its fibre connections, and therefore will be described in this paper. As stated above, it is large in *Sphenodon* and has the IVth nerve passing over its dorsal and lateral aspects.

The angles at the base of the cerebellum are bent rostrally to form the auricular lobes, thus forming an anterior furrow between them and the body of the cerebellum; but no sulcus could be seen between the ventral portion of the auricle and the medulla oblongata.

The caudal limit of the attachment of the cerebellum to the medulla is definitely marked, and lies about the level of the entrance of the Vth cranial nerve.

HISTOLOGY

The cerebellum of *Sphenodon* consists of three typical layers. These areas correspond closely to the condition found in other reptiles and even to the zones seen in the cerebellar cortex of higher vertebrates. The layers are: a molecular layer, a layer of Purkinje cells, and a granular layer (figs. 1, 10). The relations of these layers to each other can be studied in the series available, but without further Golgi preparations I am unable to give a detailed description of the types of neurones present and their ramifications.

A well-marked fibre layer is also present, lying partly between the above zones and partly through them.

The granular layer is distinct, and consists of small, darkly stained, rounded cells closely packed together. The layer is divided into various strata by the entering fibres of the cerebellum, thus giving this zone a laminated appearance in cross section. The greatest number of cells are present near the ependymal layer.

The extroversion of the cerebellum has altered the position of the granular layer from a purely caudal one. This layer, therefore, lies on the lateral surface of the auricular lobes, the ventral or ventricular surface of the base of the cerebellum, the caudal surface of the body and the dorsal surface of the tip. The thickness of the granular layer varies but slightly in the different parts of the cerebellum. It is thickest at the corpus cerebelli where the granular layer projects ventrally into the IVth ventricle on either side of the midline. In this position it forms two distinct eminences separated by a sulcus, the sulcus medialis posterior (fig. 11). The granular layer is thinnest opposite this sulcus, thickest on either side of the sulcus, and then is of almost constant thickness out to the lateral borders of the cerebellum.

The granular layer is separated from the Purkinje layer by a band of fibres which are mainly afferent in type. This band consists of commissural fibres running transversely and other fibres running longitudinally. The commissural fibres are mainly rostral to the longitudinal ones, being seen in their greatest extent in mid-sagittal section, where the longitudinal fibres are almost absent (figs. 15, 16). The fibres, which are of both medullated and non-medullated types, are not confined to the one area alone, but scatter throughout the three cell layers.

The Purkinje cells form a zone between the molecular and granular layers, or, more definitely, between the molecular and fibre layers, but scattered Purkinje cells are, however, found in the fibre layer. These cells are of the typical large ovoid shape, with darkly stained bodies and with dendritic processes, as seen in some Cajal sections, extending into the molecular layer. This stratum varies in thickness throughout the cerebellum, in some areas only one layer of cells, in others, four or five layers being seen. This variation may, in part, be due to the obliquity of the sections.

Purkinje cells extend laterally into the auricular lobes (fig. 13). They are especially numerous in the body of the cerebellum overlying the IVth ventricle. The relation of their axons to the nucleus cerebelli and the brachium conjunctivum as described by Larsell (1923) in the frog could not be definitely determined, though some fibres in the brachium conjunctivum appear to arise from regions in the cerebellum other than that of the nucleus cerebelli.

The molecular layer is seen lying in the rostral concavity due to the extroversion of the cerebellum. It is composed mainly of non-medullated fibres, though a few small, scattered, faintly stained, rounded cells are seen throughout its substance. Larsell (1923), describing this condition for the frog, suggests that these are only neuroglial cells. This layer is of approximately the same thickness as the granular layer, being of the greatest dimensions in the rostral part of the cerebellum, where it overlies the commissura cerebelli. Rostrally, it falls just short of the decussating fibres of the ventral spino-cerebellar tract. Owing to the extroversion of the cerebellum, this layer faces dorsally in the rostral part, and ventrally in the dorsal curved part of the cerebellum. The layer is related in general to the caudal surface of the optic tectum. It is bounded rostrally by the cerebellar commissure in the midline, and laterally by the arching fibres of the ventral spino-cerebellar tract.

NUCLEI OF THE CEREBELLAR REGION

The nucleus cerebelli

In the corpus cerebelli of *Sphenodon* there are present multipolar cells of large size, which bear a considerable resemblance to the Purkinje cells already described. These cells are slightly larger than the Purkinje cells, and stain less deeply. In the absence of Golgi preparations, it is impossible to describe them fully, or to trace out their connections. These cells lie in the lateral part of the cerebellum at its junction with the tegmentum of the bulb, but also extend medially into the cerebellum where it lies dorsal to the IVth ventricle (fig. 9). The cells are not collected into one mass but lie scattered throughout this region, about twenty being seen in cross section at one time. A few cells extend rostrally towards the commissura cerebelli, where they are separated from the nucleus isthmi which lies rostral, lateral, and ventral to them by the ventral spino-cerebellar tract and mesencephalic tract of the Vth nerve. Ventrally, the nucleus lies, from without in, on the tegmentum of the bulb, and the ependyma on the ventral surface of the cerebellum overlying the IVth ventricle (fig. 9). The most medial cells extend towards the midline between the granular layer and the fibre layer. Laterally, the cells are bounded by dorsal spino-cerebellar fibres and fibres of the vestibulo-cerebellar tract passing to the auricular lobe. Dorsally, the nucleus lies beneath the entering fibre tracts, while posteriorly, it comes into direct relation with the superior vestibular nucleus lying in the upper free border of the bulb (fig. 10). There is a direct continuity between the cells of both nuclei, and it is difficult to define an exact line of separation. The nucleus cerebelli lies in the midst of the ascending fibres of the vestibulo-cerebellar tract.

Thus the nucleus is brought into anatomical relationship with fibres carrying impulses from the spinal cord and also from the vestibular centres.

As stated above, the cell connections are not included in this description, but it is obvious in the sections that the fibres of the branchium conjunctivum pass ventrally and rostrally from this region of the cerebellum.

Larsell (1926) describes the deep nuclei of the cerebellum in certain reptiles as being present in two masses, medial and lateral, which are not sharply separated. The larger lateral part, he designates the nucleus cerebelli lateralis, and the attenuated medial division extending nearly to the midline of the cerebellum in the border zone between corpus cerebelli and the anterior medullary velum, is called the nucleus cerebelli medialis. The statement by Larsell that the brachium conjunctivum in *Anniella* takes origin from the lateral nucleus, is in agreement with the condition in *Sphenodon* in which the brachium conjunctivum appears to come from the more lateral cells of the nucleus cerebelli. Apart from this point there is no other means of dividing the nucleus cerebelli in *Sphenodon* into two masses.

Herrick (1914), in describing *Necturus*, states: "The cerebellar tissue in the floor of the lateral recess (eminentia ventralis cerebelli) gives rise to the greater part of the feebly developed brachium conjunctivum and is therefore probably the primordium of the roof nuclei and the nucleus dentatus of the mammalian cerebellum." He further describes the neurones lying in this region, whose neurites can be followed for only a short distance, probably entering the tractus cerebello-tegmentalis and brachium conjunctivum. He suggests that these cells are "greatly reduced Purkinje neurones."

Larsell (1926) describes cells in the frog, lying in the border zone of the eminentia ventralis cerebelli between the nucleus cerebelli and the tegmentum, of large size suggesting Purkinje cells. He regards them as a more primitive cerebellar correlating apparatus than is found in the corpus cerebelli. Both these descriptions of Purkinje-like cells can be correlated with the condition seen in *Sphenodon* in which the cells described are, however, more definitely situated in the cerebellum.

Nucleus isthmi

There exists in the literature on this subject some confusion—mainly due to the varying cell masses in the brains of vertebrates to which this term has been applied. Larsell (1924) gives an admirable introduction to the subject, in which he clears up the general point of view. Previous writers have confused the nucleus isthmi and the secondary visceral nucleus. Johnston (1906) states that the ganglion isthmi of birds is of a different character to the ganglion isthmi in amphibia and fishes. Both nucleus isthmi and secondary visceral nucleus are in close anatomical relationship in the lower vertebrates, and confusion has thus arisen. In the fishes the large size of the secondary visceral nucleus overshadows the small nucleus isthmi, while in the reptiles the reverse is the case, the nucleus isthmi being a prominent feature in the isthmus of the brain, and the secondary visceral nucleus being comparatively small. Kappers (1921) has clarified the situation by homologising the nucleus isthmi of amphibia with that of the same name in reptiles and birds. He holds that, in these forms, it is homologous with the medial geniculate body of mammals. Larsell (1923, 1924) has described carefully both the nucleus isthmi and secondary visceral nucleus in the frog, and says that they must be regarded as two distinct and unrelated nuclei which topographically are closely crowded together.

Huber and Crosby (1926), for the alligator, give a detailed description of the connections of the nucleus isthmi, but make no mention of secondary visceral nucleus. They describe the nucleus isthmi as consisting of two nuclear masses, a larger lateral portion, and a smaller medial portion. Its fibre connections correspond closely to those described by Larsell (1926) for the frog.

Huber and Crosby (1929) also give a detailed description of the nucleus isthmi in the avian diencephalon, and subdivide it still further. They describe the pars principalis as an outer or superior portion, distinctly large celled, and use the terms pars principalis parvo-cellularis and pars principalis magnocellularis for the two divisions of the nucleus isthmi in the dorsal region of the mesencephalon. They state that, associated with this pars principalis, is another nuclear group, the nucleus semilunaris of Mesdrag, for which Craigie (1928) has suggested the name pars magno-cellularis ventralis nucleus isthmi. The cells of the parvo-cellularis portion are actually medium sized and only small in comparison with the other portion. The small-celled part disappears caudally before the large-celled, and it is medial to the nucleus semilunaris. Craigie (1928) states that the whole nucleus isthmi complex is well developed in the typical avian brain. He believes that it is really a differentiation of the anterior end of the area statica, and, having connections with the latter, with the tectum, and with the cerebellum, is probably a static or visuostatic correlating area. Its considerable size may thus be correlated with that of the cerebellum and of the whole equilibratory and flight mechanism. This theory is not borne out in *Sphenodon*, in which, though the nucleus isthmi is large, the cerebellum is comparatively simple and small, and the equilibratory mechanism probably rather simple in this comparatively sluggish reptile.

The nucleus isthmi in *Sphenodon* forms a distinct projection on the brain surface, dorso-lateral to the decussation of the IVth nerve, and lateral also to the posterior corpus quadrigeminum (fig. 11). It is the most conspicuous structure in the pre-cerebellar region of the brain, the fibres of the IVth nerve passing over its external surface (fig. 20).

It is oval in shape and can be divided into two distinct nuclear groups. The dorso-lateral portion is composed of large, well-stained, multipolar cells scattered rather evenly through the medulla, while the cortex contains only a few scattered cells. This mass I have called the nucleus isthmi pars magno-cellularis (fig. 7). Medially and slightly ventrally, lies the remainder of the nucleus, closely applied to the pars magno-cellularis. It is composed of smaller, rounded, well-stained, closely packed cells, and is here called the pars parvo-cellularis (fig. 7). In addition to the division of the nucleus by the size of its cells, is the fact that the large-celled portion is also distinguishable by its dense neuropil background, a feature absent in the pars parvo-cellularis. The pars parvo-cellularis commences just caudal to the rostral pole of the pars magno-cellularis, and extends slightly caudal to the caudal pole of the latter (fig. 11). It is possible that the most caudal part of the pars parvo-cellularis may be related to the secondary gustatory nucleus, but I have not determined the exact connections of the latter nucleus, which is usually poorly developed in the reptilian brain.

The dorsal and lateral surfaces of the nucleus isthmi project on the external surface of the brain. Medially, it is related to the posterior corpus quadrigeminum, separated from it by the mesencephalic tract of the Vth nerve (fig. 21). The caudal pole of the nucleus comes into direct relationship with the lateral lemniscus (fig. 20). In all forms in which the nucleus isthmi has been described, this relationship with the lateral lemniscus has been mentioned, leading to the supposition that the nucleus isthmi is the homologue of the mammalian medial geniculate body. The caudal pole also comes to lie ventro-lateral to the cells of the nucleus cerebelli.

The hilus of the nucleus is on its rostro-lateral aspect. Fibres stream out from here to the optic tectum (figs. 18, 19, 20). It could not be distinguished in my preparations whether these were tecto-isthmial or isthmio-tectal. Larsell (1924) described both types of fibres in the frog, recognisable in silver preparations. Huber and Crosby (1926) describe the tract as I have done, and although they could not distinguish the direction of the fibres, they drew an analogy from Larsell's description in the frog. Both tracts are probably present in *Sphenodon.*

The remaining connections of the nucleus isthmi can be briefly described. Fine non-medullated fibres run from the dorso-medial aspect of the nucleus to the anterior medullary velum, and mingle with the fibres of the commissura cerebelli, probably constituting a commissural tract with the nucleus of the opposite side. In the same direction, but more rostral, fine fibres pass to the posterior corpus quadrigeminum, intersecting on their way the mesencephalic tract of the Vth nerve. Larsell (1924), in the frog, describes a quadrigemino-isthmial tract, some of the fibres of which he suggests may possibly pass through the nucleus isthmi to join the isthmio-thalamic tract.

Larsell (1924) has described two further tracts in the frog, the tractus isthmio-thalamicus, and tractus commissura transversa. The tractus isthmio-thalamicus in the frog is composed of slender fibres, staining poorly, and I have been unable to find a corresponding tract in *Sphenodon.* Larsell's tractus commissura transversa is homologous to the commissure of Gudden, and Huber and Crosby (1926) have described the same tract under the heading of the decussatio supra-optica ventralis. Cairney (1926) has described this tract as the decussatio supra-optica ventralis in *Sphenodon.* It is clearly present in the optic chiasma, but the fibres, on being followed caudally through the mesencephalon, become intermingled with other tracts and cannot be traced further. I have been unable to prove their connection with the nucleus isthmi in *Sphenodon.*

Ventral to the nucleus isthmi is a nucleus of large multipolar, well-stained cells, flattened from side to side, and lying in the stream of the lateral lemniscus (figs. 7 and 8). This evidently corresponds to the nucleus lemnisci lateralis of Huber and Crosby (1929), and to the lateral part of the nucleus semilunaris of Kappers (1921).

FIBRE TRACTS

Tractus spino-cerebellaris ventralis

This is one of the largest fibre tracts terminating in the cerebellum. In the series examined, it can be traced some distance caudally in the medulla oblongata, but, unfortunately, most of the series do not extend as far caudally as the caudal limit of the IVth ventricle. The tract passes rostrally in the lateral wall of the medulla (fig. 27), and consists of well myelinated fibres. They ascend in this position as far rostrally as the roots of the Vth nerve, lying ventral to the dorso-spino-cerebellar fibres, and having the spino-tectal tract medially.

The tract then lies ventral to the Vth roots (fig. 26), and curves round the rostral limit of these roots to pass dorsally and medially to enter the cerebellar commissure (fig. 20), where it can be distinguished as a distinct bundle. The majority of the fibres decussate in the rostral end of the cerebellar commissure where they lie just caudal to the decussation of the IVth nerve. The remainder of the fibres run dorsally to ramify in the granular layer of the cerebellum on the same side. In mid-sagittal section, the anterior medullary velum is practically negligible; the commissura cerebelli, here composed almost entirely of ventral spino-cerebellar fibres, lies adjacent to the caudal aspect of the decussatio veli, and a few of the most cephalic fibres of the commissure lie between the decussatio veli and the aqueduct of Sylvius.

The terminal ramifications of this tract appear to be in the granular layer.

Larsell (1926) discusses the varying degree of decussation of the ventral spino-cerebellar tracts in certain lizards and in a snake. The greatest amount of decussation in the specimens examined occurred in the snake, in which the cerebellar commissure appeared to be made up chiefly of decussating fibres of the ventral spino-cerebellar tract. This description for the snake is similar to that given by Huber and Crosby (1926) for *Alligator mississippiensis* and *Chrysemys marginata* where they name the tract the spino-cerebellar tract. It also corresponds to the condition seen in *Sphenodon*. The exact termination of these fibres in the cerebellum could not be accurately determined.

Huber and Crosby (1926) describe also a small cerebellar component accompanying the tractus spino-mesencephalicus in the alligator. They are undecided whether this tract corresponds to Gower's ventral spino-cerebellar tract of mammals, or whether the spino-cerebellar tract of the alligator carries fibres which, in higher forms, are incorporated into Gower's tract.

Analogous to the spino-tectal tract of other reptiles, the spino-tectal tract in *Sphenodon* is found ventral and medial to the ventral spino-cerebellar tract and lateral to the lateral lemniscus (fig. 24). The tract leaves the ventral spino-cerebellar tract at the level of the roots of the Vth nerve, and passes rostrally into the mid-brain. During its course through the medulla, this tract is with difficulty distinguishable from the lateral lemniscus. I have been unable to find the cerebellar component of this spino-tectal tract described by Huber and Crosby.

Tractus spino-cerebellaris dorsalis

Larsell (1926) describes a tractus spino-cerebellaris dorsalis (or bulbo-cerebellaris) in the reptiles. As represented in *Anniella*, the tract passes lateral to the vestibular nucleus, and may be traced caudally as a distinct bundle through the greater part of the bulb, losing its identity in the caudal region of the medulla oblongata. Larsell favours the view that it is a spinal rather than a bulbar tract. The above description applies almost exactly to the tract in *Sphenodon*. Its caudal origin could not be exactly determined. It passes rostrally along the lateral surface of the bulb becoming all the time more dorsal (fig. 27). It passes through the roots of the Vth nerve (figs. 20, 26) and runs into the cerebellum in conjunction with the vestibulo-cerebellar tract.

Huber and Crosby (1926) do not mention a dorsal spino-cerebellar tract. Though they suggest that the cerebellar component of the spino-mesencephalic tract is the homologue of the ventral spino-cerebellar tract of mammalian forms, they do not therefore attempt to homologise the spino-cerebellar tract to the alligator (ventral spino-cerebellar tract of *Sphenodon*) with the mammalian dorsal spino-cerebellar tract. The general view is to consider this reptilian ventral spino-cerebellar tract as the homologue of part of Gower's complex, and the reptilian dorsal spino-cerebellar tract as the homologue of the mammalian tract of the same name.

Tractus vestibulo-cerebellaris

This tract in *Sphenodon* is similar to that described in other reptiles. The majority of its fibres take origin in the superior vestibular nucleus. From there some fibres curve around the lateral recess (fig. 25) to pass into the stratum granulare, some to terminate on the same side and others to cross to the opposite side. Other fibres, mainly from the lateral vestibular nucleus, pass rostrally into the auricular lobe. I have been unable to find a direct vestibulo-cerebellar tract.

In the series examined, no definite tractus trigemino-cerebellaris was seen. Fibres passing rostrally from the trigeminal nucleus became so intermingled with other fibre tracts that I was unable to establish definitely a connection between this nucleus and the cerebellum. This connection was established in the frog by Larsell (1923), but he was unable to make a definite statement concerning it in the snakes and lizards (Larsell, 1926).

Tractus cerebello-tegmentalis

In addition to the brachium conjunctivum, there are efferent fibres from the ventral cerebellar eminence, possibly also from other parts of the cerebellum, passing caudally and ventrally into the tegmentum of the medulla oblongata. These fibres are few and scattered and are mainly non-medullated.

At their commencement, they are closely associated with the fibres of the brachium conjunctivum, but lie slightly more laterally. Huber and Crosby (1926), in the alligator, have suggested that this tract may be a differentiated portion of the tractus cerebello-tegmentalis mesencephali.

On being traced caudally, these fibres extend close to the motor nucleus of the Vth nerve, dorsal to which they pass. They then decussate in the midline ventral to the fasciculus longitudinalis medialis. The fibres thereafter spread out and become lost in the grey matter of the medulla.

This tract therefore places the motor nucleus of the Vth nerve, and undoubtedly other bulbar nuclei, under the influence of the cerebellum. It is evidently the same tract as that figured by Kappers (1921), for *Crocodilus porosus*, as the tractus cerebello-motorius.

Brachium conjunctivum

This tract has already been noted in connection with the nucleus cerebelli. Its fibres have their origin partly in this nucleus and partly in some more dorsal structure in the cerebellum. Larsell (1923) suggests that, in the frog, fibres of this tract originated in part as axons of Purkinje cells. This could not be accurately ascertained in *Sphenodon* preparations.

The tract is best seen in sagittal sections stained by the Cajal method (figs. 19, 20). The fibres are fine and mainly non-medullated. They are collected in a definite bundle only at their commencement. Beyond that they become more scattered, and pass rostrally and ventrally into the mid-brain. They decussate ventral to the fasciculus longitudinalis medialis, but their final termination could not be determined.

Tractus tecto-cerebellaris

This tract has been described in reptiles by Huber and Crosby (1926) for *Chrysemys marginata,* and by Larsell (1926) for *Sceloporus* and *Gerrhonotus.* A similar tract can be seen in *Sphenodon* in Cajal series, but could not be distinguished in Weigert preparations. In the silver preparations, very fine fibres can be seen running from the tectal regions first ventrally, and then caudally, dorsal to the corpus quadrigeminum posterior. Throughout their course they remain close to the midline, passing, however, dorsal to the mesencephalic tract of the Vth nerve and then ventral to the decussating fibres of the IVth nerve. They enter the anterior border of the cerebellar commissure, beyond which point they could not be traced.

Owing to its intimate relationship with certain cerebellar structures, the IVth nerve may be aptly included in the description at this stage.

Nervus trochlearis

The nucleus of the IVth nerve lies in the floor of the posterior part of the aqueduct of Sylvius dorsal to the medial longitudinal fasciculus (figs. 1, 7). The fibres emerge from the nucleus on its dorso-lateral surface, curving just dorsally and laterally and then dorsally and medially round the aqueduct (figs. 21, 22). The root is composed of a compact bundle of large coarsely medullated fibres which form, in some sections, a definite projection into the aqueduct (fig. 22). The decussation of fibres occurs in two stages, close to the dorsal surface of the isthmial region. About half the fibres decussate and emerge from the brain in the midline, and the remainder pass across to the opposite side, dorsal to the aqueduct, to emerge from the brain surface just medial to the nucleus isthmi. The two bundles immediately unite, forming the IVth nerve, which passes rostrally and ventrally over the dorsal surface of the nucleus isthmi (fig. 3).

The decussation of the IVth nerve is a very definite structure in *Sphenodon* and lies immediately rostral to the cerebellum (fig. 1). The most caudal portion of the decussation in the midline may even lie dorsal to the cerebellar commissure which here is mainly composed of fibres from the ventral spinocerebellar tract.

Larsell (1924) describes a third root in the frog which enters the cerebellum proper, joining the cerebellar commissure. He suggests that some fibres are uncrossed, and join the mesencephalic tract of the Vth nerve to pass to the region of the motor nucleus of the Vth nerve. McKibben (1913) states that, in *Necturus,* there appear to be a few uncrossed fibres which enter the IVth nerve, and which seem to be larger fibres than those which make up the trochlear nerve. They belong to the mesencephalic root of the trigeminal nerve which lies here beneath the trochlear nerve (fig. 22).

Larsell (1923) suggests that this caudal root in *Rana pipiens* contains muscle sense fibres, whose distribution is evidently to the trochlear muscle.

I have been unable to find anything corresponding to Larsell's third root entering the cerebellum of *Sphenodon.* The relationship between the IVth nerve and the mesencephalic tract of the Vth nerve is discussed in the description of the latter tract.

Tractus mesencephalicus trigemini

The fibres of the mesencephalic tract of the Vth nerve are easily discernible as they leave the optic tectum and, passing dorsally over the posterior corpora quadrigemina (fig. 21), descend on their posterior surface to reach the most ventral level of these bodies. The tract consists of fibres, heavily myelinated, arranged in small bundles, and conspicuous in Weigert series. The tract is seen as a ribbon which appears vertical in cross section. The fibres then pass caudally and also laterally to a somewhat more ventral plane. They thus reach the decussation of the IVth nerve where they turn still more laterally and ventrally to pass between the nucleus isthmi laterally and the IVth nerve medially (fig. 22). It is in this region in *Sphenodon* that some of the most medial fibres of the tract appear to pass into the decussation of the IVth nerve.

McKibben (1913) in *Necturus,* and Davidson Black (1917), and Larsell (1923), with regard to the relations in the frog, speak in favour of dendrites of the mesencephalic root of the Vth nerve joining the root fibres of the IIIrd and IVth nerves to leave the brain with their roots. This statement, Larsell says, cannot be proved with certainty in normal preparations. In the series examined by me, I have been unable to trace definitely a fibre from the mesencephalic tract of the Vth nerve into the root of the IVth nerve, though it is impossible to state that such a relationship does not exist.

Herrick (1914) describes for *Necturus,* fibres of the mesencephalic tract of the Vth nerve passing through the cerebellar commissure to reach the more posterior cells of the nucleus magno-cellularis tecti of the opposite side. In *Sphenodon,* this latter condition may occur, as a few fibres can be traced from the tract under discussion into the cerebellar commissure in its anterior part. The termination of these fibres is probably as Herrick has described for *Necturus.*

From this region the mesencephalic tract of the Vth nerve passes laterally and caudally, becoming here more ventral to the cerebellum. It lies between the brachium conjunctivum ventro-medially and the vestibulo-cerebellar tract dorsally and laterally. The tract then runs caudally, ventro-medial to the vestibulo-cerebellar tract (figs. 23, 24), and is seen in cross section as a bundle flattened from side to side. It continues in this course to reach the nuclei of the Vth nerve.

Decussatio veli

This structure in *Sphenodon* is closely related to the commissura cerebelli (fig. 1). It lies immediately rostral to the cerebellum and is composed of the decussating fibres of the trochlear nerve, the fine fibres of the tractus tecto-cerebellaris, and possibly some fibres from the mesencephalic tract of the Vth nerve.

Commissura cerebelli

The cerebellar commissure is rather a massive structure and contains several groups of fibres. Its main constituents are the decussating fibres of the ventral spino-cerebellar tract (fig. 23). Included in it also, are fibres from the mesencephalic tract of the Vth nerve, and a large number of fibres connecting the two halves of the cerebellum.

SUMMARY

The cerebellum of *Sphenodon* is a very simple structure and presents no outstanding differences from the cerebella of other lizards. It appears to be a primitive type from which have sprung the specialised forms as seen in *Sceloporus* and *Gerrhonotus.*

It is of great interest to note the close similarity of the external features of the cerebellum of *Sphenodon* to those of the cerebellum of the 27 mm. human foetus, when also the developing telencephalon of *Sphenodon* at one stage has been shown to resemble that of the 11·8 mm. human embryo.

Its internal structure clearly shows the three typical layers, molecular, Purkinje, and granular. A definite nucleus cerebelli is present, closely related to the superior vestibular nucleus both by its proximity and by fibre tracts. The nuclear mass has not yet divided into two as described in other types of lizards.

The cerebellum of *Sphenodon* possesses practically all the main fibre tracts which are described for other lizards. These include two spino-cerebellar tracts, dorsal and ventral, vestibulo-cerebellar and tecto-cerebellar, as well as the brachium conjunctivum and cerebello-tegmental fibres.

The nucleus isthmi is well developed and can be divided into two distinct nuclear masses, each with its own connections. It bears its usual relation to the lateral lemniscus and the optic tectum as a cell station between the *Nucleus cochlearis* and the optic tectum.

EXPLANATION OF FIGURES

Figs. 1 to 14 represent sections stained by the toluidin blue method, and figs. 15 to 27 sections stained by the Weigert method.

Figs. 6 to 27 have been drawn to the same degree of magnification by projection of the actual sections. Figs. 1 to 5 are drawn to a magnification $\frac{2}{3}$ of the above.

The cell size is not strictly to scale, but, where possible, variations in the size of the cells is indicated.

ABBREVIATIONS USED IN FIGURES

aur.l.	Auricular lobe.
aq.S.	Aqueduct of Sylvius.
br.conj.	Brachium conjunctivum.
cb.	Cerebellum.
co.cb.	Commissura cerebelli.
c.p.q.	Corpus quadrigeminum posterior.
dec.vel.	Decussatio veli.
f.r.	Formatio reticularis.
l.l.	Lateral lemniscus.
med.obl.	Medulla oblongata.
m.l.f.	Median longitudinal fasciculus.
n.III	Third nerve.
n.IV	Trochlear nerve.
n.V	Trigeminal nerve.
nuc.cb.	Nucleus cerebelli.
nuc.isth.	Nucleus isthmi.
nuc.isth.p.m.	Nucleus isthmi pars magno-cellularis.
nuc.isth.p.p.	Nucleus isthmi pars parvo-cellularis.
nuc.vest.	Nucleus vestibularis.
nuc.vest.sup.	Nucleus vestibularis superior.
nuc.III	Nucleus of the third nerve.
nuc.IV	Nucleus of the fourth nerve.
nuc.Va.	Afferent nucleus of the trigeminal nerve.
nuc.Ve.	Efferent nucleus of the trigeminal nerve.
op.tect.	Optic tectum.
r.III	Root of the third nerve.
r.IV	Root of the fourth nerve.
r.V	Root of the fifth nerve.
r.Va.	Afferent root of the fifth nerve.
r.Ve.	Efferent root of the fifth nerve.
r.VIId.	Afferent root of the seventh nerve.
r.VIIe.	Efferent root of the seventh nerve.
st.gr.	Stratum granulare.
st.mol.	Stratum moleculare.
st.Pur.	Stratum Purkinje.
sul.post.	Sulcus posterior.
tr.isth.tect.	Isthmio-tectal tract.
tr.mes.V	Mesencephalic tract of the fifth nerve.
tr.sp.cb.d.	Dorsal spino-cerebellar tract.
tr.sp.cb.v.	Ventral spino-cerebellar tract.
tr.sp.tect.	Spino-tectal tract.
tr.vest.cb.	Vestibulo-cerebellar tract.
vent.III	Third ventricle.
vent.IV	Fourth ventricle.
VIII.coch.	Cochlear nucleus.
VIII.vest.	Vestibular nucleus.

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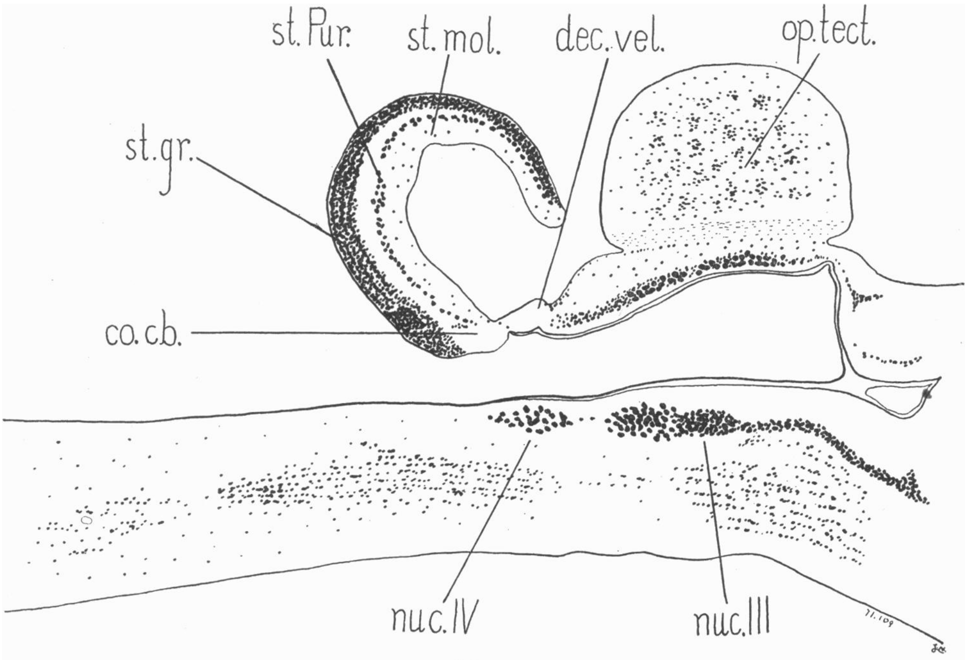

Fig. 1

Figs. 1–5. Sagittal sections of one brain from medial to lateral.

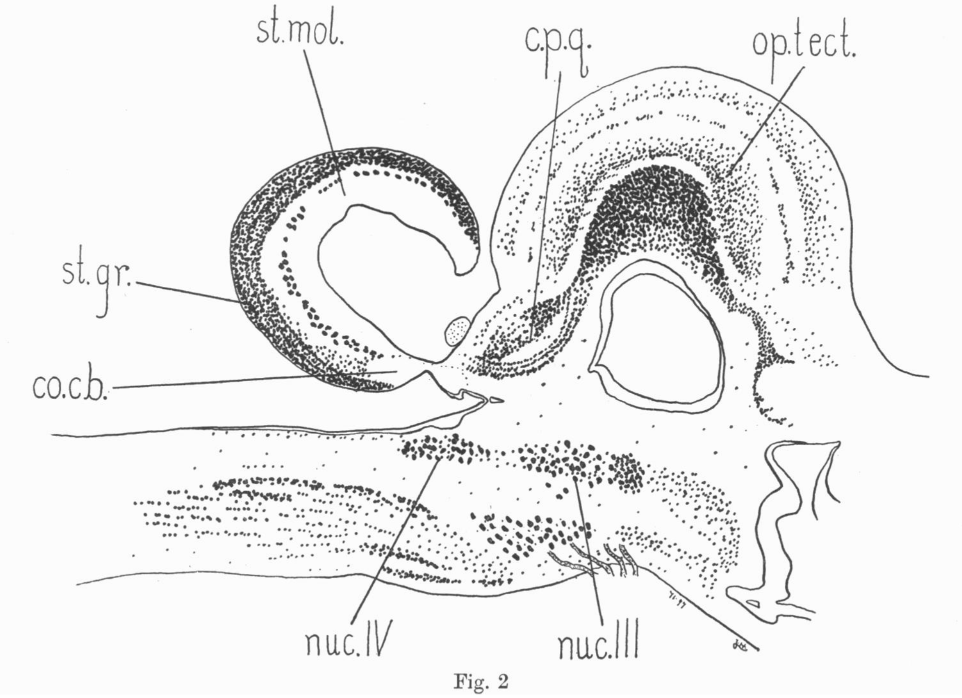

Fig. 2

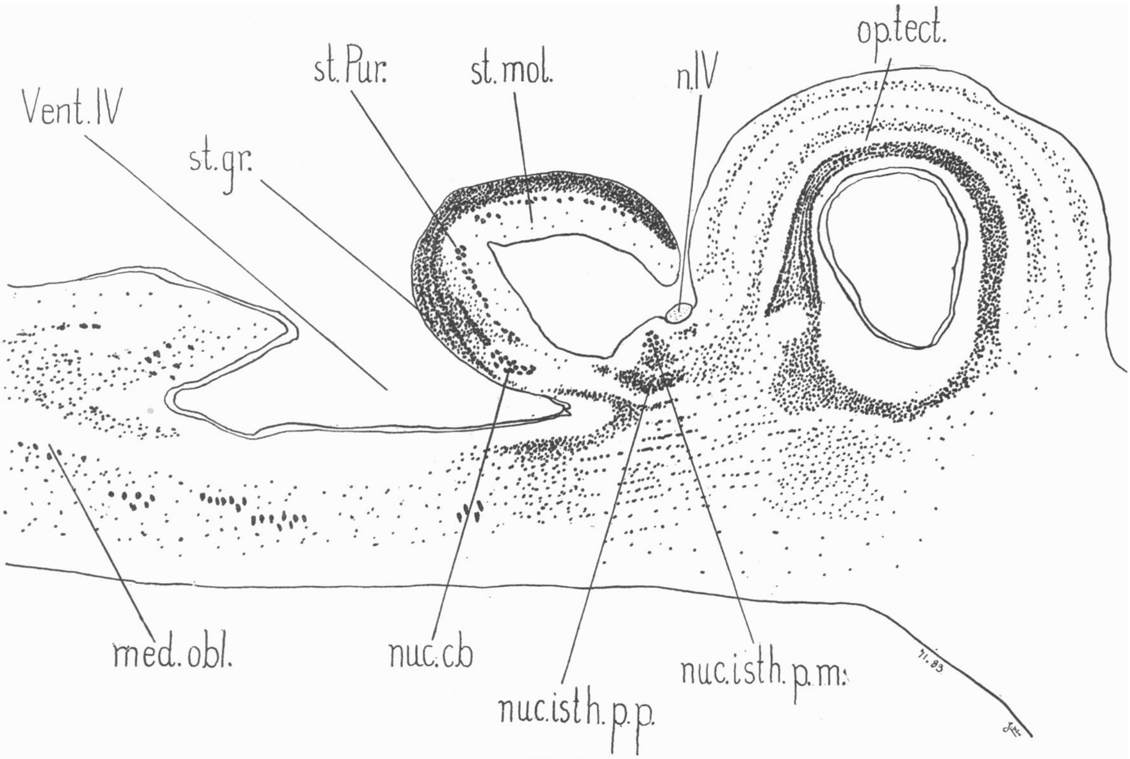
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Fig. 3

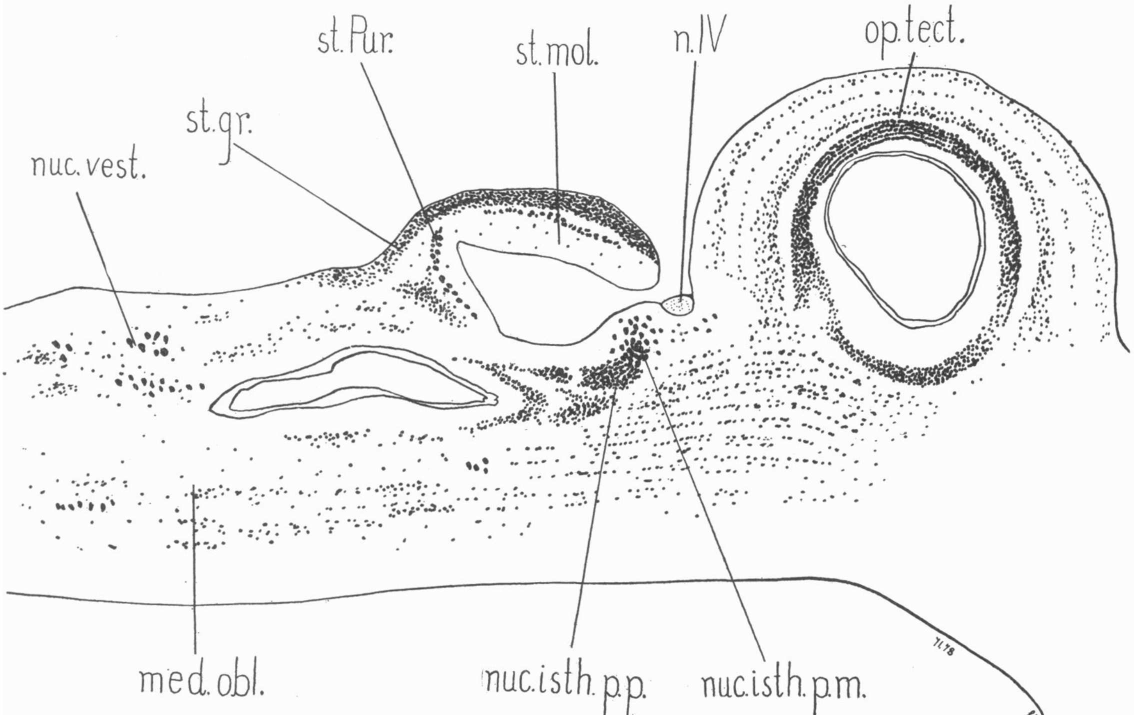
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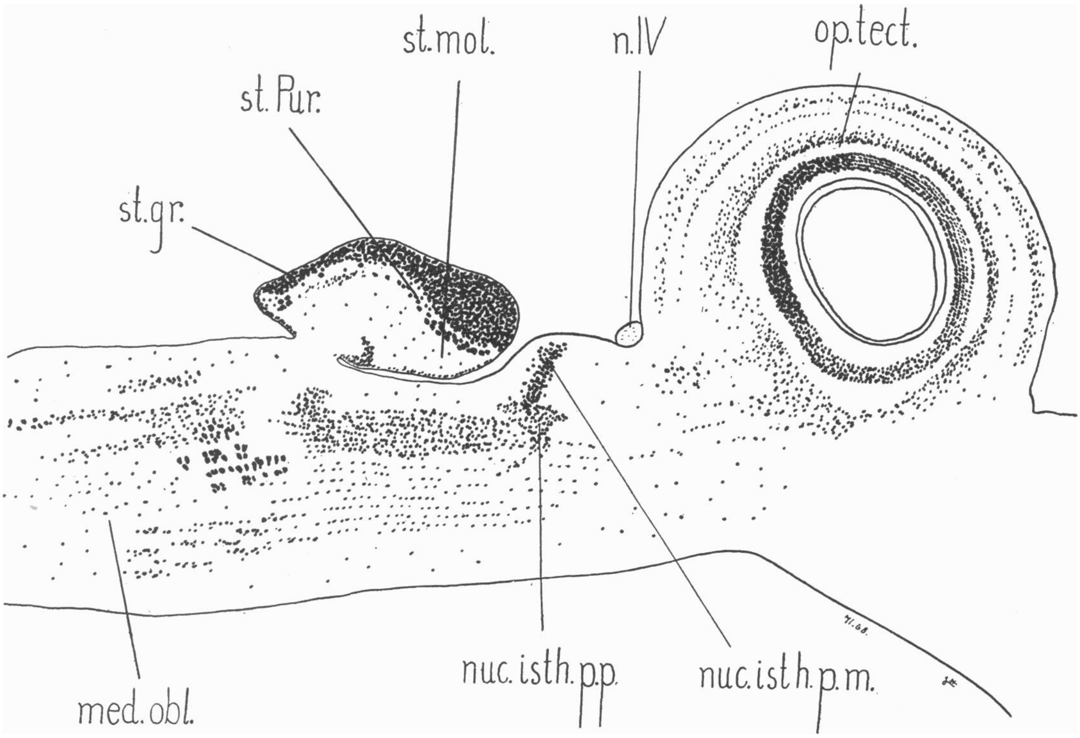
Fig. 4



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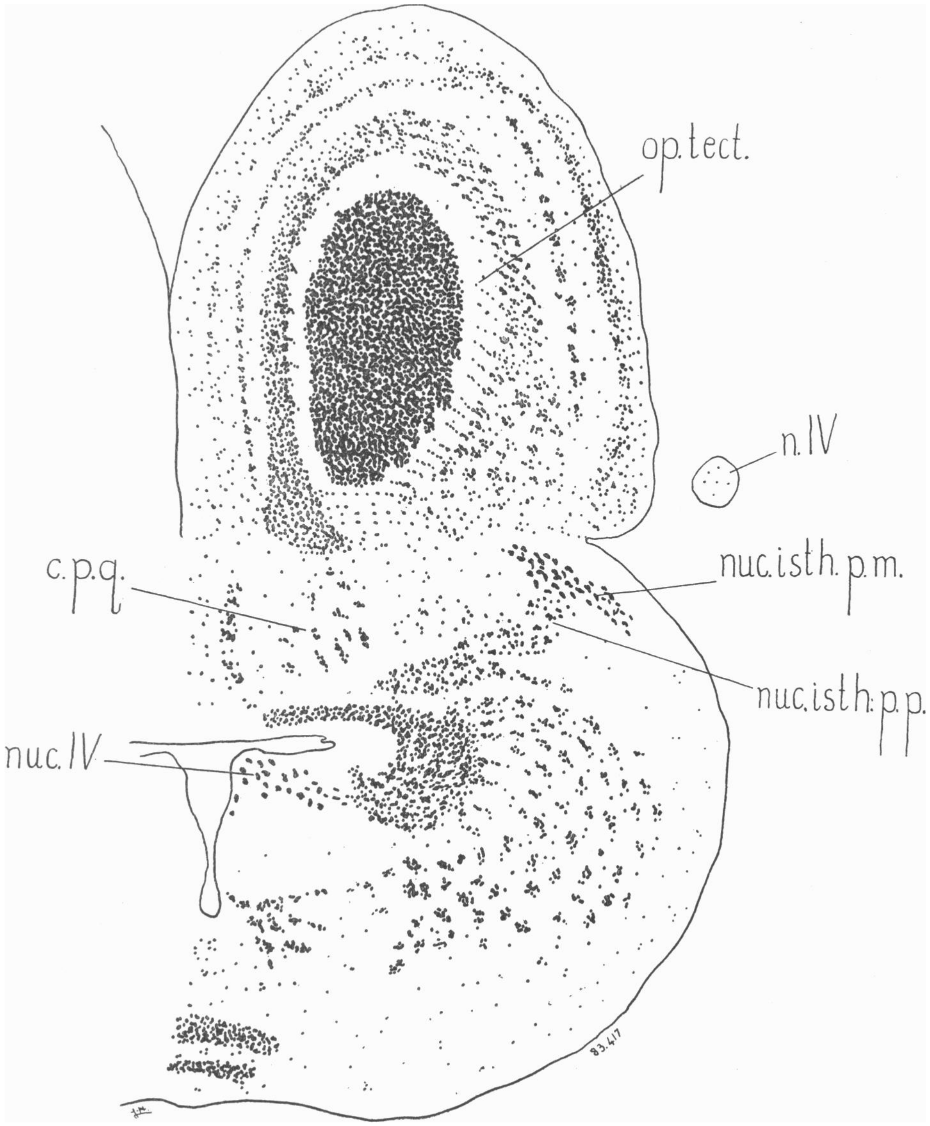

Fig. 6

Figs. 6–10. Transverse sections from before back through the cerebellar regions.

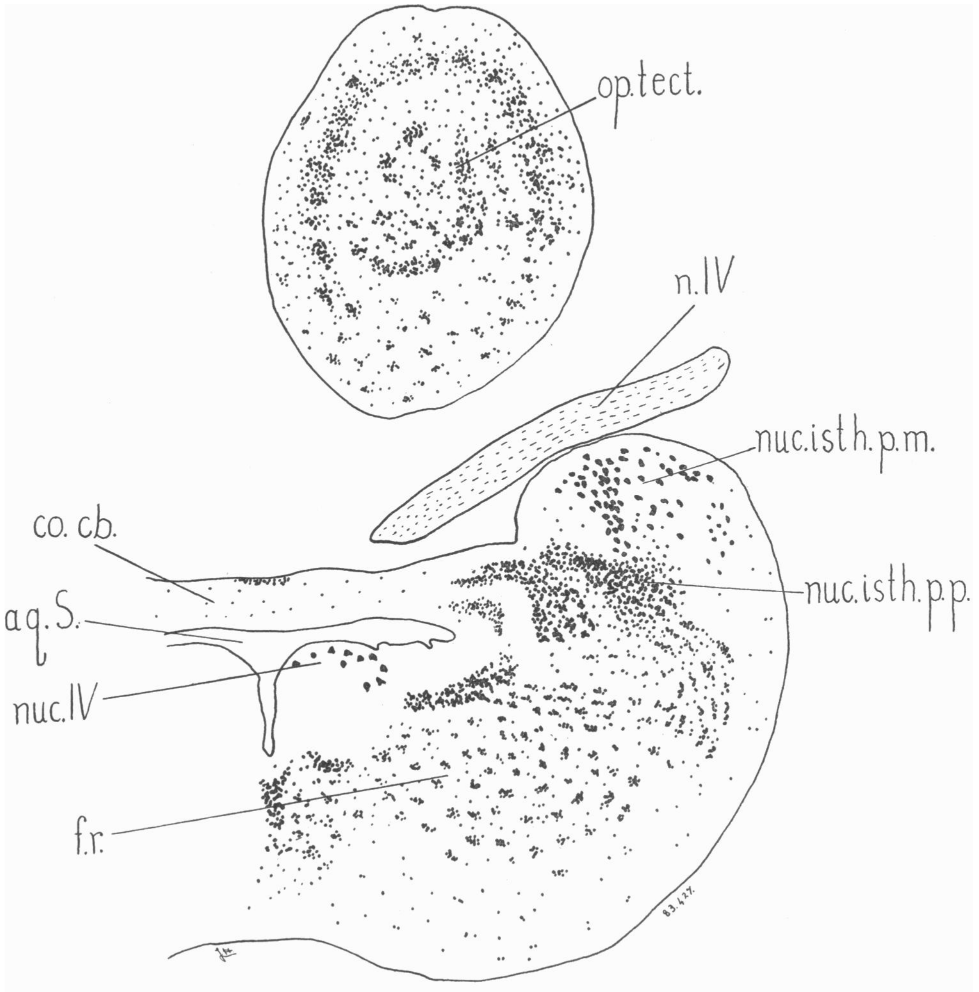
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Fig. 7

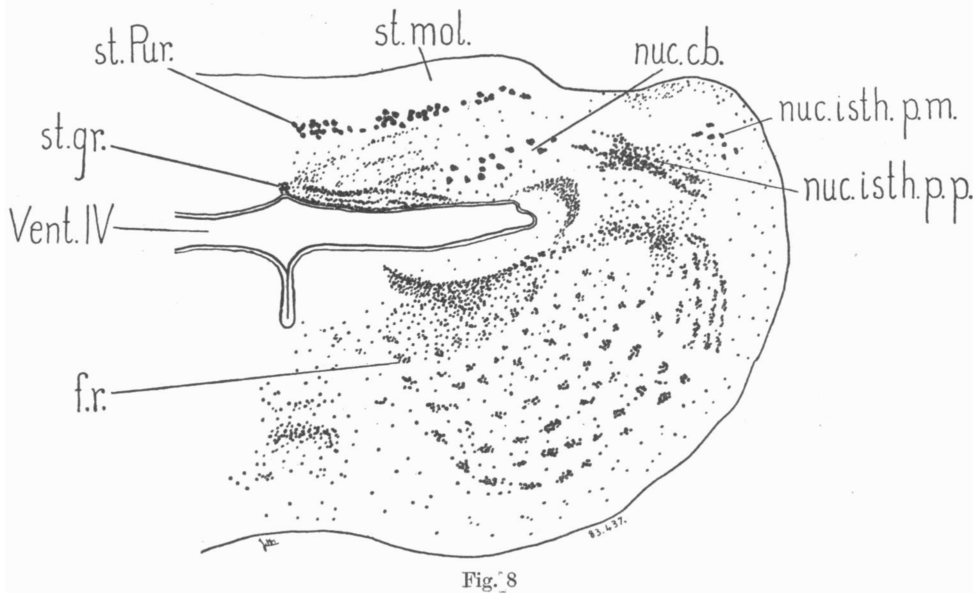
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Fig. 8

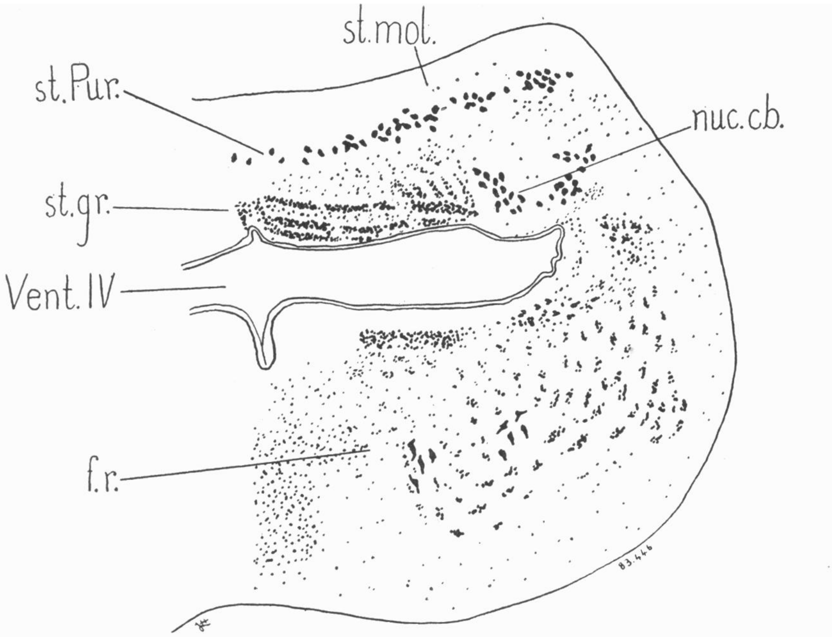
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Fig. 9

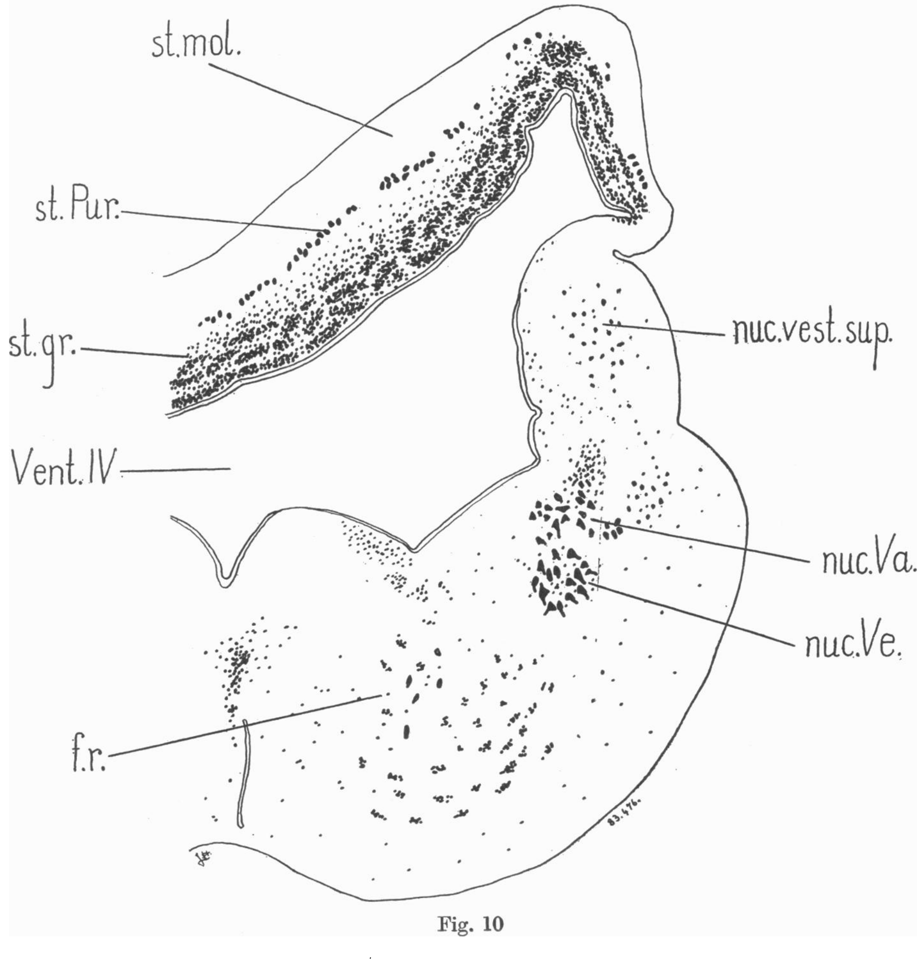
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Fig. 10

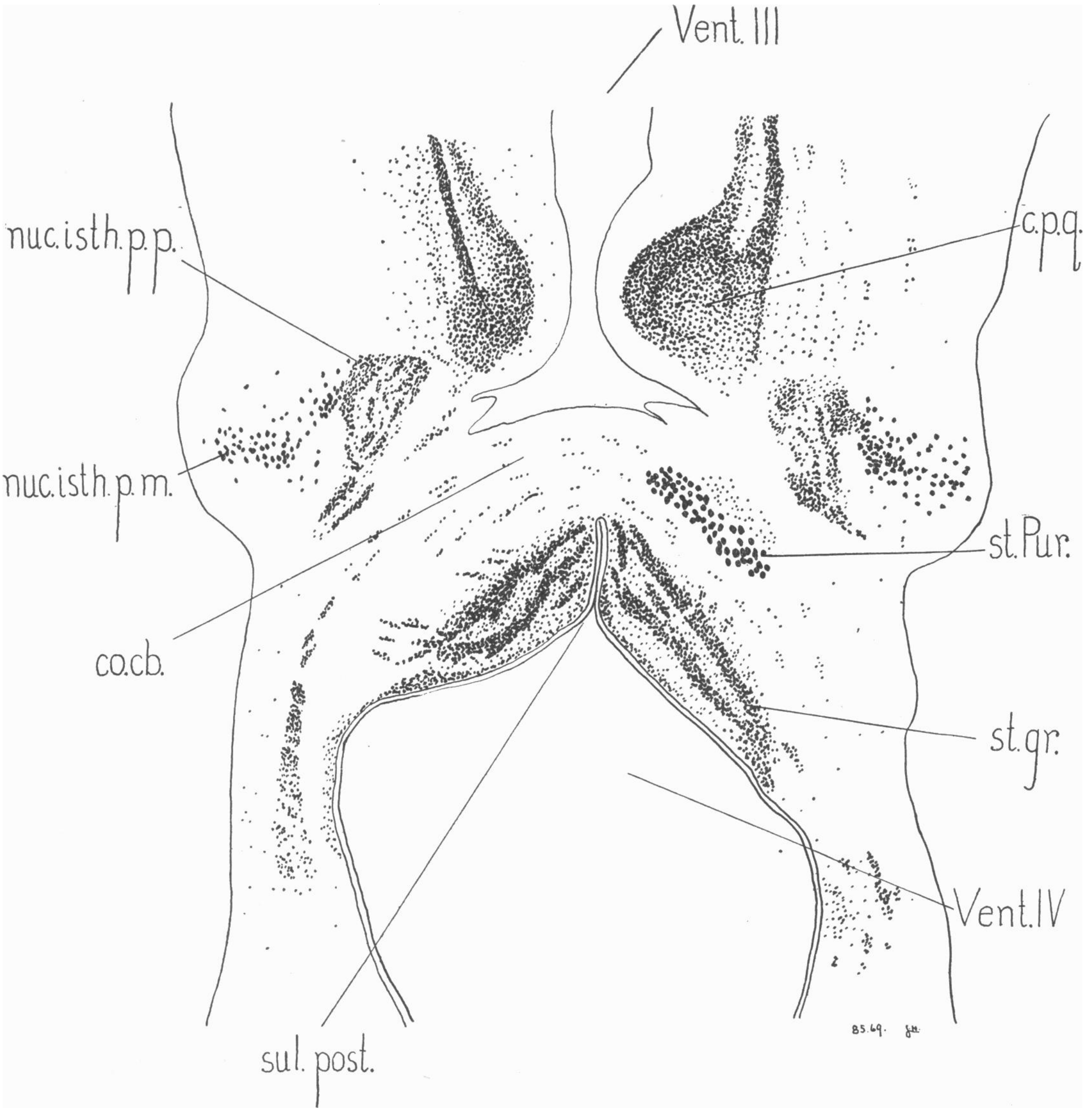

Fig. 11

Figs. 11–13. Horizontal sections of one brain from ventral to dorsal. Fig. 13 shows three separate sections through the cerebellum itself from ventral to dorsal.

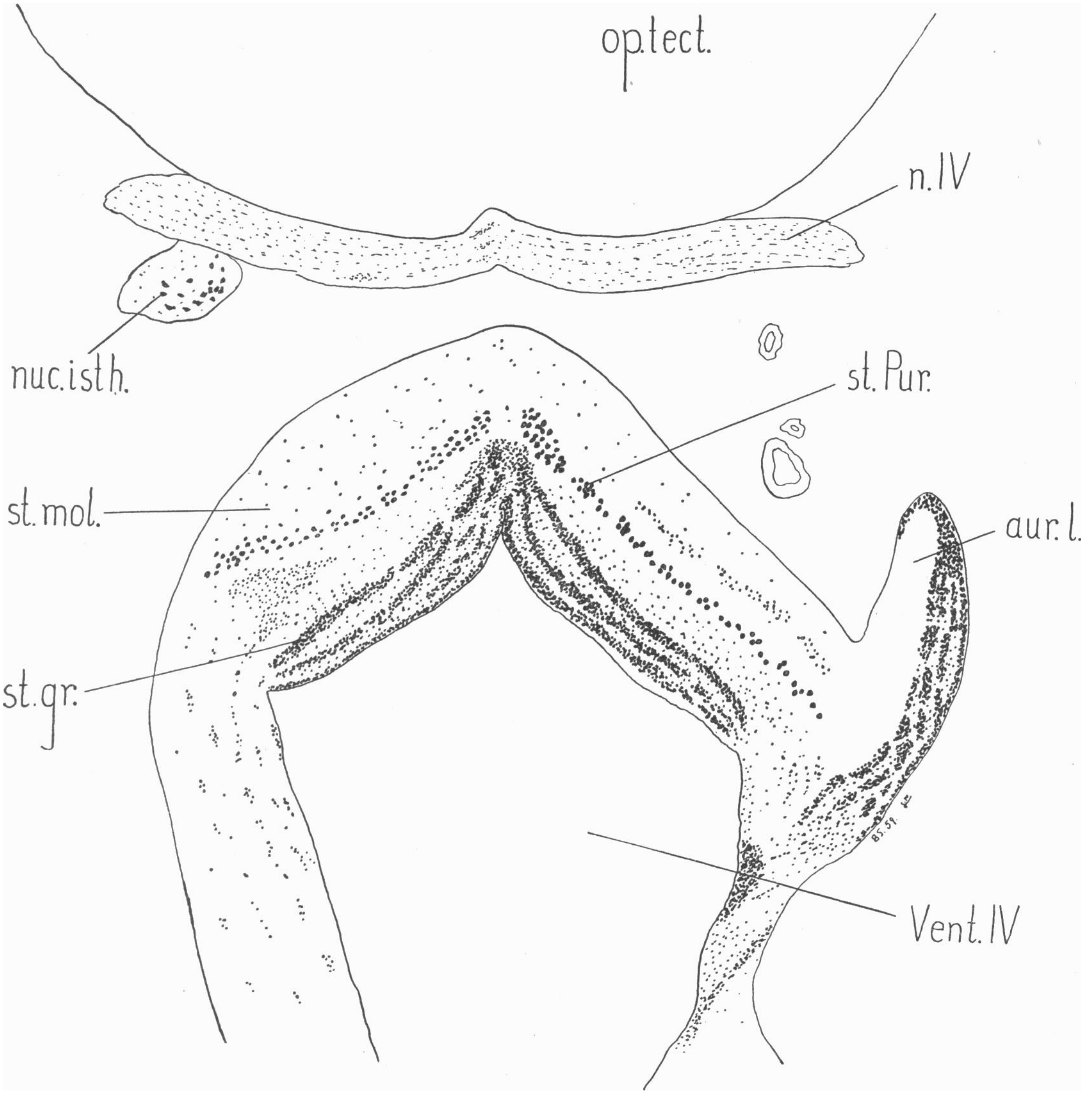

Fig. 12

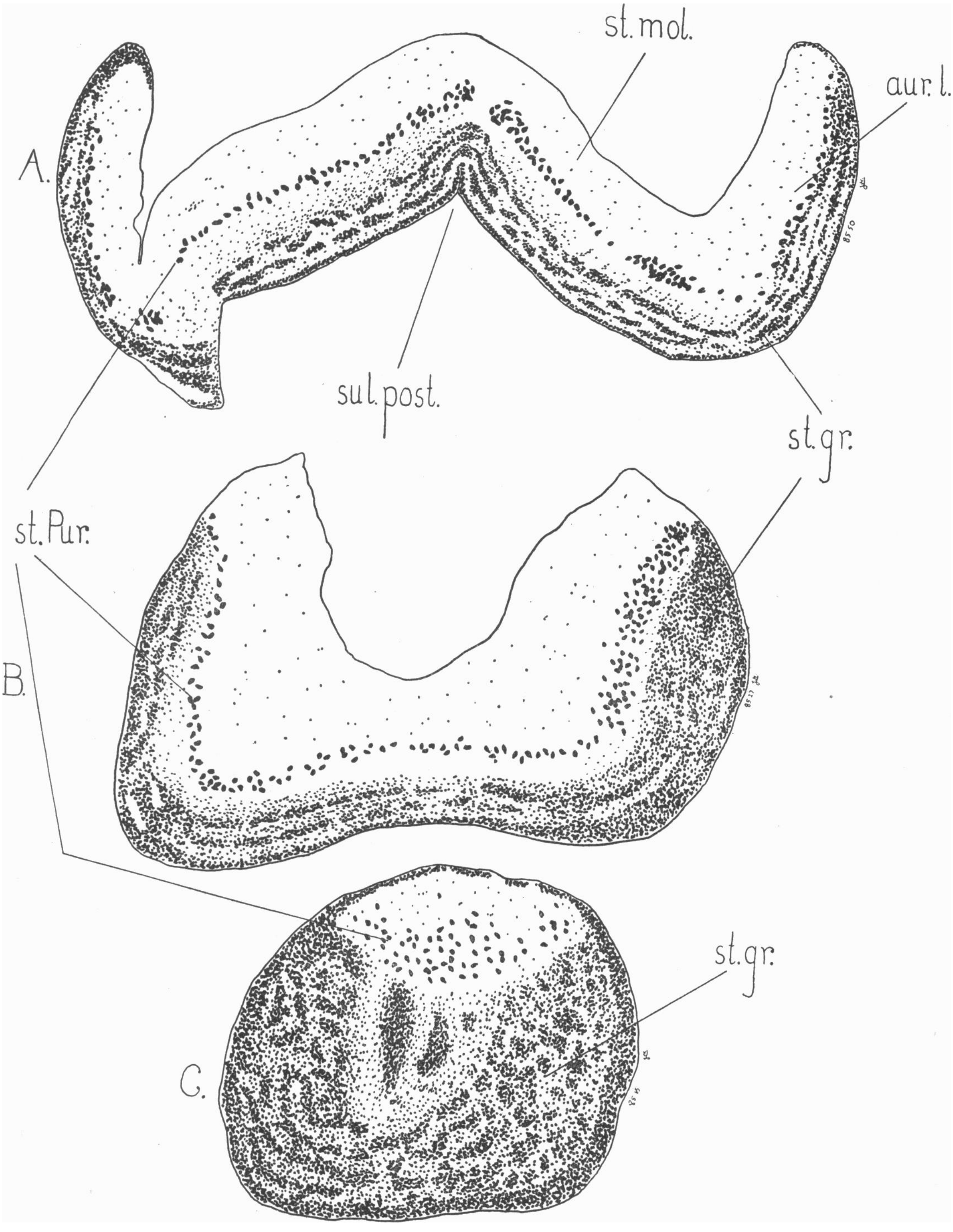

Fig. 13

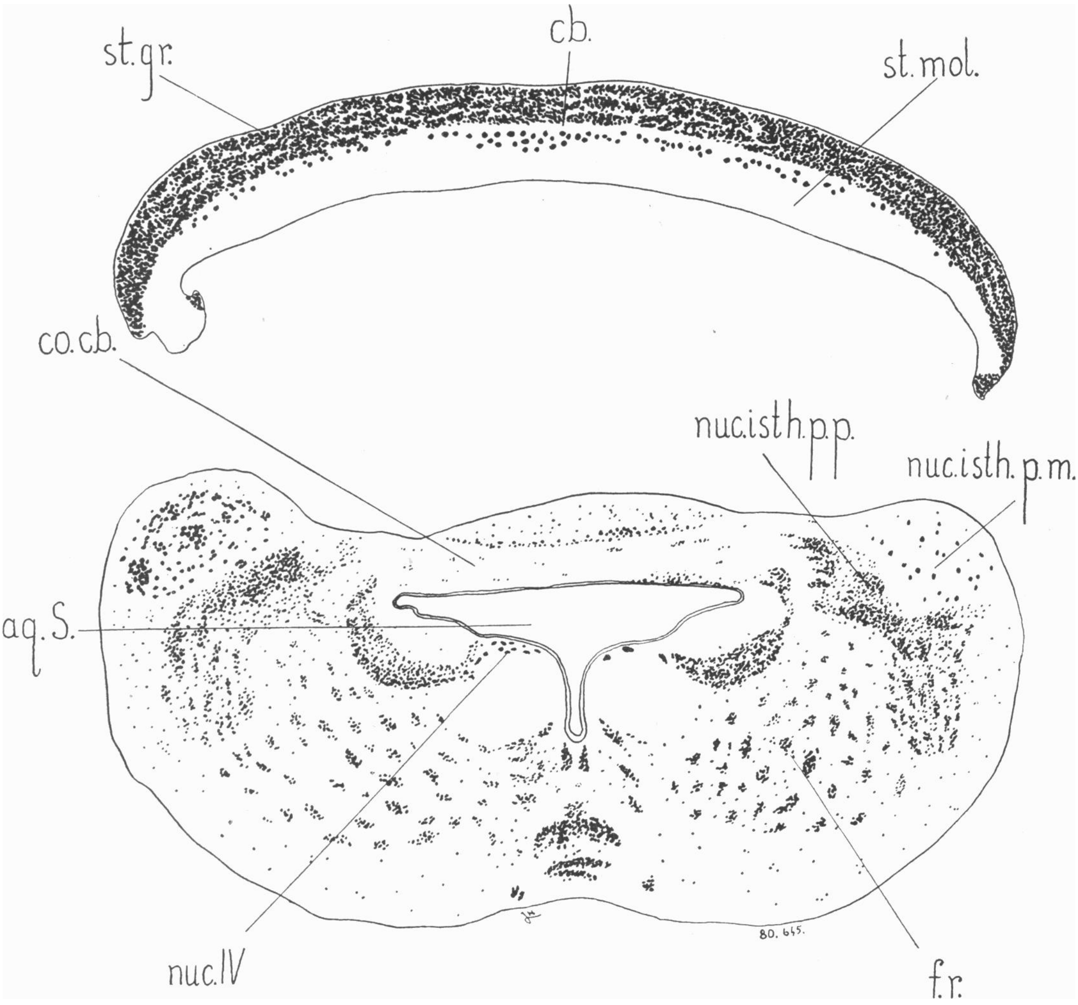

Fig. 14. This is a typical transverse section through the cerebellar region of *Sphenodon*.

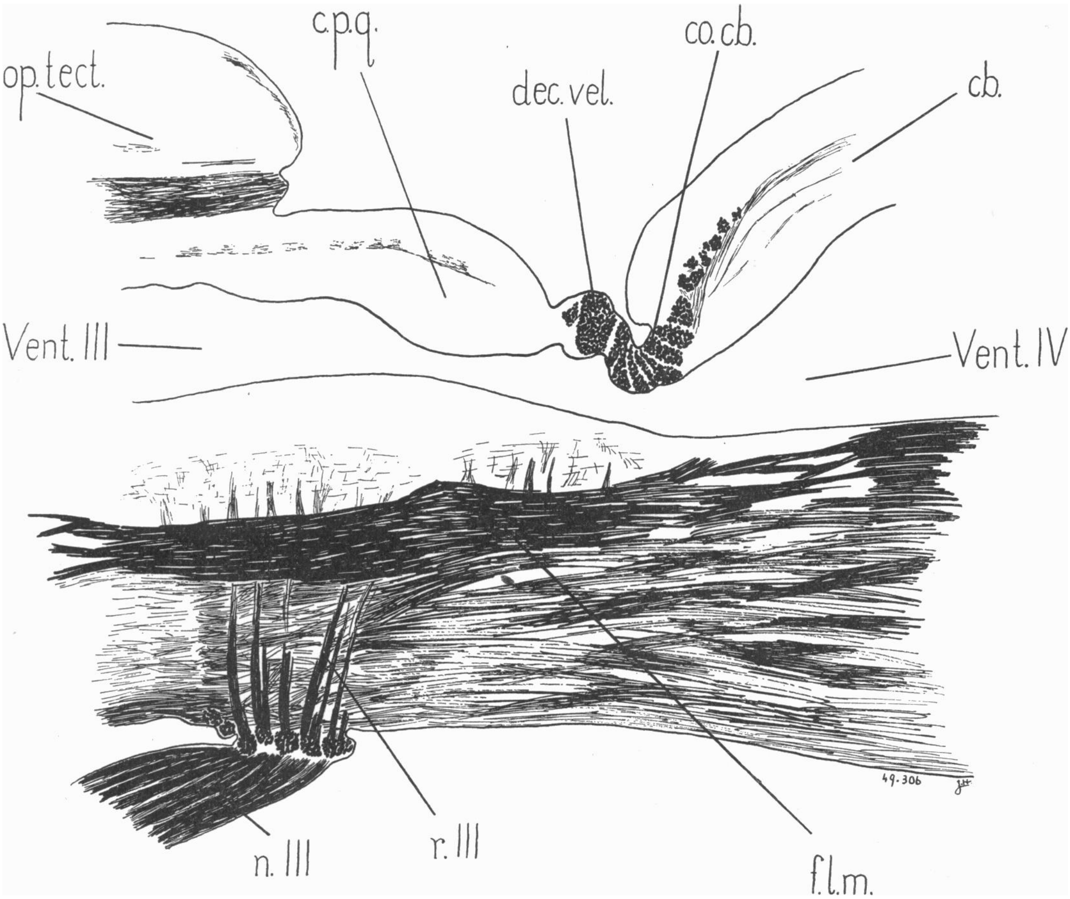

Fig. 15

Figs. 15–20. Longitudinal sections of one brain from medial to lateral.

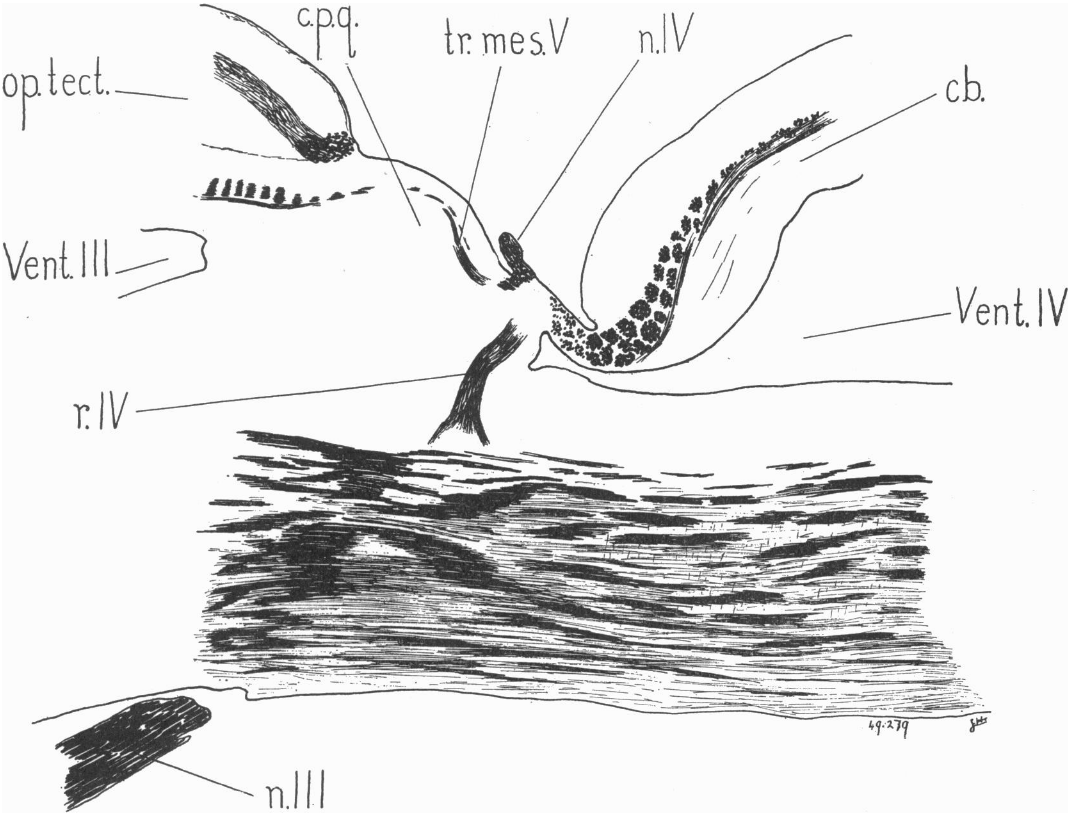

Fig. 16

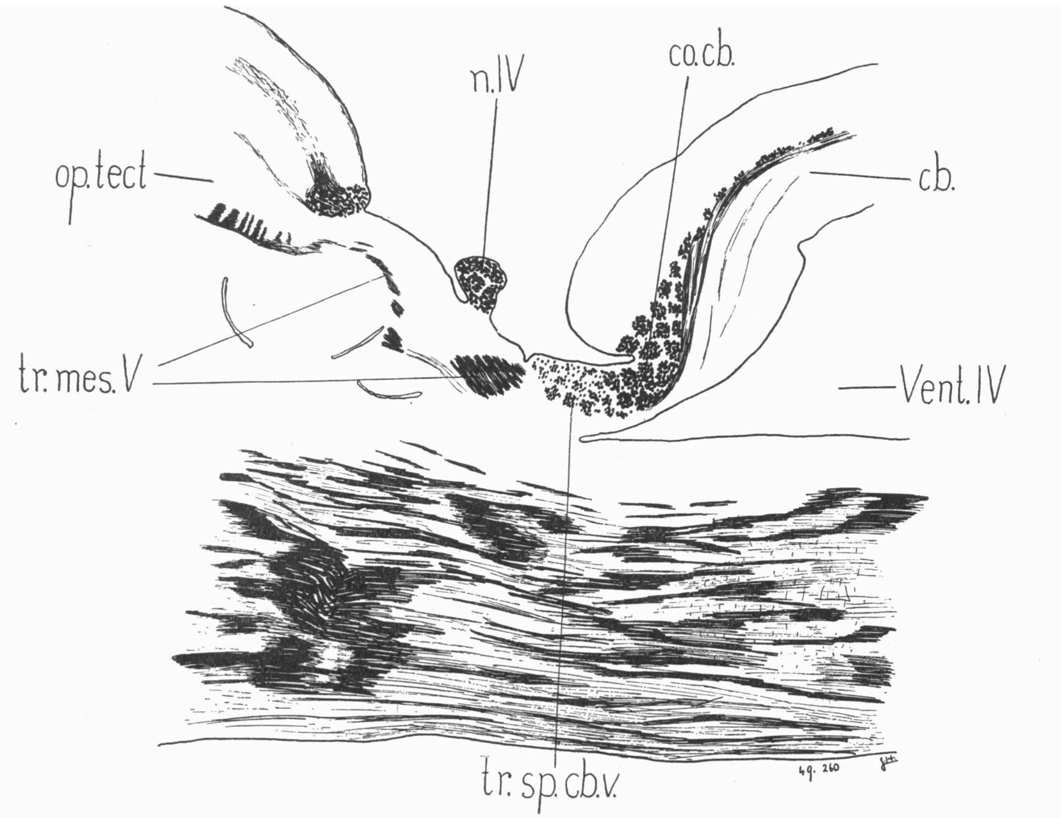
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Fig. 17

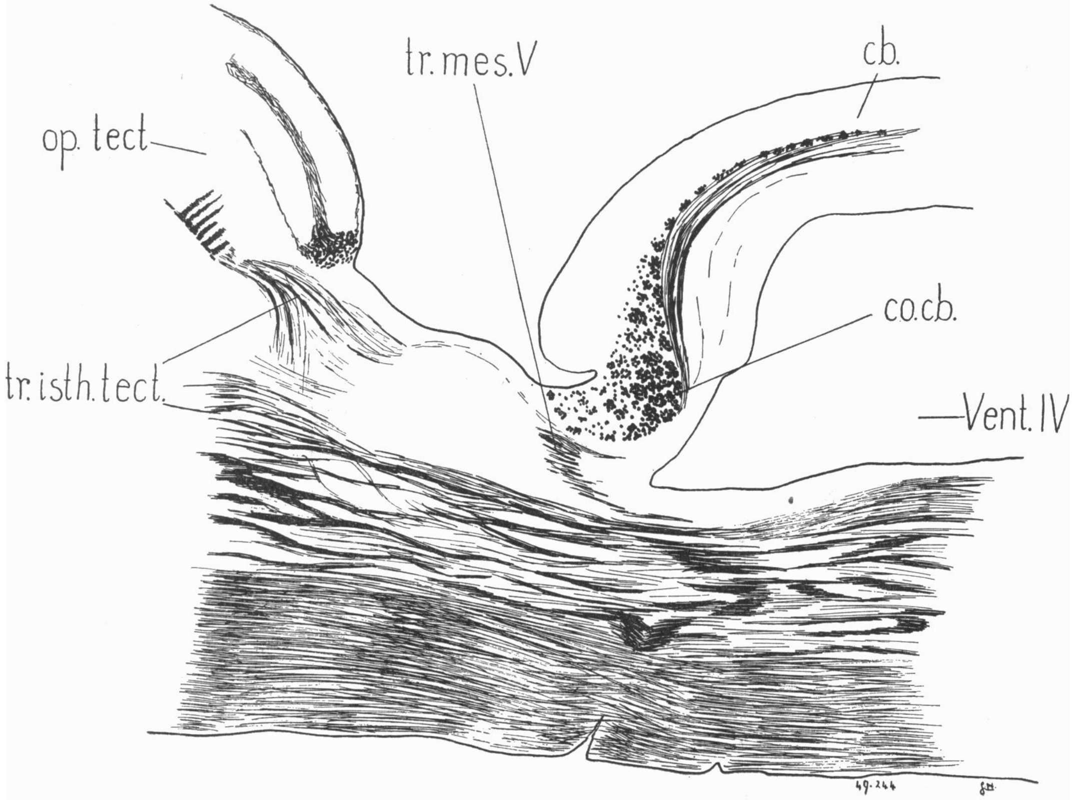
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Fig. 18

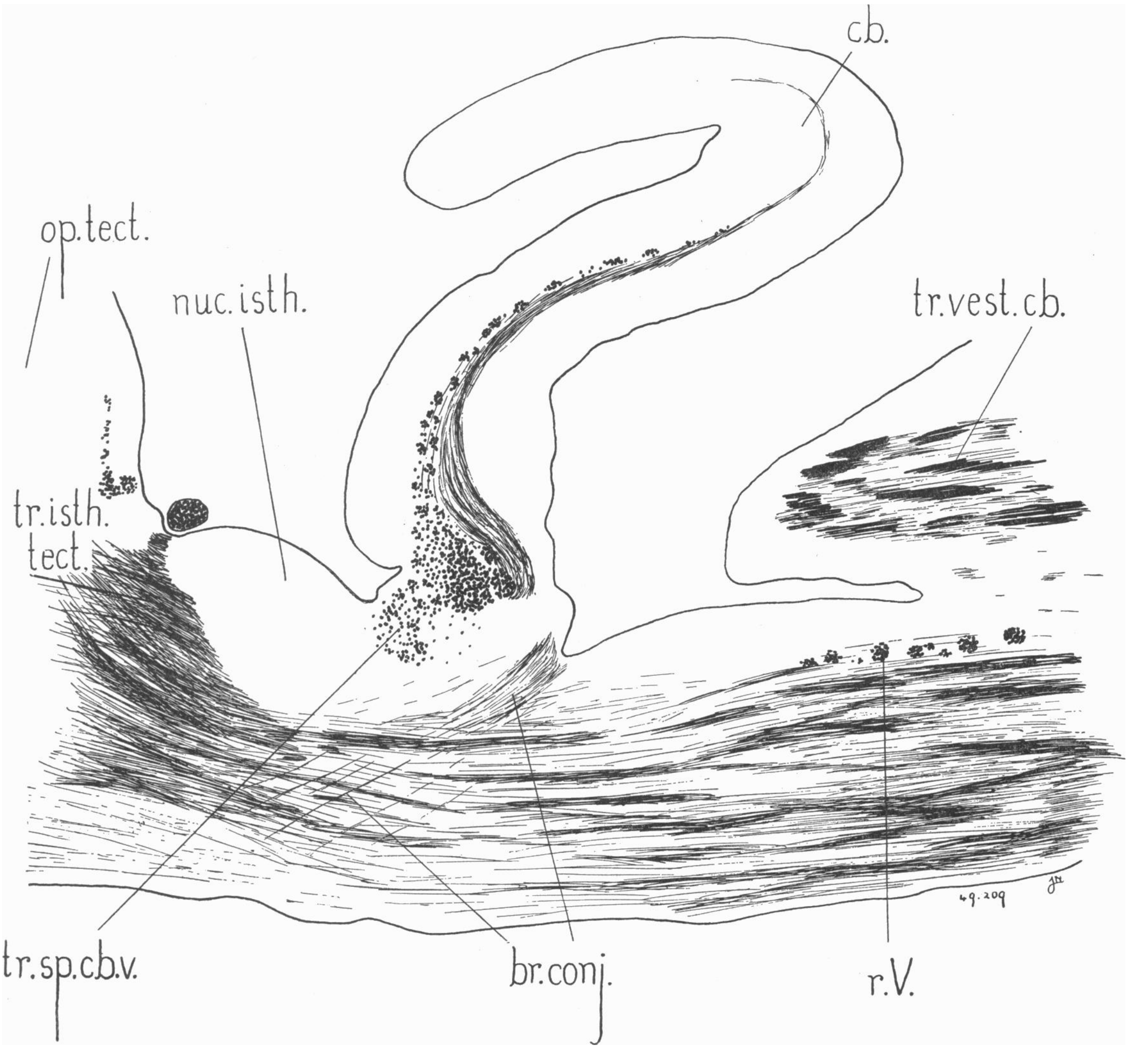
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Fig. 19

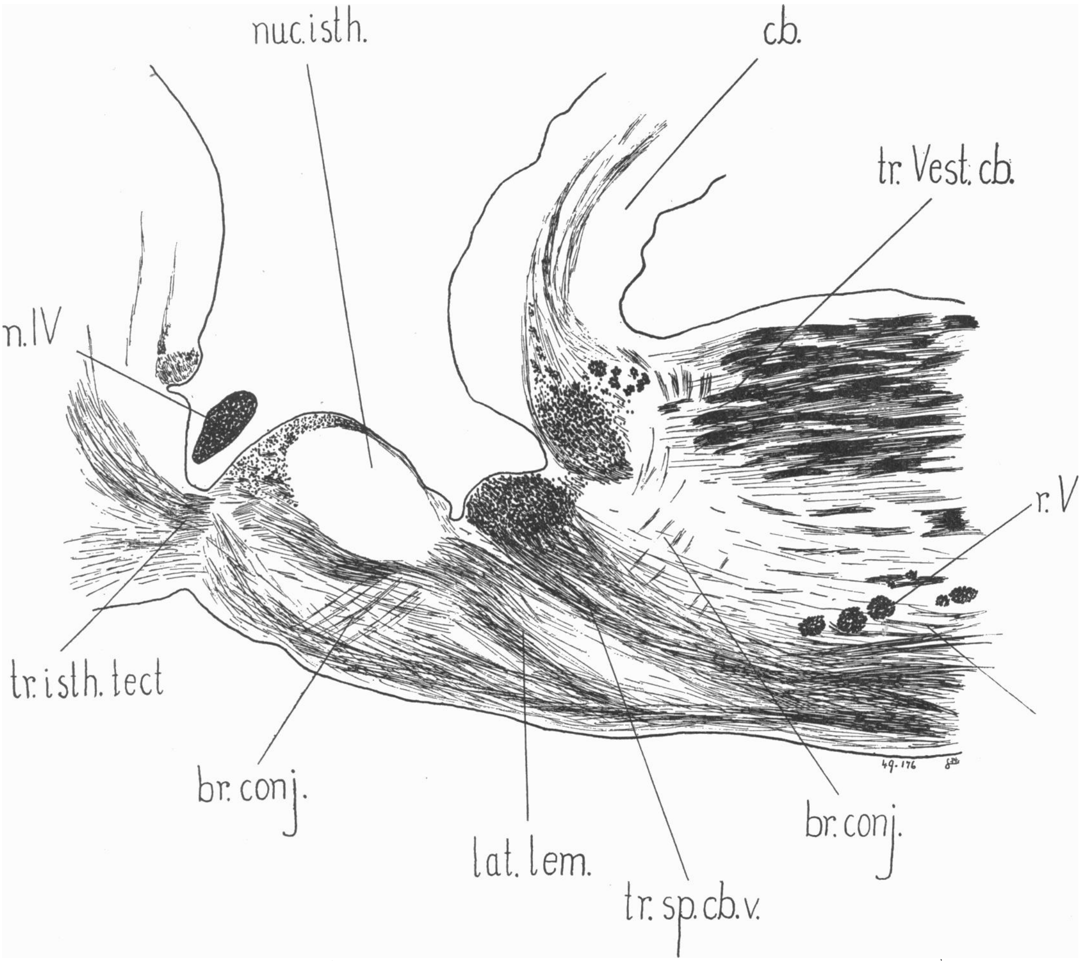
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Fig. 20

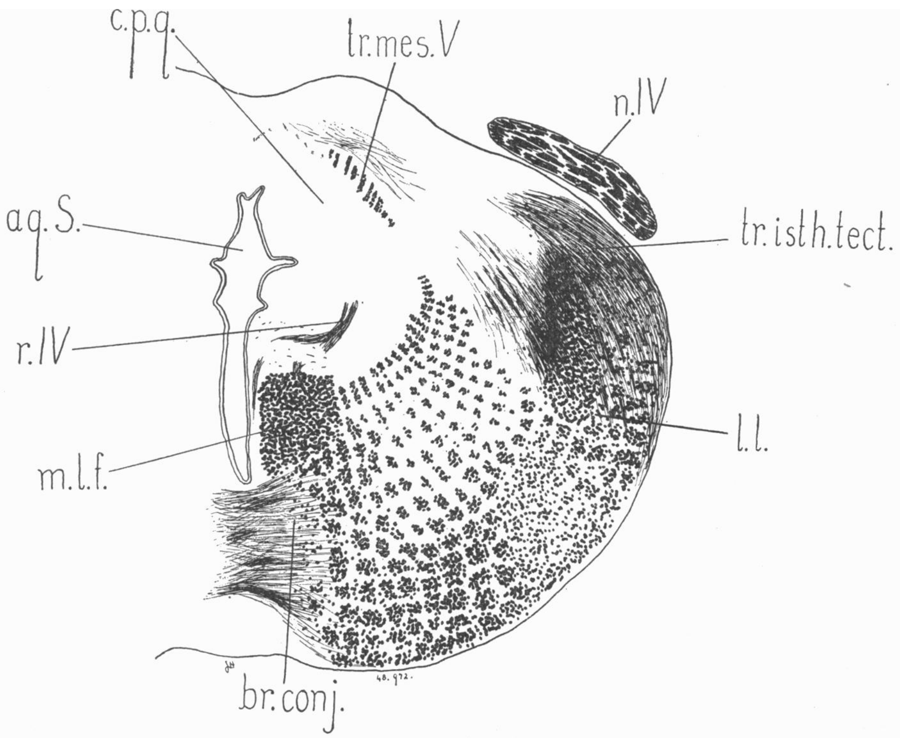

Fig. 21

Figs. 21–27. Transverse sections from before back through the cerebellar region of one brain.

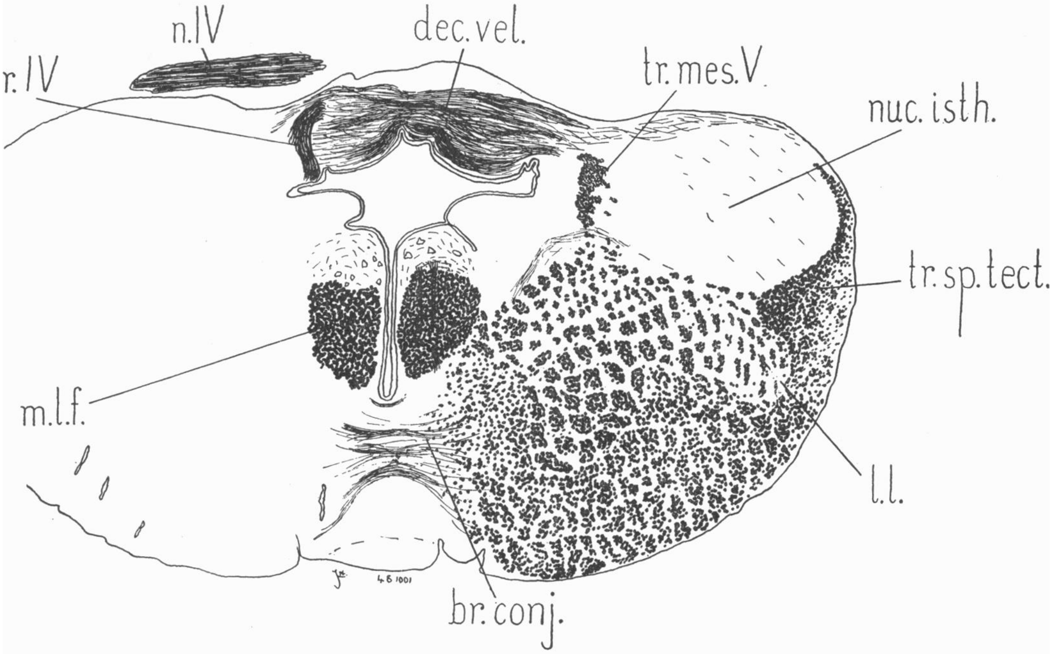

Fig. 22

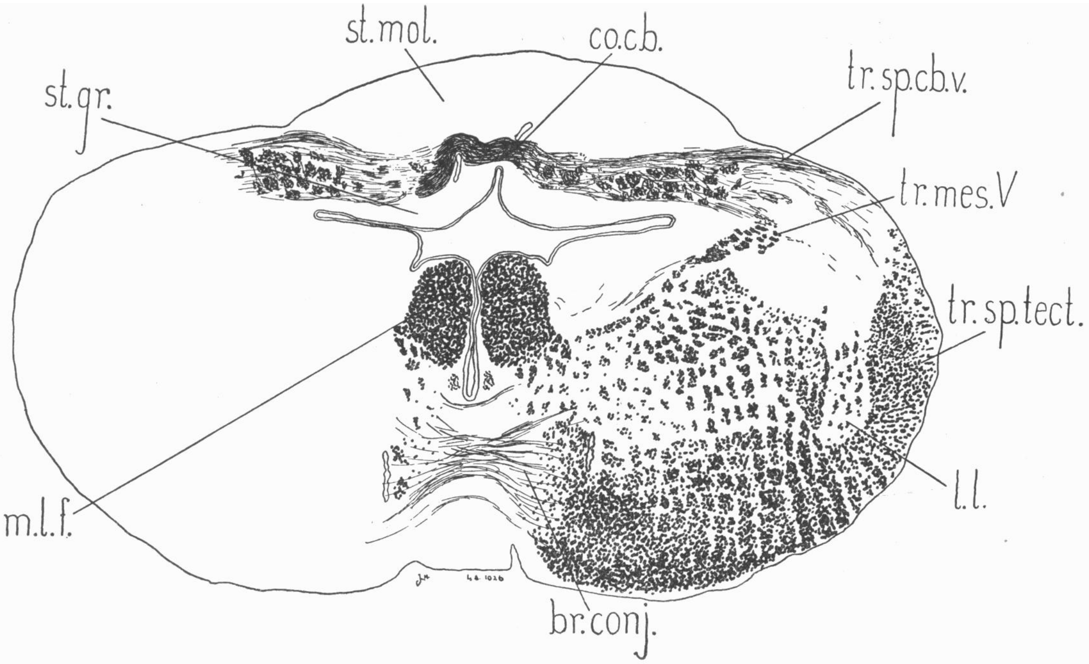
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Fig. 23

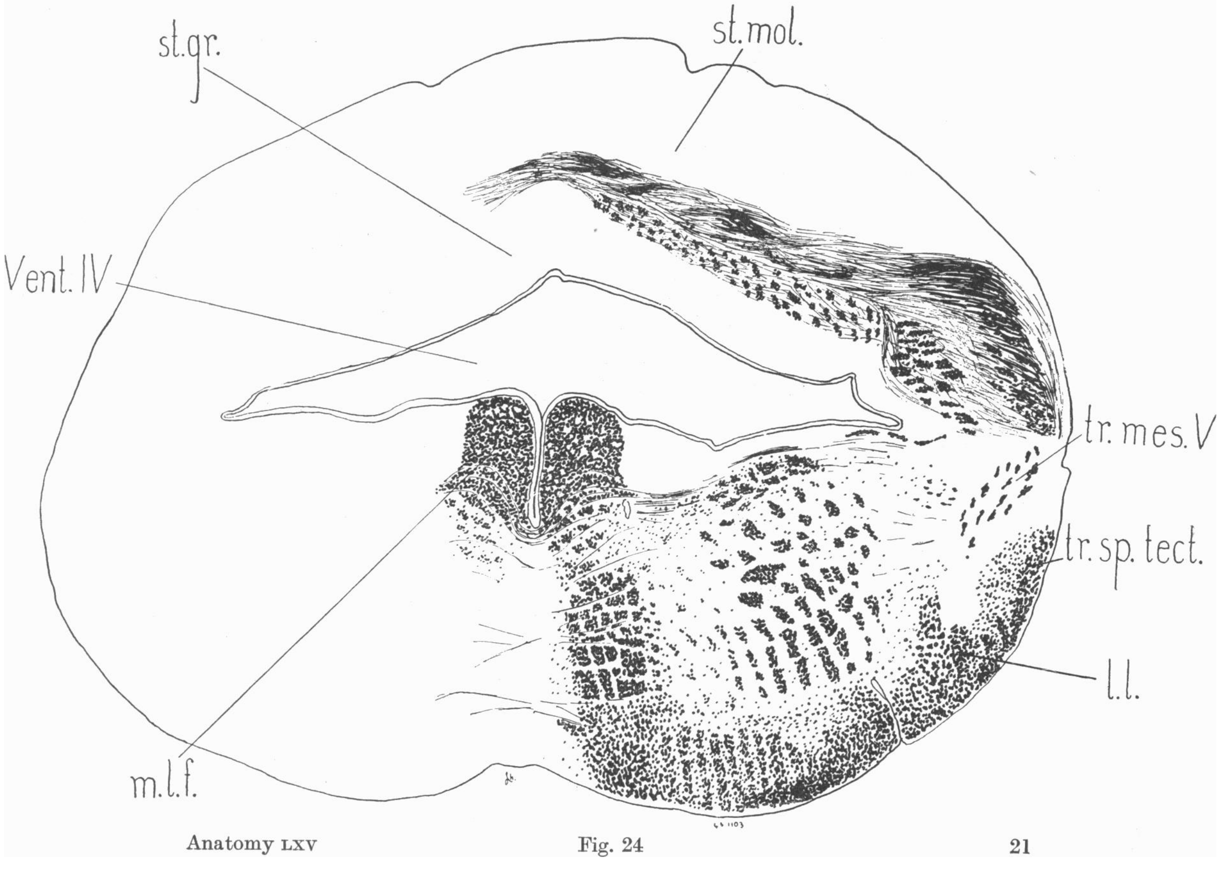
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Fig. 24

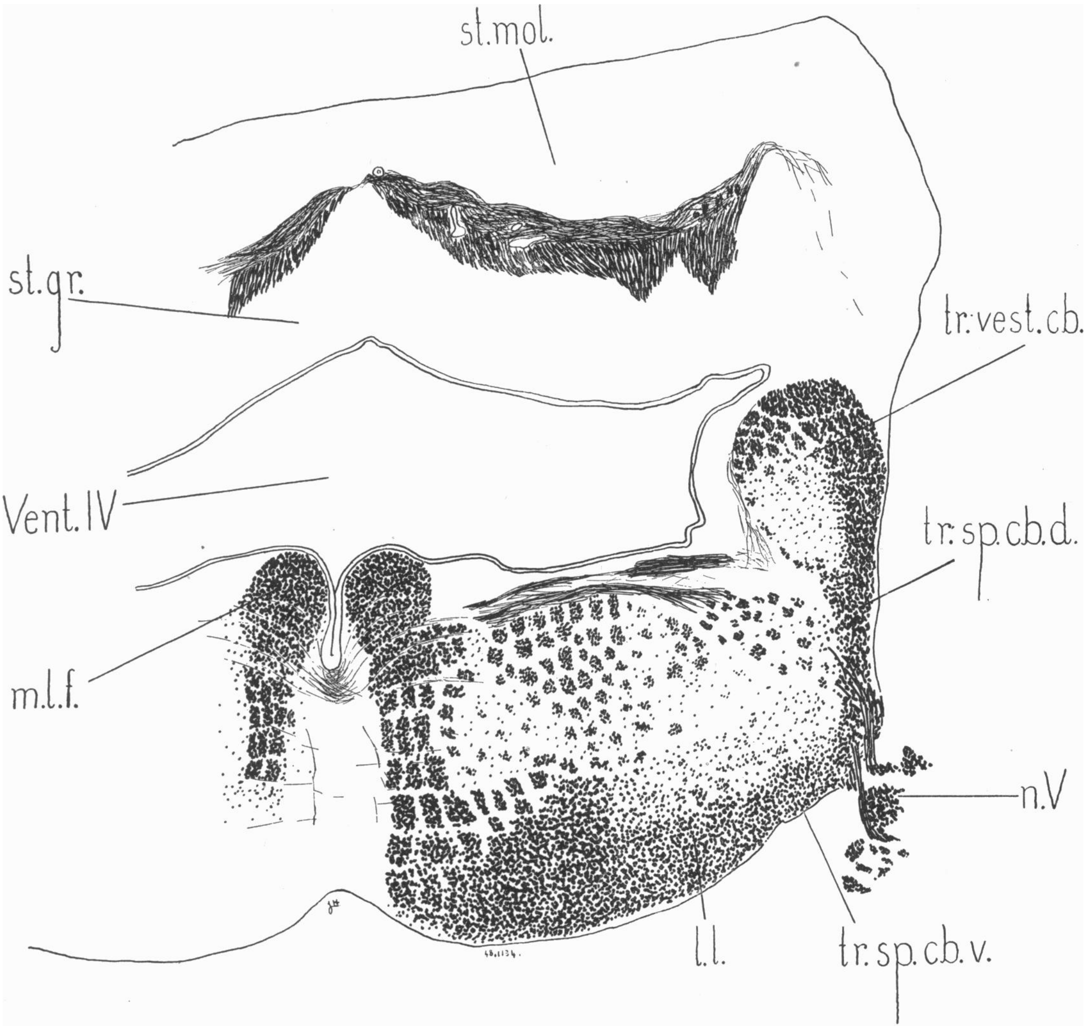
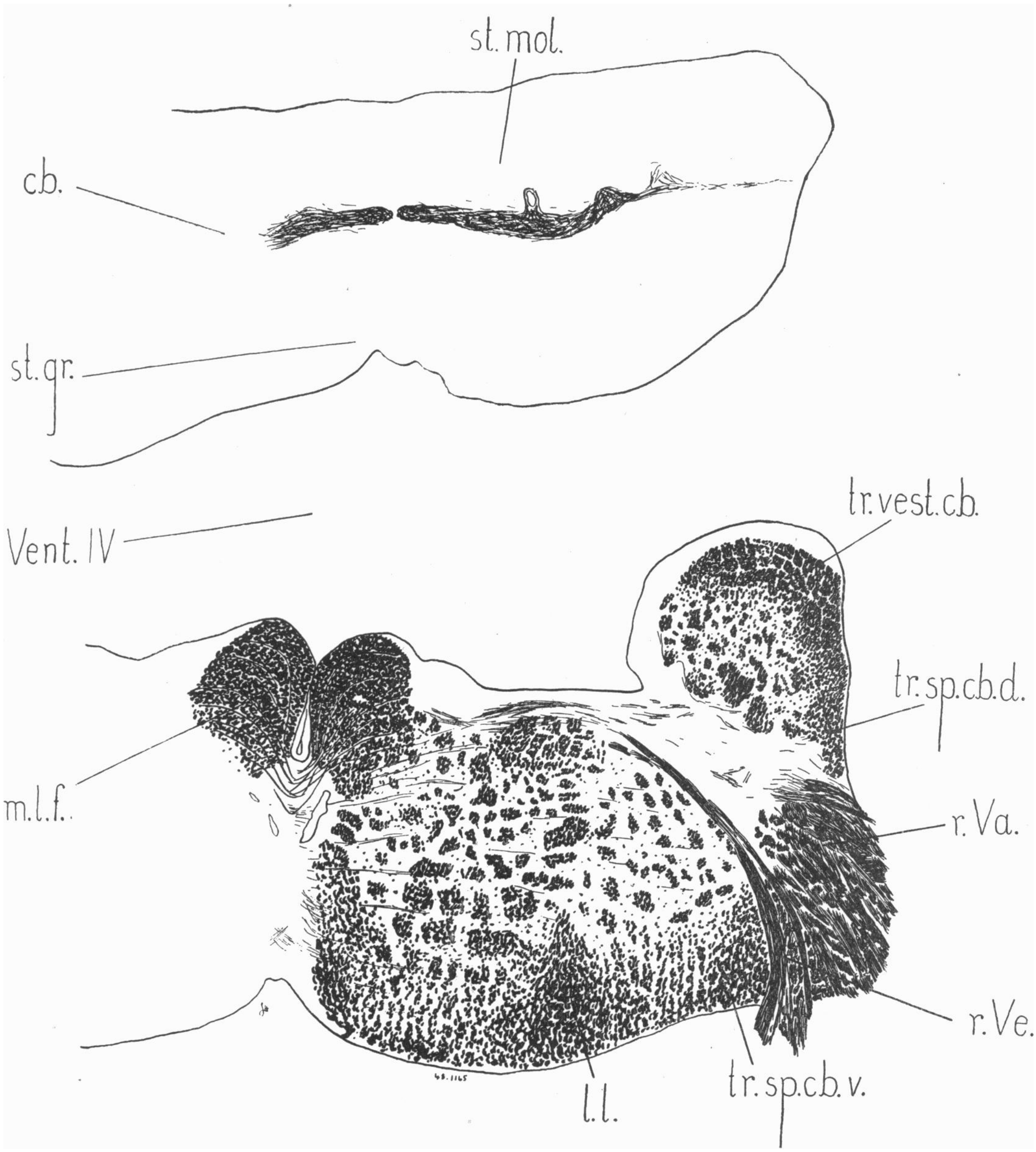


Fig. 25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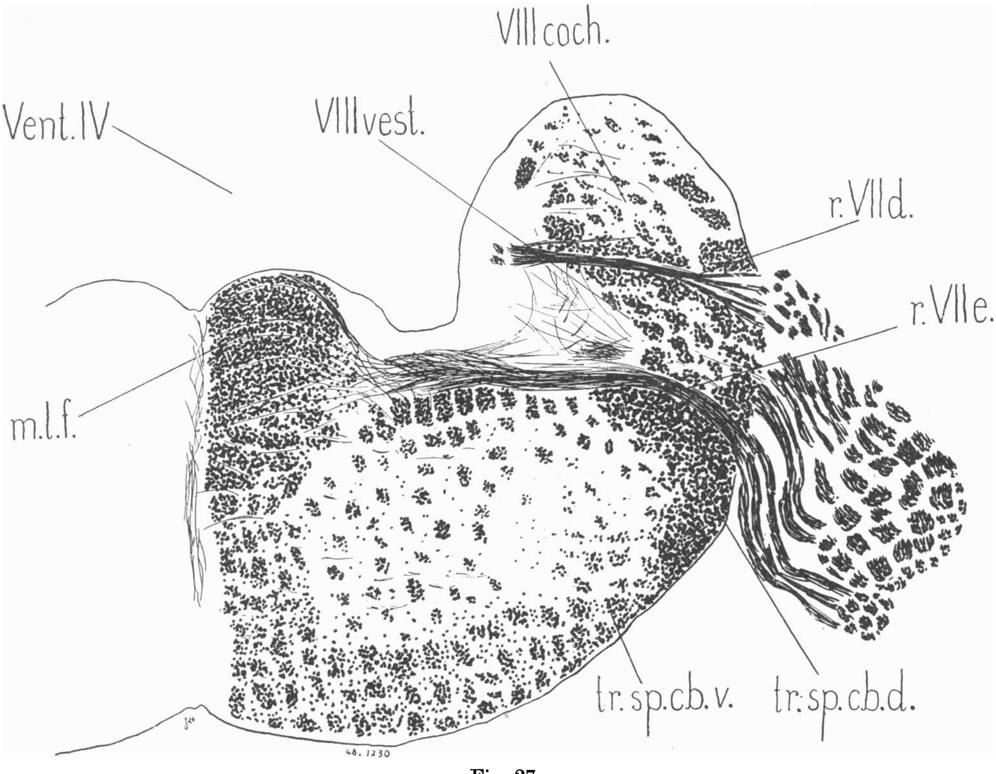
l.l.

Fig. 26


VIII coch.
Vent. IV
VIII vest.
r. VII d.
r. VII e.
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tr. sp. cb. d.
48. 1230

Fig. 27