

THE DEVELOPMENT OF THE CEREBELLAR  
FISSURES IN CERTAIN MAMMALS.

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A Thesis

Presented to the Faculty of the Graduate School of the  
University of Oregon.

In partial fulfillment of requirements for the degree of  
Master of Arts.

February 1934.

## Preface.

This thesis has been prepared from the observations made on the development of the cerebellum in the genus *Corynorhinus*. The work was done in the Anatomy Laboratories of the University of Oregon Medical School. All the materials necessary for this study were made available to me by the Department of Anatomy.

It is with pleasure that I acknowledge my indebtedness to Dr. Olof Larsell, whose criticism, counsel and encouragement have been most valuable to me in this study. I wish to express my thanks to all others who have assisted in any way in the preparation of this thesis.

### Introduction.

The cerebellum is an organ which has received the attention of the anatomist for many centuries. He failed here, as in many other fields, to gain a concept of its true structure because he confined his observations to adult forms which were highly specialized and extremely intricate in their patterns. As a result, his knowledge remained superficial and fragmentary and will continue to remain so until "nature -----teaches him to unravel her tissue in the same order in which she herself composed it." Emanuel Swedenborg (1744).

Kuithan (1894) and Stroud (1895) made the first real attempts to study the cerebellum from the standpoint of its embryological development. Elliot Smith (1902-05) and Bradley (1904-05) further advanced our knowledge of cerebellar structure, each offering his own classification for lobes and fissures, but both based upon its ontogeny and phylogeny. Bolk (1906), Ingvar (1918) and others who have added to our knowledge have used facts gleaned from the field of comparative neurology and embryology.

The studies of Herrick (1914-24), Larsell (1920, '23, '25, '31, '32) and others on the amphibians and Larsell (1926, '32) and others on the reptiles has further stimulated interest in attempts to unravel the puzzle of the cerebellum.

The bat, *Corynorhinus*, has been chosen as the subject of this study because: (1) It is a mammal, (2) it has a simple cerebellum which may be studied in the adult with comparative ease, (3) the brain is small enough to lend itself to serial section methods, (4) such a study has never, to our knowledge, been attempted heretofore.



### Review of the Literature.

The cerebellum was known to the ancients. Aristotle called it "parencephalis" according to Tilney (43). The older anatomist described the cerebellum in the human in some detail but their terminology failed to fit the mammalian group as a whole because they were dealing only with a highly specialized form. Stroud (44) states in his paper (1895),

"Perhaps the greatest cause for this misconception lies in the fact that at first it was not thought worth while to study other than human brains. So the human condition was taken for the standard; and when the brains of lower animals came to be studied they were warped into an agreement with the assumed standard condition found in man."

"Now this is a serious error, for the human cerebellum represents a highly specialized form. It is, in fact, a morphological monstrosity and can in no sense be taken for the typical mammalian organ."

The anatomy of the cerebellum at this period before a real study of simpler forms had been attempted may be summarized from Gray's Anatomy (11) (New American from the Eighth and Enlarged English Edition.--1878) pp. 632-635. Here we find the weight, size and shape of the cerebellum given in detail. The surface anatomy is discussed with the different areas usually named from a descriptive standpoint. The main parts were two lateral hemispheres, an inferior and a superior vermiform process. The inferior vermiform process was divided from the inferior region upward into nodulus, uvula, pyramid and the commissura brevis. The inferior surface of the hemisphere was divided in the same direction into flocculus, (sometimes called pneumogastric lobule, because of its situation behind the pneumogastric nerve) tonsil, digastric and slender lobes. The superior or upper surface of the hemispheres which is separated from the above parts by the great horizontal fissure consists of two lobes on each side. These are called the inferior or semilunar lobe and the anterior or square lobe. The inadequacy of such a nomenclature, when attempting to apply it to lower forms, is evident.

One of the first and best works on the development of the cerebellum is that of Bert Brenette Stroud (44), which appeared in the Journal of Comparative Neurology in 1895. His review of the earlier literature on this subject will be quoted directly as most of the references are not available to me. He states pp. 85-



"During the first quarter of this century an interest began to be manifest in the development of the cerebellum. The writings of one French and three German investigators upon this subject are recorded. The first work that I have found mentioned was in 1812, by Ios, et Car. Wenzel (51). It is quoted by Burdach (8) (3,419), who states that in a child three years old the ratio of the cerebellum to the cerebrum was 1:6.

In 1814 Ignaz Döllinger (10) stated that at the middle of fetal life the cerebellum is proportionally the smallest, being to the cerebrum as 1:24, but that it rapidly increases until at one month after birth the ratio is 1:17, and in the adult it is 1:6.

In 1815 Serres (40) stated that in the human embryo the cerebellum does not appear until the seventh week of development, and in the fowl until the sixth day of incubation. He also says that the organ is formed in the following manner: two laminae spring from the crura of the cerebellum (Kleinhirnschenkeln) and come to rest against each other at the mesen. Later they gradually grow together, after which new lamellae are added, both cephalad and caudad, and transverse furrows appear and multiply.

In 1816 Fiedemann (47) says, 'At the beginning of the second month a soft fluid substance occupies the place of the cerebellum, later in the month two small thin plates arise from each side of the oblongata, along the fourth ventricle, turn inward and rest against each other, but do not unite until later. In the third month they have increased in size and represent the corpora restiformia, called peduncles by Willis and crura by other anatomists'.

There follows a period of about forty-one years during which no attention appears to have been given to the subject.

The next reference that I find is a work on the development of the brain by Krishaber published in 1865; the next to a description of a fetal brain by Callender (9) in 1870.

1874. His, (18) says, 'The cerebellum, in most orders of mammals, is divided into a middle part (vermis) and two lateral pieces separated from it by a furrow. The vermis is formed from the mesal roof of the brain tube, i.e., out of such constituents as were present before the development of the lateral masses (hemispheres).'

1876. Mihalkovics (36) says, 'The roof of the opencephal (Hinterhirndecke) forms an expanded lamella which arches over the epicoelo. At the right and left it bends over into the epicoelian floor. Cephalad, it is separated from the mesocoelian roof by a constriction and becoming thinner caudad, merges into the metatela. From the caudal aspect, because of the wedge-like cephalic point of the metatela, this lamina looks like a pair of lateral plates. This plate may be called Kleinhirnlamella, (lamina cerebelli) because it is the proton (Anlage) of the future cerebellum. The cerebellum is formed from this lamella in the following manner: the cephalic portion of this lamella thickens, while the caudal edge at the transition into the metatela becomes sharpened.'

This thin margin bends ventrad and there results a plait-like folding in along the caudal edge of the 'Kleinhirnlamella.' The cephalic, thickened part of this transverse plain (or fold) is the proper proton (Anlage) of the cerebellum. The caudal is the 'hinteres Marksegel,' (velum medullare posticum, v. Tarini) or what the writer (Stroud) calls kilos. From his own observations the writer (Stroud) can not accept this view as to the development of the cerebellum.

1877. Alix (1) published a paper on the fetal brain.

1878 Killiker (26) says, 'The cerebellum is developed as a thickening of the cephalic part of the roof of the opencephal (Hinterhirn), which soon assumes the form of a transverse plate. From the lateral aspect it looks as though it bent around the opencephal (Hinterhirn).'

1884 Wilder (52) figures the cerebellum of a human embryo in which the lateral parts are massive, the mesal region is thin and presents a wide groove upon the dorsal surface. It is probably a little older than the embryos shown in Figs. 54 and 56 Pl.V.

1890 Hertwig (16) says, 'The wall of the fourth brain vesicle undergoes a considerable thickening in all of its parts, and surrounds its cavity in the form of a ring, differentiated into several regions. The floor furnishes the pons. From the lateral walls arise the pedunculi cerebelli ad pontem. But it is the roof that grows to an extraordinary extent and gives to the cerebellum its characteristic stamp. At first it appears as a thin transverse ridge which overhangs the thin attenuated roof of the medulla.'

1891. C. L. Herrick (13) describes his investigations upon the brains of rodents and certain reptiles. He obtains results which throw a new light upon the



cerebellum and mark an epoch in the study of its histogenesis. He has discovered proliferating regions in the epicoolian roof which apparently are identical with the writer's (Stroud) lateral protons. Professor Herrick makes a strong plea for the application of the comparative method to the study of neurologic problems. To this the writer (Stroud) joins his most hearty support.

1891 His (19) discusses the development in the human brain of the region from the isthmus to the myel, during the period from the end of the first to the beginning of the third month. He includes the entire region under one segment, the Rautenhirn, but does not deal especially with the cerebellum.

1892 His (20) gives a brief description of the development of the cerebellum. He says, 'The embryonic ependymal (Hinterhirn) appears as a conical tube of which a portion of the metatela (Rautenfeld) forms a part. Its caudal limit is at the pons flexure, its cephalic, if we first subtract the constituents of the isthmus, is at the isthmus flexure. Between the pons flexure and the isthmus flexure lies the dorsally convex knee of the ependymal. The metatela narrows rapidly caudad from the knee, but a narrow extension of it, whose edges are nearly parallel, extends cephalad. The floor of the metopicole (fourth ventricle) is formed from the ventral zone, (Grundplatte) the cerebellum from the dorsal zone (Flügelplatte). Its hemispheres are formed in the higher vertebrates from the part of the dorsal zone lying caudad of the knee, the vermis from the part lying cephalad of it.'

1893 Schäfer says, 'The roof of the fourth ventricle inferiorly becomes greatly thinned and expanded. Superiorly the tube becomes gradually more contracted and the roof thicker. This thickening being the rudiment of the cerebellum and of the valve of Vieussens. In the human embryo, the cerebellum is seen as early as the second month as a thin plate arching over the cephalic part of the metopicole (fourth ventricle). From this plate, which enlarges only gradually, is formed the middle lobe; later the lateral lobes grow out at the sides.'

'The cerebellum consists of two lateral hemispheres joined together by a median portion called, from its peculiar appearance caused by the transverse furrows or ridges upon it, the worm or vermiform process.....in mammals it is the first part to be developed and to be marked off into subdivisions.' (Idem., Vol. III Part I, p. 69). I shall show that the vermis is not the first part to be developed and marked off into subdivisions.'

1894. Schaper (39) published an account of his exhaustive investigations upon the development of the cerebellum in Teleosts. He confirmed Herrick's discoveries



and made further observations of great value. His work, and also that of Professor Herrick, will remain as landmarks in the history of the comparative development of the cerebellum.

Having thus given a brief resume of the opinions of the men who have made a special study of the development of the cerebellum during a period of nearly a century, I proceed to a consideration of the facts which lead me to differ from some of the views hitherto advanced."

Before considering the findings of Stroud, reference should be made to the work of Kuithan (29) (1894-95). In as much as the original articles are not available at this time I will quote from Ingvar's (21) summary of his work. He states, "Kuithan studied the embryonic development of the Cerebellum of the sheep and compared it with certain stages in the human. The cerebellum has, according to him, very early, first an unpaired stage in the form of an arched membrane, then a paired stage, existent out of 2 thickenings in the forward part of the "roof of the after brain", directly in front of the roof plate. These enlarge and gradually fuse in the midline, which procedure begins in the anterior part of the "Anlage". Now the transverse fissures appear. The first fissure, to be observed, is in the midline on the dorso-frontal surface of the cerebellum which continuing to become deeper divides the cerebellum into two parts. This furrow was named the sulcus primus. Immediately after appears the fissure uvulo-nodular, which gradually divides the nodulus from the uvula, and without fail at a similar time a furrow divides the uvula from the Pyramis, which later authors have called the fissura secunda". He identified the sulcus primus as the sulcus superior anterior of man.

In 1895 Stroud (44) published his work as is referred to above. This work will be discussed in some detail as it is felt that the observations are accurate and fundamental, yet for some reason have been neglected by later writers. He studied the brains of many mammals including specimens from every mammalian order but two. He, however, never published any description of these brains nor does he give any figures of them in any of his papers that have been available to me. He also studied the development of the cerebellum in the fetal stages of the cat and human and, less completely, in the pig. He used gross dissection with carefully made drawings, and microscopic sections cut in three planes.

Stroud first shows that the cerebellum is developed from bilateral alar plates fuse across the midline forming a single structure. This is a distinct contribution as

previous workers, including Kuithan, had held that the "cerebellum has very early, first an unpaired stage in the form of an arched membrane." (Kuithan see above). Stroud's observation has come to be generally accepted for we find in Streeter's section on the development of the cerebellum in the human, in "Manual of Human Embryology, Keibel and Mall (25)" The character of the cerebellum at the end of the first, second, and third months is shown in Figs. 34, 44, and 45 respectively. This covers the period from the time when it exists as simple bilateral alar plates to the time when it fuses across the median line as a transverse mass consisting of a median vermis and two lateral lobes."

This early conception has been strengthened by the more recent work of Herrick and Larsell on the phylogenic history of the cerebellum.

Stroud (44) finds the dorsal aspect of the cerebellum of the 'fairly late embryo' to be divided into the following divisions which he considers fundamental.

- (1) The vermis, unpaired.
- (2) The pilea, paired. (Hemispheres)
- (3) The paraflocculus, paired; in the lower mammals each is divided into supraflocculus and mediflocculus.
- (4) The flocculus, paired.

Of all these, the separation of the vermis from the rest he found took place last.

He states that the first distinct furrow to form is the parafloccular sulcus which separates the paraflocculus from the pileum. Examination of his figures 8, 9, 10, and 11 (cat) and 56, and 57, (human) would lead one to believe that the floccular fissure was the first formed and the most prominent at the stages illustrated. He shows the uvular nodular sulcus as developing dorsal to the floccular fissure.

He describes the paraflocculus in detail and notes the great reduction in its size in the human. The supraflocculus is said to join the post pileum by "substantial nervous substance". The mediflocculus is also observed to join the post-vermis by a ridge of nervous substance which he names the vermian tract. These connections are obscured in the adult stages particularly in the human due to the superficial development of adjacent parts.

The flocculus is recognized as a separate structure from the paraflocculus. It is described as connected to the posterior vermis but not to the nodulus directly. In summarizing the later relations of flocculus and paraflocculus to the vermis, particularly in the human he



states, "They are compressed and forced lateral by the enormous growth of the postpileum (posterior part of the hemisphere) which finally overshadows and dwarfs them. Their mesal extensions are submerged by the growth of the adjacent parts; they apparently exist only as bundles of fibers running to the post-vermis, imbedded in the foundation mass of alba."

Elliot Smith (41,42,43) published many articles on this subject all of which were not available to me. They appeared from 1899 to 1903. The article most frequently quoted and the one which has so profoundly influenced later workers in this field was published in the Anat. Anz. in 1903 (43). As it most clearly expresses his final opinion on the subject it will be reviewed in some detail.

He studied the adult brains of many mammals and the developmental stages of *Dasyurus*, *Trichosurus*, *Macropus* and *Homo*. From these varied types he concludes that the following fissures are constantly present in all mammals:

- (1) Fissura Floccularis,
- (2) Fissura Parafloccularis,
- (3) Fissura Postnodularis, (uvulo-nodular)
- (4) Fissura Prima and
- (5) Fissura Secunda.

He observed in the pouch specimen of the *Dasyurus vevorrimus* that at an early stage in its development the fissures flocculus and paraflocculus cut into the lateral margin of the cerebellum and separate two appendages, the flocculus ventrally and the paraflocculus dorsally. In his division of the cerebellum, recognizing as he does the fact of their separate formation, he places them in one lobe the "lobus floccularis". He tells us that, "The medial portion of the organ soon becomes subdivided by the remaining three fissures listed above. They begin in the medial portion and extend laterally. Although again recognizing that the postnodular fissure is the first to appear he neglects it for the other two and uses them to determine the boundaries of his divisions of the cerebellum. These he names the lobus anticus, (anterior to the fissura prima) the lobus medius, (between the fissura prima and secunda) and the lobus posticus which includes the uvula and nodulus. His explanation for this decision is because "they are so small and present so many features in common that it is convenient to group them together as one lobe". He also describes in detail the cerebellum of the *Notoryctes typhlops* (Sterling), the marsupial mole, both in its gross characteristics and the outline and relations of the cerebellar surface and the stratum granulosum as they are revealed by a serial section cut in the sagittal plane.



The median sagittal section shows the cerebellum divided by the three medial fissures mentioned above, into four simple leaves of unequal size. He states, "Each tapering lateral extremity of the posterior lobe and the ventral lateral part of the posterior surface of the middle lobe is prolonged laterally into direct continuity with the lobus flocculus." On examining the serial section he is convinced that the uvula takes no part in this but that the granular layer of the nodulus is continuous with the lower part of the lobus flocculus, and that the granular layer of the middle lobe becomes constricted to a tail like process, which remaining independent of the lateral extensions of both uvula and nodulus finally terminates in the upper pole of the lobus flocculus. The former vermal connection he names the "ala noduli", the latter the "copula pyramidis". He finds the granular layers of the lower part, presumably flocculus, is freely continuous with that of the dorsal portion, presumably paraflocculus.

In analysing his figures (pp. 374 and 376) Smith (43) fails to show where the fissure between the flocculus and paraflocculus is, and which part of the lobus flocculus is flocculus and which part is paraflocculus. He does not state whether the shallow fissure in Fig. 17 remains as he proceeds laterally nor does he name it. He does not tell us what happens to the tiny lobe in Fig. 10. The assumption is that this is the flocculus which then enlarges laterally to form the larger lobule seen in Fig. 11, whose granular layer is very clearly "in free continuity" with that of the rest of the lobe. These structures are not labelled separately nor is the transition from Fig. 10 to Fig. 11 shown clearly enough for one to be sure that such a transition does occur. Is it possible that Smith's lobus flocculus as labeled is in reality the paraflocculus alone? Against this possibility is his definite statement that the stratum granulosum of the lobus flocculus is continuous with that of the nodulus.

For purposes of comparison I am including a copy of the Diagram of the Mammalian Cerebellum as conceived by Elliot Smith, taken from the reference quoted above of 1903 (43) (Fig. 1). One can see from the above diagram that Smith considers the relation of the suprapyramidal fissure and the parafloccular fissures to be quite variable both to each other and to the other fissures in the posterior lobe. His position in this regard can best be given by the use of a few short quotations.

No suprapyramidal fissure was present in the specimen of *Notoryctes* described, although there was a slight indication of one on some of the others examined.

He tells us that in the Perameles the suprapyramidal fissure is present and becomes confluent with the para-floccular fissure. The paraflocculus is separated from the flocculus by a definite fissura floccularis. This arrangement holds also for most of the smaller mammals examined. An occasional anomaly occurs in which the paraflocculus is partially or wholly attached to the uvula. Fig. 19, which is "the caudal aspect of the abnormal cerebellum of a pouch-specimen of *Trichosurus vulpecula*", is sighted as an example of the condition. He ascribed a similar finding of Bradley (see below) in the *Lepus* to an anomaly also found such an arrangement in the foetal brain of the calf.

"Such anomalies show that it is misleading to speak of the paraflocculus as 'belonging' to any part of the vermis, because the purely mechanical factors of fissure formation may produce all sorts of fortuitous combinations of surface area." In a foot note at this point he says, "At the same time it shows that the term 'copula pyramidis' cannot be applied to all mammalian cerebelli."

At another place we find these words, "I have already referred to the supra-pyramidal and parafloccular fissures resulting in the formation of a peculiar band, which I have called the copula pyramidis. In my earlier memoirs on this subject I have perhaps attached undue importance to this really insignificant phenomenon, common though it be in the mammalia."

"In the larger mammals the parafloccular fissure cuts into the alar parts of the middle lobe (Smith's) without becoming confluent with any important fissure."

The next contributor to the subject which we are discussing is O. Charnock Bradley (4,5,6). His first paper (4) appeared in 1899 on the cerebellum of the horse. It was not until 1905, however that his work (5) on the Development and Homology of the Mammalian Cerebellar Fissures was published in the *Journal of Anatomy and Physiology*, London. Recognizing the work of Stroud as "undoubtedly the best work that has been done in the way of attempting to clear away morphological difficulties" of the mammalian cerebellum. He nevertheless criticises all the previous workers including Stroud, Kuitan, and Platau and Jacobsohn, for their apparent desire "to find, if possible, homologies to the lobes of the cerebellum of man." This, he felt, was a mistake and states, "In questions of this sort the brain of man should be lost sight of as far as possible, since it is admitted to be an organ which has far outdistanced, in its evolution, the brain of the average mammal." In his first paper



he does not mention the work of Elliot Smith although it is dealt with at length in his later work.

It is of interest that Bradley first intended to study the development of the cerebellum in the shrew, prompted by the description of the brain of the shrew and the bat by Miss Arnback-Christie-Linde (2) in 1900. Due to the difficulty in obtaining sufficient embryos in this species he chose the rabbit for his first report. He also studied the development of the cerebellum of the pig embryo and in a later study (6) in 1904 and 1905 reports the development in the sheep, calf, horse and the human, the last 3 being far from complete.

In addition he gives us detailed descriptions with figures of the adult cerebellum of many different species. In order to avoid any dependence on human anatomy and its nomenclature, Bradley devised a system of letters and numbers to label the lobes and fissures of the mammalian cerebellum (Fig. 2). Schematically the lobes described by Bradley (See Fig. 2) and their corresponding areas as they are known today are indicated below.

| Fissures                                |           | Lobes |                         |
|---|-----------|-------|-------------------------|
| Bradley's                               | Bradley's |       |                         |
|   | A1        |       |                         |
| c fissura precentralis(Smith)           |           | A     |                         |
| I fissura preculminatis(Smith)          | A2        |       | Anterior Lobe           |
| II Fissura Prima                        |           | B     | -----                   |
| b Sulcus postclivalis (human)           | C1        |       |                         |
| a Sulcus horizontalis magnis<br>(human) | C2        | C     | Middle Lobe             |
|   | C3        |       |                         |
| III Fissura prepyramidalis              |           |       | -----                   |
| d Fissura secunda                       | D1        |       | Pyramis                 |
|   |           | D     |                         |
| IV Fissura Uvulonodularis               | D2        |       | Uvula                   |
|   |           |       | Post. Lobe of<br>Ingvar |
|   |           | E     | Nodulus                 |

Bradley (5) found that the fissures in the rabbit and pig appear in the following order: IV, II, III, I. Contemporaneous with the appearance of fissure II a pair of depressions grow in from either side to mark off the paraflocculus from the rest of the hemisphere. These two fissures finally join with fissure III and thereby make the paraflocculus the lateral outlying territory of lobe D. He believes that fissure IV separates lobe E



(nodulus), the posterior medullary velum and the flocculus from the rest of the cerebellum and that the flocculus is the lateral outlying territory of Lobe E (nodulus). It will be noted that he describes no fissure d in the rabbit and states that it does not occur until the squirrel is reached. This is in direct contradiction to Elliot Smith's statement that this is one of the 5 fissures common to all mammals. In the higher mammals he finds this fissure more constantly present and very early dividing lobe D into two parts (pyramis) D1 and D2, (uvula). When present this fissure not only divides Lobe D but extends laterally into the paraflocculus and divides it into a dorsal and a ventral portion, which is joined to D1 (pyramis) and D2 (uvula) respectively. These primitive connections may be lost in the adult condition or may persist as is the case in the horse. In adult brains he finds the paraflocculus connected to the pyramis more commonly than to the uvula. He differs from Smith in:

1. The use of the Fissura Secunda as the division between two main lobes; (Bradley classing this as the intralobular fissure, d.)

2. The grouping of flocculus and paraflocculus together into lobus floccularis, and uvula and nodulus together into lobus posticus without sufficient regard for the constant presence of the fissures which early separate them;

3. In the statements concerning the relations of the parafloccular fissure to the vermal structures, as being variable in different animals and of the frequent continuity of the paraflocculus with the parapyramidal area both pars biventralis and pars tonsillaris.

One of the chief points of difference seemed to center about the relation of the posterior vermal structures to the paraflocculus. Following my own observations on the rat, reported in part below, it was apparent that Bradley's labelling of the separate lobes of the rats cerebellum was different than mine after having watched their development. On comparing the early stages of the rat with those of the rabbit as given by Bradley I found them very similar but the fissure which I feel is Fissura Secunda, Bradley calls Fissure III and the one he calls Fissure 'a' I would label fissure prepyramidal. If one would compare figures 7 or 10, pp. 128 to that of the sheep in a later article one is struck by their similarity, yet what appears to be the same fissure is labeled Fissure (prepyramidal) III, in the rabbit and 'd' (Fissure secunda) in the sheep. Elliot Smith also interpreted this fissure III in the rabbit to correspond to his fissura secunda for he criticizes Bradley, largely on the basis of his statement concerning



the relations of paraflocculus and uvula, believing that the pyramis lay above this fissure. If he had waited for the conclusion of Bradley's paper, he would have learned that Bradley really considered this fissure to be the fissure supra-pyramidal. This would have given Smith even more to criticize, especially, in that Bradley fails to identify any fissure secunda below the squirrel. This statement does not seem reasonable when one considers the careful work of Elliot Smith on the marsupials. It might be argued that Smith should have named his fissure secunda, "the fissure preapylamidal". However, in Bradley's final opinion he would identify the fissure III as that fissure which becomes confluent with the parafloccular sulcus while the parafloccular sulcus in *Notocytes* proceeded medially well above the F. secunda and in the *Peramylis*, a very similar marsupial it is continuous with the preapylamidal fissure. It is of interest at this point to note that he found "not much" difficulty in tracing the continuity of his rabbit fissure III with the parafloccular sulcus and in describing the rabbit brain at birth he states, "Fissure III fades away in the groove or depression behind the paraflocculus, as does also fissure A." My observations on the development of the fissures in the rat would lead me to believe his 'fissure A' of the rabbit is as close to continuity with the parafloccular sulcus as is the fissure which he has labelled III. Observations on the rat as yet unreported show his fissure III to apparently separate the paraflocculus into dorsal and ventral portions, a function he repeatedly assigns to the fissure d in the pig and other forms. A further comparison of Bradley's figures will convince one that he has confused these fissures in all forms, below the squirrel which he figures, the only exception being those of the hare. If one, however, would change the labels on the rabbit to those I suggest one is struck by the close resemblance to the hare's cerebellum; a resemblance which one would expect to be present considering the similarity of the two species.

Ingvar's (21) figure of the cerebellum of *Mus musculus* (Fig. 45 p. 309) is labeled as I have suggested that Bradley's should have been and is identical to my conception of the fissures in this type of cerebellum.

In conclusion an observation of even greater significance than the conclusions concerning the status of the relations of paraflocculus to vermis is the significant fact that with all their disagreeing and difficulty of interpreting, Smith and Bradley both agree on this fact, that the uvulo nodular fissure is the first to form and that, at a very early stage, it becomes confluent with the floccular sulcus. Bradley further tells us that the relations of flocculus and nodulus are the most constant and the least variable of any parts of the cerebellum.



Bradley emphasized again and again the distortion of the fundamental relationships of lateral areas to vermician structures and the loss of their connection one with the other by the growth of the superimposed parts of the cerebellum.

The next contribution of importance added to our knowledge of the cerebellum was that of Louis Bolk, (7) whose monograph, "Das Zerebellum der Säugetiere", appeared in 1906. In this work he does not discuss the development of the cerebellum except in the human. He follows the ideas of Elliot Smith as closely as any previous worker, referring to all others with the exception of Stroud whom he seemingly neglects.

He devised a scheme of lobes and fissures which was undoubtedly original and for his purpose very convenient. It was based in large part upon his detailed observation of the brain of the adult Lemur albifrons (Fig. 3)(Fig. 4).

He then studied the cerebella of many different animals and attempted to correlate the peculiar muscular development of a particular animal with the development of the separate lobes of its cerebellum. From this study he then inferred the localization of function in the cerebellar cortex. He was very successful in this work for his findings have been, in most instances, verified by physiologists.

His research opened a new field for investigations and have been of great value in the study of cerebellar function. He did however disagree with other workers on his anatomical analysis of the cerebellum and this, I believe, because he studied the folial pattern of highly complex adult cerebella without due regard for developmental relationships of the various areas of the cerebellum.

He conceives the cerebellum to be a chain of lobes. His first main division is into anterior and posterior lobes by means of the fissura prima. The region anterior to this is divided into four lobules; labeled from anterior to posterior 1, 2, 3, and 4. He does not consider that there is any division into lateral and middle regions in the anterior lobe. The area immediately posterior to the fissura prima he calls the lobulus complicatus. This is divided into lobulus lateralis posterior and lobulus medianus posterior. The lobulus C2 (made up of declive, folium cacuminis and tuber valvulae), the lobulus C1 (pyramis), the lobulus b (uvula) and the lobulus a (nodulus) comprise the lobulus medianus posterior. The lobulus lateralis posterior is divided into three parts; the most lateral he calls the lobulus ansiformis, consisting of the Crus primum superiorly, and the Crus secundum, inferiorly; medial to the lobulus ansiformis is located the second part, the



lobulus paramedianus, while directly continuous with the latter and extending laterally from it is the formatio vermicularis. The latter is divided into crus circumcludens, pars floccularis, uncus terminalis, and the lobulus petrosus. In some of his diagrams he labels a portion of the formatio vermicularis the pars tonsillaris. This is very different from Bradley, Smith, and Ingvar who consider the tonsil to correspond to Bolk's lobulus paramedianus. Ingvar and others have also criticized his grouping of flocculus, paraflocculus, and lateral extensions of the middle lobe all into one part, the formatio vermicularis.

His work is undoubtedly a real contribution to our knowledge of the cerebellum but his folial pattern does not seem to be in accord with other workers nor with my own observations in the bat.

Ingvar (21), in his outstanding work on the cerebellum, traces this organ through the amphibians and fishes; records observations on the reptiles and birds including a most important study of the development of the cerebellum in the chick. He studied the morphology of the mammalian cerebellum but called upon previous workers in large part for his material as to the developmental morphology of the mammals. His major contribution here is in the study which he made of the endings of the vestibular and the spinocerebellar fibers in the cortex of the cerebellum. These he also observed in the birds. In addition he has done many important experiments in the study of cerebellar localization and function which have no specific bearing upon this subject.

He divides the cerebellum into three lobes, (See Fig. 5) Anterior, Middle and Posterior, and in the mammals the most recent acquisition the lobus anseparamedianus. The fissure prima divides the anterior from the middle while the prepyramidal fissure separates the middle from the posterior lobe. The latter region then includes the pyramis, uvula and nodulus, in the midline, and the flocculus and paraflocculus laterally.

He came to choose this classification after having observed a division into these three lobes during his investigations on the cerebellum of the developing chick. He was impressed by the fact that the anterior and posterior regions behaved similarly in their development. They formed their transverse fissures at the same time while the middle region did not become differentiated until some time later. By comparative studies in the birds he observed that there was a striking conservatism to the morphology of the anterior and posterior lobes while the size and shape and folial pattern was extremely variable in the different species.

After examining mammalian cerebella he concluded that these three main divisions which he had found in the birds also occurred in mammals.

Realizing that he had used branches of the phylum which have diverged very early in evolution, he sought in their common ancestors, the reptiles, for the foundation of his fundamental division of the cerebellum. On examining the cerebellum of the alligator he found two transverse fissures which he believes divide the cerebellum into three lobes which are homologous with his three lobes of birds and mammals. He further quotes Larsell to the effect that an indication of such a division may be found in even lower reptiles.

Ingvar's important investigation into the distribution of afferent cerebellar tracts is also of interest in this discussion. He found that in the cat the dorsal and ventral spino-cerebellar tracts send fibers to the anterior and posterior lobes, whereas the middle lobe is free of these fibers except for a few ending in the lobulus simplex. This distribution holds regardless of the part of the cord from which they come. These tracts were found to end in corresponding areas in the pigeon. It is of interest to note that the only other parts of the cerebellum which are entirely free of spinal fibers besides the middle lobe, are the nodulus and the flocculi. Here he finds the termination of the direct vestibular root fibers, and although also distributed to the uvula and lingula, in the latter areas they are mixed with spinal fibers.

Following these important observations Ingvar presents a novel and illuminating concept of the relations of the different parts of the cerebellum to each other. He compares the cerebellum to a three story building. The basement or first floor he calls the 'vestibular floor'. He includes in this floor those basal portions where the direct vestibular root fibers end. The second floor he calls the 'spinal floor' which is situated centrally and above the vestibular floor. This area includes those parts of the cerebellum which receive the termination of the spino-cerebellar fibers. The top floor which includes the middle lobe and the hemispheres is called the 'cerebral floor' because it is these areas which receive the ponto-cerebellar fibers.

Speaking of this concept of the cerebellar morphology he says, (22) "This conception does not pretend to be more than a crude schematic one. There undoubtedly exists an overlapping in the cerebellar cortex of the different afferent fiber systems. In spite of its crude schematic character it expresses succinctly, to my mind, not only the evolution of the cerebellar functions but also the functional localization of the organ."



Now light has been thrown on the problem of the development of the cerebellum by the careful examinations of the origins of the cerebellum in the amphibia and fishes and a complete and careful analysis of the reptilian cerebellum in the light of the new knowledge of the lower forms. In 1924 C. Judson Herrick (15) reviewed this work in an article entitled "Origin and Evolution of the Cerebellum". He called upon the work of Johnson (23), 1902, Tretjakoff (50) 1909, Herrick (14) 1914, and Larsell (29) (30), 1920 and 1923, chiefly for his discussion of the cerebellum in the amphibia and fishes. He tells us, in reviewing the origin of the amphibian cerebellum, that "two centers of differentiation appear in the rhomboid lip on opposite sides of the wide lateral recess, and the functional factors involved in the elaboration of these two regions can be clearly read."

1. The lip in the lower border thickens from behind forward and is nothing other than a differentiation of the rostral end of the octavolateral area, for root fibers in the vestibular and lateral line nerves run throughout its length. With the loss in the lateral line nerves in the land forms this area becomes dominated by the vestibular fibers.

2. The thickening of the rhomboidal lip in its upper border of the lateral recess takes place under the influence of a different group of functional connections. Optic, acoustic, and somesthetic fibers from the adjacent roof of the midbrain and spinocerebellar fibers of proprioceptive type all terminate or send collaterals in to this area. The latter becomes the dominant type.

In the elasmobranchs we have an elaboration of the two areas.

1. The vestibulo-lateral area consists of the paired auricle and lower lip. This area receives vestibular and lateral line nerves at the lower or ventral lobes of the auricles and the remainder seems to be concerned chiefly with vestibulo-lateral line adjustments.

2. The dorsal Median body, which is an enlargement and dorsal evagination of the dorsal wall, between the tenia of the fourth ventricle and the decussation of the fourth nerve. Its origin can readily be traced for it receives the large spinocerebellar tracts and also fibers from the inferior olives, midbrain and hypothalamus. It is thought that it is developed in response to the enlargement and segregation of the non-vestibular functional systems. That this area in the dogfish is physiologically independent of the vestibular apparatus has been confirmed by the experiments of Tilney in 1923.

The higher fishes show an even greater enlargement of the lateral line and vestibular areas including the development of cerebellar crests, laterally, and the valvula, a median cerebellar structure, invaginated and thrust forward into the cavity of the midbrain. As these are specialized areas in themselves I will not go further into their development.

In 1932 Olof Larsell published a paper in which he summarized all the previous work on the cerebellum of the reptiles including Cajal, DeLange, Kappers (24), Van Hoëvell, Ingvan (21) Huber and Crosby, a previous work by himself (32), Christensen, Hausman (12) and Shanklin. The study concerned itself with the development, fissures, homologues, cerebellar nuclei, cellular layers, cellular elements, and fiber tracts both afferent, efferent and commissural, of this organ as is found in the reptiles.

In the summary to this latest work, Larsell (35) points out the major findings of Herrick (14,15) and himself (29,30) on the lower forms, including not only the investigations discussed by Herrick in 1924, but additional work of Larsell in 1925, '31, and '32 (31, 33,34). He emphasizes the derivation of the cerebellum from "two bilaterally paired sets of primitive coordinating centers, namely, the auricular lobes and the corpora cerebelli." He calls our attention to first a fusion of these two areas on the same side with each other and then a fusion of the two corpora cerebelli. This fusion takes place by the migration of cells medially along the commissure between the two corpora cerebelli. In the amphibians he also finds a commissure between the auricular lobes of the two sides, but contrary to previous teaching that the vestibular or vestibular lateral areas were the most primitive, Larsell showed in the larval amblystoma that the commissure between the corpora cerebelli and the trigeminal areas was the first to appear.

Although there is a commissure between the auricular lobes across the midline in the amphibia, an actual fusion of the auricular lobes across the midline is not found until the reptiles. Here he finds the evidence of a similar migration of cells to that described along the commissure of the corpora cerebelli in the amphibia, except that these cells originate in the floccular lobes and go in a caudo-medial direction along the vesticulolateral commissure. "The paired masses fuse in the midplane caudoventral to the body of the cerebellum formed by the corpora cerebelli, which have previously fused.

He then describes a furrow between the corpus cerebelli and the floccular lobe (auricle) and its extention caudomedially which was just described. This furrow he considers to be homologous with the parafloccular fissure,



laterally, and the uvulonodular fissure, medially, of birds and mammals. This stage is clearly shown in his figures of turtle and alligator embryos. It would appear from a detailed study of the development of the primitive mammalian forms, such as our present study endeavors to be, that this sulcus laterally is rather the homolog of the floccular sulcus. Larsell states further, "This parafloccular (floccular) uvulonodular fissure is the first marking to appear on the cerebellar surface."---"It marks off the two functionally distinct primitive regions of the reptilian cerebellum, namely, the vestibular floccular lobe, and the corpus cerebelli with spinal, bulbar, and mesencephalic connections."

He considers that the fissures which Ingvar (21) and others have used to subdivide the cerebellum into anterior, middle and posterior lobes are simply folds produced in the corpus cerebelli to accommodate its further enlargement which is such a conspicuous part of the later development of the cerebellum. The use of these fissures as the fundamental divisions of the cerebellum places the nodulus and flocculus in the same primary area as parts derived from the corpus cerebelli.

Larsell at this point injects this new thought into the literature on this subject. "On developmental grounds, both phylogenetically and ontogenetically, such a combining of primary and secondary structures into one lobe does not appear warranted, although it fits well into the pattern of the adult cerebellum from the higher reptiles and upward in the vertebrate scale."

Further references which should be mentioned are the following:

Zur Anatomie des Gehirnes niederer Säugetiere, by Augusta Arnbeck-Christie-Line, (2) Anat. Anz. 18:8, 1900. This is a description of the brain of the bat and the shrew, including some material on the cerebellum.

The Genesis of Cerebellar Functions. By Frederick Tilney (48), Arch. of Neurology and Psychiatry, 9:137, 1923. A comparative morphological study and review which is criticized by Herrick in 1924.

Cerebellar localization in the Light of Recent Research. By Davidson Black, (3) Journal of Lab. and Clin. Med. 1:417. Summarizes the work of Bolk, Van Rijnberk and Barany's as it bears on the subject he discusses.

Die vergleichende Anatomie des Nervensystems der Wirbeltiere un des Menschen by C. U. Ariens Kappers (24). Haarlem 1921. A work that is standard for workers in the field of comparative neurology.

The various contributions not already mentioned which appear in the volume entitled *The Cerebellum*, Baltimore 1929. The most important for our purpose being: Riley, Henry Alsep (37). "The Arbor Vitae and the Folial Pattern of the Mammalian Cerebellum. pp. 37 to 192.

Hausman, Louis (12) "The Comparative Morphology of the Cerebellar Vermis, the Cerebellar Nuclei, and the Vestibular Mass: Experimental Investigations.

After reviewing the mass of material already available on the subject it would seem at first glance that further work would be unnecessary, but following the findings of Larsell (26, 32) as above in the reptiles it seemed of value to follow closely the various stages in the development of the cerebellar fissures in an animal whose size and simplicity of cerebellar organization would lend itself to such a study.

#### Material and Methods.

##### I. Dissection preparations of *Corynorhinus*.

|     |    |                     |                    |
|-----|----|---------------------|--------------------|
| 1.  | 1- | 12 mm.              | Crown rump length. |
| 2.  | 1- | 13 mm.              | " " "              |
| 3.  | 1- | 14 mm.              | " " "              |
| 4.  | 1- | 16 mm.              | " " "              |
| 5.  | 1- | 16 <sup>a</sup> mm. | " " "              |
| 6.  | 1- | 18 mm.              | " " "              |
| 7.  | 1- | 19 mm.              | " " "              |
| 8.  | 1- | 21 mm.              | " " "              |
| 9.  | 1- | 22 mm.              | " " "              |
| 10. | 1- | 21 <sup>a</sup> mm. | " " "              |
| 11. | 1- | Young Bat.          |                    |
| 12. | 1- | Adult Bat.          |                    |

##### II. Sagittal Serial Sections of *Corynorhinus*.

|    |    |        |                                    |
|----|----|--------|------------------------------------|
| 1. | 1- | 13 mm. | Crown rump length.                 |
| 2. | 1- | 15 mm. | " " " Different embryo than No. 3. |
| 3. | 1- | 16 mm. | " " " Same embryo as No. 4         |
| 4. | 1- | 18 mm. | " " " Different embryo than No. 6. |
| 5. | 1- | 22 mm. | " " " Different embryo than No. 9. |



## III. Models.

1. 1- 15 mm. Crown rump length. Same embryo as Series No. 2. Model of the lateral  $\frac{1}{2}$  of left half of cerebellum.
2. 1- 16 mm. Crown rump length. Same embryo as Series No. 3 and Dis. prep. 4. Model of entire cerebellum.
3. 1- 18 mm. Crown rump length. Same embryo as Series No. 4. Model of the lateral  $\frac{1}{3}$  of the left half of the cerebellum.

The dissections were made under a binocular microscope of low magnification. The drawings were made to measurements observed under the binocular microscope and are as near 10x as was possible. The drawings were then labeled and photographed.

Outline drawings were made of all the series at regular intervals. The sections drawn are somewhat closer together near the lateral portions where the changes are more rapid. These drawings were made with an accurately adjusted projectoscope and are all drawn 50x. This same magnification was used in the tracings for the models.

The models were prepared by the use of blotter paper tracings cut out and pasted together with library paste. Every section was used in the tracings for the models. As transverse sections were not made it was impossible to check the accuracy except by constant comparison with the corresponding gross specimen under the microscope. The transverse diameter was measured frequently as the model was being built so that the finished model was 50x in all diameters. Series No. 4 from which Model No. 3 was made was accidentally cut a few degrees off of the true sagittal plane.

The photographs given in Figs. 6 to 78 are reduced in varying degrees of the original drawings and models. The enlargement as corrected is given for each figure.

One specimen examined which measured 21 mm. was so different in the relative size and shape of the cerebellum as compared to the other bats observed it was thought that the specimen was from some other species. The drawing of this cerebellum is not included in the present paper. As these animals were wild the age of the fetuses was not known and the only measurement taken

was the crown rump length. As will be seen, this does not correspond to the degree of differentiation of the cerebellum in every case. The specimens are described however in the order of their degree of development, regardless of their length measurements.

### Description.

The smallest embryo I have examined is one measuring 12 mm. C.R.L. (Fig. 6 & 7). The cerebellum, at this stage, is an arch with the lateral portions obviously increased in thickness as compared to the medial part. The cerebellum has fused in the midline but that part below the uvulonodular fissure is still quite narrow. There is no doubt that the uvulonodular fissure is the first to develop and at this stage is continuous, around the "U-shaped bend" of Stroud, (44) with the floccular sulcus which surrounds the developing flocculus. (Fig. 7). The flocculus at this stage has many of the characteristics of the auricle of lower forms. There is no indication of a fissura prima or secunda. It would appear that the single fissure present, the uvulonodular, was formed first laterally; for at this stage it is more marked around the flocculus although continuous across the midline.

The series which most closely approximates the above stage is Series I. C.R.L. 13 mm. (Figs. 28 to 35). Fig. 28 shows a midline section through the cerebellum, IV ventricle and its floor, choroid plexus, and mesencephalon. In this series the uvulonodular fissure is the most prominent and can be traced to the floccular fissure although the continuity is followed with a little difficulty between the sections seen in Figs. 29 and 30. There can be seen a very early beginning of the fissure prima in Figs. 28 and 29, and a questionable fissure secunda in Figs. 29 and 30. Fig. 32 shows a slight depression on the superior border which may indicate a beginning parafloccular sulcus; but this is far from definite at this stage. Fig. 31 shows the relation of the roots of the Vth and VIIth cranial nerves to the cerebellum and the medulla. Figs. 34 and 35 show the flocculus to be the most lateral parts of the cerebellum. In Fig. 34 we see the lateral extremity of the corpus cerebelli, possibly the anlage of the paraflocculus.



Figs. 8 and 9 show the posterior superior and left lateral views, respectively, of the cerebellum of a bat embryo 13 mm. C.R.L. The uvulonodular fissure is present and is easily traced to the floccular sulcus with which it becomes continuous. The nodule is more prominent in the midline than in the 12 mm. stage. (Figs. 6 & 7). Another fissure has been added which is visible under the dissecting microscope. It is the fissure secunda of Elliot Smith (41,42,43). The area just lateral and below its lateral extremity is beginning to increase in size. It is beginning to produce a concavity in the floccular sulcus below (Fig. 9). By pulling the mid-brain forward it is possible to see the fissura prima extending 1/3 of the distance to the lateral extremity of the cerebellum on either side.

The <sup>and 15 mm.</sup> 14 mm. stages have been studied by drawings, Figs. 10 and 11, a sagittal series, Figs. 36 to 44, and a model of the lateral  $\frac{2}{3}$  of the left half of the cerebellum, Fig. 73. The uvulo-nodular fissure is the only fissure extending the entire width of the cerebellum. The continuity between flocculus and nodule is clearly shown. Figs. 10 and 11. The paraflocculus has appeared as an out growth in the lateral part of the corpus cerebelli, superior to the flocculus (par. Fig. 10). The parafloccular sulcus proceeds medially superior to the fissura secunda without becoming continuous with any fissure as yet. The fissura prima and secunda are both well marked medially but disappear laterally without joining any lateral sulcus. The model Fig. 73 bears out these relationships in almost every detail. Root V is seen in Fig. 38 and Root VII or VIII in Fig. 39. There is a beginning fissure which I have called fissura preculminata (Smith) (43) which no doubt corresponds to Bradley's (5,6) Fig. I. There is no indication of a prepyramidal fissure at this stage. In following the sections there are a few sections, between those seen in Figs. 37 and 38, where the uvulo-nodular fissure becomes almost entirely obliterated. This may also be seen on the model. The continuity however, is unmistakable under the dissecting microscope.

The 16 mm. stage has been studied by means of posterior and left lateral drawings under the dissecting microscope, Figs. 12 and 13, by a sagittal series, Figs. 45 to 53, and by a model of the entire cerebellum Figs. 74, 75 and 76. Here we find the size of the paraflocculus increased over the previous stage. All the fissures are deepened with the possible exception of the uvulo-nodular. There is no prepyramidal fissure present. The sections and the model of the right side of this cerebellum shows clearly the continuity of the floccular and uvulo-nodular fissure Fig. 74, but on the left side the growth of the medial portion of the paraflocculus has already begun to

obscure this relationship and flatten out this sulcus which had appeared so early, Figs. 74 and 49, and whose continuity at this position is most definite in the earlier stages. (See Figs. 30 to 34). The parafloccular sulcus is well defined and runs medially to a point well above the fissura secunda. This can be seen in Figs. 13, 13, 47, 73, 74, and 75. Fig. 74 the right side of the model there is some indication of a fusion of this fissure with the fissura secunda. This is not born out however by a close scrutiny of the sections from which this part of the model was made.

The 16mm. stage, Figs. 14 and 15, one sees a deepening of all fissures described above plus a faint beginning of a fissura prepyramidalis (fis. ppd.) in Fig. 15. There is no indication as yet of a junction of the parafloccular sulcus and the prepyramidal fissure. Figs. 14 and 15. It is well to note here that the sulci floccularis and parafloccularis begin laterally while all the fissurae with the possible exception of the uvulonodular begin in the medial region and extend laterally and that any junction of these fissures take place after they are formed. One exception I believe occurs, namely, the uvulonodular which is present in its entirety in the earliest stages of the bat available but is more pronounced laterally.

The 18 mm. stage has been studied by posterior and lateral drawings under the dissecting microscope, Figs. 16 and 17, by serial sections cut sagittally, Figs. 54 to 60, and by a small model of the lateral 1/3 of the left half of the cerebellum. Fig. 77. The series of this stage, was cut slightly obliquely and is not a true sagittal. There is a well marked prepyramidal fissure present in all the specimens examined. The specimen from which the sections were drawn and the model was made is, I believe, somewhat further developed than the specimen shown in Figs. 16 and 17 regardless of their equal length. Fig. 16 and 17, show the parafloccular fissure on the left side to still remain separate from the prepyramidal fissure. There is a faint indication on the right however, that they are to join. In the series there can be no doubt as to their unity. Figs. 54 to 59. In studying the sections between those illustrated in Figs. 56 and 57 the depression becomes quite shallow but the continuity is present. The lateral extension of the uvulonodular fissure is plain, as followed in the series, until beyond the section shown in Fig. 57. Between Fig. 57 and Fig. 58 the fissura secunda definitely disappears, and the uvulonodular fissure becomes so shallow that it is impossible to locate it in some of the sections. There is some indication that it is continuous with a broad depression marked (g) in Figs. 58 and 59. The sulcus labelled (h) would most nearly correspond to the floccular fissure and the tiny lobe formed on the



model, Fig. 77 would most nearly correspond to the flocculus. This is formed by the appendages of several sections of which the one in Fig. 59 is a fair example (floc). This sulcus (h) is definitely not continuous with the uvulo-nodular fissure as seen in Figs. 54 to 57. In all the stages of the bat from this one on the flocculus is so tiny that it can hardly be identified at all. There does exist a rounded eminence on the under surface of the paraflocculus which is probably all that is present. The paraflocculus is very prominent and completely overshadows the flocculus from here on.

The 19 mm. C.R.L. embryo was studied only under the dissecting microscope and is represented by Figs. 18 and 19. Here we find the nodule completely hidden by the overhanging uvula. The flocculus is seen as a small projection under the caudo-ventral surface of the paraflocculus. The lateral extremity of the uvula is apparently not completely cut off from continuity with the paraflocculus. It is markedly narrowed, as compared to Figs. 12 and 13 of the 16 mm. stage. One can now see the reason for the dispute as to the relation of the paraflocculus to pyramis or uvula or both for the paraflocculus begins as an outgrowth independent of any vermian fissure and establishes its relation later in its development. That, at some stages in its development it is continuous with some parts of the cerebellar cortex, both above and below the fissura secunda, all are agreed. It must further be noted that the fissura prepyramidalis is formed later in the bat than the fissura secunda. This is in direct disagreement with Bradley's (4) idea that the fissura secunda is not even found in these simpler forms. The only way that one can harmonize his findings with other workers including myself is to conclude that his Fig. III in the rabbit and similar animals was really the fissura secunda of Elliot Smith (43) rather than the prepyramidal fissure that Bradley (5) thought it to be. It is in this stage that we first can note any division into vermis and hemispheres. This is indicated by the very shallow broad sulcus labeled the paravermian sulcus (s.p.) in Fig. 18.

The 21 mm. stage is also studied only by the aid of the dissecting microscope and is represented by Figs. 20 and 21. Aside from the deepening of all fissures and sulci including the one I have called the paravermian sulcus. From this stage on we get a tremendous increase in the bulk of the hemispheres which lie lateral to the lobus medius of Ingvar (21) (lo. med.).

The 22 mm. stage was drawn under the dissecting microscope as seen in Figs. 22 and 23, and a saggital series was made as well, Figs. 61 to 69. The uvula in

this stage has completely overshadowed the nodulus as seen either from the side or from the posterior superior aspect. In the gross specimen the uvulonodular sulcus cannot be traced laterally to join with any remnant of the floccular sulcus for by this time the flocculus can hardly be distinguished from the bulk of paraflocculus lying above it. Neither can the uvulonodular fissure be followed up along the dorsal surface of the paraflocculus as the fissure (g) in the gross specimen. That there is such a continuation of the uvulonodular fissure is evident however, in the sagittal sections Figs. 64 to 67, and all the intermediate sections show clearly the continuity of the (fis. un.) Fig. 65 and 64 to the sulcus labelled (g) in Fig. 65, 66, and 67. The explanation of this condition that exists in the bat will be discussed following a brief description of similar stages as observed in the rat. There appears a shallow sulcus in Fig. 66 which I have labelled (h). As to whether this corresponds to the sulcus so labeled in the 18 mm. series I cannot say. (Figs. 58 and 59).

The rest of the cerebellum at this stage is very clear cut and is not difficult to identify. The lateral extremities of the middle lobe are greatly enlarged and possess a horizontal fissure, which I have called the sulcus intercruralis. This divides the hemisphere proper into two lobes which are labeled Crus primum of the lobulus ansiformis and Crus secunda of the same lobe. All the above nomenclature was taken from Bolk (7). Although on first appearance it might seem that the dorsal part of the base of the paraflocculus was continuous with the Crus secunda, an observation recorded by Stroud (44) calling this same area the post pilcum, on more careful observation it is clear that the prepyramidal fissure or parafloccular sulcus (s. par.) completely encircles the paraflocculus. This observation is born out by the series of this stage noting the complete separation of the paraflocculus from the lobulus ansiformis by the parafloccular sulcus Figs. 64 to 67. The parafloccular sulcus and the prepyramidal fissure are plainly continuous both in the gross specimen and in the series examined.

The 21 mm. stage which may be seen in Figs. 24 and 25 shows an increase in all the markings described above. The lateral extension of the prepyramidal fissure can be seen at the bottom of the groove produced by the superior semicircular canal encircling the base of the paraflocculus. (s. par.). At this stage there is a fissure forming on the caudo-lateral surface of the paraflocculus which I have called the intra-parafloccular sulcus. (s. i. par.). It is entirely a secondary structure



and is not homologous to the fissure (g) as above which is medial to this fissure and has a different direction.

The young bat Figs. 26 and 27, shows a continued increase in the size of all parts and a continued secondary distortion of the fundamental relationships of the earlier stages.

Except for an increase in size the adult bat Fig. 70 does not differ from the brain of the young bat Figs. 26 and 27. The median part of the uvula shows some growth. The paraflocculus has been limited laterally by the large semicircular canals and the cochlea and to allow for its growth it has forced a small projection of the inferior portion caudo-medially through the center of the posterior semicircular canal. The lateral extremity of the uvula is so thin that its continuity with the inferior part of the paraflocculus is seen only by careful examination under the dissecting microscope. The nodulus is completely hidden from view. There is a small lip above the lateral recess of the fourth ventricle which may represent the flocculus. The lobulus ansiformis is greatly increased in size. There is a small median fissure in the middle lobe just above the prepyramidal fissure. It is thought to be Bradley's fissure (a) which he thought was represented in the human by the fis. Hor. ~~Mag~~. It is not continuous with the intercrural sulcus. The prepyramidal fissure separates the paraflocculus from the hemispheres as described in the earlier stages. Its relations can only be seen however by retracing the overhanging postero-lateral edges of Crus secunda and following the fissure around the paraflocculus where it lies in the fossa as described above.

Because of the difficulty of separating the flocculus from the paraflocculus in the bat, it was thought wise to include a part of the observations now being made on the development of the brain of the white rat in this thesis. This will make no attempt to be complete but to only point out certain stages in an animal in which the flocculus and paraflocculus both develop into well defined separate structures in the adult. The white rat was found to be satisfactory and closely graded stages were readily available.

The earliest stage examined was an 18 day rat fetus. The cerebellum, at this stage, is even simpler than any described above. A saggital series shows a lack of any fissures or sulci. There is some indication of the presence of a "rautenlippe" but no nodulus or flocculus could be identified with certainty.

The next stage was supposed to be a 21 day fetus whose mother had died of pneumonia on the date of expected delivery. Whether this affected the development I do not know but the cerebellum shows a more primitive stage than is found in other newborn rats. In this fetus we find a well marked floccular sulcus which is continuous medially with a fissure which extends to within  $1/3$  mm. of the midline on either side. This is in accord with the suggestive findings in the bat although the actual observation that the floccular, uvulo-nodular fissure began laterally, was not made in that animal. The flocculus resembles closely the auricle of the lower forms. It corresponds very closely to the 12 mm. bat embryo shown in Figs. 6 and 7. There are no other fissures present in this specimen.

The next stage is shown by Fig. 78 which is a model of the cerebellum of a newborn rat. The uvulo-nodular fissure and floccular sulcus are continuous and are the only fissure extending the entire width of the cerebellum. There are two other fissures forming in the lateral parts of the corpus cerebelli. The faint beginning of the parafloccular sulcus is seen in only a few sections just caudal to the lateral extremity of the prepyramidal fissure. The latter fissure appears to begin laterally, which is different from the occurrence in the bat.

A newborn rat obtained from a different source shows a more interesting stage than the model in some respects. It is shown in a lateral view in Fig. 71. It should be noted that the fissure I have labeled "prepyramidal" was called fissure (a) by Bradley (5) and my fissure secunda he called the fissure III or prepyramidal both in the adult rat and in the developmental stages in a similar animal, the rabbit. For a discussion of this point I refer you to pp. 12, 13 above. The parafloccular sulcus is seen definitely below the prepyramidal fissure. The paraflocculus arises lateral to the pyramis and the uvula as in the bat but the prepyramidal fissure is not continuous with the parafloccular sulcus and as a result the upper part of the pyramis is continuous with the hemisphere proper while the lower part is continuous with the paraflocculus. In no stage was I able to demonstrate a union between the parafloccular sulcus and the fissura secunda.

The one day old rat shows little change from the stage described above. The lateral extension of the uvula is becoming narrowed and the parafloccular sulcus is extending toward the fissura secunda but it definitely does not join it.



The two day rat is shown in a posterior superior view in Fig. 72. Here we find the paraflocculus enlarged and its sulcus deeper but continuing to maintain the same relationship to the medial fissures as described in the earlier stages. The lateral extension of the prepyramidal fissure cannot be seen unless the paraflocculus and hemisphere be separated. If this be done this fissure above and the parafloccular sulcus below mark off a narrow folium which gradually becomes more and more compressed as the adjacent lobes enlarge.

Attention is called to the fact that although the remainder of the cerebellum is fissured as deeply as is the adult corynorhinus the uvulo-nodular fissure is well developed and shows no indication of extending up toward the paraflocculus. One possible explanation is the fact that following the course of the shallow groove labeled (g) in Figs. 66 to 69 there is constantly present an artery of relatively large size. The final opinion as to the significance of this groove (g) must wait for further investigations on the development of the deeper connections in this area of the mammalian cerebellum.

Further development of the rat is not of importance here and will be reserved for a subsequent report.

#### Summary and Conclusions.

1. A review of the literature dealing with the development of the cerebellar fissures is presented, with the following points emphasized:

(a) Elliot Smith's (41, 42, 43) grouping together of flocculus and paraflocculus into a single lobus floccularis and a similar grouping of the uvula and nodulus into a single lobus posticus, without regard for their early separation by the uvulo-nodular fissure, which he himself recognized as being the earliest to form, is criticized.

(b) Smith's (43) description of the cerebellum of the *Notocytes* is shown to be lacking in a clear differentiation between the separate components of his floccularis in his figures of the sagittal sections through the cerebellum of this animal.

(c) Attention is called to his opinion (43) relative to the variability of the relations between the parafloccular sulcus and the "vermian" fissures of the posterior part of the cerebellum.

(d) O. Charnock Bradley's (5,6) emphasis on the separation of flocculus and nodulus from the rest of the cerebellum, is mentioned.

(e) Bradley's (5) opinion concerning the late appearance of the fissura secunda is discussed. Evidence is presented to show that Bradley has confused the fissura secunda with the prepyramidal in the developing rabbit and also in all of the adult mammalian brains below the squirrel which he has described, with the exception of the hare.

(f) Bolk's (7) work is presented in part and the criticism of Ingvar and others concerning his classification of flocculus, paraflocculus, and parts of the middle lobe into one body, the formatio vermicularis, is mentioned.

(g) Ingvar's (21,22) ideas concerning the cerebellum are presented. His findings, in the cat concerning the endings of spinal cerebellar and direct vestibular fibers in the cerebellar cortex, are discussed. Attention is called to the presence of direct vestibular endings in the nodulus and flocculus without any fibers from the spinal cord ending there, a condition which is found in no other part of the cerebellum.

(h) The origin of the cerebellum in the amphibians and fishes is presented from the work of Herrick (14,15) and Larsell (29, 30, 31, 33, 34). The new concept that this organ is derived from the two fundamental commissures, one vestibulo-lateral in nature and the other, called the corpora cerebelli, receiving components from the spinal cord, and optic, acoustic, and somesthetic fibers from the midbrain, is discussed.

(i) Larsell's (32,35) use of this knowledge in his description of and conclusions concerning the reptilian cerebellum is pointed out. His criticism of all previous workers, who have classed parts of the mammalian cerebellum which are derived from these two fundamental divisions into one posterior lobe, is quoted.

(j) Attention is called to Larsell's (35) choice of the term fissura parafloccularis as denoting the lateral extension of the first sulcus of the reptilian cerebellum and to his opinion, as stated at that time, that the floccular lobe of the reptiles is homologous to the lobus floccularis of birds and mammals which includes both paraflocculus and flocculus. In this, he is in agreement with Ingvar. A careful examination of early stages of the cerebella of mammalian embryos from those described by Stroud, down to and including my own findings, will indicate that the flocculus alone is derived from



the "auricular lobe" and that the paraflocculus is formed from the postero-lateral part of the corpus cerebelli. That Larsell has recognized this fact is seen in a later article, not yet in print, but which he has kindly allowed me to see in manuscript. He has, however, continued to use the term parafloccular sulcus in his description of the brain of the embryo mole where we use the term floccular sulcus. The nomenclature used in this thesis corresponds closer in my opinion to that used by Stroud, Smith, Bolk and Ingvar in their diagrams of the mammalian cerebellum.

In concluding the summary of the review of the literature let me state that the paper by Bert Brenette Stroud (44) was found to be of great value. In it was found the most complete review of the literature from 1812 to 1895 that I have been able to find in any work that has been available to me. In addition, his early observations are accurate and his interpretations worthy of more careful attention than has been given them by more recent writers.

2. A detailed description of the development of the fissures in the bat, *Corynorhinus*, is given. This is based on observations made on closely graded embryos of this animal by the following methods:

- (a) the observation and drawing of all stages under a dissecting microscope;
- (b) serial sections in the sagittal plane of important stages;
- (c) the preparation and study of blotting paper models of some of the stages.

These findings were supplemented by additional observations on the developing cerebellum in the white rat by the same methods as were used in the bat.

3. The *Corynorhinus* has six "vermian" fissures which appear in the following order: 1. uvulonodular fissure, 2. fissura prima, 3. fissura secunda, 4. pre-culminate fissure, 5. prepyramidal fissure, and 6. a very late fissure which I have labeled fissure 'a' after Bradley (5,6). This last fissure is not of sufficient importance to merit indication in the schemes of Smith (43) or Ingvar (21). Bradley (6) considered his fissure 'a' to be homologous with the fissura horizontalis magna of man. These median fissures are supplemented by three lateral sulci which appear in the following order: 1. floccular sulcus, 2. parafloccular sulcus, and 3. inter-cerebral sulcus.

4. The floccular sulcus is thought to be the earliest cortical marking in the bat and there can be no doubt that this is true in a slightly earlier stage observed in the rat.

5. The fused floccular sulcus and uvulonodular fissure is the first marking to appear across the midline and from side to side. This occurs in the *Corynorhinus* before any other fissure is formed and thereby divides the cerebellum into two unequal parts.

6. The paraflocculus forms as an independent outgrowth from the postero-lateral portion of the larger of these two early divisions and in the *Corynorhinus* maintains even in the adult its cortical continuity with both the pyramis and the uvula. In this animal the parafloccular sulcus fuses secondarily with the pre-pyramidal fissure. In the rat the parafloccular sulcus does not become continuous with any "vermian" fissure in any of the stages examined. The variability shown here is in agreement with the views of Elliot Smith.

7. The fissura prima soon becomes the deepest fissure in the cerebellum of the *Corynorhinus*.

8. The uvulonodular fissure, precocious as it is, loses its continuity with the floccular sulcus early in the development of the cerebellum in the bat examined.

9. The flocculus in this bat is either an extremely tiny lip overhanging the lateral recess of the fourth ventricle or has been "swallowed up" by the enormous growth of the paraflocculus. The final relationship of these two structures can not be learned until a detailed study of the fiber connections in this region is made.

10. The flocculus in the rat persists throughout its development and in the adult, as a well defined lobe. The uvulonodular fissure and floccular sulcus likewise maintain their continuity in this animal until a stage in advance of the adult bat cerebellum is reached.

11. The middle lobe (Ingvar) contains a shallow fissure (a) confined to the vermis and a deeper fissure laterally which divides the lobulus ansiformis of Bolk into two crura.

12. The anterior lobe has no indication of any division into vermis and hemispheres and consists of two long simple folia separated from the middle lobe by the fissura prima and from each other by the preculminate fissure or fissure I of Bradley.

13. The uvulonodular fissure is continuous, in the sagittal series of the 22 mm. bat, with a groove



labeled (g). This shallow groove extends onto the dorsal surface of the paraflocculus. Such a condition is not visible in the gross specimen of the bat; it has not been observed by previous workers in the development of any other mammal; nor have I observed it in the stages I have examined in the rat. There are two possibilities to explain this phenomena; one, that this represents the groove formed by an artery which constantly follows such a course; the other that this might indicate a step in the process of a secondary fusing of paraflocculus and flocculus into a true lobus floccularis as described by Elliot Smith. A determination of the fiber connections in this region is necessary before a final decision can be reached in this regard.

14. Viewing this whole subject in retrospect, one is struck by the presence of numerous arguments and differences of opinion relative to the other parts of the cerebellum and a great regularity in the findings concerning the early development of the floccular sulcus and uvulonodular fissure. In the two animals I have described one can observe an identical early stage where this is the only fissure developed. The other fissures, however, show a dissimilarity which increases as the later the fissures are formed. This emphasis rightfully placed on the importance of the uvulonodular fissure and floccular sulcus is further substantiated by the newer work on the origin of the cerebellum in the lower vertebrate forms.

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ABBREVIATIONS USED IN FIGURES.

- a.m.v., anterior medullary velum  
aq., aqueduct of Sylvius  
cb., cerebellum  
c. cb., corpus cerebelli  
cer., cerebrum  
Cr.I.,l.a., Crus prima, lobulus ansiformis (Bolk) (7)  
Cr.II.,l.a., Crus secunda, lobulus ansiformis (Bolk) (7)  
d.par., dorsal lobe of the paraflocculus  
fis.'a', fissure 'a' of Bradley (6). (fissura horizontalis  
magnus, of the human).  
fis.pc., preculminate fissure (Smith) (43)  
fis.ppd., fissura propyramidalis  
fis.pr., fissura prima  
fis.sec., fissura secunda  
fis.un., fissura uvulonodular  
floc., flocculus  
(g), sulcus of unknown significance  
G.V., ganglion of the trigeminal nerve  
G.VIII., ganglion of the acoustic nerve  
(h), sulcus of unknown significance  
i.e., internal ear  
lo.med., lobus medius (Ingvar) (21)  
med.obl., medulla oblongata  
mes., midbrain  
n.V., trigeminal nerve  
n.VIII., acoustic nerve  
nod., nodulus  
par., paraflocculus



pl.ch., choroid plexus

p.m.v., posterior medullary velum

pyr., pyramis

r.l., lateral recess of the fourth ventricle

R.VIII., hole where the roots of the acoustic nerve  
were torn out in the dissection.

s.fl., sulcus floccularis

s.i., sulcus intercruralis (Bolk) (7)

s.i.par., sulcus intraparafloccularis

s.par., sulcus parafloccularis

s.pv., paravermian sulcus

t.ch., tela choroidia

uv., uvula

v.4., fourth ventricle

v.par., ventral lobe of the paraflocculus.

Description of Figures.

- Fig. 1. Elliot Smith's diagram of the mammalian cerebellum spread out in one plane and showing variable relationships of the lateral extensions of the posterior lobe fissures. (Smith, Anat. Anz., vol. 23, pp. 369, 1903). (43)





Fig. 2. O. Charnock Bradley's schemae of the average mammalian cerebellum arranged in one plane and in sagittal section. (Bradley, J. Anat. & Physiology, vol. 39, pp. 117, 1903) (5).



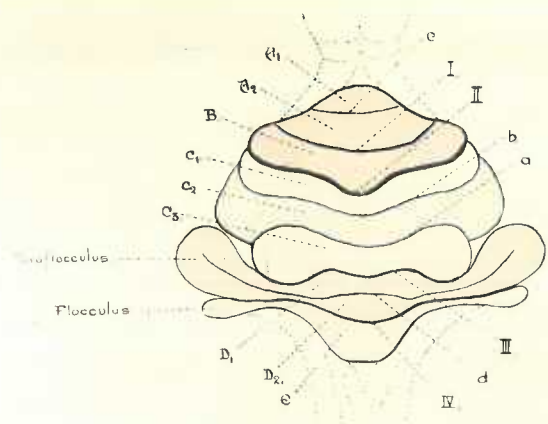


FIG. 75.

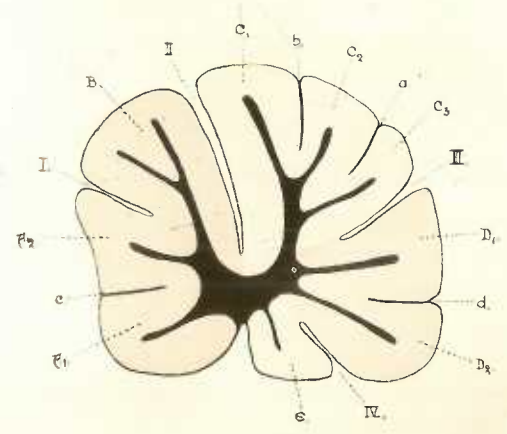


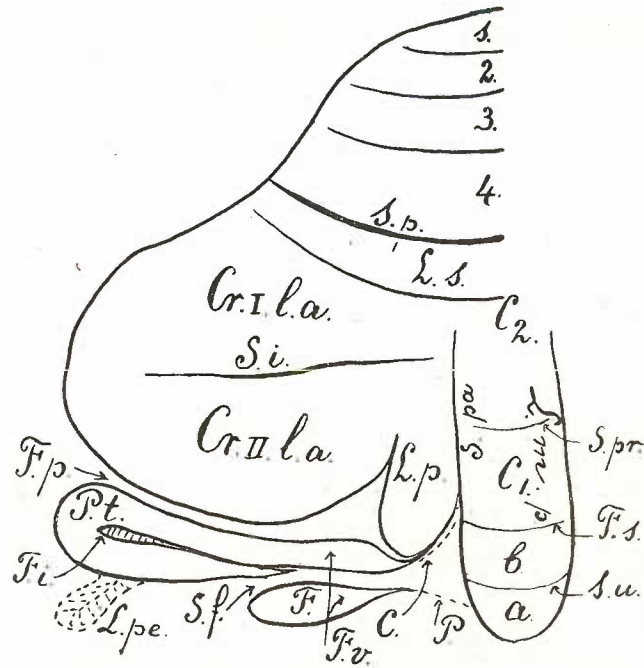
FIG. 76.

Professor O. CHAENOCK: BRADLEY ON THE MAMMALIAN CEREBELLUM: ITS LOBES AND FISSURES.

Fig. 8.

Fig. 3 Louis Bolk's diagram of the mammalian cerebellum spread out in one plane. (Bolk, Das Cerebellum der Säugetiere. Jena 1906. pp. 297) (7)





Der Bau des Säugercerebellum schematisch dargestellt. 1—4. Die vier Sublobuli des Lobus anterior. *S.p.* Sulcus primarius. *L.s.* Lobulus simplex. *Cr. I.*, *Cr. II l. a.* Crus primum, secundum lobuli ansiformis. *S. i.* Sulcus intercruralis. *L. p.* Lobulus paramedianus. *F. p.* Fissura parafloccularis. *P. t.* Pars tonsillaris. *L. p. e.* Lobulus petrosus. *S. f.* Sulcus flocculo-tonsiilaris. *F.* Flocculus. *C.* Copula pyramidis. *P.* Pecten medullare *F. i.* Fissura intervermicularis. *F. v.* Formatio vermicularis. *L. m. p.* Lobulus medianus posterior. *S. p. a.* Sulcus paramedianus. *a. b.* *C. 1.* *C. 2.* Sublobuli des Lobulus medianus posterior. *S. p. r.* Sulcus praepyramidalis. *F. s.* Fissura secunda. *S. u.* Sulcus uvulo-nodularis.

Fig. 4 Louis Bolk's chart of the folial pattern of the mammalian cerebellum. (Bolk, Das Cerebellum der Säugetiere. Jena 1906. pp. 48-49) (7).



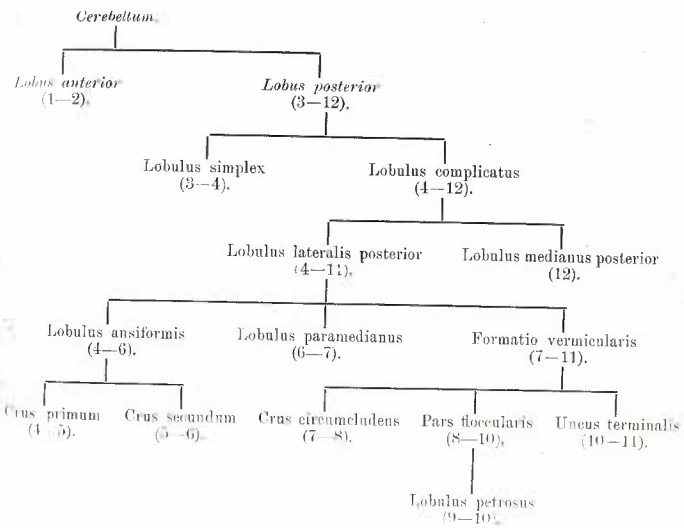
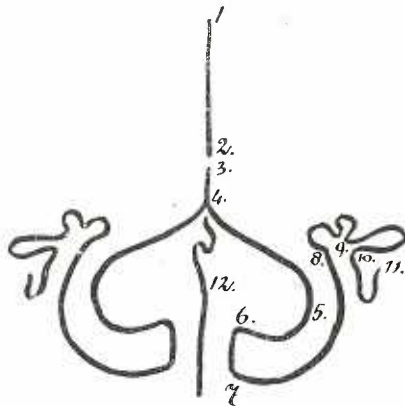


FIG. 4.

Fig. 5 Sven Ingvar's diagram of the mammalian cerebellum spread out in one plane and showing the cortical endings of the different affer-systems in the cerebellum. (Ingvar, John's Hop. Hosp. Bull., vol. 43, pp. 324, 1928) (22).



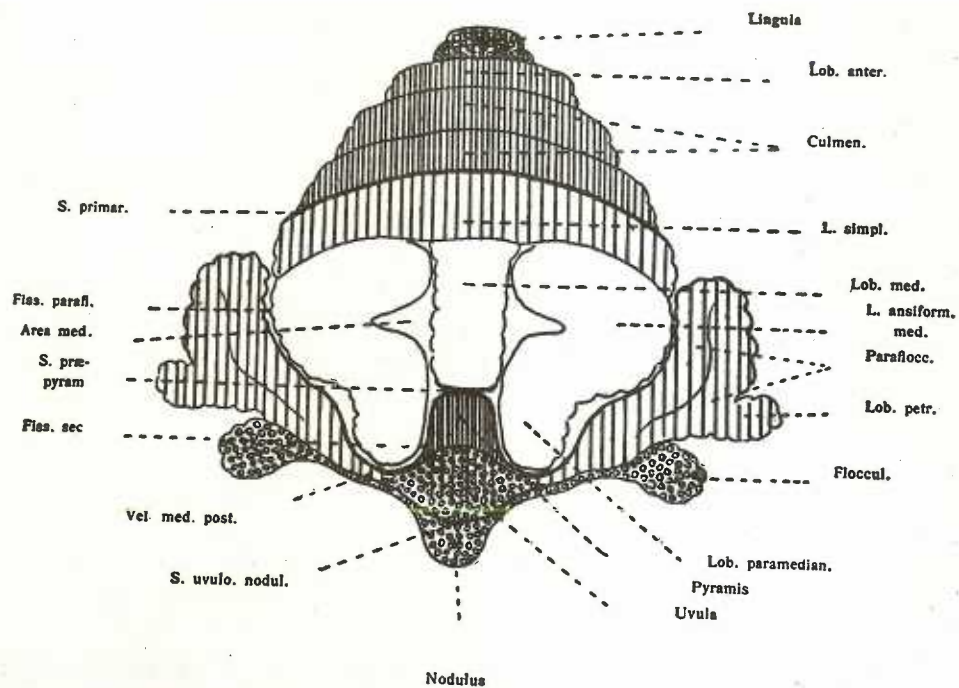


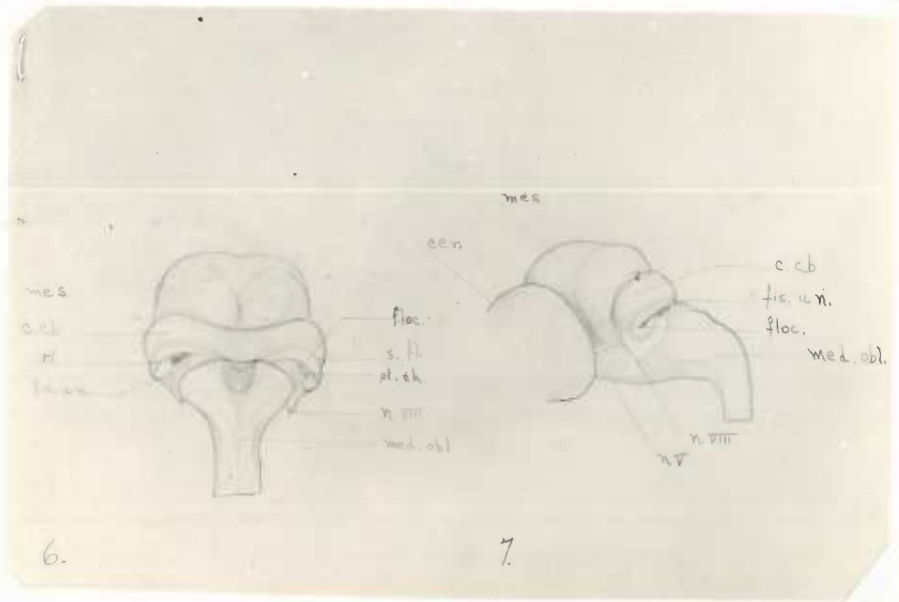
FIG. 3. DIAGRAM OF THE MAMMALIAN CEREBELLUM, THE CORTEX BEING SPREAD INTO ONE PLANE

Vertical lines mark the endings of the spino-cerebellar tracts; circles mark endings of direct fibres from the vestibular nerves. The surface of the cerebellar cortex is conceived of as being spread in one plane; the periphery of the figure corresponds to the base of the organ, that is, the parts situated in the immediate vicinity of the fourth ventricle and especially of the vestibular nuclei.

Fig. 6 Posterior superior view of the cerebellum of the  
Corynorhinus embryo, C.R.L. 12 mm., 6.1x

Fig. 7 Lateral view of the cerebellum of a Corynorhinus  
embryo, C.R.L. 12 mm., 6.1x.





6.

7.

- Fig. 8 Posterior superior view of the cerebellum of a *Corynorhinus* embryo C.R.L. 13 mm., 6.1x
- Fig. 9 Lateral view of the cerebellum of a *Corynorhinus* embryo C.R.L. 13 mm., 6.1x.
- Fig. 10 Posterior superior view of the cerebellum of a *Corynorhinus* embryo C.R.L. 14 mm., 6.1 x.
- Fig. 11 Lateral view of the cerebellum of a *Corynorhinus* embryo C.R.L. 14 mm., 6.1x.

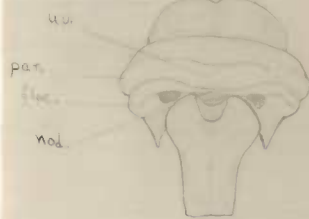




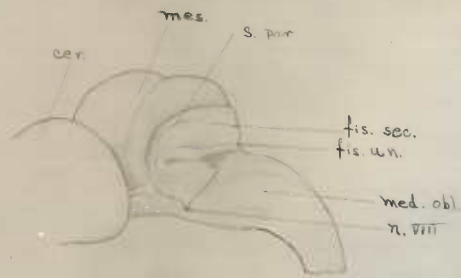
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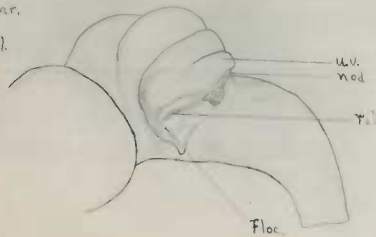
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- Fig. 12 Posterior superior view of the cerebellum of a Corynorhinus embryo 16 mm., 6.1x.
- Fig. 13 Lateral view of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 6.1 x.
- Fig. 14 Posterior superior view of the cerebellum of a Corynorhinus embryo C.R.L. 16mm., 6.1x.
- Fig. 15 Lateral view of the cerebellum of a Corynorhinus embryo C.R.L. 16mm., 6.1x.





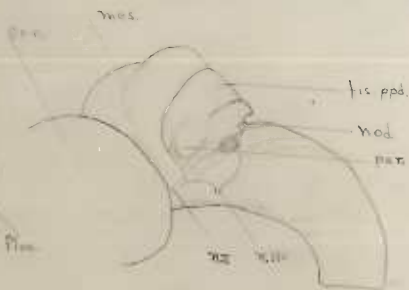
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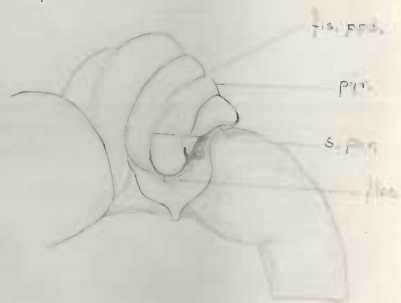


15.

- Fig. 16 Posterior superior view of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 6.1x.
- Fig. 17 Lateral view of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 6.1 x.
- Fig. 18 Posterior superior view of the cerebellum of a Corynorhinus embryo C. R. L. 19 mm., 6.1x.
- Fig. 19 Lateral view of the cerebellum of a Corynorhinus embryo C.R.L. 19 mm., 6.1x.



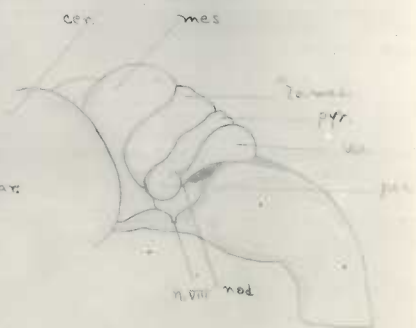
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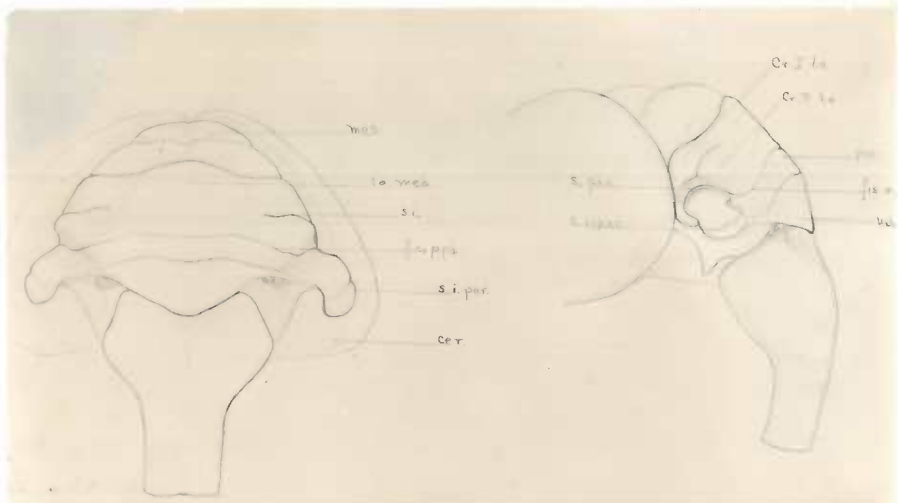


- Fig. 20 Posterior superior view of the cerebellum of a *Corynorhinus* embryo C.R.L. 21 mm., 6.lx.
- Fig. 21 Lateral view of the cerebellum of a *Corynorhinus* embryo C.R.L. 21, mm., 6.lx.
- Fig. 22 Posterior superior view of the cerebellum of a *Corynorhinus* embryo C.R.L. 22 mm., 6.lx.
- Fig. 23 Lateral view of the cerebellum of a *Corynorhinus* embryo C.R.L. 22 mm., 6.lx.



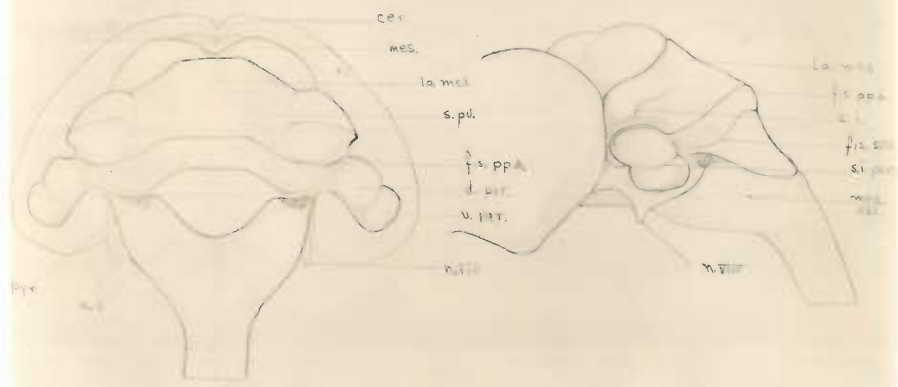
- Fig. 24 Posterior superior view of the cerebellum  
of a *Corynorhinus* embryo C.R.L. 2 1/2 mm., 6.lx.
- Fig. 25 Lateral view of the cerebellum of a  
*Corynorhinus* embryo C.R.L. 2 1/2 mm., 6.lx.
- Fig. 26 Posterior superior view of the cerebellum  
of a young *Corynorhinus*, 6.lx.
- Fig. 27 Lateral view of the cerebellum of a young  
*Corynorhinus*, 6.lx.





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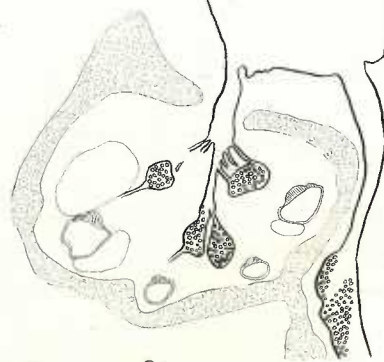
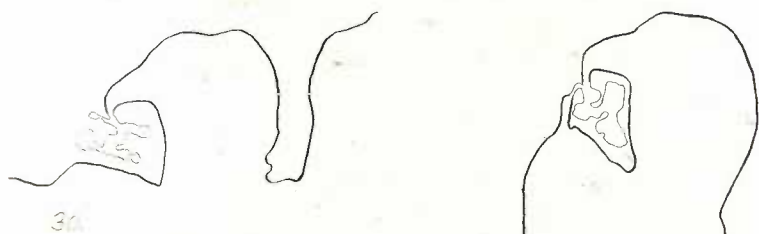
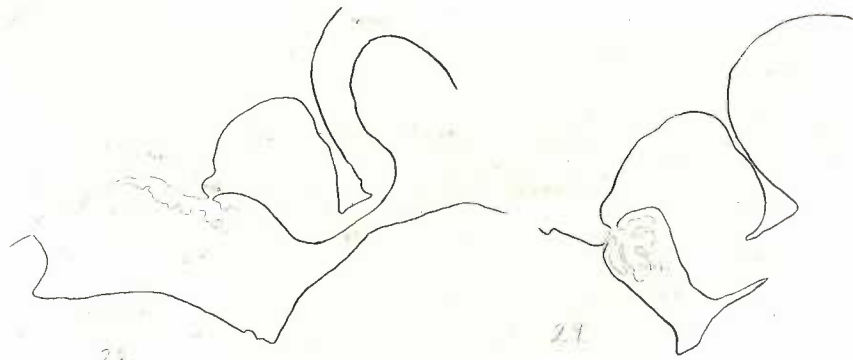
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- Fig. 28 Mid sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x.
- Fig. 29 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (0.48 mm. lateral to the mid sagittal section).
- Fig. 30 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (0.96 mm. lateral to the mid sagittal section and 0.48 mm. lateral to the section shown in Fig. 29).
- Fig. 31 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (1.2 mm. lateral to the mid sagittal section and 0.24 mm. lateral to the section shown in Fig. 30).
- Fig. 32 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (1.44 mm. lateral to the mid sagittal section and 0.24 mm. lateral to the section shown in Fig. 31).
- Fig. 33 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (1.56 mm. lateral to the mid sagittal section and 0.12 mm. lateral to the section shown in Fig. 32).
- Fig. 34 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (1.62 mm. lateral to the mid sagittal section and 0.06 mm. lateral to the section shown in Fig. 33).
- Fig. 35 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 13 mm., 28.8x. (1.68 mm. lateral to the mid sagittal section and 0.06 mm. lateral to the section shown in Fig. 34).



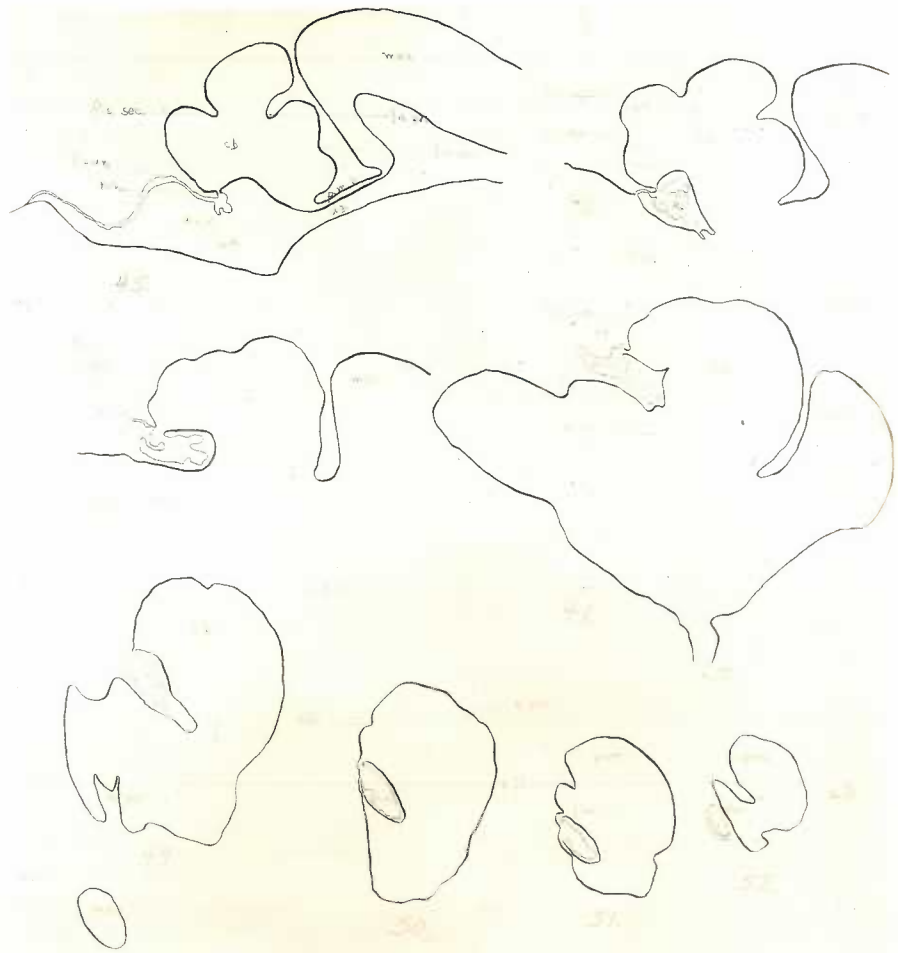


- Fig. 36 Mid sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x.
- Fig. 37 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (0.48 mm. lateral to the midsagittal section.)
- Fig. 38 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (0.96 mm. lateral to the mid sagittal section and 0.48 mm. lateral to the section shown in Fig. 37.)
- Fig. 39. Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (1.2 mm. lateral to the mid sagittal section and 0.24 mm. lateral to the section shown in Fig. 38).
- Fig. 40 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (1.26 mm. lateral to the midsagittal section and 0.06 mm. lateral to the section shown in Fig. 39).
- Fig. 41 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (1.38 mm. lateral to the mid sagittal section and 0.12 mm. lateral to the section shown in Fig. 40.)
- Fig. 42 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (1.50 mm. lateral to the mid sagittal section and 0.12 mm. lateral to the section shown in Fig. 41.)
- Fig. 43 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x (1.56 mm. lateral to the midsagittal section and 0.06 mm. lateral to the section shown in Fig. 42.)
- Fig. 44 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 15 mm., 28.5x. (1.62 mm. lateral to the mid sagittal section and 0.06 mm. lateral to the section shown in Fig. 43.)

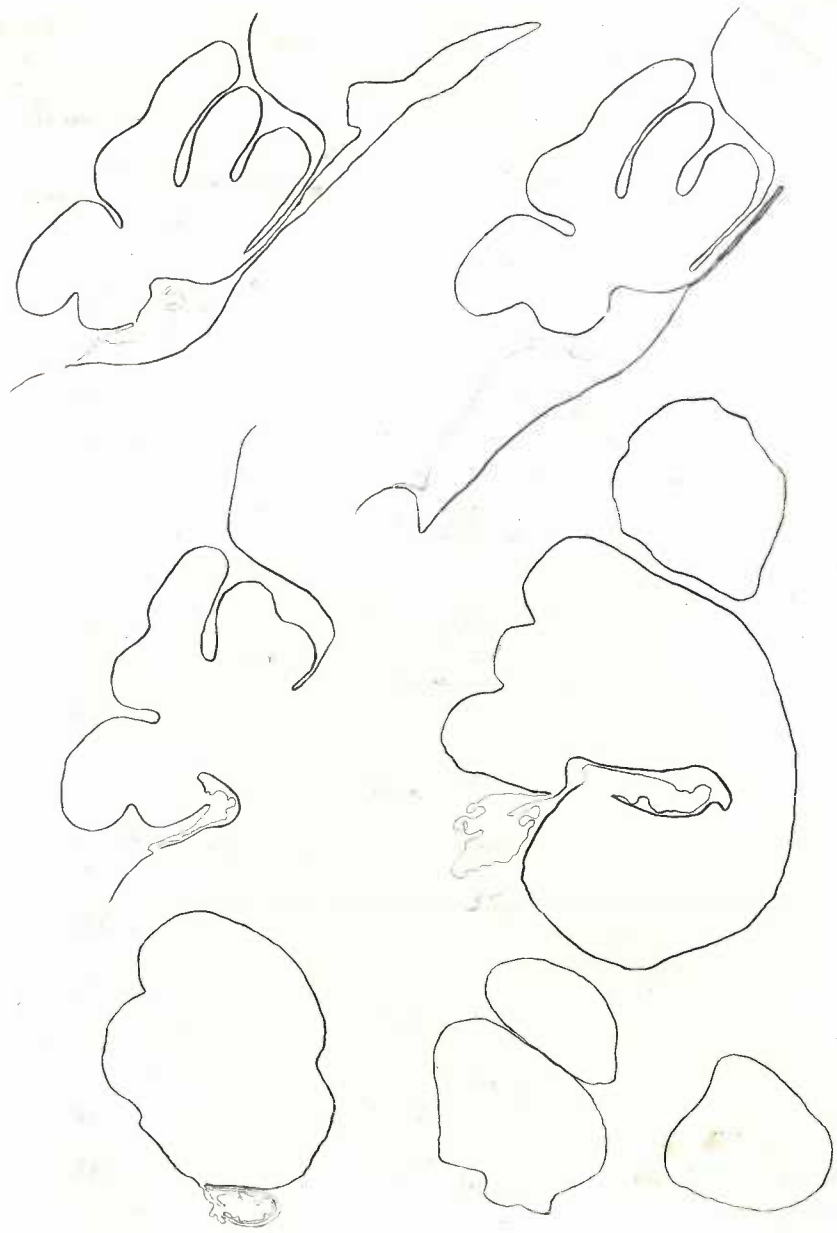


- Fig. 45 Mid sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x.
- Fig. 46 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (0.54 mm. lateral to the mid sagittal section).
- Fig. 47 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x (0.9 mm. lateral to the mid sagittal section and 0.36 mm. lateral to the section shown in Fig. 46.).
- Fig. 48 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.08 mm. lateral to the mid sagittal section and 0.18 mm. lateral to the section shown in Fig. 47.)
- Fig. 49 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.26 mm. lateral to the mid sagittal section and 0.18 mm. lateral to the section shown in Fig. 48.)
- Fig. 50 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.44 mm. lateral to the mid sagittal section and 0.18 mm. lateral to the section shown in Fig. 49.)
- Fig. 51 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.53 mm. lateral to the mid sagittal section and 0.09 mm. lateral to the section shown in Fig. 50.)
- Fig. 52 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.62 mm. lateral to the mid sagittal section and 0.09 mm. lateral to the section shown in Fig. 51.)
- Fig. 53 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 16 mm., 25.5x. (1.71 mm. lateral to the mid sagittal section and 0.09 mm. lateral to the section shown in Fig. 52).



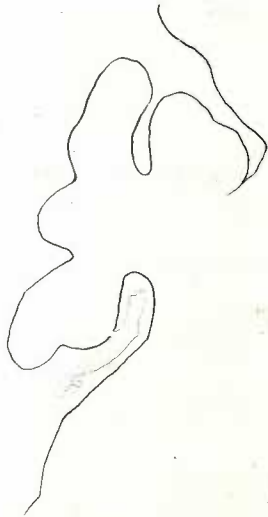
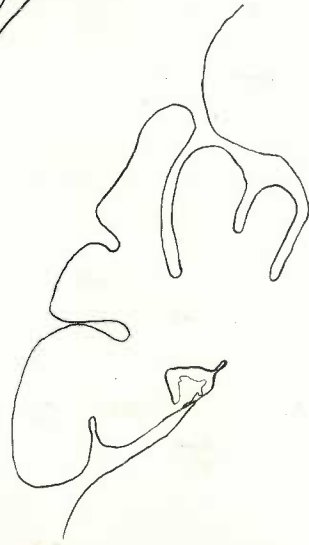
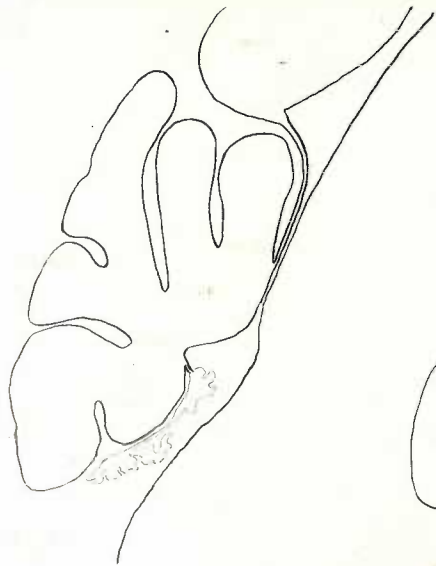


- Fig. 54 Mid sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x.
- Fig. 55 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (0.48 mm. lateral to the mid sagittal section).
- Fig. 56 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (0.96 mm. lateral to the mid sagittal section and 0.48 mm. lateral to the section shown in Fig. 55.)
- Fig. 57 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (1.44 mm. lateral to the mid sagittal section and 0.48 mm. lateral to the section shown in Fig. 56).
- Fig. 58 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (1.68 mm. lateral to the midsagittal section and 0.24 mm. lateral to the section shown in Fig. 57).
- Fig. 59 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (1.755 mm. lateral to the mid sagittal section and 0.075 mm. lateral to the section shown in Fig. 58).
- Fig. 60 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 18 mm., 28.5x. (1.92 mm. lateral to the mid sagittal section and 0.165 mm. lateral to the section shown in Fig. 59).





- Fig. 61 Mid sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.7x.
- Fig. 62 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.7x. (0.75 mm. lateral to the mid sagittal section).
- Fig. 63 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.7x. (1.125 mm. lateral to the mid sagittal section and 0.375 mm. lateral to the section shown in Fig. 62.)
- Fig. 64 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.7x. (1.5 mm. lateral to the mid sagittal section and 0.375 mm. lateral to the section shown in Fig. 63.)



- Fig. 65 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.5x. (1.695 mm. lateral to the mid sagittal section and 0.195 mm. lateral to the section shown in Fig. 64.
- Fig. 66 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.5x. (1.875 mm. lateral to the mid sagittal section and 0.18 mm. lateral to the section shown in Fig. 65).
- Fig. 67 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.5x. (2.070 mm. lateral to the mid sagittal section and 0.195 mm. lateral to the section shown in Fig. 66.
- Fig. 68 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.5x. (2.250 mm. lateral to the mid sagittal section and 0.180 mm. lateral to the section shown in Fig. 67.
- Fig. 69 Sagittal section of the cerebellum of a Corynorhinus embryo C.R.L. 22 mm., 27.5x. (2.445 mm. lateral to the mid sagittal section and 0.195 mm. lateral to the section shown in Fig. 68.
- Fig. 70 Posterior superior view of the cerebellum of the adult Corynorhinus, 6.1x.



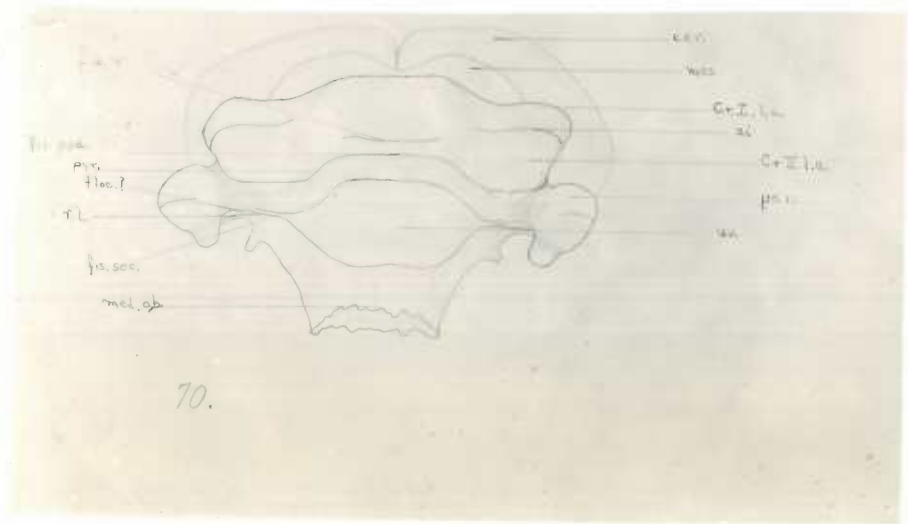
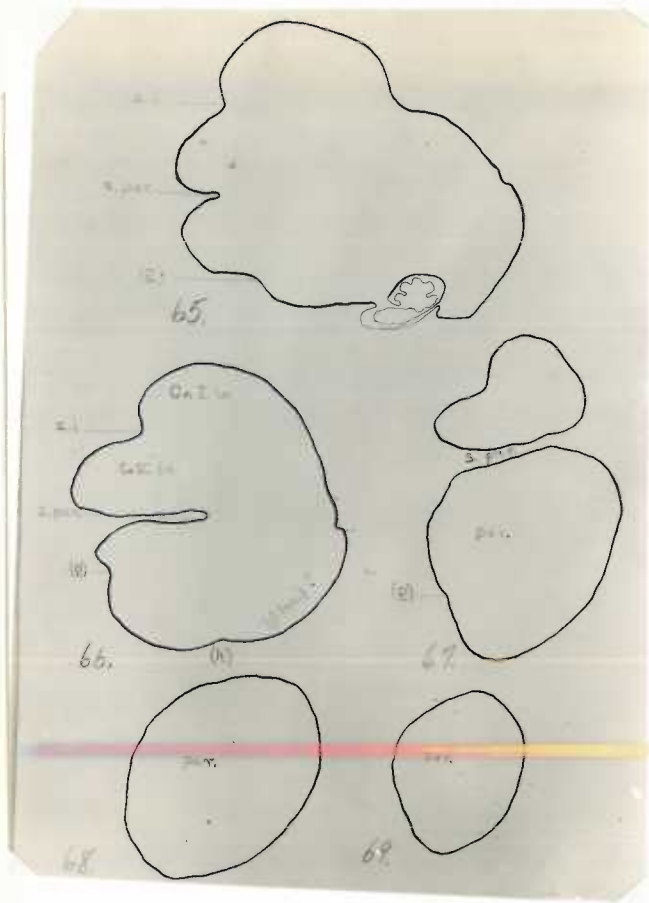
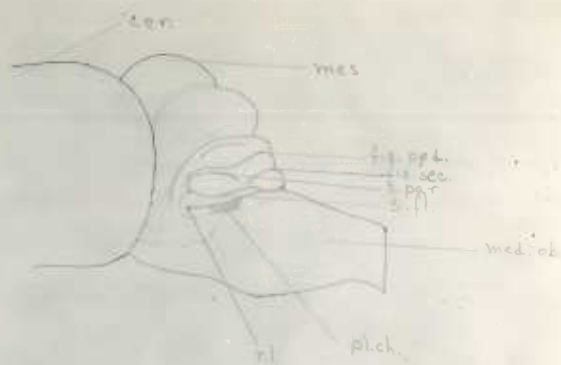


Fig. 71 Lateral view of the cerebellum of a new  
born white rat, 6.lx.

Fig. 72 Posterior superior view of the cerebellum of  
a 2 day old white rat, 6.lx.

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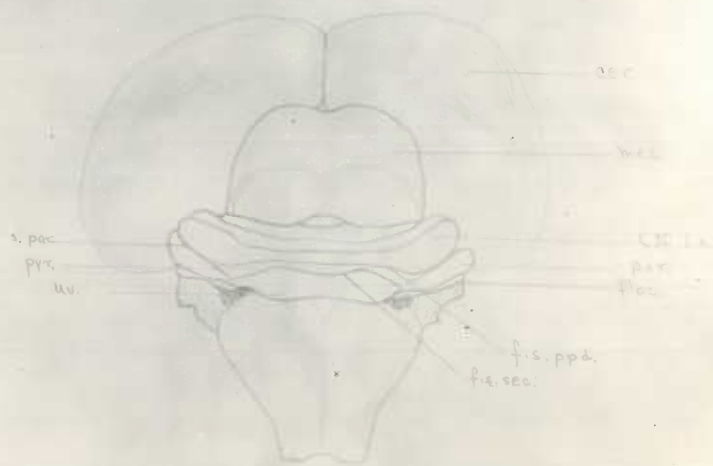




Fig. 73 Photograph of a model of the lateral part  
of the cerebellum of a *Corynorhinus* embryo  
C.R.L. 15 mm., 31.5x. (lateral view).



Fig. 73.

Fig. 74 Photograph of a model of the cerebellum  
of a *Corynorhinus* embryo C.R.L. 16 mm.,  
28.5x. (right lateral view).





Fig. 74

Fig. 75 Photograph of a model of the cerebellum of  
a *Corynorhinus* embryo C.R.L. 16 mm., 27.9x.  
(left lateral view).

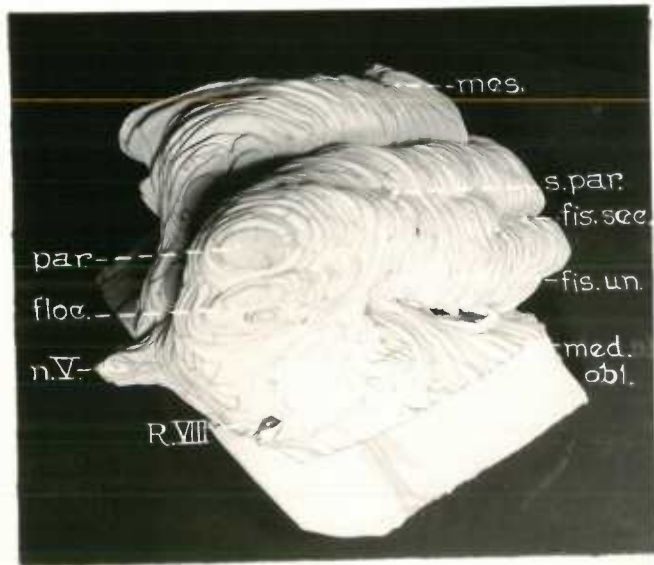


FIG. 70



Fig. 76 Photograph of a model of the cerebellum of  
a *Corynorhinus* embryo C.R.L. 16 mm., 27.8x.  
(posterior superior view.)

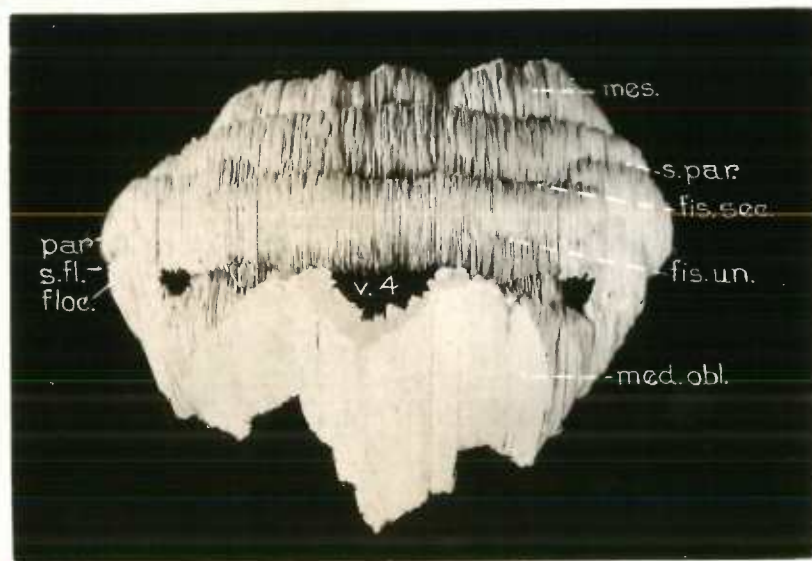


FIG. 70.

Fig. 77 Photograph of a model of the lateral extremity  
of the cerebellum of a Corynorhinus embryo  
C.R.L. 18 mm., 34x. (lateral view).



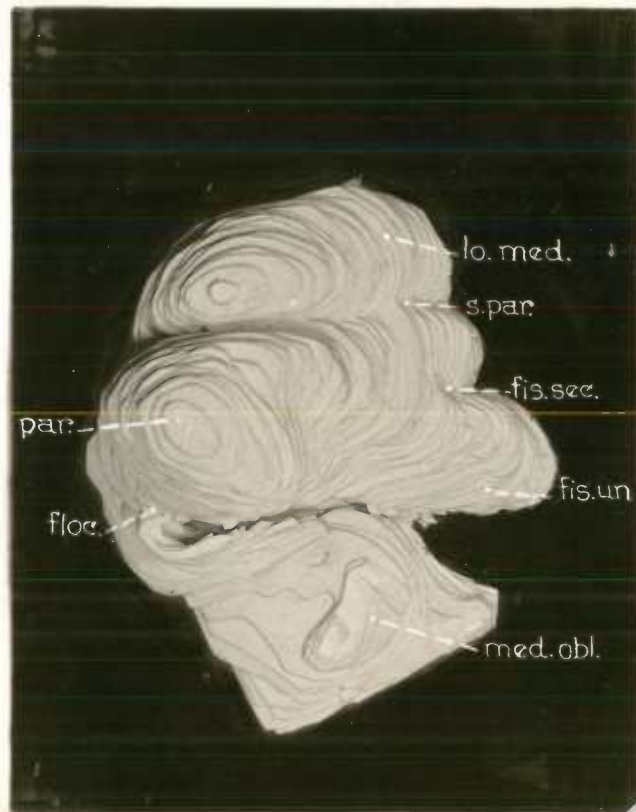


FIG. 77.

Fig. 78 Photograph of a model of  $1/2$  of the cerebellum  
of a new born white rat, 26.4x. (lateral view).

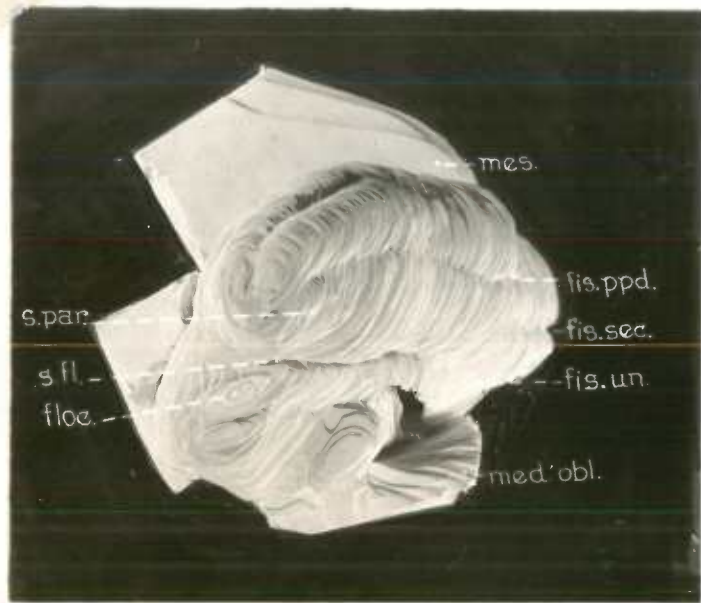


Fig. 70.