University of Edinburgh.

THESIS FOR THE DEGREE OF D.Sc.

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CONTRIBUTIONS TO THE DEVELOPMENT AND MORPHOLOGY OF THE MAMMALIAN HIND-BRAIN.

Part I.

1. "On the Development and Homology of the Mammalian Cerebellar Fissures," *Jour. Anat. and Phys.*, vol. xxxvii.
2. "The Mammalian Cerebellum: its Lobes and Fissures," *Jour. Anat. and Phys.*, vols. xxxviii. and xxxix.
3. "Neuromeres of the Rhombencephalon of the Pig," *Rev. Neur. and Psych.*, vol. ii.

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ON THE DEVELOPMENT AND HOMOLOGY OF THE MAMMALIAN CEREBELLAR FISSURES.[1]

By O. Charnock Bradley, M.B., *Professor of Anatomy, Royal Veterinary College, Edinburgh.* (Plates XII.–XVI.)

Part I.

Very few serious attempts have been made to discover if there is any regular plan of arrangement of the fissures and lobes of the mammalian cerebellum. If we leave out of account those scattered descriptions of the cerebellum of a single animal, or of one or two animals—such, for instance, as Ganser's (1) classic and oft-quoted investigation into the anatomy of the brain of the mole, Krause's (2) monograph on the rabbit, and Miss Ärnbäck-Christie-Linde's (3) paper on the brain of the shrew and bat; not to mention more of a like nature—we find that the literature on the comparative anatomy of the cerebellum can only be described as meagre. Undoubtedly the best work that has been done in the way of attempting to clear away morphological difficulties is that which has appeared from the pen of Stroud (4). Another paper worthy of mention in this connection is that of Kuithan (5), which appeared almost contemporaneously with Stroud's. These two writers stand practically alone, inasmuch as they did not rest satisfied with an examination of the adult brain, but demanded to know what embryology had to say. Stroud traced the development of the cerebellar fissures in the cat and in man; and Kuithan examined embryos of the sheep and man.

The latest attempt—as far as is known by the present writer—which has been made to establish the homology of the lobes of the cerebellum of mammals appears in the large work by Flatau and Jacobsohn (6) on the central nervous system. The value, great though it still remains, of this last piece of work is impaired by the fact that only adult material was used, and in many cases apparently second-hand descriptions were accepted.

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[1] The work, of which the present paper is the outcome, was done by the writer as a Research Student of the University of Edinburgh.

The ideal method, in a question of this kind, appears to be a combination of the embryological and the comparative anatomical. Stroud recognised this, and suggested that it would be necessary to examine into the intrauterine history of every mammal—a colossal task, verily. This being beyond the compass of the powers of one man, he examined two animals embryologically, and gave a long list of adult animals which he stated he had compared with each other. Unfortunately his description of the adult cerebella, seemingly promised in his first paper, is not as yet forthcoming.

Kuithan did not attempt the examination of a series of adult cerebella, but contented himself with the consideration of the development of the fissures in sheep and in man.

In the case of Stroud, Kuithan, and Flatau and Jacobsohn the investigation was apparently begun with the determination to find, if possible, homologies to the lobes of the cerebellum of man. To the mind of the present writer this was a mistake. 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. It is only after many (if possible, all) mammals have been passed under review that man may be brought in to complete the list as the highest and most richly endowed.

Acting upon the conviction that the brain of man should not be taken as the standard, but that the simplest cerebella should form the starting-point, the present investigation was commenced with a search for the smoothest and least complicated mammalian cerebellum. This was discovered—thanks in part to the paper of Miss Ärnbäck-Christie-Linde—in the shrew and some of the bats. The shrew's was therefore taken as the initial cerebellum; and had it been possible, shrew embryos would have been examined with a view to noting the time and order of appearance of the various fissures. Owing to the difficulty of obtaining a sufficiency of shrews at all periods of intrauterine life, and because of the comparative ease with which rabbit embryos of all ages could be obtained, it was decided to start the embryological part of the investigation with the latter; and indeed the rabbit possibly served the purpose better than the shrew would have done, since the cerebellum of the adult is built on simple lines, and yet there are parts in it in miniature which attain considerable magnitude in the larger mammals.

Seeing that the rabbit has a cerebellum so very much more simple than, say, that of the carnivora or the ungulates, it seemed well that the development of the fissures in one of the larger animals should also be watched. For this purpose, because of the little difficulty in getting material, the pig was chosen. As it happened, I was able to command material at practically any stage of development, and therefore the ages of both the rabbit and the pig embryos were, with one or two exceptions, absolutely known.

In addition to the examination of the developmental history of the fissures in two mammals, as many kinds of adult cerebella as could be obtained have also been compared.

In this paper are stated the results of the investigation, starting with an account of the appearance of the fissures in the rabbit. Until the time arrives when it is necessary to summarise results, the fissures and lobes will be known by the simplest designations, viz., figures and letters, to the end that the mind may not be influenced by the use of terms which have acquired a certain fixed significance.

RABBIT.

20 *days embryo*, 37 *mm. long* (fig. 3).—When the entire brain of the rabbit is examined at this stage, the cerebellum appears as two fairly prominent lateral projections jutting out on each side just below the mid-brain. A narrow connecting band is also seen running transversely between the mid-brain and the medulla. No fissures are visible to the naked eye; and on making a sagittal microscopic section in the mesial plane, the contour is even except at the posterior lower part of the cerebellar lamina, where a curved hem-like portion is marked off by a shallow fissure (fig. 3, IV.). This fissure makes its first appearance about the 18th day (fig. 1). The hem-like edge of the lamina is continued laterally over the lateral recess of the ventricle, to become continuous with a similar lip belonging to the medulla (fig. 2). It is apparently the Rautenlippe (His).

21 *days embryo*, 42 *mm. long* (fig. 4).—At this stage the cerebellum is very similar in appearance, to the naked eye, to that of the preceding day. The middle portion is somewhat more obvious, but no other visible change has occurred. A mesial sagittal section presents an outline which may be roughly described as triangular, the base of the triangle looking towards the medulla and pons. The two other sides of the triangle constitute what it will be convenient to call the anterior and posterior slopes of the cerebellum. Such a section again shows the fissure mentioned in the description of the 20 days embryo, but it is now farther removed from the extreme edge of the lamina (fig. 4, IV.). There is also a faint indication of another fissure at the upper part of the anterior slope (fig. 4, II.). It may be noted also that the future anterior medullary velum is better marked, as a result of a slight forward growth of the anterior part of the cerebellar lamina.

22 *days embryo*, 50 *mm. long* (figs. 5, 6 and 7).—A distinct advance has been made in development. The cerebellum is still very obviously made up of two prominent lateral masses, connected by a slighter intermediate portion, but the disparity in volume of these three parts is not so evident (fig. 5). In addition to a mere growth in size, other important changes have taken place. On an examination with the naked eye, it is clear that a portion of each lateral projection is about to be differentiated from the main bulk of the mass. This is shown by faint fissures, or rather grooves, slightly indenting the surface (figs. 5 and 6). Moreover, on sagittal section, the fissure, faintly foreshadowed in the 21 days embryo at the upper part of the anterior slope, is unmistakably a definite entity, and cuts the anterior slope into two almost equal parts (fig. 7, II.). The fissure which was the first to appear is still farther from the edge of the lamina (fig. 7, IV.). Further, there is the promise of a third fissure, this being indicated at this stage by a depression on the posterior slope (fig. 7, III.).

At this stage there are therefore evidences of three transverse fissures cutting at least the mesial part of the cerebellum into four portions; and in addition, indication of a subsequent complication of the lateral part.

23 *days embryo*, 50 *mm. long* (figs. 8, 9 and 10).—There is

now undoubted evidence of the rudiments of the three parts of the adult cerebellum. The central portion has increased considerably in volume, and there are shallow antero-posterior grooves marking off the future vermis and hemispheres.

The fissure on the posterior slope, which was not more than hinted at in the 22 days embryo, is now sufficiently deep to be visible by means of an ordinary pocket lens (fig. 8, III.). By the same means two transverse fissures are distinguishable on the anterior slope (fig. 9). The more superior corresponds to that already noticed in the previous stage. The lower one of the two is very shallow, and it is necessary to examine sections in order to be definitely certain that it is in reality the rudiment of a fissure.

Sagittal sections show three fissures, with the commencement of a fourth. The deepest corresponds to the one on the anterior slope of the 22 days cerebellum (fig. 10, II.).

In an embryo of 55 mm. in length, apparently some hours older than the one now under consideration, four fissures can be distinguished without any difficulty (fig. 11). It is desired to call especial attention to this stage, for it is believed that here we have the same number of fissures and lobes in the vermis as belong to the simplest form of mammalian cerebellum. Without applying any special names to these fissures and lobes, and without anticipating the attempt, which will be made later, to homologise them with similar features in the cerebella of other mammals, let it suffice for the present to designate the fissures as I., II., III. and IV., and the lobes as A, B, C, D and E, in each case commencing the enumeration anteriorly. Of the four fissures we may consider II. to stand in the first place of morphologic importance. It appears at an early date in all animals of which we have any embryological account. Moreover, it maintains its supremacy of depth throughout the whole of embryonic life, and on into the adult state. As has been pointed out by previous writers, it is the deepest and most constant fissure of the cerebellum.

In the hemisphere of the 23 days embryo a fissure is growing inwards towards fissure III. of the vermis, and is consequently dividing the most lateral part of the hemisphere into two somewhat unequal parts, the more posterior of which projects the more laterally.

24 *days embryo*, 59 *mm. long* (fig. 12).—To the naked eye the only change is one of increased size and greater distinctness of the fissures. In microscopic sections the fissures are obviously deeper than they were in the preceding stage, and there are indications of a future fissure in lobe A (fig. 12, *c*).

25 *days embryo*, 64 *mm. long* (figs. 13, 14 and 15).—The distinction of vermis and hemispheres is now very clear, and the fissures are more definite. Fissure I. is now of considerable depth and extends completely across the vermis. Fissures II. and III. have invaded the groove marking vermis from hemisphere. The fissures indenting the lateral part of the hemispheres are deeper and approach fissure III. a little more closely. Two pairs of additional fissures can be distinguished in lobe C, these being in the groove between vermis and hemisphere; one pair on the anterior slope, the other on the posterior (fig. 13, *a*, fig. 14, *b*).

In sections, the fissure whose beginning was seen in lobe A of the 24 days cerebellum has attained some depth, and another fissure is forming below it. The former may be called, for the present, fissure *c* (fig. 15).

27 *days embryo*, 67 *mm. long* (figs. 16, 17 and 18).—All the fissures are deeper and much more lateral in extent. The outstanding projection of the hemisphere is now very sharply marked off from the rest of the hemisphere, and when the cerebellum is viewed from the front, is becoming separated from a smaller eminence which has developed in connection with the roof of the lateral recess of the ventricle. The upper and larger projection we shall henceforth speak of as the *paraflocculus*, and the lower as the *flocculus* (fig. 17). These terms were suggested by Stroud, and are useful as indicating that the two structures are not equivalent to the flocculus of man. They arise each in its own particular way. The paraflocculus is a part of the hemisphere proper. The flocculus, on the other hand, has developed in the same manner as lobe E, *i.e.* in close relationship to the Rautenlippe.

The two lateral fissures on the posterior slope of lobe C have now run together in the middle line, and constitute a single transverse fissure cutting the lobe into two parts (fig. 16, *a*, fig. 18, *a*).

28 *days* (?) *embryo*, 67 *mm. long* (figs. 19, 20 and 21).—On the posterior slope the only change is one of depth and distinctness of the fissures, there being no additions. But when the cerebellum is viewed from the front, it is evident that development has here gone on more rapidly. Fissure II. is now in the form of a crescent, extending almost to the borders of the hemisphere. The fissures in the lateral parts of lobe C are also longer and deeper than in the stage described above. An additional fissure has made its appearance in lobe B. The paraflocculus and flocculus are separated by a still deeper depression, and the paraflocculus is more sharply separated from the rest of the hemisphere (fig. 20).

For the sake of subsequent description, we may indicate the fissure on the posterior slope which divides lobe C into two parts by the letter *a* (fig. 19, *a*, fig. 21, *a*). That this fissure, shallow though it is even in the adult rabbit, is of considerable morphologic importance, is brought out in the section of this paper which deals with the various adult cerebella.

At birth.—At the time when the rabbit is born, the cerebellum is not a replica in miniature of the adult organ, since development progresses rapidly for some days after birth.

The cerebellum at birth has its principal fissures of considerable depth, and some of its accessory fissures have begun to form (figs. 22 and 23). The paraflocculus is now completely surrounded by a fissure, with the exception of its posterior part, where there is no fissure, but merely a shallow depression. The flocculus is also completely bounded by a fissure, but as yet its surface is not sculptured by any lines. Fissure III. fades away in the groove or depression behind the paraflocculus, as also does fissure *a* (fig. 22). Even in the adult the lateral parts of these fissures are not deep.

2 *days after birth.*—After birth, as has been said, there is a fairly rapid change for a few days, until the cerebellum comes to resemble the adult organ.

At the end of the second day the exact connection of the paraflocculus with the vermis is more precisely indicated. Fissure III. has grown more laterally, and it is now evident that the paraflocculus really belongs to lobe D. Lobe E can hardly be said to extend into the hemisphere at all, fissure IV. disappearing in the groove between vermis and hemisphere. In the earlier stages this lobe was continuous, without any fissure of demarcation with the posterior medullary velum; but from the 22nd day onwards it projects backwards more and more, and consequently a limiting fissure is formed.

Adult cerebellum (figs. 24, 25, 26 and 28).—In giving a description of the adult cerebellum of any animal, it is both convenient and rational to take fissure II. as the dividing line between an interior and a posterior portion. In the cerebellum of the rabbit this fissure lies wholly in the anterior surface, a surface presenting a concavity into which the mid-brain fits. Fissure II. occupies a comparatively high position in the vermis, but slopes rapidly downwards and outwards across the hemisphere to its border. Its great depth is brought out best by making a sagittal section of the vermis (fig. 28, II.). Below this fissure lie some seven folia, the two uppermost of which are separated from the rest by a fairly deep fissure, which we have seen makes its appearance about the 23rd day of intrauterine life, and which has been referred to in the previous paragraphs as fissure I. This is the deepest fissure in that part of the vermis which lies anterior to fissure II. When traced outwards it is found to fail to reach the extreme lateral border of the hemisphere (fig. 24, I.). At a distance of two folia below fissure I. is fissure *c* (as referred to in the embryonic cerebella), not quite so deep as the former, but reaching the lateral border. From the presence of fissure *c* lobe A is divided into two portions, which may be called lobule A_1 below the fissure, and lobule A_2 above it. In lobule A_1 the folia do not extend farther in a lateral direction than to a line corresponding to the lateral limits of the vermis, *i.e.* no hemisphere can be distinguished in this part of the cerebellum. The question of whether there is a lingula in the rabbit corresponding exactly to that of man is one which seems best answered in the negative. There are certainly no folia adherent to the anterior medullary velum.

The vermis and hemispheres behind fissure II. are divided into three lobes (C, D and E), corresponding to those first indicated in the 22 days embryo. Lobe C of the vermis usually carries eight folia, the majority of which are not carried directly into the hemisphere. The fissures between these folia are for the most part shallow, but two of them go to a greater depth than the rest, and are held to be of greater importance. Not only are they deeper than the others, but they appear at an earlier period. A reference to the 25 days embryo shows the forerunners of these fissures as two pairs of depressions; one on the anterior, the other on the posterior slope. In the adult brain the more anterior of the two occurs between folia 2 and 3 (counting from fissure II.), and on being traced into the hemisphere is seen to run for some distance parallel to fissure II., into which it ultimately opens. For more immediate purposes we shall speak of this fissure as fissure *b* (fig. 24, *b*, fig. 28, *b*). An offshoot leaves it in the groove between vermis and hemisphere, and curves outwards and backwards to the border of the hemisphere.

The other deep fissure of lobe C separates folium 6 from folium 7, and corresponds to the fissure resulting from the union of the pair of grooves on the posterior slope which first appeared on the 25th day, and which met in the vermis two days later. This has already been referred to as fissure *a*. In the adult it can be traced to the outermost limits of lobe C. If we recognise the fissures just mentioned as being of importance, it follows that lobe C must be looked upon as consisting of three portions or lobules. These, for the present, will be called lobules C_1, C_2 and C_3, starting the enumeration anteriorly.

The fissure between lobes C and D (fissure III.) is of moderate depth in the middle of the vermis (fig. 28, III.), but becomes very shallow at its lateral borders. In some specimens, however, there is not much difficulty in tracing its curved course outwards and upwards until it is lost in the deep fissure which separates the paraflocculus from the rest of the hemisphere. Lobe D is confined to the vermis, but in most specimens there is a low white ridge connecting it with the paraflocculus. Its surface is formed by three folia (sometimes a shallow fissure divides the lowest folium into two). Of the two fissures between these folia the lower is slightly the deeper, and the lower folium extends rather farther towards the hemisphere than the other two. These facts are mentioned because of the belief that lobe D of the rabbit corresponds to two lobules in more complicated cerebella.

Lobe E is entirely confined to the inferior aspect of the cerebellum, and, like lobe D, has no direct continuation into the hemisphere.

The paraflocculus projects markedly from the lateral part of the hemisphere, from which it is separated by a deep fissure in front and above, and by a depression behind. It is entirely enclosed in a special fossa formed by the temporal bone (lobulus petrosus). As has been seen in tracing its development, it is really a piece of the hemisphere which has been cut off from the rest. Its developmental connection with lobe D is a point upon which it is desired to lay emphasis.

The flocculus consists of two or three folia, seen best when the cerebellum is viewed from the front, and lying anterior to the paraflocculus (fig. 25). It is in contact with the lateral extremity of lobe B, from which it is separated by a fissure which contains the middle cerebellar peduncle (fig. 24).

Lepus timidus (fig. 27).—The differences between the cerebellum of the rabbit and that of the hare are not perhaps very great, but they seem sufficiently important to merit mention. Lobes A, B and C are practically identical with those of the rabbit. Lobe C has again eight folia in the vermis, and a fissure, *a*, deeper than the rest, separates folia 6 and 7. This fissure is much more definite in hemisphere of the hare than it is in the rabbit.

The most important differences exist in lobe D. Here the number of folia is at least four, as against three in the rabbit; and the uppermost of the four is more definitely joined to the paraflocculus by a ridge which is slightly foliated along its upper border as it approaches the paraflocculus. This fact is mentioned as being the ground upon which the statement, that in the adult rabbit lobe D is connected with the paraflocculus, is based. In many specimens of the rabbit's cerebellum the adult connection is obscure; therefore the evidence afforded by the brain of the hare is welcome.

Before passing to the consideration of the development of the much more complicated cerebellum of the pig, it is perhaps well to describe those adult cerebella which are built on the same or similar lines as obtain in the rabbit.

Sorex vulgaris (fig. 29).—As previously stated, apparently the simplest form of mammalian cerebellum is found in the shrew and some of the bats. An examination of sagittal sections of the shrew's cerebellum shows that the vermis is divided into fine lobes by four fissures, *i.e.* that the numerical condition as found in the brain of a rabbit embryo of about 24 days is maintained into adult life. Fissure I. is of moderate depth, but does not extend much, if at all, beyond the vermis. Fissure II., on the other hand, is very deep, and passes far out into the hemisphere. Its importance as a morphologic entity probably stands out more plainly in the shrew, and some few animals with a similar simple cerebellum, than it does in many of those in which the fissures are more numerous.

Fissure III. is the shallowest of the fissures of the vermis, and does not invade the hemisphere, or at any rate only slightly. There is a fissure in the hemisphere occupying a corresponding position, but microscopic sections show that there is no union of the two. Fissure IV. very early disappears in a series of sections. There is a projection, from the lateral part of the hemisphere, enclosed in a cell in the temporal bone, and doubtless corresponding to the paraflocculus of the rabbit. It seems very doubtful if a flocculus proper is developed.

Erinaceus Europæus (figs. 30, 31, 32, 33 and 34).—The hedgehog has a cerebellum which, in degree of complexity, may be considered to stand between that of the shrew and that of the rabbit. The vermis is divided into five lobes by four fissures, of which the second (fissure II.) is by far the deepest. This is visible in the vermis when the cerebellum is examined from above, but it leaves the dorsal to gain the anterior surface in the shallow groove which marks vermis from hemisphere. In the hemisphere it slopes rapidly downwards and outwards, in much the same manner as in the rabbit. Fissure I. is second in point of depth. Unlike the corresponding fissure in the rabbit, it reaches the borders of the hemispheres. Fissures III. and IV. are of moderate depth, and run into one another at the lateral boundary of the vermis.

Lobe A is, as a rule, beset by three folia, and, unlike the corresponding lobe in the rabbit, is not divided by a fissure, *c*. Lobe B has never more than two folia, so far as can be gathered from an examination of some ten brains. Lobe C has five folia in the vermis, the four anterior of which are separated from the fifth by a fissure which corresponds to *a* in the brain of the rabbit, and which is continued into the hemisphere in a like manner. Lobe C, anterior to fissure *a*, becomes much expanded in the hemisphere, and its folia are increased in number. The folium behind fissure *a* retains its single character after its prolongation into the hemisphere (lobule C_3). Lobes D and E have each two folia, and are confined to the vermis.

The paraflocculus is fairly well marked, but does not produce the projection (lobulus petrosus) which is so prominent in the rabbit. The flocculus is rather smaller in the hedgehog than in the rabbit, but has approximately the same position and shape as in the latter animal. Sagittal sections show very clearly the close relationship of this lobule with the posterior medullary velum. As successive sections are examined in a direction away from the vermis, the velum is seen to become thickened by grey matter, which is directly continuous with the grey matter of the flocculus.

Talpa Europœa (figs. 35, 36 and 37).—In the vermis of the cerebellum of the mole, the four fundamental fissures are easily distinguished. Fissure I. is relatively a slightly greater depth than in either the rabbit or the shrew. It is, as usual, limited to the anterior surface, and runs almost vertically downwards in the line of boundary between vermis and hemisphere. Fissure II. is of very considerable depth. Its course is very sinuous, beginning on the anterior surface of the vermis, then taking a sharp bend backwards over the anterior superior border of the cerebellum to gain the dorsal surface, where it again turns sharply forwards and outwards to once more become included in the anterior surface, down which it runs almost vertically. Fissure III. is more distinct than in the shrew. Fissure IV. is of about the same depth as in Sorex.

Lobe A is almost entirely in the vermis, though it expands a little in the lower part of the anterior surface. Its surface possesses two fissures, the lower of which is more pronounced, and may possibly be comparable to fissure *c* of the rabbit; a fissure not represented in the shrew. Lobe B is constricted in the vermis, where it is constituted by a single folium; but, owing to the erratic course taken by fissure II., it expands considerably in the hemisphere. That part of lobe C which is included in the vermis is comparatively extensive. This lobe is constricted at the junction of vermis and hemisphere, to become again extensive in the hemisphere itself. There are a few shallow fissures in the vermis, but one of them is of slightly greater depth than the rest, and corresponds to fissure *a*. Lobule C_3 consists of a narrow folium in the vermis, but expands in the hemisphere (fig. 35). This is a point of some moment, because in the more complicated cerebella, to be hereafter described, the expansion of this particular lobule in the hemisphere is a prominent feature. Lobes D and E are simple and call for no remark, except that a very thin and narrow band runs outwards and forwards from D, but is entirely hidden by the bulk of the hemisphere. This band extends as far forwards as the base of the paraflocculus.

The paraflocculus is in the form of a rounded lobule, with fissured surface, connected with the hemisphere by a narrow neck, and enclosed in a fossa of the temporal bone. No flocculus can be made out with certainty.

Mus decumanus (figs. 38, 39, 40 and 41).—The cerebellum of the rat is decidedly more complicated than that organ in the mole or hedgehog, and approaches more nearly that of the rabbit. Fissures I. and II. resemble those of the rabbit, except that I. always reaches the margin of the hemisphere, and the central part of II. is visible of the dorsal surface. Fissures III. and IV. are also very similar to those of the rabbit's cerebellum.

Lobe A is divided into two parts by a fissure, *c*, which is almost as deep as I. The upper part of this lobe (lobule A_2) has two folia; the lower part (lobule A_1) a variable number, separated by shallow fissures (fig. 41). Lobe B has two folia, and resembles the like lobe in the rabbit both in position and size. In lobe C there is a deep fissure, *a*, cutting the vermis to almost the same depth as fissure III., and separating a single folium, which is continued into the hemisphere. The rest of lobe C, which is contained in the vermis, has about three folia, of which the most anterior is the largest. A definite fissure, *b*, cannot be made out. The hemisphere part of lobe C, anterior to fissure *a*, is of considerable size. Lobes D and E are confined to the vermis, the former having three folia, the latter two.

The paraflocculus projects from the hemisphere by a narrow neck, and is received into a fossa in the temporal bone, the investment of bone being less close than in the rabbit. There is a small, simple flocculus lying anterior to the paraflocculus, and touching the lateral borders of lobes A and B.

In the mouse (*Mus musculus*) the cerebellum very closely resembles that of the rat. The paraflocculus has possibly a slightly narrower neck and is more closely invested by bone.

Arvicola amphibius (figs. 42, 43 and 44).—The water-vole has a cerebellum which differs from that of the brown rat in minor points only. Its fissures are the same in number. As a rule, fissure I. does not quite reach the border of the hemisphere. Lobe A is divided by a fairly deep fissure, *c*. Lobule A_2 has two folia, lobule A_1 only one. Lobe B is narrow (as in the rat), and possesses two folia in the vermis. The vermis portion of lobe C has six folia, fissure *a* separating the sixth from the rest. The sixth folium (constituting the central part of lobule C_3) is continued into the hemisphere without either increase in size or accession of fissures. There is possibly a fissure, *b*, placed between the 2nd and 3rd folia, and continued outwards and forwards into the anterior surface of the hemisphere.

Lobes D and E are limited to the vermis, D having two folia, E only one. The paraflocculus and flocculus are almost identical with those in the rat.

The cerebellum of the field-vole (*Arvicola agrestis*, fig. 45) only differs from that of the water-vole inasmuch as its folia are fewer in number.

Pteropus poliocephalus (figs. 46, 47, 48 and 49).—A sagittal section through the middle of the vermis of this large bat discloses an arrangement of lobes not very unlike that of the hedgehog. The number of lobes and fissures is the same, but the folia are somewhat more numerous. Fissure I. is rather shallow, but fissure II. is of great depth; of fissures III. and IV. there is nothing remarkable to note. Lobe A is small and carries about three folia. There is apparently no fissure *c*. Lobe B, on the other hand, is large, and is provided with five or six folia. There are seven folia in the vermis in lobe C, the seventh of which is separated from those anterior to it by an unmistakable fissure *a*. This single folium of the vermis is connected with two folia in the hemisphere. In Talpa, lobule C_3 increased in size in the hemisphere, but did not acquire any intrinsic fissures. In Pteropus it also expands, and in addition is sculptured by a fissure. It seems good to call attention to this point, in the light of other facts presently to be set forth. Lobes D and E belong exclusively to the vermis; the former has three folia, the latter two.

A noteworthy development appears in the paraflocculus. It consists of two parts, an upper and a lower. In the cerebella to be described in the following pages, the morphologic importance of this feature of the paraflocculus will become evident. The lower portion of the paraflocculus of Pteropus consists of a lobulus petrosus; *i.e.* it projects into a bony fossa and has a narrow neck. Both portions of the paraflocculus are foliated (figs. 46 and 47). The flocculus is small, and divided into two by an almost vertical fissure, only seen when the cerebellum is viewed from the side.

It is interesting to notice the great difference in the cerebellum of the Megachiroptera as shown in Pteropus, and that of the Microchiroptera as exemplified in *Vesperugo pipestrellus*, described and figured by Miss Ärnbäch-Christie-Linde (3). Vesperugo has a cerebellum not more complex than that of the shrew, whereas the cerebellum of Pteropus is as complex as that of the rabbit, or possibly more so.

Sciurus vulgaris (figs. 50, 51, 52 and 53).—The squirrel offers a most instructive degree of complexity in the fissures and lobes of its cerebellum, inasmuch as it exhibits a condition intermediate between the simpler forms, which have already been described, and those of a more complicated nature, still to be considered. For this reason the squirrel's cerebellum is peculiarly serviceable to anyone desiring to establish homologies in the lobes and fissures of mammals in general.

Fissure I. in the squirrel, as in the rabbit, stands second in point of depth. Also, as in the rabbit, it fails to reach the margin of the hemisphere. Fissure II. is far and away the deepest of all the fissures. It is visible in the vermis, on the dorsal surface; but turning forwards abruptly, it runs down the anterior surface of the hemisphere, with only a slight degree of obliquity. Fissure III. is of considerable depth, and on reaching the border of the vermis, turns at almost a right angle, and runs nearly vertically downwards for some distance. Then, curving outwards and afterwards forwards, it is traceable into the deep fissure separating the paraflocculus from the hemisphere (figs. 51 and 52, III.). Fissure IV. resembles the same fissure in the rabbit, and offers no noteworthy feature.

The greatest interest centres itself in the lobes. Lobe A is of considerable size, consists of five folia, and is indented by a fissure, *c*, between the 2nd and 3rd folia. Another fissure, of a depth almost equal to that of *c*, occurs at a distance of two folia below the latter. Lobe B consists of three or four folia and is not very noteworthy. Lobe C has five folia in the vermis. The anterior four expand in the hemisphere, in the customary manner, and are separated from the fifth by a fissure, *a*. The fifth folium, instead of remaining as a single folium when traced into the hemisphere, as in the rabbit, suddenly expands and forms a not inconsiderable lobule, clearly differentiated from the rest of lobe C by a continuation of fissure *a* (fig. 52). Lobe D is relatively large and carries six folia. It is divided into two approximately equal parts by a fissure of a depth only slightly, if at all, inferior to that of fissure III. We shall refer to this latest fissure as *d* in future descriptions, as its value as a division between parts of the vermis is unquestionable (figs. 51, 52 and 53, *d*). That part of lobe D which lies above fissure *d* (and which we may call lobule D_1) consists of two folia, which becoming one, curves round the inferior border of lobule C_3, and losing its grey cortex, gives place to a white ridge passing directly to the upper part of the paraflocculus. That part of lobe D inferior to fissure *d* (known in the succeeding descriptions as lobule D_2) is not continued into the hemisphere. Lobe E is comparatively small, and consists of only one definite folium.

The paraflocculus is large when compared with the similar lobule of the cerebella already described, and presents the appearance of a rounded foliated band which has been doubled upon itself and placed with its long axis approximately in the direction of the long axis of the head. The bend is in front (figs. 51 and 52). The flocculus is small and compressed. It lies below the paraflocculus, and can only be seen from the side or front of the cerebellum.

The points in the foregoing description to which it is desired to draw especial attention are as follows:—(1) The increasing complexity of lobe A as compared with the same lobe of all the other animals so far discussed. (2) The considerable expansion in the hemisphere of lobule C_3. (3) The division of lobe D into two parts by the fissure *d*, and the lateral continuation of the upper part (lobule D_1) of this lobe. (4) The arrangement of the paraflocculus in the form of two parallel portions, continuous with each other in front, and the connection of lobule D_1 with the upper portion of the paraflocculus.

The cerebella which remain to be described are all built on much more complicated lines than are those which have been passed under view in the foregoing sections. This being so the examination of the development of the fissures in an animal possessing a richly fissured and foliated cerebellum in adult life will greatly aid in the task of recognising homologies. Therefore pig embryos will be examined, with a view to noting the time and order of appearance of the various fissures.

(*To be continued.*)

REFERENCES.

(1) Ganser, S., "Vergleichend-anatomische Studien über das Gehirn des Maulwurfs," *Morpholog. Jahrbuch.*, Bd. 7, 1882, p. 591.

(2) Krause, *Die Anatomie des Kaninchens*, 1884.

(3) Ärnbäck-Christie-Linde, Augusta, "Zur Anatomie des Gehirnes niederer Säugetiere," *Anat. Ang.*, Bd. xviii., 1900, p. 8.

(4) Stroud, B. B., "The Mammalian Cerebellum," *Journ. Comp. Neurology*, vol. v., 1895, p. 71.

Ibid., "A Preliminary Account of the Comparative Anatomy of the Cerebellum," *Proc. Assoc. American Anatomists*, May 1897.

Ibid., "Morphology of the Ape Cerebellum," *Proc. Assoc. American Anatomists*, Dec. 1897.

(5) Kuithan, W., "Die Entwicklung des Kleinhirns bei Säugetieren," *S. B. Ges. Morph. Physiol.*, München, 1894, and *Münchener Medicinische Abhandlungen*, vii. Reihe, 6 Heft, 1895.

(6) Flatau, E., und Jacobsohn, L., "Handbuch der Anatomie und vergleichenden Anatomie des Centralnervensystems der Säugetiere," Berlin, 1899.

PLATES XII.–XVI.

EXPLANATION OF FIGURES.

In all the figures the same letters and figures are used for corresponding fissures or lobes. The application of the letters and figures is explained in the text.

p.m.v. (in figs. 1 and 3) = posterior medullary velum.
a.m.v. (in figs. 4 and 7) = anterior medullary velum.
ch.pl. (in figs. 1, 2 and 3) = choroid plexus.

All the sections (with the exception of that shown in fig. 2) are in the median plane and sagittal in direction.

Fig. 1. Rabbit embryo, 18 days, 21 mm. Mesial sagittal section through the cerebellar lamina.
Fig. 2. Same embryo. Sagittal section where the cerebellar lamina and the medulla are joining. *lat. rec.* = lateral recess.
Fig. 3. Rabbit embryo, 20 days, 37 mm. Mesial sagittal section through the cerebellar lamina.
Fig. 4. Rabbit embryo, 21 days, 42 mm. Mesial sagittal section.
Fig. 5. ,, 22 days, 50 mm. Posterior view. × 2.
Fig. 6. ,, 22 days, 50 mm. Left lateral view. × 2.
Fig. 7. ,, 22 days, 50 mm. Mesial sagittal section.
Fig. 8. ,, 23 days, 50 mm. Posterior view. × 2.
Fig. 9. ,, 23 days, 50 mm. Anterior view. × 2.
Fig. 10. ,, 23 days, 50 mm. Mesial sagittal section.
Fig. 11. ,, 55 mm. Mesial sagittal section.
Fig. 12. ,, 24 days, 59 mm. Mesial sagittal section.
Fig. 13. ,, 25 days, 64 mm. Posterior view × 2.
Fig. 14. ,, 25 days, 64 mm. Anterior view. × 2.
Fig. 15. ,, 25 days, 64 mm. Mesial sagittal section.
Fig. 16. ,, 27 days, 67 mm. Posterior view. × 2.
Fig. 17. ,, 27 days, 67 mm. Anterior view. × 2.
Fig. 18. ,, 27 days, 67 mm. Mesial sagittal section.
Fig. 19. ,, 28 days (?) 67 mm. Posterior view. × 2.
Fig. 20. ,, 28 days (?) 67 mm. Anterior view. × 2.
Fig. 21. ,, 28 days (?) 67 mm. Mesial sagittal section.
Fig. 22. Rabbit, 30 hours after birth. Posterior view. × 2.
Fig. 23. ,, 30 hours after birth. Anterior view. × 2.
Fig. 24. ,, adult. Anterior surface. × 2.
Fig. 25. ,, ,, Left lateral surface. × 2.
Fig. 26. ,, ,, Posterior surface. × 2.
Fig. 27. Lepus timidus. Posterior view. × 2.
Fig. 28. Rabbit, adult. Mesial sagittal section.
Fig. 29. Sorex vulgaris. Mesial sagittal section.
Fig. 30. Erinaceus Europæus. Mesial sagittal section.
Fig. 31. ,, ,, Anterior surface. × 2.
Fig. 32. ,, ,, Left lateral view. × 2.

Fig. 33. Erinaceus Europæus. Superior view. × 2.
Fig. 34. ,, ,, Posterior view. × 2.
Fig. 35. Talpa Europæa. Superior-posterior view. × 2.
Fig. 36. ,, Anterior surface. × 2.
Fig. 37. ,, Mesial sagittal section.
Fig. 38. Mus decumanus. Posterior view. × 2.
Fig. 39. ,, Superior view. × 2.
Fig. 40. ,, Anterior surface. × 2
Fig. 41. ,, Mesial sagittal section.
Fig. 42. Arvicola amphibius. Superior surface. × 2.
Fig. 43. ,, ,, Anterior surface. × 2.
Fig. 44. ,, ,, Mesial sagittal section.
Fig. 45. Arvicola agrestis. Mesial sagittal section.
Fig. 46. Pteropus poliocephalus. Superior view. × 2.
Fig. 47. ,, ,, Posterior view. × 2.
Fig. 48. ,, ,, Anterior surface. × 2.
Fig. 49. ,, ,, Mesial sagittal section.
Fig. 50. Sciurus vulgaris. Anterior surface. × 2.
Fig. 51. ,, Superior view. × 2.
Fig. 52. ,, Posterior view. × 2.
Fig. 53. ,, Mesial sagittal section.

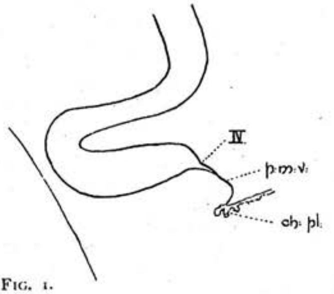
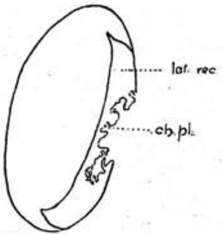


FIG. 1.



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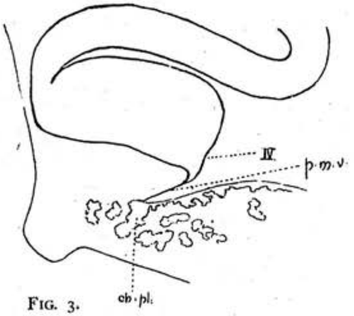

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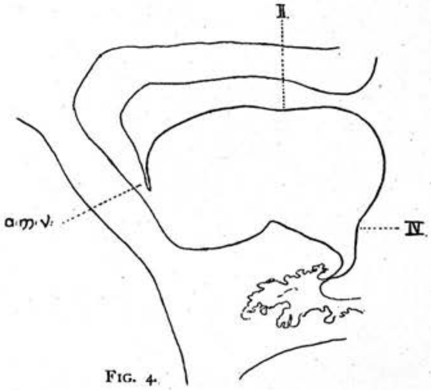

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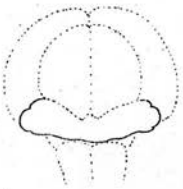

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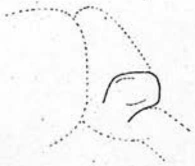

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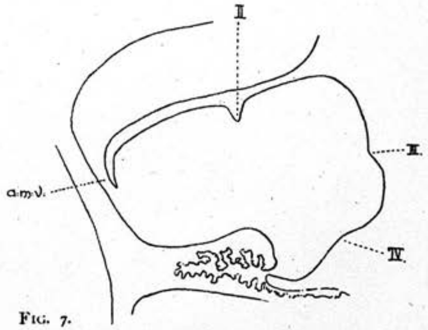

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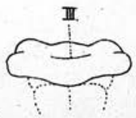

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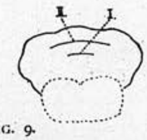

FIG. 9.

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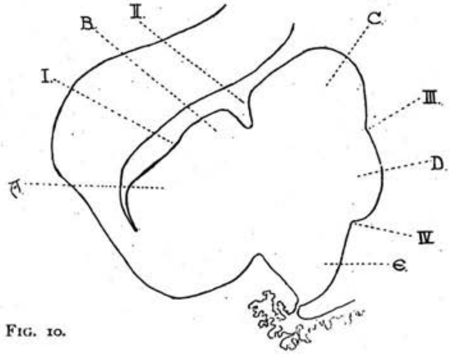

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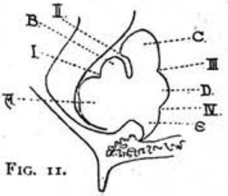

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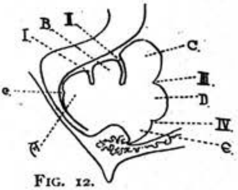

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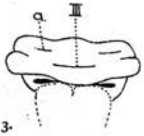

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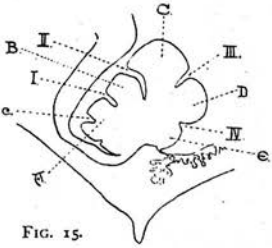

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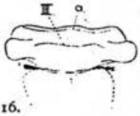

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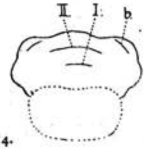

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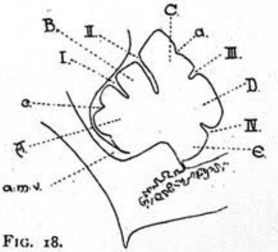

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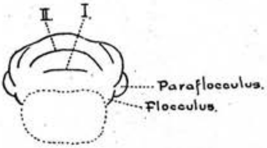

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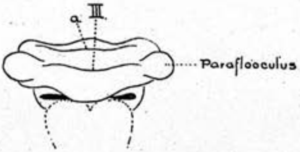

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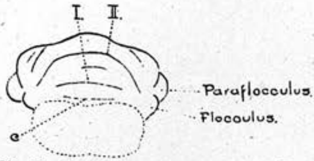

FIG. 20.

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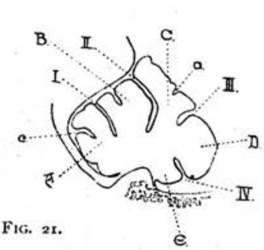

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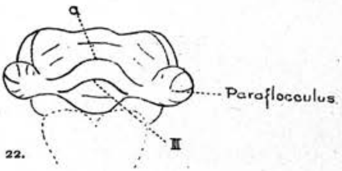

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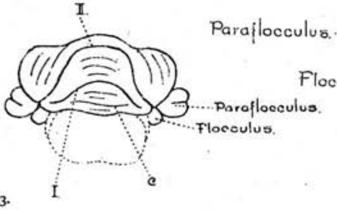

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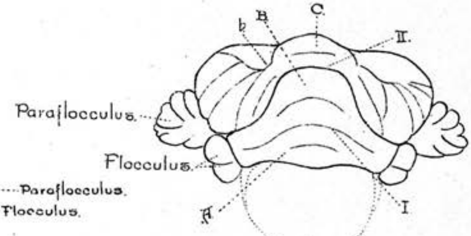

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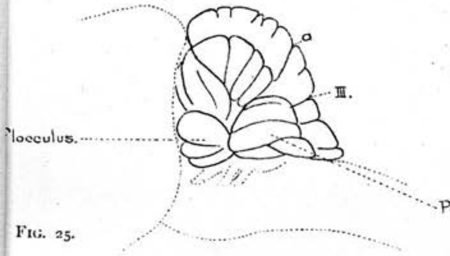

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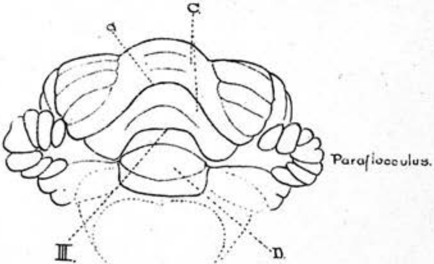

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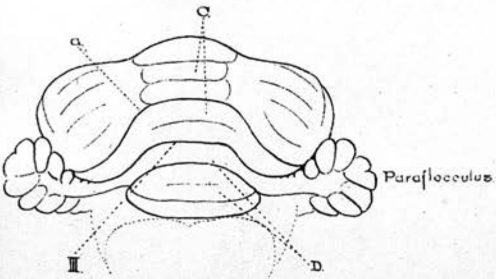

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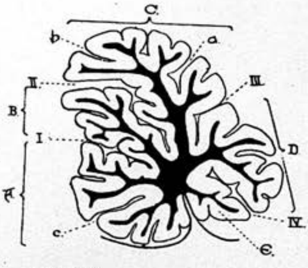

FIG. 28.

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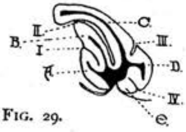

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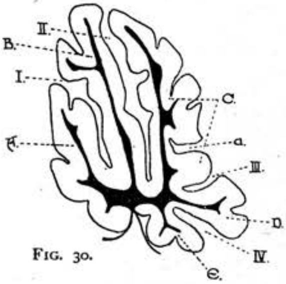

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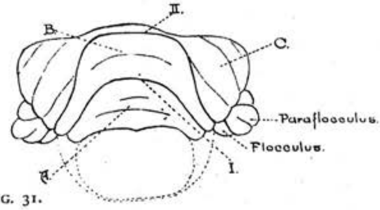

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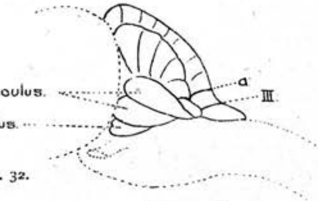

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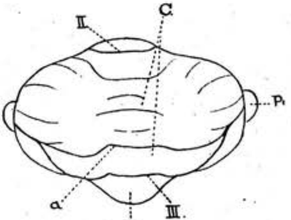

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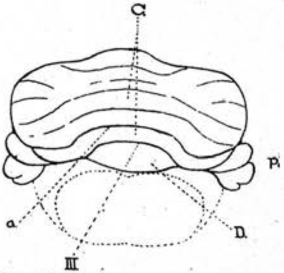

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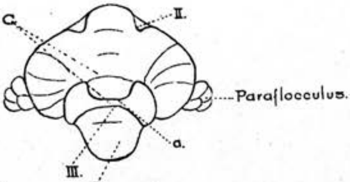

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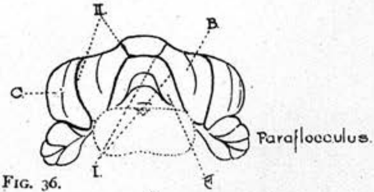

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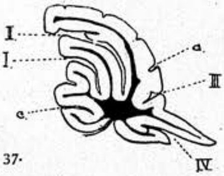

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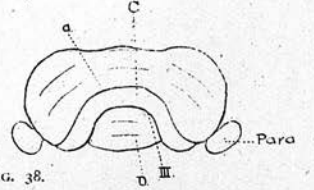
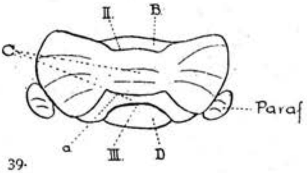


FIG. 38.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.



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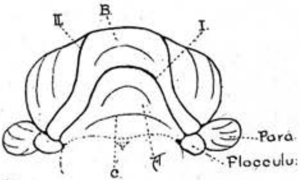

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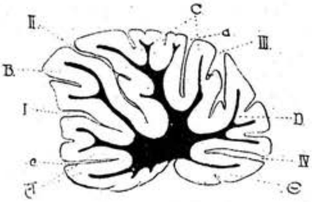

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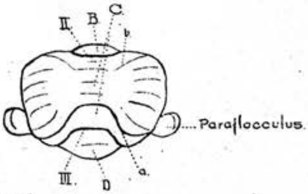

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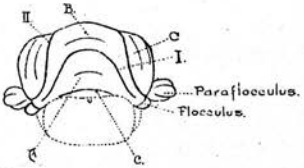

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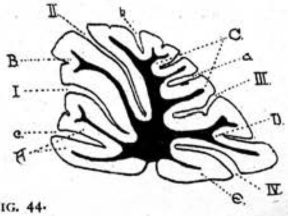

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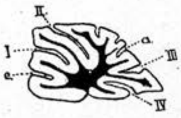

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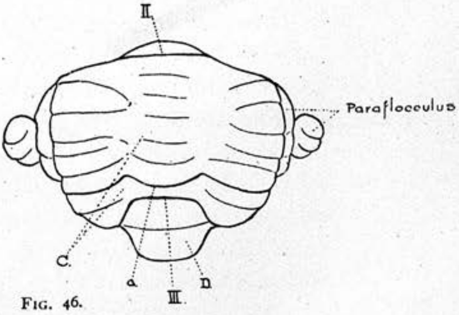

FIG. 46.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.

ON THE DEVELOPMENT AND HOMOLOGY OF THE MAMMALIAN CEREBELLAR FISSURES.[1]

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PART II.—PIG.

40 *days embryo*, 52 *mm. long* (figs. 54, 55 and 56).—At this stage the cerebellum of the pig embryo bears a certain likeness to that of the rabbit on the 20th day of gestation. No fissures are visible to the naked eye, but when sections are made and microscopically examined there is noticed a somewhat thin lip-like plate projecting from the lower posterior corner of the section of the cerebellar lamina (fig. 56). This is comparable in every respect to the same feature in the rabbit's brain on the 20th day, and there develops a homologous lobe in connection with it.

44 *days embryo*, 64 *mm. long* (figs. 57, 58 and 59).—Development has proceeded rapidly during the interval between the last stage and the present. A naked-eye examination shows a sufficiently clear distinction between the future vermis and hemispheres. There is also visible on the anterior slope a fissure (II.) of considerable length (fig. 58). Microscopic sagittal sections show fissure IV. as before, and fissure II. of some depth. There are also possibly faint indications of two other fissures in that part of the vermis lying between II. and IV. There is as yet no trace of a separation of a paraflocculus from the hemisphere.

48 *days embryo*, 80 *mm. long* (figs. 60, 61 and 62).—Develop-

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[1] The work, of which the present paper is the outcome, was done by the writer as a Research Student of the University of Edinburgh.

ment has again progressed rapidly; indeed, it is something of a misfortune that a stage intermediate between 44 and 48 days could not be obtained. But though this is a misfortune, it is not one which offers any insuperable difficulty in the solution of the problem before us.

An examination of a 48 days cerebellum reveals a fissure (II.) which is prolonged for some distance into the hemisphere. Below it the two other fissures are faintly marked. These develop into fissures I. and *c*. On the posterior slope there are two faint fissures in the vermis. Subsequent development shows that these become fissures III. and *d*. In the hemisphere there is an indication of a fissure, which, growing inwards from the lateral part of this portion of the cerebellum, ultimately demarcates the paraflocculus. Another faint foreshadowing of a fissure is also seen indenting the margin of the hemisphere anterior to the one just mentioned. This latter, growing inwards, ultimately forms part of fissure *a* (fig. 60, *a*).

Microscopic sections afford additional evidence as to the actuality of the faint depressions seen with the naked eye (fig. 62). They also show that a number of fissures are about to complicate that portion of lobe A which lies below fissure *c* (lobule A_1). Lobe E has increased in volume, and is now, in consequence, sharply defined from the posterior medullary velum. A flocculus is becoming evident, and its development from the boundary of the lateral recess is clearly indicated. Its boundaries are not as yet rigidly set down, but it reveals itself as a thickening and bulging in the region in which, in the future, it is to become conspicuous (fig. 61).

Embryo, 86 *mm. long*.—In the cerebellum of an embryo of 86 mm. in length (of which the age is not certainly known, but is estimated at about 50 days) the anterior surface is quite richly fissured. Fissure II. now reaches the extreme margin of the hemisphere, and fissure I. almost does so. On the posterior slope, fissure *a* runs completely across the cerebellum, but is shallow at the junction of vermis and hemisphere. Fissure III. crosses the vermis and invades the groove between it and the hemisphere. The fissure which is about to cut off the paraflocculus is deep, and is growing inwards towards fissure III. of the vermis, with which it finally becomes continuous.

Fissure *d* is, if anything, rather longer than fissure III. The paraflocculus forms a distinct projection, and is now clearly separated from the flocculus. Sections show that lobe B is becoming divided by a shallow transverse fissure.

51 *days embryo*, 88 *mm. long* (figs. 63, 64 and 65).—The difference between this and the above stage is only one of depth of fissures.

55 *days embryo*, 100 *mm. long* (fig. 66).—To the naked eye the fissures have obviously deepened since the 51st day, but no new ones can be made out. Sections, however, show that a fissure, *b*, has begun to invade that part of lobe C which is in the vermis. It seems likely that this fissure first made its appearance, on the anterior slope of the hemisphere, about the 48th day (fig. 61), and that the two parts gradually grew together in the vermis. It is interesting to notice at what an early period fissure *a* came into existence, and how comparatively late fissure *b* is in making its appearance in the vermis. This should be compared with the constancy of the former fissure in the cerebella of the type of the rabbit, and the inconstancy or difficulty of determination of fissure *b* in the cerebella of the same order of complexity.

The fissures in lobule A_1 are now of considerable depth. Lobule A_2 retains its comparatively small size. Lobe B is larger, and contains a moderately deep fissure, which is the forerunner of a like feature in the adult brain.

59 *days embryo*, 118 *mm. long* (figs. 67, 68 and 69).—As in the rabbit, the anterior part of the pig's cerebellum has advanced more rapidly than the posterior part during the earlier stages of development. By the 59th day the anterior surface is bearing a strong resemblance to the adult condition, but the posterior part is still comparatively simple. Fissure *b* is now of some depth and can readily be recognised by the unaided eye. Fissure *a* has gained considerably in depth. Fissure III. has become continuous with the lateral fissures, which, making an early appearance, first indicated the limits of the paraflocculus.

Fissure *d* is of great lateral extent, being indeed the longest fissure of the cerebellum at this stage (with the possible doubtful exception of fissure II., which has a curved course). Fissure *d*, it should be noted, is growing forwards into the paraflocculus, which is, by it, being divided into an upper and a lower part, connected together in front (fig. 67). It is desired to emphasise the fact that there is a strong, well marked connection between lobe D and the paraflocculus. This connection at this stage is not confined to the part of lobe D above fissure *d* (lobule D_1), but belongs to the entire lobe. Nothing could show more clearly that the paraflocculus and lobe D are parts of one and the same morphologic unit. This point is illustrated much better in the pig than it was in the rabbit.

The paraflocculus has enlarged, and its anterior surface shows signs of foliation (fig. 68).

65 *days embryo*, 132 *mm. long* (figs. 70, 71, 72, 73 and 74).—The anterior surface has now very closely approached the adult condition, both in its external appearance and also in those features which can only be adequately appreciated by means of sagittal sections.

Fissure II. is of great depth, its lowest part being not far removed from the summit of the roof of the 4th ventricle (fig. 74). Lobe B shows definite evidence of its future bipartite condition. Lobule A_1 has now lost its former arrangement of indefinitely arranged folia, and has collected them into three sub-lobules such as are found in the adult brain. Fissure *b* is now of some depth, and fissure *a* makes an important landmark on the posterior slope. Fissure *d* is deeper than fissure III., and both parts of lobe D are becoming foliated (fig. 74). Lobe E remains relatively small and simple, but is now separated from the posterior medullary velum by a conspicuous fissure.

The paraflocculus is now divided into two parts, both of which are now foliated. The whole lobule now closely resembles the same lobule in the adult squirrel. The division into two parts has obviously been brought about by an extension in a forward direction of fissure *d*. This extension was beginning in the previous stage. The upper part of the paraflocculus is connected with lobule D_1 by a rounded non-foliated ridge. The connection between lobule D_2 and the lower half of the paraflocculus has almost become obliterated, but it should be kept in mind that such a connection did at one time exist. The flocculus is small and, to the naked eye, not yet provided with folia. On examining microscopic sections, however, slight fissures are found to exist.

70 *days embryo*, 150 *mm. long* (fig. 75).—Except in richness of foliation, no marked change has occurred in that part of the cerebellum which is anterior to fissure II. The posterior portion of the organ, however, has now entered into a more active phase of development, and is rapidly assuming the adult appearance. That part of lobe C which is anterior to fissure *a* (lobules C_1 and C_2) has grown considerably in a lateral direction. Further, the vermis portion has also grown so much in an antero-posterior direction that it can no longer be accommodated in the strict mesial plane, but has become distorted by being thrust over to one side. Fissure *b* is now a very important feature. It extends all the way across the cerebellum. Lobule C_3 has also altered considerably in appearance. It no longer forms a band of practically uniform width, running from one margin of the cerebellum to the other. It now fails to extend as far laterally as the more anterior part of lobe C. Its vermis portion has increased in volume in a sagittal direction, and, like that part of the vermis immediately in front of it, is now distorted by being pushed to one side. The hemisphere portions, too, have enlarged in a sagittal direction, and are now in the form of rounded masses, connected with the vermis by a comparatively narrow isthmus. This lobule has therefore come to resemble that of the squirrel.

The two parts of lobe D have also enlarged, and their folia are more numerous. The connection between lobule D_1 and the corresponding part of the paraflocculus is still smooth. Lobe E remains small, and to the naked eye appears to have no connection with the flocculus beyond that established by means of the posterior medullary velum. But microscopic sections show that there is still a low smooth ridge running between the two structures.

The paraflocculus has not increased much in size, and, because of the lateral expansion of lobe C, is now not so prominent a feature on the lateral surface of the hemisphere. The flocculus is still small, and to the naked eye smooth.

Embryo, 165 *mm. long, age unknown* (figs. 76, 77, 78, 79 and 80).—This is the last embryonic stage which it is necessary to examine, as it brings us within a short distance of the condition of the adult cerebellum. Lobule A_1 is now certainly composed of three sub-lobules, the uppermost of which has beyond doubt an extension into the hemisphere. One single small folium still adheres to the anterior medullary velum, and therefore may possibly be looked upon as an attenuated example of a lingula. Lobule A_2 is relatively small, and has a rather shallow fissure dividing it into two parts. Fissure II. begins on the dorsal surface of the vermis; curving forwards at the lateral boundary of the vermis, it runs obliquely down the anterior surface. Lobe B is divided into upper and lower portions by a fairly deep fissure, whose advent has been noted in earlier stages. Lobe C has again made great advances. So much is this the case that lobule C_2 is very considerably distorted. Lobule C_3 is now clearly divided into three parts—one in the vermis and one in each hemisphere—connected by narrow bands. The connection between lobule D_1 and the upper part of the paraflocculus is becoming slightly marked by fissures, and has become in part hidden by the posterior extremity of lobe C.

The paraflocculus is now quite complicated, from the presence of numerous folia; but there is no difficulty in recognising its constitution as two tiers. The flocculus is now foliated.

Adult cerebellum (figs. 81, 82, 83 and 84).—Having traced the development of the fissures and lobes up to an advanced stage, it does not seem necessary to give an additional detailed description of the adult organ. It will suffice to briefly indicate the changes which have occurred since the 165 mm. stage.

The cerebellum anterior to fissure II. has not undergone any radical change. It has taken additional folia upon itself, but that is all. In the posterior part of the cerebellum more decided changes have occurred. Fissure *b* is now very distinct crossing vermis and hemisphere, and reaching the border of the latter. A further displacement of the vermis portion of lobe C has taken place, so that in the adult brain fissure *a* is decidedly oblique. The connections between the vermis and hemisphere portions of lobule C_3 have become very much reduced. The upper part of lobe D has shared in the general distortion of this region of the vermis. Its connection with the paraflocculus now consists of a transversely foliated ridge (fig. 83). Lobule D_2 has merely increased in size and become more thickly foliated. Lobe E remains very small and inconspicuous (fig. 84).

In many cerebella the paraflocculus has become a somewhat jumbled collection of folia, but in most brains it has retained a closer resemblance to its earlier condition. There is usually little difficulty in tracing its two-tiered character, but it appears as though the lower tier had been turned forwards at its posterior end. The flocculus in the adult is in the form of a row of vertically placed folia, and runs in an antero-posterior direction, immediately below the paraflocculus. Its extremities only are visible when the cerebellum is looked at from before or from behind.

Having now learnt the characters of the fissures and lobes in the pig, we are in a position to examine those cerebella which are constructed after a similar plan.

Mustela furo (figs. 85, 86, 87 and 88).—In this animal is a good example of the backward retreat that fissure II. makes in some of the more complex cerebella. The vermis is about equally voluminous in front of and behind this fissure, this being the result of an increase in the number of lobules in the more anterior section of the vermis.

Lobe A is divided into two slightly unequal parts by a fissure, *c*, which is almost entirely visible when the cerebellum is looked at from the front, and which reaches the margin of the hemisphere. Lobule A_1 is divided into two parts, each carrying two or three folia. Lobule A_2 is also divided into two portions, but the fissure is not so deep as that in lobule A_1. Lobe B is cut by a curved fissure which almost reaches its lateral boundaries. It will be seen that lobes A and B are very similar to the corresponding lobes in the pig, except that the lower component of A is divided into two instead of three sub-lobules.

Lobe C forms a very considerable constituent of the hemisphere. It has fissures *a* and *b*, but the lobules in the vermis between *a* and *b* and *a* and III. are comparatively simple; *i.e.* they are not developed to such an extent that their accommodation necessitates distortion of the vermis. The connection between vermis and hemisphere segments of lobule C_3 is very narrow, as in the pig, and partly or wholly concealed. Lobes D and E are confined to the vermis; and D is divided into two lobules by a fissure, *d*.

The paraflocculus is arranged in the form of two tiers of folia joined together anteriorly. From the lower tier a lobulus petrosus projects for some distance. The connection between paraflocculus and lobe D cannot be made out in the adult. It is somewhat difficult to satisfactorily distinguish a flocculus, but it is apparently present, and visible when the cerebellum is viewed from the side or from behind.

Mustela erminea and *M. vulgaris* have both been examined, but they so closely resemble *M. furo* that no further description is necessary.

Meles taxus (figs. 89, 90, 91 and 92).—As compared with lobe B, lobe A is smaller in the badger than it is in the pig. Only a comparatively small portion of it is visible on the anterior surface of the cerebellum. Lobule A_2 is also small. Below fissure *c* there are two groups of folia, that group lying more inferiorly being further partially divided.

Lobe B is large, and divided by a deep fissure into upper and lower lobules, each of which is again somewhat deeply indented by a fissure (fig. 92).

In lobe C, fissure *b* extends to the border of the hemisphere, as it does in the pig (fig. 90). Lobule C_2 consists of a vermis portion, whose folia—unlike those of the pig—run transversely; and a hemisphere part, considerably removed from the vermis, because of the large development of those parts of lobule C_3 which belong to the hemisphere. The three segments of lobule C_3 are very unequal in size, the hemisphere portions being very extensive. There is practically no distortion of lobule C_3 in the vermis (fig. 91). Lobes D and E call for no special remark. The double character of the paraflocculus is very evident, the two portions being arranged in an oblique plane, and very clearly continuous in front (figs. 89 and 90). The connection between paraflocculus and vermis is very difficult to establish. In the brain examined, a very prominent lobulus petrosus was present on the right side, and was received into a fossa formed by the temporal bone. On the left side the corresponding lobule was curved forwards underneath the lower part of the paraflocculus (fig. 89). The question arises as to the possibility of the lobulus petrosus always representing the posterior extremity of the lower portion of the paraflocculus. This may be the case. If we accept this as being a true interpretation of the facts, then we should consider that, as the paraflocculus increases in size in different animals, it tends to press forwards, since the lobulus petrosus is often found in cerebella having small paraflocculi.

The flocculus consists of a single folium lying between the lateral recess of the ventricle and the most posterior part of the paraflocculus.

Canis familiaris (figs. 93, 94, 95 and 96).—The anterior part of the cerebellum of the dog does not differ very materially in the arrangement of its fissures and the disposition of its lobes from the corresponding part of the badger's cerebellum. In lobes C and D, however, there are differences of sufficient magnitude to warrant mention. Fissure *b* is present in a position very similar to that of the badger. It can readily be followed across the vermis and hemisphere to the border of the latter, running almost parallel to fissure II. Lobule C_2 has a very considerably distorted vermis portion, and its hemisphere dependencies show several fissures of some depth, which give the impression that it consists of several distinct sub-lobules. The central segment of lobule C_3 is also much twisted, and on superficial examination appears to have no connection with those vertically elongated masses which form its hemisphere segments. On opening up the groove between vermis and hemisphere, however, the connection can be distinguished. The displacement and sinuousness of the vermis in lobules C_2 and C_3 only appears after birth. In a new-born dog the vermis is perfectly straight and its folia entirely transverse.

Lobule D is connected to the upper part of the paraflocculus by a low white ridge, which can only be discovered by removing the lowest and most posterior part of lobe C. The rest of lobe D and lobe E call for no remark.

The paraflocculus is relatively larger than that of the badger, to which it bears a close resemblance in the manner in which its two tiers are arranged. It has not, however, a lobulus petrosus; or, at any rate, there is not more than the merest attempt at the formation of one, this occurring at the posterior end of the lower tier, and being only occasionally present. The flocculus is small and consists of a few folia, placed, under cover of the paraflocculus, at the most anterior limit of the lateral recess of the ventricle (fig. 95).

Canis vulpes (figs. 97, 98 and 99).—The general shape of the cerebellum of the fox is very different from that found in the dog. The fox's cerebellum has a greater vertical height in comparison with its antero-posterior diameter. Its anterior surface is depressed for the reception of the corpora quadrigemina, and its posterior surface is also concave from above downwards. The posterior concavity is rendered all the more obvious because of the backward projection of lobe D over the medulla. This projection is confined to lobule D_2, and is so great that this lobule can be seen very distinctly when the cerebellum is viewed from above. These differences being recognised, the cerebellum of the fox otherwise resembles that of the dog. The only points to which it seems necessary to draw attention are two, as follows: The vermis in the region of lobules C_2 and C_3 is possibly a little shorter in an antero-posterior direction, and somewhat less distorted in form. The lower part of the paraflocculus carries a definite lobulus petrosus (figs. 97 and 98).

The flocculus is small in the fox, and only just visible from behind (fig. 98).

Felis domestica (figs. 100, 101 and 102).—In the domestic cat the anterior part of the cerebellum is so similar to the same portion in the dog, both as regards its superficial characters and also its appearance in sections, that no detailed description is needed. The most important features are those presented by the organ when viewed from behind. Several cerebella of the cat have been examined, and in all a very striking character is the extreme to which the distortion of the central portions of lobules C_2 and C_3 is carried (figs. 100 and 101). In the brain from which the figures were made this distortion is very marked, possibly more so than is the case in the average cerebellum; but they serve to show to what lengths this twisting of the vermis may go. It will be observed that lobules C_2 and C_3 are arranged in the form of an S-shaped curve, the bends of which are very abrupt. This curvature of the vermis is continued into lobe D, but here its bends are not so sudden (fig. 101). There can be little doubt that this exaggerated displacement of the vermis is to be interpreted as meaning that, in the cat, lobes C and D are relatively more developed (so far as those parts of them which belong to the vermis are concerned) than is the case in the other mammals examined. The lateral parts of lobule C_3 are relatively smaller in the cat than in the dog, badger, or fox (fig. 101). They do not extend so far downwards as to blot out the connection between parafloceulus and the vermis. This connection is in the form of one or two folia, resting upon the medulla below, and in contact with the lowest part of lobule C_3 above.

The paraflocculus resembles that structure in the dog. There is considerable difficulty in distinguishing a flocculus with any degree of certainty in the adult animal. That it is present is undoubted from the observations made by Stroud on its development. But its clear definition in the embryo appears to become obscured at a later date.

Goat and Sheep (figs. 103, 104 and 105).—In many respects the cerebellum of ungulates departs, in the way of details, from the plan found in those carnivora just described.

When viewed from the front, the cerebella of the goat and sheep show fissures *c*, I., II. and *b* very distinctly (fig. 103), all of these reaching the margins of the hemisphere. Fissure *c* crosses the vermis almost perfectly transversely. Lobule A_1 has only a very imperfectly developed hemisphere portion; indeed it is doubtful if the hemispheres can be considered to extend into this region. Fissure I., possibly a little shallower than *c*, has a curved direction. Fissure II. is very acutely curved, as in the dog. Lobule A_2 and lobe B are almost entirely confined to the vermis, their lateral prolongations being very small. Indeed, in this region it is difficult to set definite bounds between the vermis and the hemispheres. There is some amount of lateral displacement, with consequent curvature, in the vermis in lobules C_2 and C_3, but this is not greater in amount than that found in the dog.

In the sheep and goat, and in ungulates generally, the lateral divisions of lobule C_3 are not nearly so large as they are in the carnivora. In the carnivora their uppermost ends are commonly visible, either on one or both sides, when the cerebellum is regarded from the front. This has never been found to obtain in those ungulates which have been examined for the purposes of this research. Again, these lobules do not reach so far down as to touch the medulla, other than in exceptional cases. The result of this vertical abbreviation is to allow of the connection of the paraflocculus to be traced directly to the vermis, as is the case in the simpler forms of cerebellum (fig. 104). As we have seen, this connection is easily made out in the adult pig. In the sheep and goat, however, it is not quite so evident on a superficial examination; it is necessary to open up the groove between vermis and hemisphere.

The form of lobule D_1 is somewhat peculiar in both the sheep and goat (fig. 104). It has a central, well developed portion in the vermis, and smaller offshoots reaching into the hemispheres, a constriction of greater or less tenuity intervening.

Lobe E is of larger size than in the pig and the carnivora. The paraflocculus and flocculus resemble those parts of the cerebellum of the pig.

Bos taurus (fig. 106).—In the cerebellum of the cow, although the same lines are followed as in the sheep and goat, the arrangement of fissures appears at first sight to be very complicated. This remark applies only to the superior and posterior views, as lobes A and B and lobule C_1 are almost identical in form with those parts in the average carnivore or ungulate brain. It may be added that it is impossible to make out any hemisphere in lobe A. Even in lobe B the hemisphere is very attenuated.

On closely examining the posterior part of the cerebellum, it is found that the complexity is more apparent than real, and is due to a distortion which rivals that of the cat's vermis. Apart from this disturbance of form, there is little to which special attention need be directed. It may be mentioned, however, that the lateral parts of lobule C_3 commonly extend farther in a downward direction than obtains in the sheep and goat, this extension bringing them almost or quite in contact with the medulla. Not infrequently lobe E is so large and projects so far backwards as to be visible as one or two folia on the posterior aspect of the cerebellum.

Equus caballus (figs. 107, 108 and 109).—A very striking feature in the horse's cerebellum is the comparatively posterior position of fissure II. Fissures *c*, I., II. and *b* are distinct and deep. Fissure *c* is of very considerable depth, and fissure I. is almost as deep as fissure II. (fig. 109). It should be noted—as distinguishing the cerebellum of the horse from that of the sheep and goat, and especially from that of the cow—that lobe A is certainly, though not very strongly, continued into the hemisphere.

The posterior part of the horse's cerebellum shows one or two points of interest and importance. As in the ungulates already mentioned, the lateral parts of lobule C_3 are small as compared with the carnivora. In the horse their connections with the vermis are not difficult to follow. There is, further, no difficulty in making out the connecting link between lobule D_1 and the paraflocculus (fig. 108).

In some specimens lobule D_2 is continued into the hemisphere for a short distance, but this continuation has only once been found on both sides in the same brain. Its presence, though inconstant, is interesting, as being apparently the remains of that undoubted connection which we have seen to exist between lobule D_2 and the lower part of the paraflocculus during the embryonic life of the pig. In the majority of animals all trace of this primitive unity is lost as the brain grows into its adult form; but in some, possibly in man, evidences remain.

Lobule E is, if anything, smaller in the horse than it is in the sheep, goat and cow. The paraflocculus shows its two-tier character more clearly than in the other ungulates examined, in this respect resembling the paraflocculus of the carnivora. It should be remembered that in ungulates generally the lower tier shows a tendency to curve forwards at its posterior end. This is so well marked in the horse that there are practically three tiers produced. In an earlier part of this paper the suggestion has been thrown out that possibly the lobulus petrosus of the rabbit, etc. represents only the posterior extremity of the lower part of the paraflocculus of more complex cerebella. It may be asked, further, whether in those animals like the horse, in which the paraflocculus turns forwards at its posterior end, this recurved extremity may not be equivalent to a lobulus petrosus, unenclosed in a special fossa of bone. The supposition that this may be so is strengthened when the condition found in the badger is taken into account. In the cerebellum of *Meles taxus*, of which a description has already been given, on one side a lobulus petrosus was found; but on the other side the corresponding part of the paraflocculus was turned forwards underneath the lower tier.

The flocculus is usually easily distinguished in the horse, and is visible from the side and from behind. In some specimens a distinct white ridge, independent of the posterior medullary velum, passes from the flocculus to lobe E of the vermis. This ridge is indicated on the left side of fig. 108. It has not been met with elsewhere than in the horse—possibly because an insufficient number of cerebella have been examined—but its occurrence in this animal is of importance, as showing evidence, in the adult, of the embryonic unity of the structures between which it passes.

Equus asinus.—The cerebellum of the donkey is so like that of the horse in all but the merest details that an extended description is not necessary. It may perhaps be well to say that lobule C_2 in the hemisphere carries several fairly deep fissures, whose presence give the surface a complex appearance. Lobule D_1 shows the tendency, remarked in the sheep and goat, to extend into the hemispheres in the form of lateral appendages. The connection of this lobule with the paraflocculus is not so superficially evident as it is in the horse. The flocculus of the donkey has a greater antero-posterior extent than is the case in the horse.

In the foregoing pages the steps by which the fissures, and consequent lobes and lobules, of the cerebellum came into existence have been traced in two mammals. It has also been sought to discover the simplest form of mammalian cerebellum, and this having been done, to endeavour to recognise, in the complex as well as in the simpler forms, a likeness to this elementary pattern. Apparently the cerebellum in which the fissures are fewest and the lobes smoothest belongs to the shrew and the smaller bats. In the shrew there are four fissures only; and of these only one (the second, *i.e.* II.) extends through both vermis and hemisphere. The remaining three do not belong to the hemisphere, being confined to the vermis or its immediate neighbourhood.

In following the development of the cerebellum of the rabbit, it was found that this five-lobed and four-fissured stage was reproduced. But in the adult rabbit the number of fissures is increased. In the development of the pig, it appears possible that the five-lobed condition may obtain in its simple form for a time, but it quickly gives place to a much greater complex of fissures.

In both rabbit and pig fissure IV. was the first to appear, and this in association with the Rautenlippe, which, continuing round the lateral recess of the ventricle, blends with the Rautenlippe of the medulla. The association of fissure IV. originally seems beyond doubt. But as development goes on it becomes more and more removed from the edge of the cerebellar lamina, because of the growth of lobe E and the flocculus.

In both rabbit and pig the second fissure to develop is fissure II., which has been recognised by several writers to be of paramount importance, and which is declared by both Stroud and Kuithan to be the first fissure visible in the developing cerebellum.

The next fissures, in point of time of appearance and importance as dividing lines of the cerebellum, are fissure III. and those demarcating the paraflocculus from the rest of the hemisphere. These three are in reality the three elements of one and the same fissure, which, becoming continuous, they ultimately form.

By the presence of the above mentioned fissures, the cerebellum becomes divided transversely (but not completely as yet) into four unequal portions. (1) A part anterior to fissure II.; this becoming itself divided later into lobes A and B by fissure I. (2) Lobe C, lying between fissure II. and fissure III., with its lateral elements. (3) Lobe D, to which the paraflocculus belongs. And (4) lobe E, of which the flocculus is an outlying dependency.

Fissure I., separating lobes A and B, appears shortly after fissure III. in the rabbit, and somewhere about the same time in the pig. The other fissures, which are formed either at the same time to divide the cerebellum into two primary parts, is evident, and has been pointed out and insisted upon by Stroud. The comparative method clearly shows that sulcus preclivalis (*furcal sulcus* of Stroud) forms the real and fundamental dividing line.

In that part of the cerebellum which falls anterior to fissure II. (sulcus preclivalis), difficulties arise in the use of human anatomical terms. For *sulcus postcentralis* of the human anatomist corresponds to fissure *c*; a fissure secondary both in point of time of appearance in the embryo and in morphologic value. In the current descriptions of the human brain, as given in this country, no sulcus is mentioned as equivalent to fissure I. The result is that the culmen of human anatomy includes lobe B and lobule A_2. Lobule A_2 probably corresponds to the "ascending part of the monticulus" of some German writers (Flatau and Jacobsohn, for instance), but I am not certain that the expression is used for lobule A_2 alone or always.

The following table shows the parts in the human brain corresponding to the various divisions of the mammalian cerebellum as described in this paper.

Fissures.	Lobes.		
	Lobus centralis.	A_1.	A.
c. Sulcus postcentralis			
		A_2.	
I. (Not named by Schäfer)	Lobus culminis		
			B.
II. Sulcus preclivalis			
	Lobus clivi.	C_1.	C.
b. Sulcus postclivalis			
	Lobus cacuminis.	C_2.	
a. Sulcus horizontalis magnus			
	Lobus tuberis.	C_3.	
III. Sulcus postpyramidalis			
	Lobus pyramidis.	D_1.	D.
d. Sulcus prepyramidalis			
	Lobus uvulæ.	D_2.	
IV. Sulcus postnodularis			
	Lobus noduli.		E.

It will be observed that I have only examined the cerebella of placental mammals. Lack of suitable material has precluded a first-hand investigation of Monotremes and Marsupials. But, judging from the descriptions and figures given by Ziehen (7), it is clear that the scheme, as elaborated in the foregoing pages, will apply to Marsupials at least. These mammals evidently fall into the group of animals in which the cerebellum follows the simpler type. Whether Monotremes also can be included in this group is not so obvious from the descriptions available. It seems not unlikely that their cerebella belong to a group separate from the rest of the mammalia.

In carrying out the work of this investigation, so much assistance, in the form of material, has been afforded by so many persons, that it is impossible to make suitable acknowledgment without going to considerable length. Let it suffice to say, that my debt of gratitude is not to be computed from the extent of the avowal here made. Much of the microscopic work has been done in the Physiological Laboratory of the University of Edinburgh, where, through the courtesy of Professor Schäfer and his assistants, every facility that could be wished for has been afforded.

REFERENCE.

(7) Ziehen, Th., "Das Centralnervensystem der Monotremen und Marsupialier. Thiel I. Macroscopische Anatomie," *Jenai'sche Denkschriften*, vi., 1897.

PLATES XVII.–XXIII.

EXPLANATION OF FIGURES.

Fig. 54.	Pig embryo,	40 days, 52 mm.	Posterior view. × 2.
Fig. 55.	,,	40 days, 52 mm.	Left lateral view. × 2.
Fig. 56.	,,	40 days, 52 mm.	Mesial sagittal section.
Fig. 57.	,,	44 days, 64 mm.	Posterior view. × 2.
Fig. 58.	,,	44 days, 64 mm.	Anterior view. × 2.
Fig. 59.	,,	44 days, 64 mm.	Mesial sagittal section.
Fig. 60.	,,	48 days, 80 mm.	Posterior view. × 2.
Fig. 61.	,,	48 days, 80 mm.	Anterior view. × 2.
Fig. 62.	,,	48 days, 80 mm.	Mesial sagittal section.
Fig. 63.	,,	51 days, 88 mm.	Posterior view. × 2.
Fig. 64.	,,	51 days, 88 mm.	Anterior view. × 2.

Fig. 65. Pig embryo, 51 days, 88 mm. Mesial sagittal section.
Fig. 66. ,, 55 days, 100 mm. Mesial sagittal section.
Fig. 67. ,, 59 days, 118 mm. Superior posterior view.
Fig. 68. ,, 59 days, 118 mm. Anterior view. × 2.
Fig. 69. ,, 59 days, 118 mm. Mesial sagittal section.
Fig. 70. ,, 65 days, 132 mm. Posterior view. × 2.
Fig. 71. ,, 65 days, 132 mm. Superior view. × 2.
Fig. 72. ,, 65 days, 132 mm. Anterior view. × 2.
Fig. 73. ,, 65 days, 132 mm. Left lateral view. × 2.
Fig. 74. ,, 65 days, 132 mm. Mesial sagittal section.
Fig. 75. ,, 70 days, 150 mm. Superior view. × 2.
Fig. 76. ,, 165 mm. Posterior view. × 2.
Fig. 77. ,, 165 mm. Superior view. × 2.
Fig. 78. ,, 165 mm. Left lateral view. × 2.
Fig. 79. ,, 165 mm. Anterior view. × 2.
Fig. 80. ,, 165 mm. Mesial sagittal section.
Fig. 81. Pig, adult. Anterior surface. × 1.
Fig. 82. ,, ,, Superior view. × 1.
Fig. 83. ,, ,, Posterior view. × 1.
Fig. 84. ,, ,, Mesial sagittal section. × 1.
Fig. 85. Mustela furo. Anterior surface. × 2
Fig. 86. ,, Superior view. × 2.
Fig. 87. ,, Posterior view. × 2.
Fig. 88. ,, Mesial sagittal section.
Fig. 89. Meles taxus. Anterior surface. × 1
Fig. 90. ,, Superior view. × 1.
Fig. 91. ,, Posterior view. × 1.
Fig. 92. ,, Mesial sagittal section.
Fig. 93. Canis familiaris. Anterior surface. × 1.
Fig. 94. ,, Superior view. × 1.
Fig. 95. ,, Inferior surface. × 1.
Fig. 96. ,, Mesial sagittal section.
Fig. 97. Canis vulpes. Superior view. × 1.
Fig. 98. ,, Posterior view. × 1.
Fig. 99. ,, Mesial sagittal section.
Fig. 100. Cat. Superior view. × 1.
Fig. 101. ,, Posterior view. × 1.
Fig. 102. ,, Mesial sagittal section. × 1.
Fig. 103. Ovis aries. Anterior view. × 1.
Fig. 104. ,, Posterior view. × 1.
Fig. 105. Goat. Mesial sagittal section. × 1.
Fig. 106. Bos taurus. Mesial sagittal section. × ½.
Fig. 107. Equus caballus. Anterior superior view. × ½.
Fig. 108. ,, Posterior view. × ½.
Fig. 109. ,, Mesial sagittal section. × ½.

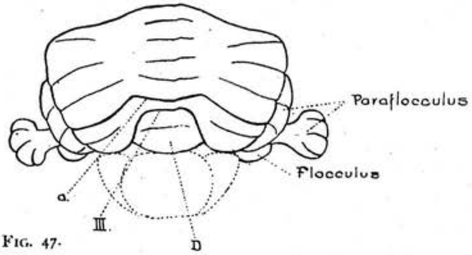


FIG. 47.

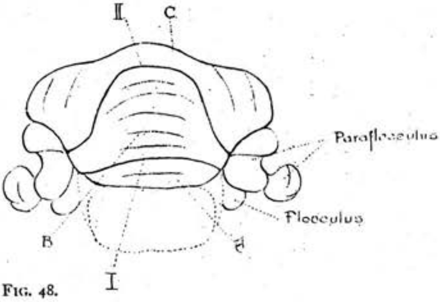
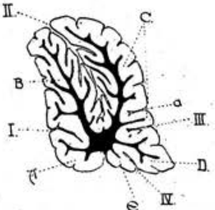


FIG. 48.



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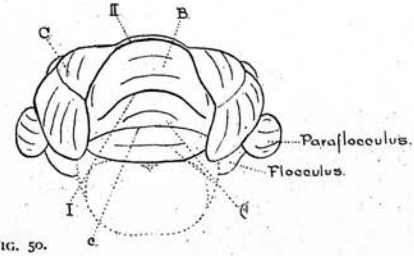

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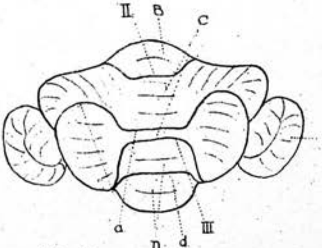

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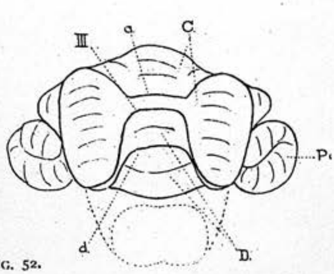


FIG. 52.

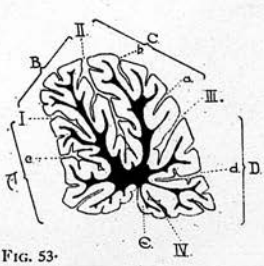
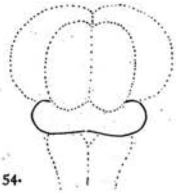


FIG. 53.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.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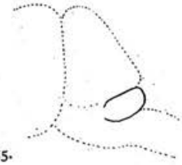
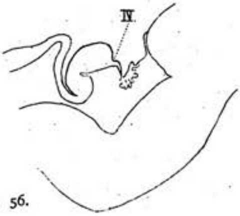


FIG. 55.



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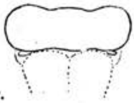
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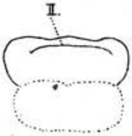
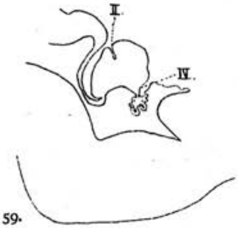


FIG. 58.



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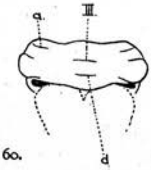
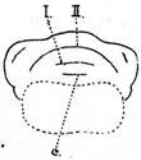


FIG. 60.



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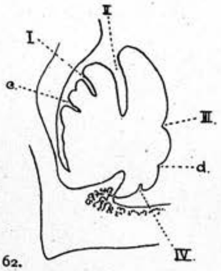

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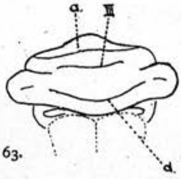

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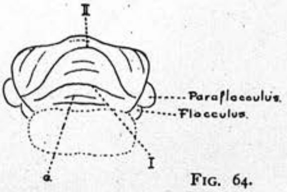


FIG. 64.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.

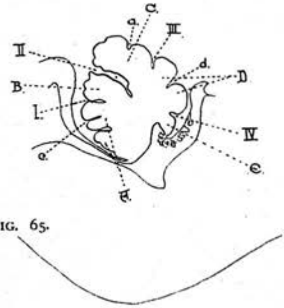
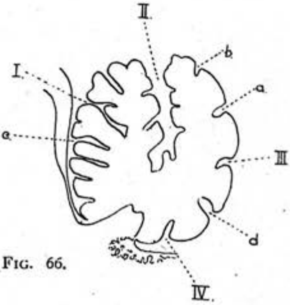


FIG. 65.



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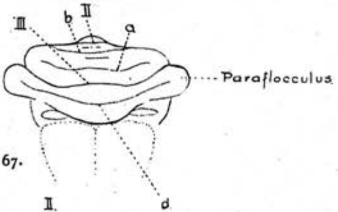

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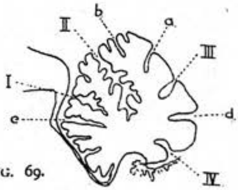

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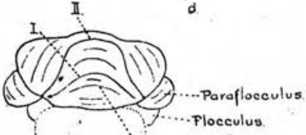

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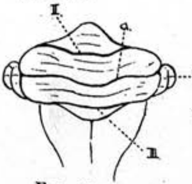

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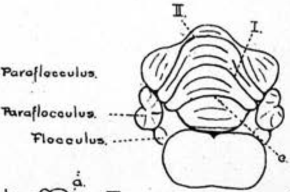


FIG. 72.

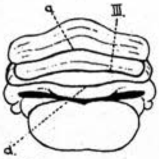
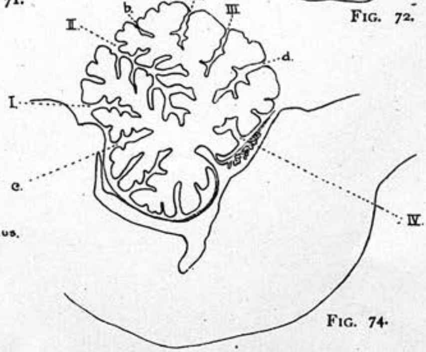


FIG. 70.



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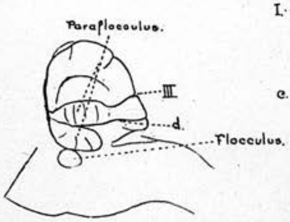

FIG. 73.

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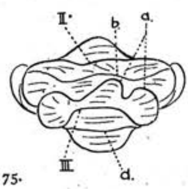


FIG. 75.

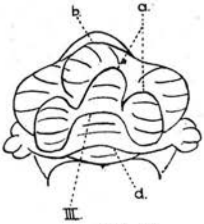


FIG. 76.

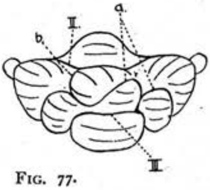
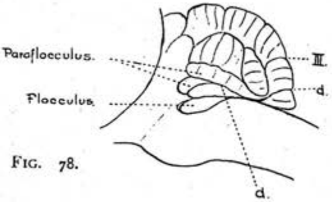


FIG. 77.



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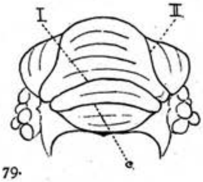

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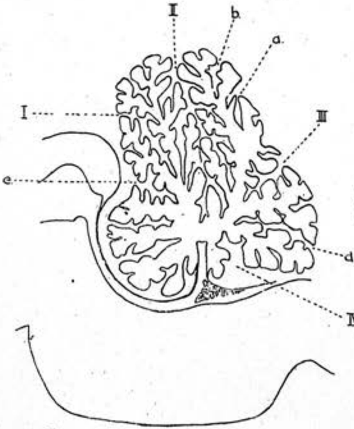

FIG. 80.

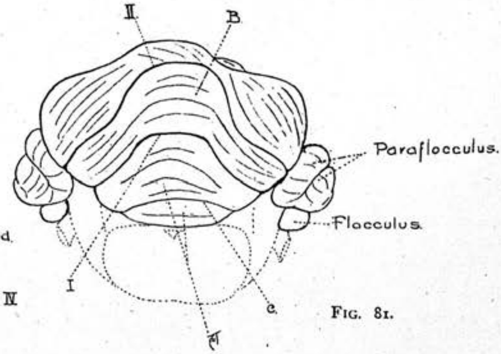

FIG. 81.

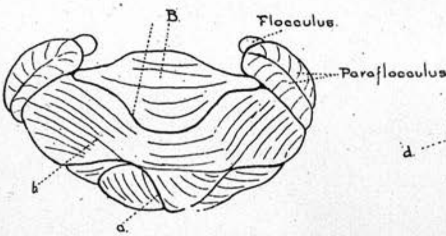

FIG. 82.

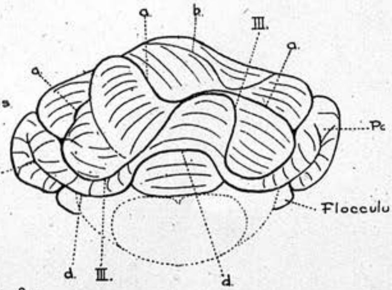

FIG. 83.

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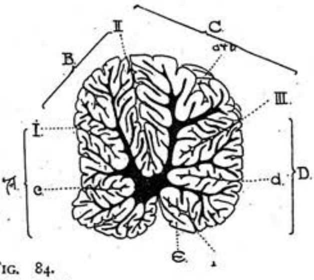

FIG. 84.

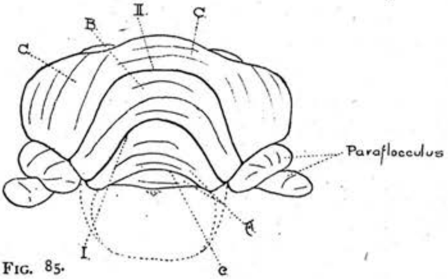

FIG. 85.

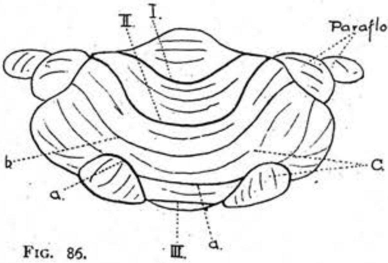

FIG. 86.

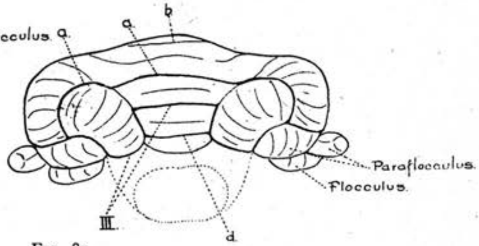

FIG. 87.

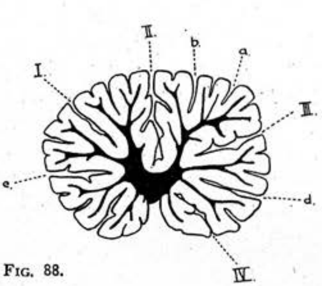

FIG. 88.

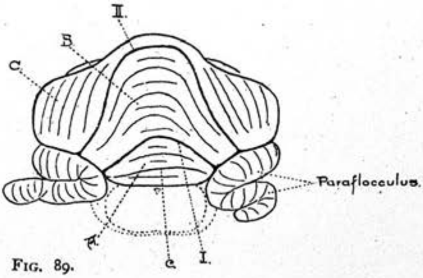

FIG. 89.

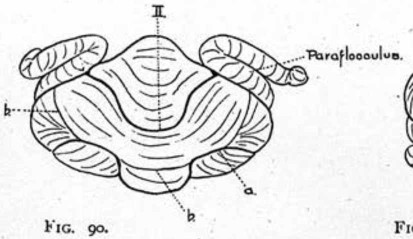

FIG. 90.

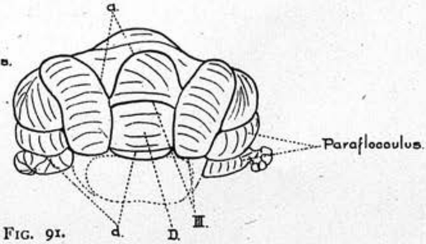

FIG. 91.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.

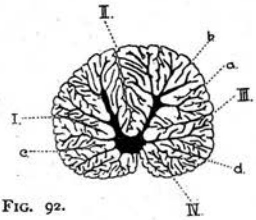

FIG. 92.

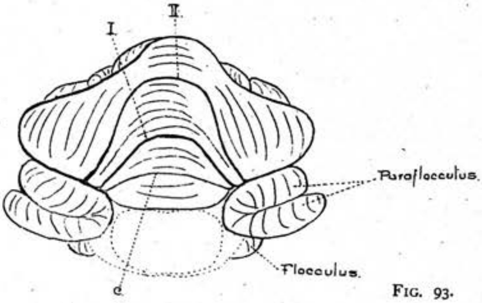

FIG. 93.

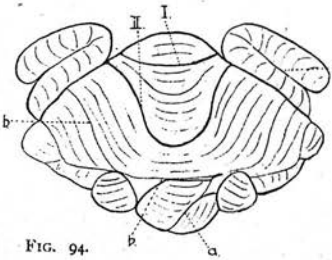

FIG. 94.

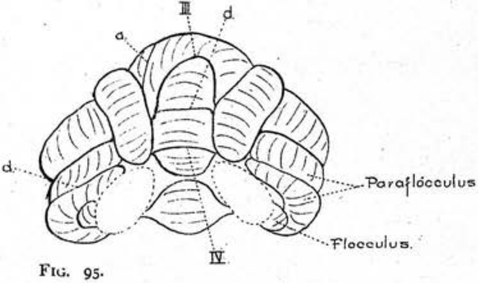

FIG. 95.

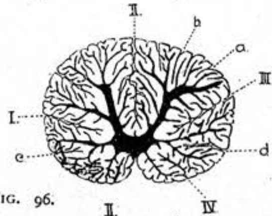

FIG. 96.

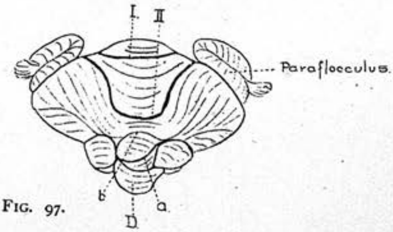

FIG. 97.

FIG. 99.

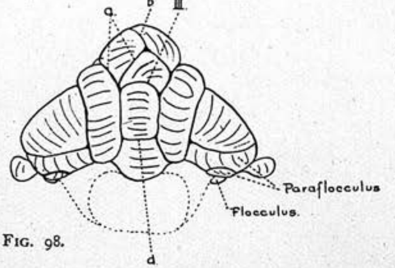

FIG. 98.

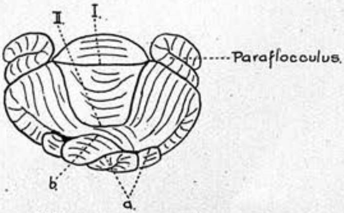

FIG. 100.

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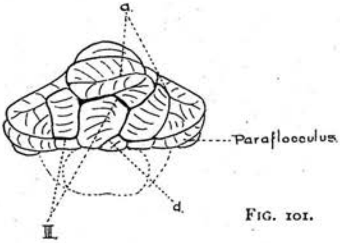

FIG. 101.

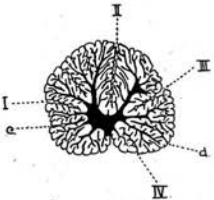

FIG. 102.

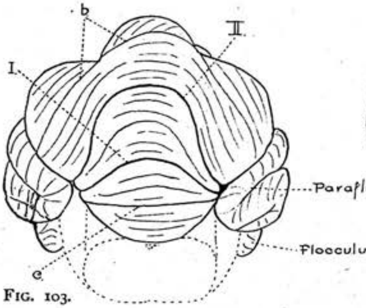

FIG. 103.

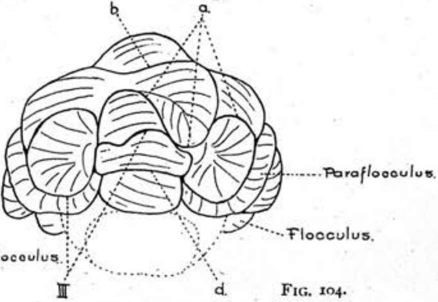

FIG. 104.

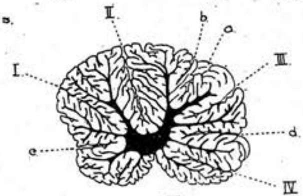

FIG. 106.

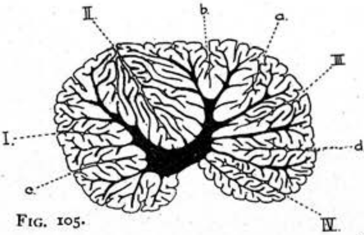

FIG. 105.

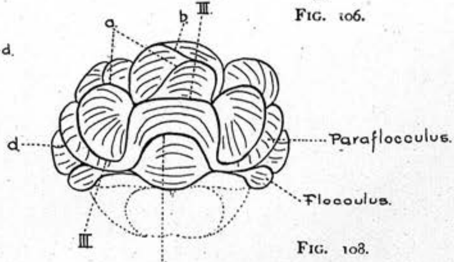

FIG. 108.

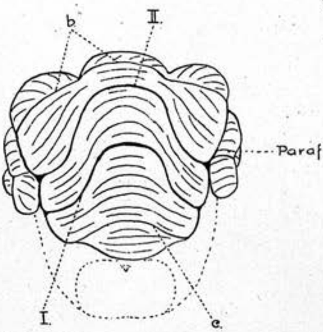

FIG. 107.

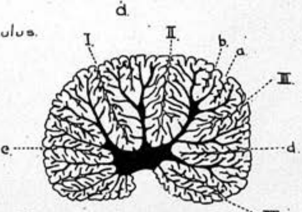

FIG. 109.

Professor O. CHARNOCK BRADLEY on the Development and Homology of the Mammalian Cerebellar Fissures.

THE MAMMALIAN CEREBELLUM: ITS LOBES AND FISSURES.

By O. CHARNOCK BRADLEY, M.B., F.R.S.E., *Royal Veterinary College, Edinburgh; Goodsir Fellow, University of Edinburgh.* (PLATES XLVI.–L.).

PART I.

So far as I am aware, no serious attempt was made to establish the morphology of the mammalian cerebellum upon a rational basis before the year 1895, when Stroud (1) published a paper dealing with the development of that organ in the cat and man. As a result of his investigations, Stroud came to the conclusion that there is a fundamental plan after which the cerebella of all mammals are formed. He recognised certain very important features which are always present. Among other points he discounted the use of the sulcus horizontalis magnus as the essential line of division of the cerebellum into two parts, and emphasised the importance of a much deeper and absolutely constant fissure, which is equivalent to that found in the human brain separating the culmen from the clivus, and to which he gave the name of *furcal sulcus.* That part of the cerebellum in front of the sulcus furcalis he called the *pre-ramus,* and to that part posterior to the sulcus he applied the name of *post-ramus.* Each of the lateral parts of the post-ramus he designated *pileum,* consisting of a post-pileum and pre-pileum, separated by an *inter-pilear sulcus* (in the cat), or a *peduncular sulcus* (in man). In man the pre-pileum is formed by the clivus and its lateral prolongations. In the cat it consists of the clivus, cacumen, and tuber, and their lateral prolongations. It seems a pity that some more uniform division could not have been resolved upon.

A very important fact which was brought out by Stroud's investigations was the lack of correspondence between the human flocculus and the so-called flocculus of the majority of mammals. It was shown that the flocculus of man is present in the lower animals, but only forms part, and a comparatively insignificant part, of the lobe lying to the side of the cerebellum of the cat. To the major part of this lobe the name of *paraflocculus* was given. The value of this discovery can hardly be overstated.

Almost contemporaneously with the publication of Stroud's paper appeared one in which Kuithan (2) traced the development of the cerebellum in the sheep and in man. Here, again, the morphologic importance of the constant deep fissure, called sulcus furcalis by Stroud, was pointed out. From its early appearance during development, Kuithan named it the *sulcus primarius cerebelli.* From the circumstance that the sulcus primarius is the deepest fissure in the vermis, while what he took to be the sulcus horizontalis magnus is the deepest in the hemisphere, Kuithan proposed to divide the mammalian cerebellum into three lobes, of which these fissures would form the boundaries. The anterior lobe (Vorderlappen) would, by this method of division, consist of lobi centralis and culminis; the middle lobe (Mittellappen) would include lobi clivi and cacuminis; and the posterior lobe (Unterlappen), lobi tuberis pyramidis, uvulæ, and noduli. This is a variation of the division suggested by Schwalbe (4) in his description of the human cerebellum. Schwalbe also divided the cerebellum into three lobes, but his middle lobe consisted of lobi cacuminis, clivi, and tuberis; and this recognition of the three parts as constituting one single lobe is supported by embryological evidence, as will be shown later. Kuithan does not appear to have grasped the significance of the paraflocculus and flocculus, for he simply named the upper part of the paraflocculus of the sheep the *vermis lateralis,* and made no suggestion regarding its homology. Kuithan further fell into the error of allowing his ideas to be governed by what he knew to be the condition of things in man. His endeavours appear to have been largely in the direction of showing that the cerebellum of the sheep contains the same divisions as does that of man. Although this circumstance marred his publication considerably, the residual value is very great.

In 1897 Ziehen (3) published an elaborate paper on the brain of monotremes and marsupials, but he treated his subject from the purely descriptive side, and did not venture into the field of speculation as to homologies. He did, however, recognise a fissure which he named the sulcus horizontalis magnus, on the assumption that it corresponded to the fissure bearing that name in man; and he called attention to *sulci cerebelli superior*, *anterior*, and *posterior*, the former of which is obviously the homologue of the sulcus furcalis (Stroud) and the sulcus primarius cerebelli (Kuithan). He further remarked upon the *lobus flocculi* and its connection with the rest of the cerebellum, but he did not draw any distinction between a paraflocculus and a flocculus. He appeared to fall into error in giving the name of 'flocculus' to a projecting part of the lobus flocculi which, doubtless, corresponds to the lobulus petrosus of the paraflocculus.

In 1899 G. Elliot Smith, in his detailed description of the brain of the Edentates (5), struck out an entirely new line in his manner of dealing with the cerebellum. He recognised the individuality of the lobus flocculi, which is separated from the rest of the cerebellum by a deep limiting fissure, for which he suggested the name of *fissura flocculi* (parafloccular sulcus of Stroud). He followed Stroud in dividing the lobus flocculi into two parts, a flocculus and a paraflocculus, the latter being subdivided into upper and lower portions—*paraflocculus dorsalis* and *paraflocculus ventralis*. After the lobus flocculi had been subtracted from the cerebellum, Elliot Smith considered the residuum to consist of three azygous lobes, separated from each other by two fissures—a *fissura prima* and a *fissura secunda*. The fissura prima corresponds to Stroud's sulcus furcalis; the fissura secunda separates lobes apparently homologous with the pyramid and uvula of man. The lobes limited by these fissures were called *lobus anticus*, *lobus centralis*, and *lobus posticus*. The lateral part of the lobus centralis was named the *area crescens*, "for it will be found that in the higher mammals it is the exuberant increase of this part of the cerebellum which is the main factor in the evolutionary process." A point of very considerable importance was clearly stated in this paper—this being the recognition of the connection of the pyramid with the caudal extremity of the upper part of the paraflocculus. It was also stated that the area crescens can be subdivided into three portions, lying the one behind the other. It is perhaps only fair to point out that the term 'pyramid' was only used tentatively. "In the meantime," says the writer, "I shall use the term *pyramid* with the reservation that the validity of its homology with the similarly-named part of the cerebellum in man remains to be proved. This point can be satisfactorily settled only by embryological investigation, and neither Kuithan nor Stroud has attempted to solve the problem."

The large work published in 1899 by Flatau and Jacobsohn (6) on the comparative anatomy of the central nervous system of mammals contains a mass of material descriptive of the cerebellum. These writers, like those previously quoted, admitted that the deep and constant sulcus superior anterior (Ziehen) is the true dividing line by which the cerebellum is separated into two parts. Their descriptions, however, have all the end in view of finding, in the average mammalian cerebellum, representatives of the lobes of the human structure.

In the early part of 1902 the present writer embodied the results of a somewhat extended investigation, on the development and homologies of the mammalian cerebellar fissures, in a paper which was not published until the beginning of 1903 (7). The investigation had been carried out on the following lines. The simplest form of cerebellum known to the writer was taken as the starting-point, and the parts of this simple form sought for in the more highly-developed and elaborated cerebella, this method being considered more rational than that of assuming that the simpler form must contain, in a simplified condition, the divisions of the more complicated brains. The simplest workable type of cerebellum was found to be one in which a mesial sagittal section shows five lobes separated from each other by four fissures. In order to avoid confusion, no pre-existing names were applied to these lobes and fissures, but the simplest method of designating them—that of letters and figures—was employed. The five lobes were called A, B, C, D, and E, commencing the enumeration with the most anterior, or rather with the one nearest to the anterior medullary velum. The fissures were similarly designated as I., II., III., and IV. Of the four fissures, II. was found to be constantly the deepest, and therefore corresponds to the sulcus furcalis of Stroud, the sulcus primarius cerebelli of Kuithan, and the fissura prima of Elliot Smith. Embryological evidence was sought in an animal in which the five lobes are comparatively simple, viz., in the rabbit. It was found that the fissures appear in this animal in the following order: IV., II., III., I. Contemporaneous with the appearance of fissure II. a pair of depressions—one growing inwards from each lateral border of the cerebellum—start to cut off the future paraflocculus from the main mass of the future hemisphere. These two fissures finally join fissure III., thus indicating that the paraflocculus is the most lateral part of lobe D. Lobe E begins its existence in intimate association with what is to become the posterior medullary velum, and the flocculus does the same at the most lateral part of the pontine flexure. For this reason it was held that the flocculus is an outlying territory of lobe E. The next fissure found in a mesial section was one involving lobe A, and was named *c*. As a consequence of the presence of this secondary sulcus, lobe A is subdivided into lobule A_1, the more inferior part, and lobule A_2, the part above fissure *c*.

Shortly after the advent of fissure *c* a pair of sulci become apparent in the lateral (hemisphere) part of lobe C. These were known as fissures *a* and *b*—*a* being the more posterior. The two halves of fissure *a* gradually approach each other in the middle line, and finally fuse, the two portions of fissure *b* doing the same a little later. Lobe C is now subdivided into three lobules—C_1, C_2, and C_3—the enumeration being from before backwards.

The constancy of these fissures was established by the examination of a number of cerebella differing only very slightly from that of the rabbit. Very important modifications were found in the cerebellum of the squirrel, which, as a consequence, served as a connecting link between the simpler and the more complicated cerebella. The modifications consisted in the antero-posterior expansion of the hemisphere portion of lobule C_3; of the appearance of a fissure (named *d*) which divided lobe D into lobule D_1 and lobule D_2; and of an increase in size of the paraflocculus and the arrangement of its folia in two tiers (*paraflocculus dorsalis* and *ventralis* of Elliot Smith), the upper of which was found to be connected with lobule D_1.

Next, the development of the cerebellum of the pig was traced. This was found to follow the same main lines as that organ in the rabbit, but additional important evidence was discovered. The most striking point, and the one to which most weight was attached, was the evident connection, at one stage of development, of the two portions of the paraflocculus with the two portions of lobe D. Indeed, it was clear that the paraflocculus was divided into two parts by the lateral growth of fissure *d*. The connection between paraflocculus dorsalis and lobule D_1 was found to persist into adult life, but that between paraflocculus ventralis and lobule D_2 disappeared in the later stages of intra-uterine development. It was obvious, however, that not only is the paraflocculus as a whole a part of lobe D, but that the two parts of the paraflocculus belong to the two parts of lobe D, each to each.

From the examination of a number of adult cerebella from various animals, it was found that the disappearance of the connection between lobule D_2 and the paraflocculus ventralis is the rule; but in one specimen of the horse's cerebellum, traces of the original connection were found. In many animals the continuity of lobule D_1 also becomes faint, but on the other hand it may persist, and often does so.

Since the above conclusions were put into writing, Elliot Smith and Louis Bolk have made additions to the literature. The former has made several communications regarding the morphology of the cerebellum in mammals in general. A short paper, published by Elliot Smith at the time my MS. was in the hands of the Editor of the *Journal of Anatomy and Physiology*, is mainly a condensation of what he has already said in his monograph on the brain of the Edentates (8). In it he adheres to his original statement of the division of the mammalian cerebellum into two floccular lobes and a large inter-floccular mass subdivided into three azygous lobes (anterior, middle, and posterior) by the fissura prima and the fissura secunda. No exception whatever can be taken to the importance attached to the fissura prima. As has been previously stated, it is the furcal sulcus of Stroud and the fissura primarius of Kuithan, and its morphologic status is beyond question. But it appears to me that there are objections to placing the fissura secunda on the same level.

There seems little doubt that it corresponds to my fissure *d*, which I have given reasons for considering as secondary in character. It is only an inter-lobular fissure, and owes its importance mainly to the fact that it divides lobe D into portions, linked together at the oral end of the paraflocculus, as Elliot Smith's diagram and description admit. Further, there does not appear to be sufficient distinction made between flocculus and paraflocculus. That such distinction should be made is indicated by the difference in the development of the two structures. There is, indeed, a danger that the name of 'lobus flocculi,' as applied to the two parts, may lead the reader into error. It would be better to always speak of them as *flocculus* and *paraflocculus* separately and distinctly; though it must be admitted that their close relation to each other makes a collective name very convenient.

As a consequence of exalting fissura secunda into a sulcus of primary value, the nodulus and uvula (mesial portions of lobe E and lobule D_2) are thrown together as constituting the 'posterior lobe,' which is stated to be connected with the flocculus. As has been previously remarked, development appears to pretty clearly indicate that the flocculus belongs to lobe E alone; and no adult cerebellum that I have examined has demonstrated any other connection. This is another reason for clearly distinguishing the flocculus from the paraflocculus.

The 'anterior lobe' comes in for but slight attention in this paper; nor is a great deal said of it in the memoir on the Edentate brain, although in a figure illustrating the mesial sagittal section of the cerebellum of Orycteropus (fig. 29) two fissures are marked with the letters *e* and *f* which appear to correspond very closely with my fissures I. and *c* respectively.

Apart from the above-mentioned points, Elliot Smith's views, up to the time of writing the paper just considered, do not differ very widely from those I have previously stated.[1] But in some

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[1] To prevent a misunderstanding which may arise out of a criticism by Elliot Smith (9), I may be allowed to state that at the time my first paper was written and submitted to the Editors of *this Journal* (early in 1902), Professor Elliot Smith had expressed no views on the morphology of the mammalian cerebellum beyond those contained in his Memoir on the Brain of the Edentates. When my paper was written the different opinions on the subject were conflicting in the

later communications our divergence of views is increased. In his latest paper on the cerebellum of mammals in general (10), he supplies a scheme differing in material points from that given in his earlier note (*cf.* diagram in (8) and fig. 1 (10)). He states that the suprapyramidal fissure (my fissure III.) may behave in different ways. It may join the parafloccular fissure (the fissure separating the paraflocculus from the bulk of the hemisphere, and named the fissura flocculi in the paper on the Edentates), or it may cut across area C, to join the parapyramidal fissure (a fissure not mentioned previously). Fissure secunda (*d*) may become continuous "with the floccular" (IV.) "or parafloccular fissures, or even (as usually happens in the human brain) with a fissure in the paravermis" (in area C of the earlier papers). I can only say that the material (embryological and adult) which I have examined does not lead me to conclude that these fissures are capable of such irregularity. It is now admitted that the uvula and nodule "become separated the one from the other long before the other lobes and lobules become mapped out." This fact I have already demonstrated as grounds for considering them as parts of separate lobes, but Elliot Smith still maintains that "they are so small and present so many features in common that it is convenient to group them together as one lobe." Their different development history, however, I hold as sufficient justification for their separation.

The material I have investigated leads me to further differ from Elliot Smith when he avers that the pyramid "can be shown to be continuous (in most mammals) with the parapyramidal area" (a portion of the lateral part of my lobe C), "including not only its pars dorsalis (biventralis), as is taught in Human Anatomy, but also its pars ventralis (tonsillaris)." The importance attached to the *copula pyramidis* in his earlier writings is now stated by our author to have been unduly emphasised.

Not only are the fissures of the vermis held as being erratic

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extreme, and it was therefore considered that it would be better to attack the problem *de novo*. To keep the mind of the reader as unbiassed as possible, the literature was only barely touched upon. This explains why Professor Elliot Smith's paper was not specially alluded to.

in their connections, but the parafloccular fissure in the larger mammals "cuts into the alar part of the middle lobe without becoming confluent with any important fissure." I am unable to reconcile this statement with what I have seen in the material at my disposal.

It will be seen from the above that there has been a considerable modification of the views expressed in the earlier publications, with a consequent complication of the picture of the lobus posticus and a part of the lobus medius (called formerly the lobus centralis).

Elliot Smith's latest communication deals with the morphology of the human cerebellum along the lines just discussed (11).

Among the papers treating of the mammalian cerebellum which have appeared recently is one by Professor Louis Bolk (14). It claims attention as being the expression of opinion of a well-known anatomist. Bolk commences by condemning that method of description of a cerebellum which takes the human brain for its type, and points out how such a method is a fount of error. He therefore sets aside the human organ, and the orthodox description of it, referring to it only in the later part of his paper. He states that, with the exception of the monotremes, he has examined the cerebellum in several representatives of all the orders of mammalia. In this communication it is his intention to set forth his idea of the structural type (Bautypus) as exemplified in the cerebellum of *Lemur albifrons*. He seeks, further, to observe the more important variations in different animals, and finally to answer the question—How does the human cerebellum stand with regard to that of other animals, and in what direction has it specially developed? His present statement is to be regarded as preliminary only. In the course of correspondence, he informs me that he hopes to publish his observations *in extenso* before long.

Bolk divides the cerebellum into two lobes—*lobus anterior* and *lobus posterior*—by the sulcus primarius cerebelli (Kuithan). He refuses to recognise the division into a vermis and two hemispheres as based upon firm morphologic ground, since he denies the existence of paramedian sulci in the anterior lobe of any cerebellum he has examined, with the possible exception of that of the Cetaceans. The two lobes are different in several respects, but chiefly in their method of growth. The superficial expansion of the anterior lobe is greatest in the middle line, the growth intensity (Wachstumintensität) becoming gradually smaller in a lateral direction. Bolk does not subdivide the anterior lobe, at any rate in the present paper. The posterior lobe he divides into two portions—a *lobulus simplex* and a *lobulus complicatus*. Of these the former has characteristics which ally it with the lobus anterior. Its folia are arranged transversely, and there are no paramedian sulci. Moreover, its 'growth centre' is in the middle line. Sulci paramediani are present in the lobulus complicatus, and divide it into a *lobulus medianus posterior* and two *lobuli laterales posteriores*, the former corresponding to the inferior vermis of Human Anatomy.

There are three growth centres in the posterior lobe—one in the middle line and two placed laterally. The presence of these centres, and their influence upon the surface anatomy is emphasised, and held to be of great importance. The transverse expansion energy of the middle growth centre (*i.e.* of the lobulus medianus posterior) is very limited. The bilateral centres are likewise of small activity in a direction at right angles to their long axis, but in a sagittal direction they are even more active than the median centre. As a consequence, the lobuli laterales posteriores become considerably curved in brains such as that of Lemur albifrons. In simpler brains the sagittal line of growth is not such as to produce distortion. The curvatures of the lobuli laterales posteriores produce the *lobulus ansiformis*, the *lobulus paramedianus*, and the *formatio vermicularis*. The paraflocculus and flocculus constitute the last.

It is difficult to criticise Bolk's paper adequately, seeing that it is of the nature of a preliminary statement. One will be in a better position to agree or disagree with him when his theses are expanded. As the case stands at present, there are several points which appear debatable. In the first place, the recognition of two lobes only in the cerebellum may be simple as a method of division of the whole organ, but it is one which may be considered inconvenient and insufficient for purposes of description. This is made evident in Bolk's own paper. He finds it necessary to divide the posterior lobe into two parts (lobuli simplex and complicatus). A vermis may not always be very conspicuous in the anterior lobe, indeed in many instances it is impossible to distinguish a vermis and two lateral hemispheres in this region; but a vermis is always sufficiently obvious in the posterior region. And it cannot be denied that a division into a vermis and two hemispheres is a convenience, if not a necessity, for purposes of description of the surface anatomy of the cerebellum. Though the paramedian sulci may be shallow anteriorly, still, in the majority of animals, their presence can be affirmed. Bolk's own figure of the cerebellum of the Lemur (fig. 1) shows this. At the same time it should not be forgotten that the paramedian sulci are quite secondary objects, as their late appearance shows.

In his consideration of the lobulus complicatus, Bolk appears to pay too much attention to the adult condition, and relegates the simple transverse arrangement of the fissures to too secondary a place, though he certainly does not overlook it. Indeed, he mentions the fact that originally each part of the posterior lobe consisted of two lateral portions and a middle connecting link. But, unless the embryonic condition be employed as a basis for the division of the adult organ, there is great danger of misconception when adult cerebella are considered.

As an explanation of the mode of production of the complex arrangement of the lobules of the posterior lobe, Bolk's arguments are ingenious and to the point. But the fact that the complexity is secondary must not be lost sight of. In another paper on the cerebellum of some New World monkeys (13), speaking of the posterior lobe, Bolk says that the circumstance that in Hapale and Midas the lateral parts are joined to the corresponding middle portions by means of low ridges, leads one to suppose that in the posterior as in the anterior lobe the sulci originally ran uninterruptedly from one border of the cerebellum to the other. Therefore, he maintains, one must consider that the genesis of the sulci paramediani is secondary, and of quite another nature from that of the interlamellar fissures. On this point no one who has examined the brain in embryos will express dissent.

In his second paper Bolk considers the cerebella of Hapale, Midas, Chrysothrix, Mycetes, Cebus, and Ateles, which he arranges in this order, as being the one in which the gradual growth of complexity of the lobes among the New World monkeys is best indicated. The whole paper is practically the application of his division of the cerebellum, as previously explained, to a series of concrete examples.

In the large work on Human Anatomy at present appearing under the editorship of Professor Karl von Bardeleben, Ziehen (15) describes the anatomy of the cerebellum at considerable length. He divides the cerebellum of man into eight *lobuli cerebelli*, as shown below:—

1. Lingula cerebelli.
   Sulcus postlingualis.
2. Lobulus centralis.
   S. postcentralis (cerebelli).
3. Monticulus.
   a. Culmen.
   S. superior anterior.
   b. Declive.
   S. superior posterior.
4. Folium vermis.
   S. horizontalis.
5. Tuber vermis.
   S. inferior posterior.
6. Pyramis.
   S. inferior anterior.
7. Uvula.
   S. præuvularis.
8. Nodule.

It is interesting to note that, though he recognises the importance of the sulci superior anterior, Ziehen still considers culmen and declive to be parts of one lobulus cerebelli.

A very elaborate description of the lobes and lobules follows; after which comes a section devoted to the comparative anatomy of the cerebellum. Here sundry new names are suggested. The term *lobulus impendens* is used as it was in the monograph on the brain of monotremes and marsupials; that is, it is applied to the declive and tuber vermis in those forms in which these overhang the culmen, *e.g.* in Rodentia. Ziehen's *lobulus eruciformis* is found in the hemisphere, and corresponds "without doubt to the lobuli semilunares superior and inferior (of man)." It is in the form of a worm-like complex in the carnivora. The term *lobulus palpiformis* is used to indicate a finger-like lobule lying anterior to l. eruciformis, and is evident in Ungulata. Under the name of *tabulata* is included the flocculus and paraflocculus, at any rate in some animals, and it is suggested that it may correspond, in part at least, to the 'tonsil.'

In those animals in which the lobules of the vermis are apparently fewer than in man (*e.g.* the rodents), the lobes in the posterior part of the cerebellum are considered by Ziehen to be either tuber vermis and pyramid (including uvula and nodule), or, as appears more likely, pyramid and uvula (including nodule). Facts have been adduced in an earlier part of this paper for traversing the supposition that the nodule and uvula are combined in any cerebellum.

Ziehen is doubtful as to the homology of the small lobule found below the lobulus petrosus in rodents. This has been shown to be the flocculus.

There are other points to which attention might be directed, but the above will suffice to show that Ziehen's contribution to the literature, while painstaking and detailed, would have been even more valuable if it had had an embryological basis, and had the brain of man been used as a goal, and not as a starting-point.

Still more recently Ziehen has given a description of the brain of Tarsius, Nycticebus, and Galeopithecus (17). In an illustration showing the appearance of a mesial sagittal section of the cerebellum of *Tarsius spectrum* (fig. 5), five lobes are indicated; these being a lobulus centralis, culmen, lobulus impendens, pyramis, and a lobule stated to represent the combined uvula and nodule. This last lobe is perfectly simple, but the 'pyramis' is divided into two nearly equal parts by a moderately deep fissure.

In the following pages is contained an expansion of the writer's previous research. Some additional embryonic material has been investigated, and the examination of adult cerebella has been continued. The same methods as those used in the earlier work have been followed. The brains of embryos have been carefully exposed and sketched in outline, all the fissures visible to the naked eye, or by means of an ordinary pocket lens, being introduced in their proper relative positions in the sketch. Then the whole cerebellum, or rather more than half of it when its size was considerable, was embedded in paraffin and serial sagittal sections cut. These sections have been worked through, outline drawings being made wherever alterations in the fissures were encountered. In this way the first outline sketch of the surface has been checked. The smaller adult cerebella have been treated in the same way; and in the larger organs microscopic sections have been made when the naked-eye examination left any doubt as to the connections of the lobules or the continuity of the fissures.

Sheep Embryos.—Although the development of the cerebellar fissures of the sheep has already been described by Kuithan (2), there are still certain points upon which he is silent which appear to require study. It is a matter for regret that as full a series of sheep embryos as have been already described of the pig could not be procured. But the breaks in the series can be filled, partially at least, by the material described by Kuithan.

68 *mm. embryo* (Pl. XLVI. fig. 1).—At this stage the cerebellum of the sheep presents much the same appearance to the naked eye as does that of the pig of a somewhat similar size (44 days, 64 mm.). It is very difficult to make out any fissures without the aid of a lens, and even by such assistance fissure II. is not conspicuous. Microscopic sections, however, remove any doubt as to its existence; and they further reveal the presence of two shallow depressions which turn out to be the beginnings of fissures IV. and *d*. Kuithan's figure of a section of the cerebellar lamina of a 5 cm. embryo gives a very similar picture to that presented by the present specimen. On examining a series of sections beginning in the middle line, all three fissures are soon found to disappear, fissure II. being the last to do so, as was to be expected. In sections of the lateral part of the cerebellum there is a faint fissure, which may possibly be the initiation of *a*; subsequent development lending support to this supposition.

87 *mm. embryo* (Pl. XLVI. figs. 2 and 3).—There is already the indication of a vermis and two hemispheres. Fissure II. is easily visible on the surface, and extends for a considerable distance in a slightly curved direction across the cerebellum. Posterior to fissure II. two depressions can be detected with the unaided eye when the cerebellum is undisturbed, and there is a third hidden between this structure and the medulla. These three sulci are IV., *d*, and III., the last being very shallow. Fissures IV. and *d* cross the whole of what may

be termed the vermis, and appear to be invading the hemisphere. Fissure III. does not extend so far laterally. Sections show unmistakably that fissure IV. is continued to the very lateral boundary of the cerebellum, where it curves forwards and downwards to circumscribe the anlage of the flocculus. This arrangement is one which has been met with in both the rabbit and pig. There are clear indications of the separation of the paraflocculus; that part which now represents it standing out prominently from the side of the cerebellum, limited by a fissure which curves round its anterior end. The fissure, tentatively named *a* in the previous embryo, is now sufficiently deep to be visible by means of a pocket lens. It is in the form of a slight indentation of that rounded mass of the lateral part of the cerebellum which lies between fissure II. and the future paraflocculus (fig. 2). Fissures I. and *c* have appeared in front of, or rather below, fissure II. The greater importance of I. is shown by its being a little deeper than *c*, and extending considerably farther laterally.

100 *mm. embryo* (Pl. XLVI. figs. 4, 5 and 6).—In the posterior part of the cerebellum, matters have not advanced much since the 87 mm. stage. Fissures IV., *d*, and III. are deeper, but little more can be said for them. With the exception of IV., they do not extend far into the hemisphere. The paraflocculus is rather more distinctly defined than in the previous specimen. Fissure *a* is much the same as it was before. Posterior to fissure II., therefore, development is now slow. But, as one expects from what has been found in other animals, the part in front of II. has become very active in its development. Fissures I. and *c* are easily detected. Their depth, as shown in sections, is greater than it was in the 87 mm. embryo, I. still extending farther in a lateral direction than *c*.

114 *mm. embryo* (Pl. XLVI. figs. 7, 8 and 9).—Great progress has been made, but more especially in the more anterior region. Fissure II. now clearly reaches the margin of the cerebellum, and the margin in this district is well defined. Fissures I. and *c* are very obvious; and sections show that lobule A_1 is complicated by subsidiary (intralobular) fissures. The posterior part of the cerebellum is also entering upon a period of activity. Fissures III. and *d* are not much longer (relatively) than before, but they are certainly deeper. Fissure *a* is now complete; that is, it runs across the entire cerebellum. Since the last stage a fissure *b* has made its appearance, having begun, as far as one can judge, in the middle line. The flocculus and paraflocculus are very distinct, but the latter is still a simple rounded projection from the side of the cerebellum; that is, it has not as yet begun to divide into dorsal and ventral portions. It is fortunate that a stage such as is illustrated by this embryo was procurable, for here all the fissures are firmly sketched in, the details only being wanting. It is further fortunate because the next older specimen is one in which many, if not most, of the details are added.

163 *mm. embryo* (Pls. XLVI. and XLVII. figs. 10 and 11).—Viewed from the front, this cerebellum presents features strikingly like those

found in the adult. The foliation is abundant, and the main fissures are deep. It is upon the posterior part that attention will be more particularly bestowed; because here, though development has proceeded a considerable distance towards the adult condition, the more primitive characters of the lobes are not yet lost, their original transverse disposition being still preserved. Lobule C_1 contains two folia in the vermis, but these are reduced to one in the hemisphere. Lobule C_2 has become quite characteristic. In the vermis it is composed of two folia, but in the paramedian sulcus the intralobular fissure disappears, and the lobule becomes constricted. In the hemisphere there is a notable indication of that expansion in a sagittal direction, with which one is now familiar: this part of the lobule has three folia.

Lobule C_3 is, in the main, very like C_2. It has two folia in the vermis: there is a constriction in the region of the paramedian sulcus: there is an expansion in the hemisphere. Lobule D_1 has also certain features of great value. It has two folia in the vermis, which are reduced to one in the paramedian sulcus; and then the lobule curving under the lower border of lobule C_3 becomes directly and beyond question continuous with the dorsal paraflocculus, the connecting ridge being transversely foliated. Lobule D_2 is large, but cannot be said to pass outside the limits of the vermis.

Lobe E in this embryo, and in those younger, is relatively large. If serial sections are examined, it is found to extend very considerably beyond the vermis. It disappears for a short time, and then reappears as the flocculus, which is also relatively large in sheep embryos.

The paraflocculus is now divided into dorsal and ventral limbs, but how the division has been brought about is not clear. Unfortunately, Kuithan is silent upon this point; for, as has been previously said, he did not recognise the true nature of this portion of the cerebellum. At this period the paraflocculus has advanced so far towards the adult condition as to be beset with transverse folia, especially in its dorsal portion.

Although the adult cerebellum of the sheep has been described in the former paper, it may not be out of place to revert to it here. Concerning the anterior part of it there is nothing to be said, because the adult features are recognisable at an early period in the embryo. It is to the region behind fissure II. that attention is asked. Lobule C_1 does not undergo any radical changes in the later stages of development, but lobules C_2 and C_3 alter very markedly. In the 163 mm. embryo, it has been seen that lobule C_2 is constricted in the paramedian sulcus, and is of greater antero-posterior diameter in the hemisphere than in the vermis. These features are exaggerated in the adult. The vermis grows so largely in a sagittal direction that distortion is produced. The same remarks apply to lobule C_3, except that the constrictions are even better marked, while the distortion in the vermis is little or nothing. These peculiarities in the development of lobe C will be more fully considered in connection with calf embryos, for in the ox the sagittal expansion is much greater, so far as the vermis is concerned, than in the sheep.

Lobules D_1 and D_2 retain their embryonic features, a foliated ridge joining the former to the dorsal paraflocculus. Lobe E in the adult, as in the embryo, is relatively well developed; but, unlike the condition in the embryo, it does not pass the boundaries of the vermis.

The paraflocculus and flocculus of the adult call for no remark, as the 163 mm. embryo prepares one for their appearance in the future.

Calf Embryos.—Three calf embryos have been obtained which, because of their stages of development, add greatly to the evidence in support of some of the statements previously made.

138 *mm. embryo* (Pl. XLVII. figs. 12, 13 and 14).—The cerebellum of this embryo has already become divided into a vermis and hemispheres by shallow paramedian sulci. All the main fissures are present in the vermis, and many of them extend all the way across the cerebellum. As was found in the embryos of the other animals, the anterior portion had proceeded farther in development than the posterior. Fissure II. can readily be detected on the surface; and when sections are made, it is seen to be of great depth, and with foliated sides. Fissures I. and *c* can also be clearly defined when the surface is inspected. Lobe A is comparatively simple, but lobe B is divided into two parts by a fairly deep fissure which runs across the central part of the cerebellum. In lobe C there is very unmistakable evidence of a fissure *a*, which runs a sinuous course across both vermis and hemisphere. It is interesting to note that fissure *b* is also complete, and, as seen in sections, very much deeper than *a*. Unfortunately, this embryo is too old to exhibit the method of commencement of fissures *a* and *b*. Fissures III. and *d* are present, but are almost entirely confined to the vermis. There are shallow sulci marking off the paraflocculus, but the more anterior is scarcely to be made out except in microscopic sections. It is important to notice that the paraflocculus is being divided into upper and lower portions by a depression which is deepest anteriorly (fig. 13), and which, therefore, has presumably begun its development in front, and is now growing backwards. The position of the future flocculus is marked by a comparatively slight bulging at the extreme lateral part of the pontine flexure. Lobe E is small in the middle line, but becomes a little larger laterally. Its appearance suggests that peculiarity of development from the border of the cerebellar lamina which has been observed in the rabbit and pig.

150 *mm. embryo* (Pl. XLVII. figs. 15 and 16).—Little need be said of the condition of the parts in front of fissure II. Fissures *c* and I. are both of considerable depth, and numerous intralobular fissures have developed. Lobe C is now completely divided into its three lobules. Fissure *b* has retreated from fissure II. to some extent, and is of much greater depth than *a*, as was found in the previous embryo. Fissure III. is complete, and, along with *a*, bounds a very characteristic lobule C_3, which shows the sagittal expansion which was found in other animals. Fissure *d* is more extensive than in the 138 mm. embryo, but, even now, does not reach very far into the hemisphere. It is still some little distance short of joining the fissure which has

been previously described as dividing the paraflocculus into dorsal and ventral limbs. Indeed, it appears as though the latter fissure is growing towards *d* rather than that *d* is extending much laterally. The dorsal paraflocculus is showing signs of developing folia. Fissure IV. is of considerable depth and very sharply defines lobe D, with its lateral parts, from lobe E and its connection with the flocculus.

175 *mm. embryo* (Pl. XLVII. figs. 17, 18, 19 and 20).—This specimen shows a fairly great advance in development. There is now no difficulty in distinguishing a vermis and two lateral hemispheres in all parts of the cerebellum, with the possible exception of the most anterior. The anterior surface is well foliated, and its main fissures are of good depth. But even at this stage the lateral limits of lobes A and B are indefinite (fig. 19). This is, no doubt, to be associated with the remarkably small lateral expansion of these lobes in the adult (fig. 21). Lobules C_1 and C_2, on the other hand, have very clear lateral boundaries. Again, it is to be noticed that fissure *b* is relatively very deep, and comparatively close to fissure II. Lobule C_1 is consequently narrow in a sagittal direction. Lobule C_2 is well developed in the vermis and in the hemisphere, and is beginning to show a decided constriction in the region of the paramedian sulcus. The vermis portion of lobule C_3 remains small, and still consists of only one folium. Its lateral segments have increased in a sagittal direction, and have become foliated. As a consequence of the lateral growth of lobule C_2 (which now extends as far out as the paraflocculus), lobule C_3 appears dwarfed in its transverse diameter. Fissure *d* is of good depth in the vermis, but rapidly becomes shallow in the paramedian sulcus. Though there is no direct evidence to be obtained from the present material, there can be little doubt, arguing from analogy, that it will ultimately become continuous with the fissure present in the earliest embryo, and which now divides the paraflocculus into two very distinct portions. The characteristic growth of lobule C_3 has resulted in a very clear definition of the paraflocculus. The dorsal paraflocculus carries two separate fissures; the ventral paraflocculus is still perfectly simple. Both the mesial part of lobe E and also the flocculus are small, this being in remarkable contrast to what was found in the sheep.

It is very interesting to compare this cerebellum with that of the adult animal (Pls. XLVII. and XLVIII. figs. 21, 22 and 23). Lobes A and B apparently do not alter in the later stages of development, but the lobes behind fissure II. undergo a noteworthy alteration in form. In lobule C_1 the change is merely one of increase of size, with a resulting backward displacement of fissure *b*. In lobule C_2 there is a great increase in size in the hemisphere, accompanied by an alteration in the direction of the intralobular fissures, and so considerable a growth in the vermis that this part of the lobule is bent upon itself, and even then occupies so much room that the vermis segment of lobule C_3 is crowded over to one side (figs. 22 and 23). The middle portion of fissure *a* ran in an almost perfectly sagittal direction in the specimen from which the figures were drawn. The three portions of lobule

C_3 also expand in an antero-posterior direction. As just stated, this lobule is crowded out of the vermis, and therefore comes to lie in what was once the paramedian sulcus. Those portions of the lobule which forms parts of the hemisphere are connected with the vermis by very much constricted but still quite obvious bridges of cortical substance. Lobe D shares in this antero-posterior development, and consequently its lobules present a sinuous appearance in the vermis, their folia being thrown out of the transverse direction completely. The connection between the dorsal paraflocculus and lobule D_1 is maintained in the adult state, but is, to a certain extent, obscured by the growth of lobule C_3. The paraflocculus in the adult animal is rather smaller than is usually found in Ungulates, and the arrangement in dorsal and ventral tiers is not so clear as in the embryos described. It is evident that lobe E must develop greatly after the stage illustrated by the 175 mm. embryo; for in the adult it is large and richly foliated, usually extending as far backwards as to be visible when the cerebellum is examined from behind (fig. 23). The flocculus also increases markedly in size.

The cerebellum of the ox affords a very good illustration of Bolk's 'growth-centres.' The 'centre' in the vermis expands in a sagittal but not in a transverse direction. This expansion is so great that the whole vermis behind fissure *b* is thrown into a series of billowing coils. Bolk's bilateral 'growth-centres' are also illustrated, but not in so striking a manner as that in the vermis.

Horse Embryo 18 *weeks old* (Pl. XLVIII. figs. 24, 25 and 26). I have only been able to get one embryo which shows the method of development of the fissures in the equine cerebellum, but this happens to be of a stage to which great interest is attached. There is no difficulty in distinguishing a vermis and two hemispheres, even in the most anterior region. Fissures *c* and I. are well developed, the latter being only second to fissure II. in point of depth (fig. 26). No better specimen could be desired to support the contention that fissure I. is of fundamental importance. This fissure evidently continues of great depth from the time of the 18 weeks embryo onwards, for in the adult it is only slightly shallower than fissure II. Lobule A_1 is becoming divided into its permanent three subdivisions. There is a fairly deep indentation of the surface of lobule A_2, which no doubt corresponds to the deeper of the two intralobular fissures met with in the adult. Lobe B is relatively as extensive as in the adult, and has already become subdivided. Fissure II. is as pronounced as one would expect it to be at so advanced a period. Lobe C is comparatively large, and consists of three expanded portions, separated by faint constrictions in the paramedian sulci. In it are two depressions, which may possibly correspond to fissures *a* and *b*. Fissure *b* (?) crosses the entire cerebellum, and the element of doubt which attaches to its identity is not so great as that concerning fissure *a* (?). The questionable fissure *a* is present as a shallow depression in the vermis, but does not cross the paramedian sulcus. There is a fissure running from the border of each hemisphere towards fissure *a* (?), but not joining it. If this is indeed fissure *a*—and older material is needed to remove all dubiety—then it either develops somewhat differently in the horse from what has been found in the embryos of the pig and sheep, or else a phase of its growth has been caught in this specimen which has been missed in the others. The former view seems the more probably correct.

Fissure III., though not of any great depth, is complete. Lobe D presents the most interesting feature in this cerebellum. Those portions of it which will ultimately become paraflocculi form very prominent projections from the sides of the cerebellum. They are as yet perfectly simple, but it is evident that fissure *d* is gradually growing into them, in the manner in which it develops in the pig. From the material examined, we may conclude that the dorsal and ventral portions of the paraflocculus are separated off from the primarily single mass in at least two different ways. On the one hand, fissure *d* may extend laterally, as in the pig and horse. On the other hand, an independent fissure may appear in the most lateral part of this region of the hemisphere, and grow towards fissure *d*, with which it finally fuses. The latter method is found in the ox, and possibly also in the sheep.

Concerning lobe E, one need only remark that it is fairly large in the vermis, and that the flocculus is as yet small and inconspicuous. An examination of the adult cerebellum shows that, though there is some distortion produced by the growth in a sagittal direction of lobules C_2 and C_3 in the vermis, this is not nearly so marked as in the ox, nor does it involve lobe D. The connection between lobule D_1 and the dorsal paraflocculus is always distinct in the adult.

Didelphis azaræ (Pls. XLVIII. and XLIX. figs. 27, 28, 29 and 30).—Opportunity has been afforded me of examining the cerebellum of this marsupial in a perfectly satisfactory condition, and the examination has been productive of several points of interest. The freshness of the material when it came into my hands (the animal was actually living when it reached me) allowed me to obtain sections in the best possible state.

A first glance at the cerebellum of Didelphis shows one an organ very similar to that found in some of the rodents. There is the same comparative simplicity, and the same prominent lobulus petrosus. In lobe A no paramedian sulci are present. A fissure *c* cuts off a simple undivided lobule A_1. Lobule A_2 is larger than the preceding, and is subdivided into two parts, each of which has two folia on the surface. Fissure II. is deep, transverse in direction in the vermis, curving sharply downwards and forwards on reaching the paramedian sulcus, and running in a sagittal direction in the sulcus. Lobe B, as the result of the course of fissure II., presents a four-sided area on the surface. This lobe is relatively larger than it is in most animals, and is subdivided by a fissure running almost parallel with II. Lobe C is a veritable lobulus impendens, in the sense in which the term is used by Ziehen. It is very much greater in its antero-posterior diameter in the hemispheres than in the vermis. Whether a fissure *b* is present is open to question, but there can be little doubt of the actuality of fissure *a*, which, running a curved course, much as it does in the rabbit, cuts off a distinct lobule C_3. This lobule consists of two folia in the vermis, but is reduced to one in the hemisphere. At first sight it appeared that lobule C_3 was continuous with the dorsal paraflocculus, but this was found not to be the case. Fissure III. passes for a considerable distance into the substance of the cerebellum, and runs a course similar to that of fissure *a*. Lobe D is subdivided by a fissure *d*, which sections show to be even deeper than III. Lobule D_1 has one folium only, lobule D_2 has two. Fissure IV. and lobe E do not offer anything of interest, so far as a naked-eye examination is concerned.

It was considered advisable to make perfectly sure of the arrangement and connections of lobule C_3, lobe D and lobe E. To this end serial sections of one-half of the cerebellum were very carefully worked through, and drawings made wherever crucial points were encountered. The following facts were noted. In the vermis these three parts of the cerebellum were found to consist of six folia, which may be numbered as follows:—1 and 2 belong to lobule C_3; 3 belongs to lobule D_1; 4 and 5 are parts of lobule D_2; and 6 is lobe E. In following the various folia in a lateral direction, the following was observed. Folia 1 and 2 blended with each other, 4 and 5 doing the same. That is, lobules C_3 and D_2 were reduced to one folium each. Then folium 3 gradually became less and less prominent, and finally disappeared. The next change was the termination of the single folium produced by the fusion of 4 and 5, this giving place to a wide sulcus, the bottom of which was formed of white matter. Folium 6 was next greatly reduced in size, and came to consist of a small ridge of grey matter. Now grey matter began to appear at the bottom of the sulcus left after folia 4 and 5 had come to an end. This was found to become the paraflocculus. At the same time folium 6 began to increase in size. The combined folia 1 and 2 diminished rapidly, and finally, after becoming detached from the rest of the hemisphere, ended. Folium 6 was ultimately traced into the flocculus.

To sum up. Lobule C_3 ends at the border of the hemisphere. The whole of lobe D soon comes to an end when the limits of the vermis are passed. Lobe E, however, is directly continuous, as a grey ridge, with the flocculus. This last fact adds considerably to the strength of the assertion that the flocculus is a part of lobe E, and of nothing else. The paraflocculus begins to appear in the depths of the sulcus left by the disappearance of lobe D. This might lead one to suspect the original connection of these two parts, even if one had no other evidence.

To the naked eye, the paraflocculus consists of several folia and carries a very distinct lobulus petrosus which is closely invested by bone. The flocculus consists of one folium, and its identity is only rendered clear by the aid of microscopic sections. It expands to a certain extent as it passes forwards.

Pteropus medius and *Xantharpyia* (*Rousettus*) *collaris.*—The cerebella of these two fruit-eating bats have been examined, and are found to be very similar to that of *Pteropus poliocephalus*, which is described in my former paper. In discussing the cerebellum of *P. poliocephalus*, I said that "there is apparently no fissure *c*." The new material leads me to think that this is possibly not the case. It is quite likely that the fissure marked I. in the figures should be called *c*, and that the fissure two folia distant above it should be indicated as deeper and labelled I.

Herpestes Mungo (Pl. XLIX. figs. 31, 32, 33 and 34).—In some respects the cerebellum of the mongoose departs from the average type as found among the carnivora. Its anterior portion presents nothing very remarkable, there being the usual fissures and lobules, disposed in the customary manner. If we take the deepest and most continuous fissure in lobe C to be fissure *b*, then lobule C_1 is remarkably small. It consists of three folia in the vermis, and these become two in the left hemisphere and only one in the right. There can be little doubt regarding the presence of a fissure *a* in the hemisphere, where it is in a position usual in the carnivora, but it cannot be traced with certainty into the vermis. Lobule C_2 is of moderate size in the vermis, but it becomes very narrow at the paramedian sulcus. Lobule C_3 has very typical carnivore characters in the hemisphere. In this region it is developed into a row of folia, running practically vertically, and reaching the medulla. Lobule D_1 is rather small, and both it and lobule D_2 are limited to the vermis. There is nothing remarkable about lobe E.

The paraflocculus of the mongoose differs to a certain extent from what may be considered as the type. A superficial examination would lead to the conclusion that there is but one row of folia, but on looking more closely into it two rows are disclosed. The ventral limb, however, is small, and extends backwards for only a short distance, tailing away in the interval between the flocculus and the dorsal paraflocculus. A lobulus petrosus, of some size, is carried by the ventral paraflocculus; but instead of springing from its most posterior end, it is attached anteriorly.

The flocculus is rather larger, relatively, than is mostly found in the carnivora. Its anterior end is broad, and composed of two or three folia. These fuse to form a single grey ridge, which passes inwards to become continuous with lobe E in the vermis. The connection of this ridge with the medullary velum is very intimate.

Procyon lotor (Pls. XLIX. and L. figs. 35, 36, 37 and 38).—The cerebellum of the racoon resembles, in a general way, that organ in any other moderately large carnivore. A detailed description of all its parts is not called for, since the figures in illustration of this cerebellum speak for themselves. But there are some points to which it is deemed desirable to direct attention. Fissures c and l and lobe A are very like those features in other cerebella. The large size of lobe B, however, is remarkable; as is also its almost entire inclusion in the vermis, because of the curved boundary formed by fissure II. Lobe C is of great interest. The identity of fissue *b* is uncertain. If the fissure marked *b* in the figures is really homologous with the boundary between lobules C_1 and C_2 in other animals, then one at once notices its asymmetrical arrangement. Lobule C_2 shows in a marked degree the characteristic sagittal expansion in the hemisphere, with the result that its folia run in several different directions. Fissure *a* is very decided in the hemisphere, but when traced mesially it becomes lost in the depths of fissure III. From this it follows that one cannot distinguish with certainty a lobule C_3 in the vermis, though sections show a fissure which may at one time have been part of *a*. Lobule C_3 in the hemisphere is comparatively small, consisting of a row of some half dozen folia, against which the dorsal paraflocculus abuts.

The remainder of the lobes do not depart to any very great extent from the customary arrangement. But it should be noted that lobule D_1 is continued into the hemisphere as two folia, one of which, the upper, is the larger, and touches the dorsal paraflocculus. Lobule D_2 is confined to the vermis. The paraflocculus is composed of the usual dorsal and ventral portions. The dorsal paraflocculus is much the larger, and extends backwards to a considerable amount. So far as this specimen is concerned, one might easily commit the mistake of supposing that the dorsal paraflocculus is a continuation of lobule C_3. In short, there is an appearance typical of the *lobulus ansiformis* of Bolk. So far as the naked-eye examination goes, there is no connection of lobule D_3 with the dorsal paraflocculus, though we feel fairly safe in assuming that such a connection was originally present, and that the coiled row of folia, which Bolk calls the *lobulus ansiformis*, is of secondary development. The ventral paraflocculus is small, and does not reach so posterior a level as does its dorsal companion. The flocculus, as is often the case in the carnivora, is small, and consists of one folium only; it is mainly hidden by the paraflocculus, between which and the roots of the 7th and 8th cranial nerves it lies. Its attachment to the lateral part of the posterior medullary velum is a very intimate one.

Viverra civetta (Pl. L. figs. 39, 40, 41 and 42).—In this cerebellum there is certainly no paramedian sulcus anterior to fissure II.; therefore it affords an excellent example in support of Bolk's refusal to recognise a vermis. The fissures in this region being numerous, and all of approximately the same depth, it is impossible to decide with certainty upon fissure I. and *c*. Still a fissure I. can be tentatively fixed upon from an observation of the arrangement of the rays of white matter in a mesial section. Lobes A and B have a relatively great antero-posterior diameter, which no doubt makes up for their comparatively small transverse width. This exuberance of sagittal development causes fissure II. to be placed far back in the vermis.

Lobe C is very singular. Fissures *b* and *a* cannot be distinguished, nor can the different lobules be determined upon from the disposition of the folia. The most anterior part of the lobe certainly resembles lobule C_1 as we are accustomed to see it, but its boundaries are not clear. It is, however, in the posterior part of the lobe that the most noteworthy features are found. There is the usual narrowing of the lobe at the paramedian sulcus, and the consequent reduction of the intralobular fissures. But these fissures are remarkable for the manner in which they join together just at the paramedian sulcus. In the hemisphere the fissures mostly end without joining each other.

In lobe D the paramedian sulci are much shallower than is often found to be the case in the cerebellum of a carnivore of this size. Lobule D_1 has three folia in the vermis, but in the hemisphere the lowest folium is very slender and soon fades away. Between lobes C and D, and close to the paramedian sulcus, is an uncertain area on each side (dotted in fig. 41). It is connected, quite distinctly, with both lobe C and lobule D_1, and it is impossible to decide to which it really belongs, though its position makes one think that it represents lobule C_3. Whether this is an accidental variation or the usual arrangement, can only be decided from an examination of other specimens. It may, however, be at once stated that *Viverra malaccensis* does not offer a similar enigma (fig. 43).

There is nothing peculiar in lobule D_2. It belongs exclusively to the vermis. Lobe E is fairly large, and is interesting because it shows a condition only occasionally met with. A grey lamina extends for some distance outwards from it, running under lobule D_1. This lamina is attached to the medullary velum, and reaches nearly to the posterior end of the flocculus.

The paraflocculus is very commonplace. It is composed of the usual two limbs, the ventral of which carries a lobulus petrosus at its posterior end. The flocculus is mainly concealed. At its anterior end it consists of two folia, one above the other. The upper folium is small; the lower reaches as far back as the posterior end of the paraflocculus, and is then continued by a very narrow ridge to the grey lamina or folium projecting from lobe E. This should be remembered in connection with what has already been seen microscopically in Didelphis and macroscopically in Herpestes, and with what is yet to be remarked in Cebus.

Viverra malaccensis (Pl. L. fig. 43).—This merits special attention on account of the points in which it differs from the cerebellum of *V. civetta*. Lobes A and B are the same in both animals, and there is the same difficulty experienced in determining which are the primary fissures anterior to II. It is in lobe C that the chief differences reside. One feels again the same hesitation in deciding upon a fissure *b*, but *a* can be more readily recognised. Its position in the hemisphere is clear, as it forms the upper boundary of a very typical lobule C_3 in this area, and it can be traced, though not very easily, across the vermis. Lobule C_2 shows that bending upon itself which has been frequently seen, and the radiation of its folia from a deep sulcus which has arisen secondarily as the result of the bending. The lateral extent of lobule C_3 is inconsiderable. In the vermis it consists of a vertical row of some four transverse folia; in the paramedian sulcus it is narrow. There is no uncertain area such as was met with in *V. civetta*. As in the larger animal, there is no difficulty in observing the connection of the three parts of lobule D_1. There is no continuation of either lobule D_2 or lobe E beyond the vermis.

The paraflocculus is like that of *V. civetta*, and the flocculus is small. There is no attempt at continuity of grey matter between the flocculus and the central part of lobe E.

Phoca vitulina (Pl. L. figs. 44, 45 and 46).—At first sight the cerebellum of the seal appears an inextricable tangle of fissures and coiling lobes. Beside it the cerebellum of man appears comparatively simple, for in man the fissures do run transversely in the main, but in the seal their course is in all directions. A closer examination shows that the labyrinth occurs in the hemispheres, the vermis being almost perfectly straightforward.

Taking the organ as a whole, it may be described as decidedly flattened from above to below. This is perhaps best indicated by actual measurements of the vermis of a cerebellum after being preserved in a solution of formalin, followed by alcohol. In the particular specimen from which the accompanying figures were made the vermis measured 37 mm. from before backwards, and 23 mm. from above to below. These figures are approximately equal to those given by Flatau and Jacobsohn (6), who state the dimensions of the vermis as being 4·0 cm. by 2·4 cm. This vertical flattening is even more pronounced in the hemispheres, which slope somewhat rapidly downwards and outwards from the vermis (fig. 45). The hemispheres, further, have a greater antero-posterior diameter than the vermis, since they project farther forwards (fig. 44). There is a deep and moderately wide notch in the anterior border ('incisura cerebelli anterior'), but no corresponding notch behind. The vermis appears narrow, but this appearance is doubtless fictitious, and produced by the great expansion of the hemispheres. Anterior to fissure II. there are really no paramedian sulci, but posterior to this fissure these sulci are deep. If we except fissures *a* and *b*, which are rather doubtful, there is little difficulty in recognising the various customary fissures, lobes, and lobules in the vermis. There is certainly a deep fissure in lobe C, which one feels inclined to call *a*, but its identity is lost as soon as it reaches the paramedian sulcus. There is also a moderately deep fissure anterior to *a*, but it is by no means certain that it is fissure *b*.

Unlike the vermis, the hemispheres present many instead of few difficulties. Lobes A and B are comparatively simple, the latter forming the bottom of the notch already mentioned as existing in the anterior border of the cerebellum. Lobule C_1 is only slightly more difficult to recognise than A and B. But the remaining lobules give rise to much hesitation, as they are confused and deep fissures are many. It is well-nigh impossible to follow the fissures of the vermis into the hemisphere; indeed, in some it is quite impossible to do so with any degree of certainty. The following statements, therefore, are put forth as appearing to me possibilities and probabilities, not as matters of certitude. It is difficult to see how we can be positive regarding the homologies in this particular region of the seal's cerebellum until someone has been fortunate enough to get an embryo or embryos of an age when the fissures and lobes are simple.

It appears feasible to suppose that the large lobules, which project forwards and form the lateral boundaries of the notch already spoken of, are lobules C_2. They occur as double rows of folia, connected anteriorly; and one can easily imagine that the originally few and transverse folia have increased so enormously in number that the lobule has been bent upon itself. This would demonstrate a much exaggerated activity in a sagittal direction of Bolk's lateral 'growth-centre.' If the above supposition be correct, then the lobule which is placed posterior to the large double row of folia is lobule C_3. One can speak a little more confidently of lobule D_1. It consists of an extremely well-developed vermis portion and two rows of transverse folia in each hemisphere, the three parts being moderately well connected together, *i.e.* the paramedian sulci are not so deep here as in some other places. Lobule D_2 and lobe E do not extend into the hemisphere. At first sight the paraflocculus appears to be too large to correspond to the paraflocculus of other animals, but a close examination of it leaves one little option. The doubt that the whole of it is the homologue of the paraflocculus in the rest of the mammalia is small. The dorsal paraflocculus is much larger than the ventral, and consists of a number of radiating masses of folia. From a point a little in front of the middle of its lower surface springs a lobulus petrosus. The ventral paraflocculus lies along the side of the medulla oblongata, immediately behind the pons. The flocculus cannot be seen until the ventral paraflocculus has been removed. It is moderately large, and is composed of a row of folia.

The above account differs in some points from that given by Flatau and Jacobsohn, but it is the one which seems best fitted to bring the cerebellum of the seal into line with that of other mammals.

REFERENCES.

(1) Stroud, B. B., "The Mammalian Cerebellum, part 1: The Development of the Cerebellum in Man and the Cat," *Journ. Comp. Neurol.*, vol. v. p. 71, 1895.

(2) Kuithan, W., "Die Entwickelung des Kleinhirns bei Säugetieren," *Münchener Medic. Abhandl.*, vii. Reihe, 6 Heft, 1895.

(3) Ziehen, Th., "Das Centralnervensystem der Monotremen und Marsupialier," Theil i., *Semon's Zoologische Forschungreisen in Australien und dem malayischen Archipel. Jenai'sche Denkschriften*, vi., 1897.

(4) Schwalbe, *Lehrbuch der Neurologie*, Erlangen, 1881.

(5) Elliot Smith, G., "The Brain in the Edentates," *Trans. Linn. Soc. Lond.*, Zoology, 2nd series, vol. vii. part 7, p. 277, 1899.

(6) Flatau, E., und Jacobsohn, L., *Handbuch der Anatomie und vergleichenden Anatomie des Centralnervensystems der Säugetiere*, I. Makroskopischer Teil, Berlin, 1899.

(7) Bradley, O. Charnock, "On the Development and Homology of the Mammalian Cerebellar Fissures," *Journ. Anat. and Phys.*, vol. xxxvii. pp. 112 and 221, 1903.

(8) Elliot Smith, G., "On the Primary Subdivision of the Mammalian Cerebellum," *Journ. Anat. and Phys.*, vol. xxxvi. p. 381, 1902.

(9) *Ibid.*, "Notes on the Morphology of the Cerebellum," *Journ. Anat. and Phys.*, vol. xxxvii. p. 327, 1903.

(10) *Ibid.*, "Further Observations on the Natural Mode of Subdivision of the Mammalian Cerebellum," *Anat. Anz.*, Bd. xxiii., p. 368, 1903.

(11) *Ibid.*, "The Morphology of the Human Cerebellum," *Rev. Neur. and Psychiatry*, vol. i. No. 10, p. 629, Oct. 1903.

(12) *Ibid.*, "On the Morphology of the Brain in the Mammalia with Special Reference to that of the Lemurs, recent and extinct," *Trans. Linn. Soc. Lond.*, Zoology, 2nd series, vol. viii. part 10, p. 319, Febry. 1903.

(13) Bolk, Louis, "Beiträge zur Affen-anatomia, IV. Das Kleinhirn der Neuweltaffen," *Morph. Jahrb.*, Bd. xxxi. Heft 1, p. 44, 1902.

(14) *Ibid.*, "Hauptzüge der vergleichenden Anatomie des Cerebellum der Säugetiere mit besonderer Berücksichtigung des menschlichen Kleinhirnes," *Monatsch. f. Psych. u. Neurol.*, Bd. 12, Heft. 5, p. 432, 1902.

(15) Ziehen, Th., "Makroscopische und Mikroscopische Anatomie des Gehirns," *Handbuch der Anatomie des Menschen*, herausgegeben von Prof. Dr Karl von Bardeleben, 10 Lief., Jena, 1903.

(16) Stroud, B. B., "The Morphology of the Ape Cerebellum," *Assoc. Amer. Anatomists*, Dec. 28–30, 1897, p. 107.

(17) Ziehen, Th., "Ueber den Bau des Gehirns bei den Halbaffen und bei Galeopithecus," *Anat. Anz.*, Bd. 21, p. 505, 1903.

EXPLANATION OF THE FIGURES IN PLATES XLVI.–L.

Fig. 1.	Sheep embryo,	68 mm.	Mesial sagittal section.
Fig. 2.	,,	87 mm.	Posterior view. × 2.
Fig. 3.	,,	87 mm.	Mesial sagittal section.
Fig. 4.	,,	100 mm.	Superior-posterior view. × 2.
Fig. 5.	,,	100 mm.	Anterior view. × 2.
Fig. 6.	,,	100 mm.	Mesial sagittal section.
Fig. 7.	,,	114 mm.	Superior-posterior view. × 2.
Fig. 8.	,,	114 mm.	Mesial sagittal section.
Fig. 9.	,,	114 mm.	Anterior view. × 2.
Fig. 10.	,,	163 mm.	Superior-posterior view. × 2.
Fig. 11.	,,	163 mm.	Mesial sagittal section.
Fig. 12.	Calf embryo,	138 mm.	Superior-posterior view. × 2.
Fig. 13.	,,	138 mm.	Left lateral view. × 2.
Fig. 14.	,,	138 mm.	Mesial sagittal section.
Fig. 15.	,,	150 mm.	Postero-superior view. × 2.
Fig. 16.	,,	150 mm.	Left lateral view. × 2.
Fig. 17.	,,	175 mm.	Superior view. × 2.
Fig. 18.	,,	175 mm.	Posterior view. × 2.
Fig. 19.	,,	175 mm.	Anterior view. × 2.

Fig. 20. Calf embryo, 175 mm. Mesial sagittal section.
Fig. 21. Bos taurus. Anterior view. $\times \frac{1}{2}$.
Fig. 22. ,, Superior view. $\times \frac{1}{2}$.
Fig. 23. ,, Posterior view. $\times \frac{1}{2}$.
Fig. 24. Horse embryo, 18 weeks old. Posterior view. $\times 2$.
Fig. 25. ,, 18 weeks old. Anterior view.
Fig. 26. ,, 18 weeks old. Mesial sagittal section. The section has been cut slightly obliquely; the anterior part of the figure therefore shows the fissures, etc., a little more to the right than the posterior part.
Fig. 27. Didelphis azaræ. Superior view. $\times 2$.
Fig. 28. ,, Anterior view. $\times 2$.
Fig. 29. ,, Postero-lateral view. $\times 2$.
Fig. 30. ,, Mesial sagittal section.
Fig. 31. Herpestes mungo. Anterior view. $\times 2$.
Fig. 32. ,, Superior view. $\times 2$.
Fig. 33. ,, Posterior view. $\times 2$.
Fig. 34. ,, Mesial sagittal section.
Fig. 35. Procyon lotor. Anterior view. $\times 1$.
Fig. 36. ,, Superior view. $\times 1$.
Fig. 37. ,, Posterior view. $\times 1$.
Fig. 38. ,, Mesial sagittal section.
Fig. 39. Viverra civetta. Anterior view. $\times 1$.
Fig. 40. ,, Superior view. $\times 1$.
Fig. 41. ,, Posterior view. $\times 1$. The dotted areas are connected with both lobe C and lobule D_1.
Fig. 42. ,, Mesial sagittal section.
Fig. 43. Viverra malaccensis. Posterior view. $\times 1$.
Fig. 44. Phoca vitulina. Superior view. $\times \frac{1}{2}$.
Fig. 45. ,, Posterior view. $\times \frac{1}{2}$.
Fig. 46. ,, Inferior view. $\times \frac{1}{2}$.

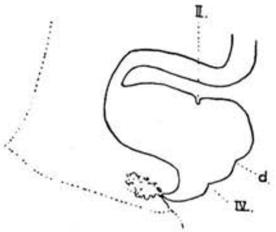
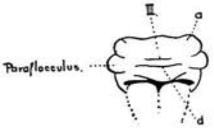


FIG. 1.



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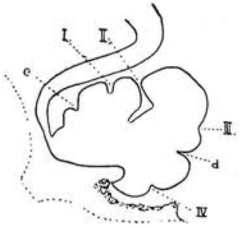
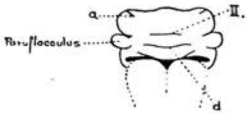


FIG. 3.



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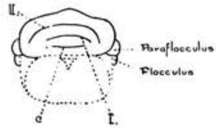

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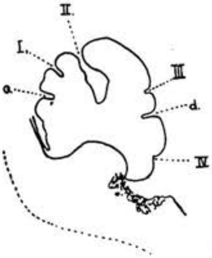

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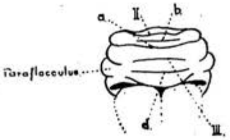

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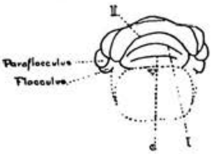
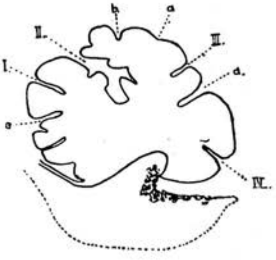


FIG. 9.



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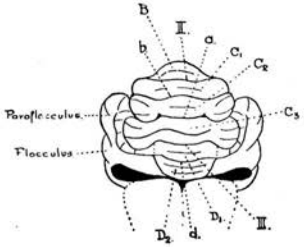
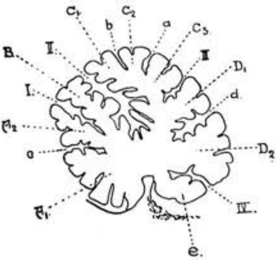


FIG. 10.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.



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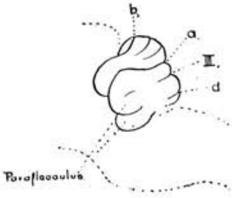

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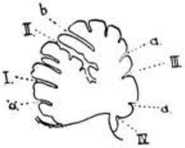

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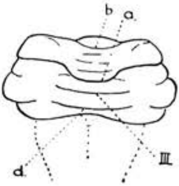

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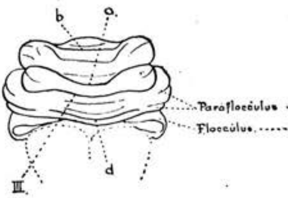

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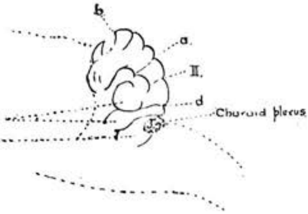

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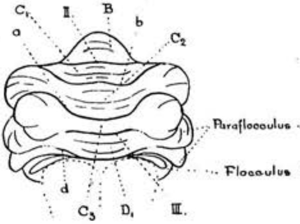

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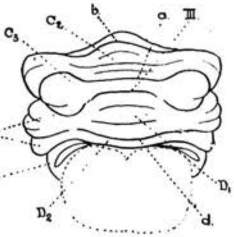

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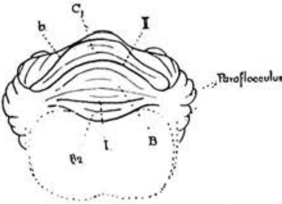

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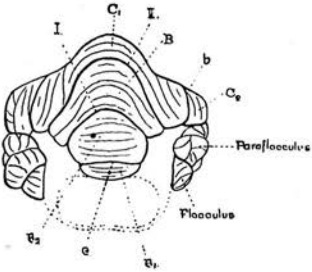

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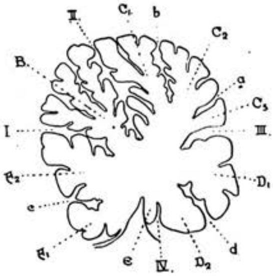
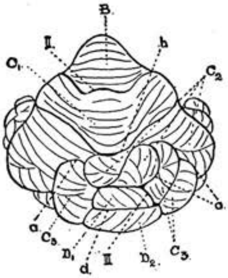


FIG. 20.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.



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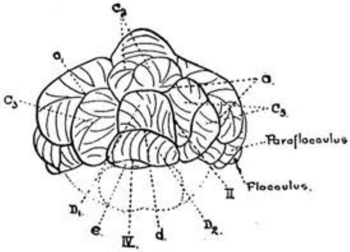

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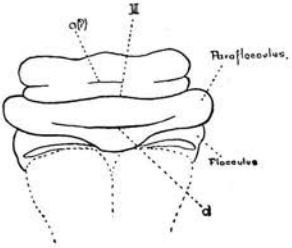

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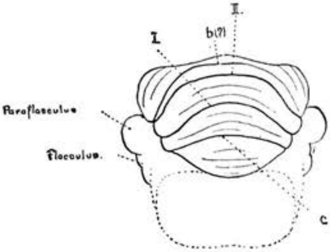

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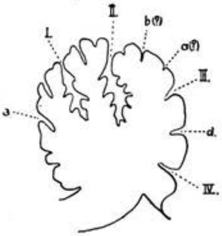

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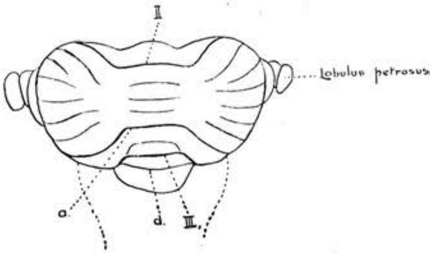

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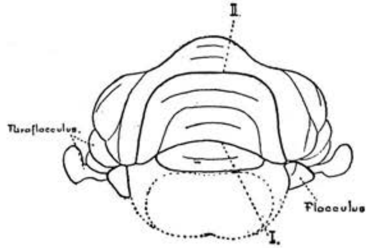

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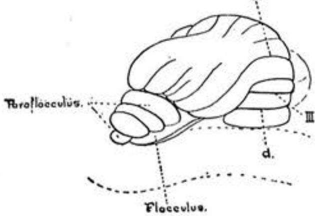
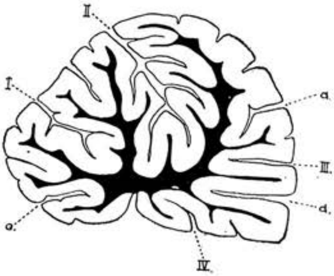


FIG. 29.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum : its Lobes and Fissures.



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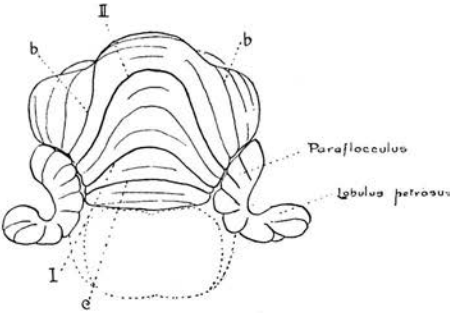

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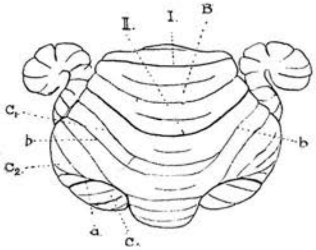

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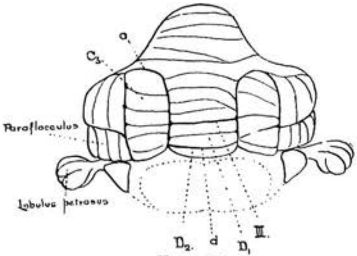

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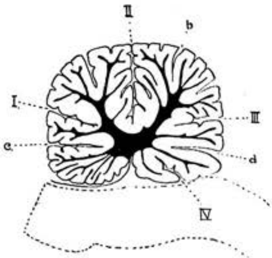

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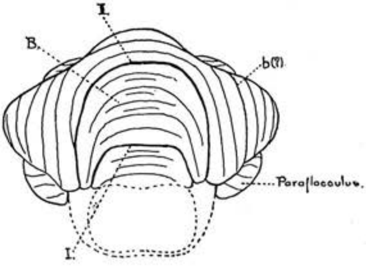
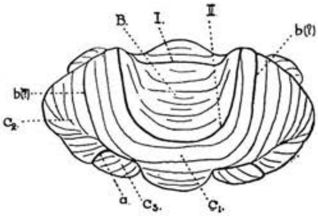


FIG. 35.



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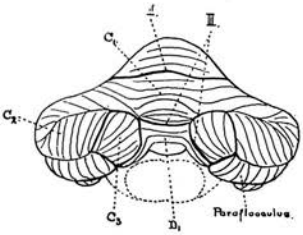
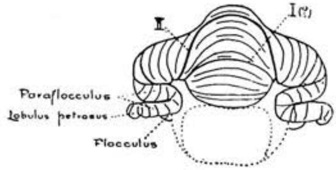


FIG. 37.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.



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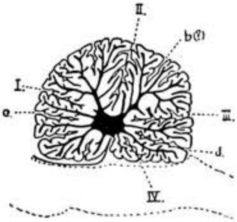

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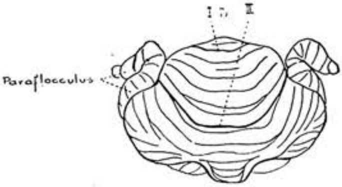


FIG. 40.

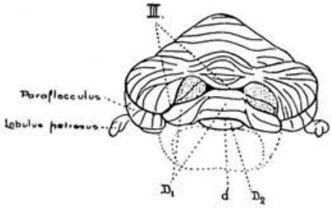


FIG. 41.

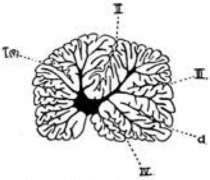


FIG. 42.

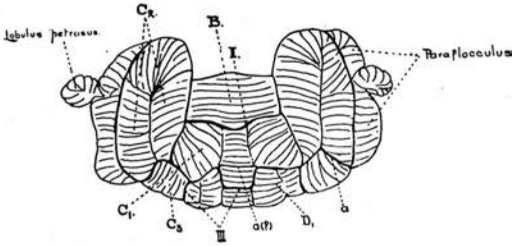


FIG. 44.

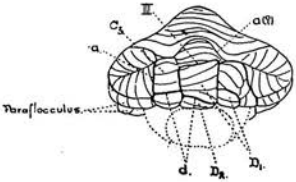


FIG. 43.

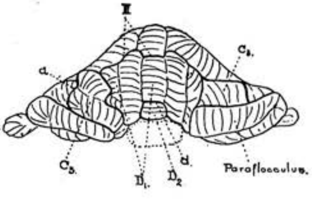


FIG. 45.

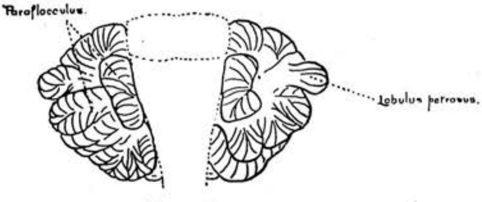


FIG. 46.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.

THE MAMMALIAN CEREBELLUM: ITS LOBES AND FISSURES. By O. CHARNOCK BRADLEY, M.B., F.R.S.E., *Royal Veterinary College, Edinburgh; Goodsir Fellow, University of Edinburgh.* (PLATES XXIV.–XXVIII.)

PART II.

The Cerebellum in Primates.

THE brains of *Hapale jacchus*, *Nyctipithecus trivirgatus*, *Cebus capucinus*, *Lagothrix humboldti*, *Ateles ater*, *Macacus rhesus* (two specimens), *Cynopithecus niger*, and *Cercocebus fuliginosus* have been examined. The description of the cerebella of the first two had better be given separately, as they differ in many respects from those of the remaining monkeys. The other specimens will be described together, since they do not differ sufficiently widely to justify individual consideration.

Hapale jacchus (Pl. XXIV. figs. 48, 49, 50 and 51).—At the very first glance, one is struck with the remarkable simplicity of this cerebellum. It is certainly not a simplicity of so severe a type as that met with in some other small mammals, but it is sufficiently pronounced to call for remark. Paramedian sulci are exceedingly faint in lobes A, B and C. In the remaining lobes they are easily recognisable, but not deep. The number of folia in the vermis is small enough to allow one to speak of the different lobes as being composed of a certain number.

Fissure I. is very easily recognised in mesial sections. Its depth is about as great as that of any other fissure with the exception of II. Lobe A consists of five folia, three of which go to lobule A_1, the remaining two to A_2. Fissure *c* is undoubted. It is difficult to say if lobe A assists in the formation of the hemisphere, owing to the doubtful character of the paramedian sulcus at this point.

Fissure II. is placed farther back than one would expect, in view of the comparative simplicity of the cerebellum as a whole. Consequently, lobe B is relatively large in the vermis, but becomes more restricted in the hemisphere, owing to the course of fissure II. in a downward and forward direction. Only one, or possibly two, of the intralobular fissures is what Bolk would describe as 'complete,' *i.e.* runs completely across the cerebellum.

Lobe C calls for a detailed description. It consists of four folia in the vermis, but in the hemisphere—following the customary behaviour of this lobe—its folia are more numerous. Three of the folia pass outwards and forwards to the border of the cerebellum without undergoing much alteration. The fourth folium is connected with several short folia, which are arranged in a radiating manner, their centre of radiation being towards the middle line. This increase in the number of the folia, with a corresponding increase in the size of lobe C, is what we have been led to expect; but the point to which attention is asked is the comparative simplicity of their arrangement in a cerebellum in which, as will be shown immediately, certain parts are much better developed than is customary in a cerebellum with a simple lobe C. Neither fissure *a* nor *b* can be determined, though serial sections through the half of the cerebellum have been made and examined microscopically, in order to settle this and some other particulars to be presently detailed.

Lobe D is divided into two lobules by a very distinct fissure *d*. Lobule D_1 consists of two folia in both vermis and hemisphere, there being no difficulty in determining the connection of the two districts, owing to the shallowness of the paramedian sulcus. Lobule D_2 also carries two folia, but does not reach the hemisphere.

Lobe E is likewise composed of two folia, or one compound folium, and microscopic sections show that it entirely disappears at the limits of the vermis, and that a white area takes its place. Considerable difficulty has been experienced in arriving at any conclusion as to the line of separation of flocculus and paraflocculus. There is a well-developed and clearly-defined lobulus petrosus which, attached to the rest of the cerebellum by a narrow neck, is closely surrounded by a capsule of bone. In addition, there are five folia lying anterior to the point of attachment of the lobulus petrosus; and it becomes a question as to how many—if any—of these belong to the paraflocculus. Unfortunately Bolk (13) affords no assistance in the reading of the riddle, since he does not mention these folia in the text of his paper, nor do they appear in his text figures. In fig. 2, taf. ii., he apparently shows two of them. But here they are simply labelled "*Form. verm.*" (formatio vermicularis). An examination of serial microscopic sections leads one to conclude that, as in the rabbit, these folia anterior to the lobulus petrosus all belong to the flocculus. In looking over sections beginning in the middle line, it is first noticed that a trace of grey matter appears in the small area of white matter which has been left on the disappearance of lobule D_2 and lobe E. This gradually increases in amount until a veritable folium is formed, which is ultimately divided into two, an upper and a lower, to the former of which the lobulus petrosus is attached. There can be little doubt that this is the paraflocculus; and, incidentally, it may be remarked that its mesial commencement lies far under lobule D_1, *i.e.* it commences within measurable distance of the vermis. No microscopic connection can be traced between the paraflocculus as just described and the five folia in the anterior part of the cerebellum; they are therefore held to constitute the flocculus, which, as in the rabbit, is far removed from the vermis.

Nyctipithecus trivirgatus (Pl. XXIV. figs. 52, 53 and 54).—The cerebellum of this Douroucouli is not unlike that of Hapale, except that it is a little more complex. In this specimen, as in the preceding, microscopic sagittal sections have been made of one-half of the organ. Instead of giving a detailed description, it will suffice to compare the cerebellum of Nyctipithecus with that of Hapale.

The differences in the anterior region are too slight to require mention, and lobe C need not be dilated upon. It is with lobes D and E that it was found especial attention was necessary. In this part of the cerebellum paramedian sulci are very pronounced, and their presence removes the obvious connection of the parts of lobule D_1 which is so clear in Hapale. When a series of sections are examined, it is found that lobule D_2 (which is larger than in Hapale) ends somewhat abruptly about the paramedian sulcus. At the same time lobule D_1 adds to the number of its folia, so that there are three of these visible in the hemisphere when the intact cerebellum is examined. Sections show a very definite continuity of them with the paraflocculus, which, though not very large, is of good size, and carries a bulky lobulus petrosus.

The mesial part of lobe E retains its grey matter slightly more laterally than lobule D_2 extends. Then all that remains is the edge of the medullary velum, above which lies fissure IV., which can be followed without difficulty until it separates the paraflocculus and flocculus.

Cebus, *Lagothrix*, *Ateles*, *Macacus*, *Cynopithecus*, and *Cercocebus* (Pl. XXV. figs. 55 to 62; Pl. XXVI. figs. 63 and 64).—These cerebella will be described together, as their resemblance is very great. In the anterior part of the organ there is little to note. Until lobe C is reached, the lobes, lobules and fissures are not unlike those met with in animals with a cerebellum of about the same degree of complexity. And it may be further stated that in all six monkeys the corresponding parts are of about the same relative size and disposition. It is in the district which lies behind fissure II. that the main features of interest are encountered.

Lobe C is marked by a pronounced antero-posterior increase in the hemisphere. With the exception of Cebus, there is little difficulty experienced in finding fissure *b*, which cuts the vermis fairly deeply, and curves downwards and forwards to the margin of the hemisphere. Lobule C_1, thus bounded posteriorly, is of about equal antero-posterior diameter throughout, and its intralobular fissures run approximately parallel. It is a perfectly good exhibition of Bolk's *lobulus simplex*. In Cebus, however, it is difficult to decide upon a *sulcus posterior* such as is figured and described by Bolk (13), fig. 13. In the other monkeys the deepest fissure in the vermis in lobe C can be traced as a continuous and deep sulcus to the margin of the hemisphere. But in the specimen of Cebus, examined for the purpose of this paper, the deepest fissure in the vermis is neither deep nor continuous in the hemisphere. Judging from the condition as described by Bolk, I can only conclude that my specimen was one illustrating the subsidiary morphological position of the fissure.

Lobule C_2 is not quite the same in all the specimens. In Cebus, as noted above, fissure *b* cannot be determined; therefore the exact limits of lobule C_2 cannot be defined. In Macacus, C_2 has *apparently* no existence in the vermis, because fissure *a* runs into fissure *b* in the paramedian sulcus. That part of it which does exist, however, has the same form as the hemisphere portion of the lobule in the other monkeys, *i.e.* it consists of a number of folia arranged in the form of a half-opened fan, the handle of which is directed towards the vermis. The fissures between the folia all disappear before reaching either fissure *a* or fissure *b*, with the exception of one which arrives at the apex of the triangle, and therefore opens into the conjoint fissure $a+b$ (Pl. XXV. fig. 61). In Cercocebus and Cynopithecus fissure *a* is deep in the hemisphere, but in the vermis is traceable into a shallow interfoliar cleft in the depths of fissure III. Lobule C_2 is therefore present and of some size in the vermis. In the hemisphere it need only be noted that it is relatively larger than in Macacus. It has the same radial arrangement as in the latter animal, and there is the same fissure running inwards towards the point of convergence of fissures *a* and *b*. It should be noted that there is a very narrow link connecting the three parts of lobule C_2 on each side, this being invisible on the surface. In Lagothrix and Ateles fissure *a* cannot be followed into the vermis, therefore the limit between lobules C_2 and C_3 is problematic.

Lobule C_3 in Cebus and Macacus consists of a narrow part in the vermis, continued into a much larger portion in each hemisphere, there being a slight stricture in the paramedian sulcus. In Cercocebus and Cynopithecus, owing to the peculiarity of fissure *a*, lobule C_3 can hardly be said to have any existence in the vermis. The most that can be said of it is that it is represented by three or four folia on the anterior wall of fissure III. In the hemisphere, however, it is large, and resembles the homologous part in the other cerebella.

Lobules D_1 and D_2 are very similar in all the specimens. D_1 is largely developed in the hemisphere, and there is little difficulty in finding its connections with the vermis. This is very easily done in Cebus, owing to the comparative lack of depth of the paramedian sulci (Pl. XXV. fig. 57). Lobule D_2 belongs entirely to the vermis. In order to ascertain if there was any continuation whatever beyond the vermis, microscopic sections of this region were made in Cercocebus. It was found that lobule D_2 ends somewhat abruptly, and gives place to a considerable stretch of white matter which underlies lobule D_1 in the mesial part of the hemisphere.

In all but Cebus, lobe E also ends at the level of the paramedian sulcus. In Cebus, however, the lowest folium is continued outwards, undiminished in size, underneath lobule D_1 (Pl. XXV. fig. 58). It proceeds laterally for some distance and then fades away, giving place, as it appears, to the posterior medullary velum to which it has been previously adherent.

The same general arrangement of the flocculus and paraflocculus obtains in all the monkeys examined. The paraflocculus consists of a single row of transverse folia, which turns downwards a little in front and *appears* to be continuous with the flocculus (Pl. XXV. figs. 55 and 60). This appearance would lead to the description of the paraflocculus as composed of dorsal and ventral parts, and to the statement that the flocculus is wanting, were it not for two circumstances which cannot be put on one side unconsidered. The one is that there is a deep sulcus separating the anterior end of the flocculus from the paraflocculus. Again, the flocculus is closely related to, and partly adherent to, the lateral prolongation of the posterior medullary velum. This is best seen in Cebus, where, owing to the lateral extension of lobe E (as described above), there is very little interval between flocculus and lobe E (Pl. XXV. fig. 58).

The paraflocculus carries a lobulus petrosus, springing from its lateral face close to the anterior end. The extent to which the paraflocculus proceeds backwards and inwards varies in some degree.

In Cebus, lobule D_1 passes on to the inferior surface of the hemisphere, and consequently sets a limit to the paraflocculus. In the other monkeys, however, the paraflocculus is continued unarrested in a mesial direction until it almost reaches the vermis. But it is not fused with any part of the vermis, as microscopic sections show; and for this reason the term paraflocculus is applied to the whole of it, however nearly it may approach the middle line.

In no specimen could one feel convinced that there was a dorsal and a ventral limb to the paraflocculus, such as Elliot Smith indicates (10). I am inclined to think that the paraflocculus of the monkey corresponds to the ventral limb of that structure in the majority of mammals, and that the dorsal paraflocculus has been replaced, so to speak, by the enlarged hemisphere segment of lobule D_1.

The Human Cerebellum.

Thanks to the kindness of Professor D. J. Cunningham, I have been enabled to examine a number of human fœtal cerebella. Although several of them are of approximately the same age, and none is illustrative of the earlier stages of development of the fissures and lobes, there are at least four of them which throw light upon some of the problems of the growth of the fissures in man. The remainder have been of the greatest use in enabling me to check my results, and in showing in what manner some of the fissures are liable to variation. Seeing that the several cerebella had been separated (along with the pons and medulla) from the rest of the brain, no definite idea could be formed as to the age of the embryos from which any one had been taken. This is perhaps not of the greatest importance, since the literature contains figures illustrating several different stages in the growth of the human cerebellum, with the age or size of the embryo appended. Anyone who is curious on the matter may compare the figures given herewith with those of previous writers (Stroud, Kuithan, Elliot Smith). The cerebella mentioned here will be known by numbers.

In *Cerebellum No. I.* (Pl. XXVI. figs. 65, 66, 67, 68 and 69), the anterior part of the organ is already provided with a fairly numerous set of folia. In the posterior part the fissures are less numerous, and it is on this district that especial attention will be bestowed, for the reason that here are located the lobes and lobules concerning which there is most difficulty in arriving at conclusions regarding homologies. In all parts of the organ a distinction can readily be made into a vermis and two hemispheres, this being the more easily done in the posterior district. When the cerebellum is viewed from the front (fig. 65), fissures *c*, I., II. and *b* can be at once recognised, their disposition being very similar to that in the adult brain. Special attention is asked to the appearance presented by a mesial sagittal section (fig. 69). A noteworthy feature here is the large size of what is no doubt to become the 'lingula.' Further, the depth of fissure I. is to be noticed, since this, as previously tentatively stated, is not recognised by the human anatomist as a fissure of any importance in the division of the vermis into its several lobes. Between fissures *c* and I. there is only one folium visible when the surface is examined, this folium being even narrower in the hemisphere than in the vermis. That part of the organ which lies posterior to fissure II. is of great interest, chiefly because, as already said, its development is not so far advanced. Appearances seem to point to the development of fissure *b* as having been from two lateral halves, which have gradually grown towards the middle line. These two halves, in this particular specimen, seem to have missed arriving at exactly the same point in the middle line, with the result that they overlap to some extent (fig. 66). In a mesial section the fissure is double, appearing as two shallow depressions (fig. 69). Fissure *a* is still in the form of two halves, which are approaching each other in the vermis. It will be observed that fissures *a* and *b* develop in man in the same manner as has been found in the pig, rabbit and sheep. Fissure III. has obviously commenced its development in the middle line (*cf.* Kuithan). It is deep in the vermis, but gradually becomes shallower as it curves outwards and downwards into the hemisphere, to disappear finally before reaching the margin of the cerebellum (fig. 67). Fissure *d* is as deep as III. in the vermis, and in each hemisphere is continuous with a curved groove which reaches the border of the organ. It is well to remark that *d* is very shallow in the paramedian sulcus.

Lobe E is small, and confined to the vermis. A simple unfoliated flocculus is visible when the cerebellum is looked at from behind or from the side (figs. 67 and 68). There are no paraflocculi in this specimen.

A few intralobular fissures have appeared in the vermis in lobules D_1 and D_2; and that part of the hemisphere which lies between fissures *a* and *d* is marked by a groove, which begins at the border of the cerebellum and, passing for some distance towards the middle line, becomes gradually less deep, until it finally ends before reaching the vermis (fig. 67). There seems little reason to doubt that this groove ultimately becomes continuous with III., and so separates lobe C from lobe D (*cf.* Stroud's figure 62 (1), and Elliot Smith's emendation of it in his figure 9 (12)). If this supposition is correct—and there seems little reason to question it—then the similarity of development of fissure III. in its entirety in man, and in the rabbit, pig, sheep and calf, is very striking.

Cerebellum No. II. (Pl. XXVI. fig. 70), in addition to showing further growth of the fissures and lobes, is interesting, since it illustrates an asymmetry in lobe C. It will be observed that fissure *b* of the left side is continuous with fissure *a* of the right; and *a* of the left and *b* of the right half of the cerebellum cross the middle line to terminate in the opposite hemisphere. If any instance were needed in the support of the contention that these fissures are of secondary importance merely, their tendency to irregularity of disposition might be cited. In this cerebellum the posterior portion has developed very considerably as compared with the same region in No I. Fissure III. is now complete, forming a series of graceful curves, of which that in the vermis is the most acute, and has its convexity looking upwards. Fissure *d* and lobule D_2 have not altered materially from the condition in the preceding specimen. The vermis portion of lobule D_2 has become foliated, but the hemisphere segments remain smooth. The flocculus is now foliated. There is a paraflocculus on one side only, and it is much smaller than the flocculus. Its connections cannot be followed with any degree of satisfaction, it being quite clear that only in much younger material can the origin of the paraflocculus and flocculus be determined beyond question.

Looking at this cerebellum as a whole, it is observed that there has been a more pronounced growth in the hemispheres than in the vermis. This growth has taken place more particularly in lobules C_3 and D_1, lobule D_2, as previously stated, being still unfoliated in the hemisphere. As a consequence of this marked local development, the hemispheres project farther posteriorly than the vermis, and overhang the medulla to a greater degree than they did in cerebellum No. I. The paramedian sulcus is deepest and best marked in lobule D_2, and it will be noticed that the connection between the three parts of lobule D_1 has become very narrow.

In *Cerebellum No. III.* (Pl. XXVII. figs. 71, 72 and 73), there is a marked resemblance to the adult organ. There is now a fairly pronounced vertical flattening. On inspecting the cerebellum from above, fissures I., II. and *b* are seen to run uninterruptedly across the surface, and lobes A and B and lobule C_1 now carry folia. Fissure *a* is still in the form of two lateral halves which approach each other, *i.e.* the vermis, but have not yet fused (figs. 71 and 72). Because of this lack of continuity there is still a portion of the vermis common to lobules C_2 and C_3. This common connection is of only small antero-posterior diameter, as indeed was the case in the younger specimens. Lobule C_2 is relatively small, and its intralobular fissures are few. Lobule C_3 in the hemisphere has again grown at a rapid rate as compared with the surrounding lobules. There is little to remark in fissures III. and *d*. They present much the same features as have been mentioned in connection with Cerebellum No. II., their depth of course being greater. Lobule D_1 has not grown as rapidly as appeared to have been the case in the interval between No. I. and No. II. The connecting link between that part of it which lies in the vermis and its more lateral segments is narrow (as in No. II.) and consists of a single folium. Lobule D_2 has not grown in a manner which calls for remark, and those portions of it which are placed lateral to the paramedian sulci are still smooth. A small and simple paraflocculus is present on both sides (fig. 73). The flocculus does not appear to have made any noteworthy progress.

The external features of *Cerebellum No. IV.* (Pl. XXVII. fig. 74) are very similar to those of No. III. There are rather more intralobular fissures, but the lobes, in the main, present no additional points of interest. It should be noticed that the two halves of fissure *a* have at length joined in the middle line. This is obvious in a mesial section (fig. 74). Attention is again directed to fissure I. as seen in section. Its depth in the middle line is great, being not much less than that of *c*. The importance of this fissure is once again insisted upon.

The only other fœtal cerebellum (*No. V.*) to which any reference is necessary is useful as affording evidence of the parts of the adult organ formed from the various lobes of the younger specimens. This cerebellum has arrived at such a stage that it, at one and the same time, resembles No. IV. and also the fully-developed structure. Its approaching identity with the adult organ removes any necessity for a detailed description. It will suffice to indicate what changes occur in the transition from the fœtal to the adult condition. It may be said, in general terms, that the most striking alteration in the form of the whole organ is produced by a growth in the hemispheres out of proportion to that of the vermis. This we have seen to begin in the comparatively early stages illustrated by the material the description of which is given above; it becomes still more evident in the later stages. As a consequence of this disproportionate growth, the vermis becomes a comparatively insignificant part of the human cerebellum, and the mesial connections of the corresponding parts in the two hemispheres is relatively reduced in a sagittal direction. This feature of development is not equally marked in all regions. In lobes A and B it is very trifling. In lobe C it is decidedly obvious, and particularly so in lobule C_3.

The growth of the hemispheres within this lobule is so great, and the fissures which cut its surface are so deep, that human anatomists have found it expedient to divide it into three parts. This enormous growth of lobe C is very characteristic of the human brain. Indeed, Bolk has said (14) that "the distinguishing feature of the human cerebellum depends upon what may almost be called the monstrous development of the *crus primum* of the *lobulus ansiformis*" (*i.e.* lobuli semilunares superior and inferior and gracilis), with the corresponding reduction of other parts to which attention will be directed later. The lateral portions of lobule D_1 also share in this developmental activity, but to a smaller extent. Lobule D_2 does not become nearly so conspicuous a focus of growth. Because of the backward projection of the hemispheres in the region of lobe C, the vermis appears to sink into the depths of a narrow valley, bounded by the steep heights of the hemispheres. For the same reason, the lateral portions of lobe D are constrained to form part of the sides of the valley. That part of lobule D_2 which contributes to the formation of the hemisphere is, indeed, so confined by the masses lying lateral to it that its growth has to take place in a sagittal direction. In the adult brain it is found to consist of two rows of folia—or rather one row doubled upon itself—radiating out from what Ziehen (15) describes as the *fossa axialis.*

Throughout the present paper, and also in the one which has preceded it, the various lobes and fissures have been known by means of letters and numbers. This plan has been followed with the intention of avoiding the use of terms—such as those employed in Human Anatomy, for instance—which would in any degree hamper us in our endeavour to approach the subject without preconceived ideas of any kind. It need hardly be said that these letters and numbers here employed are merely a temporary convenience, but I do not propose to substitute any other form of nomenclature for them in this communication except in the case of the human brain, and in this case merely in order that the conclusions as stated in the preceding paragraphs may be the more readily appreciated by the human anatomist.

Fissure *c*, then, is the *sulcus postcentralis* of man, and therefore forms the posterior (upper) limit of the *lobus centralis* (lobule A_1). Fissure I. is not recognised as being of any great importance, and is therefore unnamed in books on Human Anatomy. That it should not be relegated to a subordinate place has, it is hoped, been made clear by embryological evidence, and also by the testimony of comparative anatomy. Lobule A_2 is considered in the text-books as a part of the *lobus culminis*, though there are not lacking those who consider this lobe to be composed of two parts. Lobe B constitutes the upper part of the lobus culminis. There seems to be want of agreement between Professor Elliot Smith and the present writer in connection with the subdivision of this part of the cerebellum. What has been referred to as fissure *c* in the foregoing descriptions is evidently equivalent to the *fissura præculminata* of Elliot Smith, who, nevertheless, states that the 'culmen' of the human brain is divided into two lobules by a fissure (*a* in his figures) which may be as deep as, or even deeper than, the *fissura præculminata* (11).

Fissure II. is the *sulcus preclivalis*, fissure *b* is the *sulcus postclivalis*, fissure *a* the *sulcus horizontalis magnus*, and fissure III. the *sulcus postpyramidalis*. Lobe C therefore comprises a very large proportion of the human cerebellum. Its lobule C_1 is the *lobus clivi*, consisting of a *clivus monticuli* and its *lobi lunati posteriores.*

In the Hapalidæ the lobes are simple and of few folia; and the general direction of the fissures is transverse, *i.e.* there is none of that marked local obliquity so commonly met with in most cerebella. Lobe C can hardly be said to be subdivided at all. This circumstance, were it not relieved by an attempt at the obliquity just mentioned, would bring the lobe down to the level of the corresponding part in the rodents, insectivores, etc. Another feature of note is the small size of the paraflocculus (that is, if the statements set forth upon this point in a previous part of this paper are substantiated by further research).

In all the monkeys examined, as well as in those described by Bolk (13), there is no possibility of overlooking fissure I. In most monkeys lobule A_2 is, relatively speaking, small, whereas lobe B is well developed. In lobe C we find a gradual increase in size as we ascend from the Hapalidæ, this increase being mainly, but not entirely, in a sagittal direction. Associated with this expansion in the hemisphere is a relative reduction of the vermis posterior to fissure *b*, and an arrangement in the hemisphere of the folia belonging to lobules C_2 and C_3 in a radiating manner.

The characteristic feature of lobule D_1 is the constancy and size of those parts of it which belong to the hemispheres. So far as the marmosets and monkeys are concerned, there is nothing very striking in the form, size and disposition of lobule D_2. In all of them of which we have any account this lobule is similar to that of mammals belonging to other orders. There is therefore a remarkable difference between this lobule in the monkeys and the apes. From Stroud's observations on the Ape Cerebellum (16), it appears that in the chimpanzee, orang and gorilla, at any rate, there is a lateral continuation of lobule D_2 as in man, but in these animals it "is a relatively small tetragonal mass." It would be very interesting to find some monkey in which this condition, but on a smaller scale, is present, for then the gradations up to man would be complete in this region of the cerebellum.

The fairly uniform size of the flocculus and lobe E in general in different monkeys is noteworthy. In no order of Mammalia is there any very great variation in the dimensions of these parts; but in monkeys and apes (Stroud) the variation is even less than might reasonably be expected in a group of animals differing widely in other particulars. In monkeys, too, the paraflocculus is fairly uniform, and is peculiar in all of them in consisting of only one well-developed row of folia. In a previous paragraph it has been stated that there seems reason to suppose that this single limb corresponds to the ventral paraflocculus of other mammals, the dorsal limb being probably taken up in the development of the large part of lobule D_1 which lies within the hemisphere. It would be interesting to see what embryology has to say on this point.

In the apes, Stroud found that the paraflocculus was variable. In a gorilla he describes it as "very large and almost entirely exposed." In two orangs "it is small and concealed on the left side, only the tip showing on the right side." And in a chimpanzee it "is small and concealed on the left side; the tip is visible on the right side." The paraflocculus of the apes therefore forms a link between the well-developed lobule of the monkeys and the small, insignificant and inconstant structure in man, which is generally referred to as the "accessory flocculus."

ARBOR VITÆ CEREBELLI.

It has become a practice—not invariable, but certainly common—for those who write on the cerebellum to devote some attention to the figure presented when sagittal sections (particularly in the middle line of the vermis) are made. It is obvious that the form assumed by the white matter will vary greatly, depending upon the depth of the primary fissures, and the number, depth and disposition of the subsidiary fissures. For this reason the appearance of the arbor vitæ cerebelli differs in different animals, presenting the least intricacy in those brains in which the cerebellar fissures are few and the lobes and lobules are simple. For example, in the smaller bats the rays proceeding from the central mass of white substance are only five in number, and each ray is undivided. In the larger cerebella the rays are much more numerous and sometimes very copiously branched. Moreover, not only does the form of the arbor vitæ differ in different species of animal, but there is also variation to be noticed in different animals of the same species.

For these reasons it is difficult to arrive at any precise conclusion as to the absolutely typical form of arbor for any one class, or even species of animal, unless one is fortunate enough to be able to examine numerous specimens of that order or species. Bearing this in mind, it is with a certain amount of reserve that one speaks of the form and definite arrangement of the branches of the arbor vitæ cerebelli in any given animal. At the same time general statements may be made as to their disposition in the average mammalian cerebellum.

In all cerebella the central white mass is divided more or less into two parts by the fastigium cutting into it from below and fissure II. indenting it from above (Pl. XXVIII. fig. 76). The degree of division is far from being constant, nor is the result of the division always the same. In probably the majority of mammals the anterior area of white matter is the larger and more compact. The posterior area has a greater tendency to be drawn out in an antero-posterior direction. Springing from the anterior and posterior portions of the white mass are two strong main branches, which pass upwards into lobes B and C respectively. To these two branches Ziehen (15) has applied the names of *truncus verticalis* (to the anterior) and *truncus horizontalis* (to the posterior). It is unfortunate that these names do not indicate the direction of the branches in all, or even in most, mammals. Most frequently they are both more or less vertical.

In all but the simplest forms there are five prominent branches in addition to the two just mentioned, so that the average mammalian cerebellum has seven rays of white matter spreading out from the central mass. These seven rays pass into the following lobes and lobules. The lowest of the anterior branches passes into lobule A_1, and is very frequently not a single ray, but rather two or three. The next ray passes into lobule A_2, and arises either from the central mass directly or from the third branch. Not infrequently it is difficult to decide if these two branches come from a common point, or if the third branch gives origin to the second. The third branch, which is one of the two main and constant rays, is always thick; it forms the core of lobe B, and very frequently divides into two (sometimes more) parts. The fourth branch is usually the strongest of the seven. It curves upwards into lobe C, and in all cases, except where this lobe is incompletely or not at all divided, splits into three sub-rays—one for each lobule. The fifth branch arises in one of four ways. It may leave the central mass independently; it may arise in common with the fourth branch; it may spring from this branch; or it may have a common origin with the sixth branch. Whatever its mode of origin, its destination is lobule D_1. The sixth branch mostly arises separately and independently; but, as just said, it may share a common origin with the fifth. It runs into lobule D_2. The last branch is always the smallest; indeed in the simplest forms it is not more than a small projection from the white centre. It forms the axis of lobe E.

Seeing that there is so much diversity of form of the hemispheres in different animals, it would be exceedingly difficult to make any serviceable general remarks upon the arrangement of the white matter in these parts of the cerebellum.

General Summary.

It may be well to briefly summarise the result set forth in this paper and in the one which has preceded it, and to state the conclusions at which one has arrived. The writer is fully alive to the possibility that these conclusions may require modification in the light of further research. But at the same time they are such as have emerged from a conscientious attempt to add facts as well as theories to the literature of that part of the brain concerning which, even at the present time, opinions are far from uniform.

From the examination of embryological as well as adult material, it is again made clear—if this were in any way necessary after the work done by Stroud, Kuithan, Elliot Smith, Flatau and Jacobsohn, and Ziehen—that in all mammalian cerebella, from the simplest upwards, there is one transverse fissure of pre-eminent importance. Its future status is foreshadowed at an early period of development, and is attained to and maintained in all adult forms. Were it not that it is to a degree inconvenient to do so, the cerebellum might be described as consisting of two lobes, separated by this fissure. Largely for the sake of convenience, but also and mainly from the consideration of the comparative anatomy of the mammalian cerebellum, it is better to recognise five lobes. Each of these has its own characteristics, and, in a series of cerebella, is found to undergo modifications along certain lines. The lobe in which variation is least marked is the most posterior, or E. The greatest amount of diversity of form occurs in lobes C and D. Lobes A and B change somewhat, but to a less extent. Lobe A, in all but the simplest cerebella, is divided into two parts by a transverse interlobular fissure. Lobule A_1, the lower of the two, may remain simple, or, in the higher forms, be in its turn composed of more or less independent parts—generally two or three in number. Lobule A_2, the upper part of lobe A, is generally the smaller, and frequently remains unsegmented. The deep fissure in lobe A has been known as *c* throughout these communications; its importance has been recognised for long by human anatomists. Fissure I., which separates lobes A and B, has not been accorded that attention to which, it appears to me, it is entitled. Lobe B varies in different animals within certain limits, but these limits are fairly well defined. In all the small bats, for example, it is a single, undivided folium. It increases in size *pari passu* with the increase in size of the other lobes, until it is found to be subdivided by deep sulci. Examples of the commencing division of this lobe are supplied by the squirrel and opossum. In these animals, not to multiply examples, the lobe is found to be crossed transversely by a fissure which divides it into two practically equal portions. When there is dissimilarity of size the advantage nearly always rests with the more posterior division. In Phoca the division is very clear. In forms more complex than the opossum and squirrel the two portions of lobe B are themselves subdivided. This is also well exemplified in Phoca. Lobes A and B differ from the remaining lobes in the shallowness of their paramedian sulci, and in their small transverse expansion. These points have been emphasised by Bolk (14), and are excellently demonstrated in some of the Ungulates (Bos, for example). The embryology of lobes A and B is also different from that of C, D and E. In the earlier stages they lag behind in development; then comes a period of activity, in which they outdistance the posterior lobes, and so come to resemble the adult lobes while C, D and E are still comparatively rudimentary.

Lobe C occupies a developmental and anatomical position peculiarly its own. Even in the simpler forms its surpassing importance is obvious, for even here its great antero-posterior diameter in the hemispheres attracts attention. In higher forms it is clearly divided into three lobules by two fissures—*a* and *b*. These two fissures are not of equal consequence. From what has been seen in the embryos examined, *a* probably always (horse excepted?) begins its existence in the hemisphere and grows into the vermis. Fissure *b* seems to begin either in the hemisphere (rabbit and pig) or in the vermis (sheep), and nearly always becomes complete, *i.e.* grows across the whole cerebellum. It is highly probable that fissure *a* frequently remains as two lateral segments which do not join in the vermis, or if they do, their union is apparently later than the conjunction of the two parts of *b*. Even when fissure *a* is complete, it may not cut the vermis very deeply. These variations, and the potentiality for irregularity, demonstrate the secondary importance of fissures *a* and *b*.

Lobule C_1 apparently corresponds to Bolk's *lobulus simplex*, and does all that Bolk claims for it. It is unmistakably of a like constitution with lobes A and B, but it differs from them in its greater lateral extent. Lobules C_2 and C_3 are peculiar in possessing a power of growing in a sagittal direction, especially in the hemispheres. Upon this peculiarity depends the most striking differences in a series of mammalian cerebella. For this reason Elliot Smith gave the name of *area crescens* to the lateral part of what he then called the *lobus centralis* (now named by him *lobus medius*). Sagittal expansion is also possible in the vermis, but it is generally smaller in amount here than in the hemisphere. Phoca may be used as an example of the possible exuberant expansion of the hemisphere, and Bos as an instance of a similar growth, but to a less extent, in the vermis.

The two lobules which compose lobe D have different characters. Lobule D_2 is much the simpler. It is usually limited to the vermis except in the highest forms (apes and man), and does not show any sagittal expansion such as will produce distortion of the vermis. Lobule D_1 may be confined to the vermis, but is frequently continued into the hemisphere (as shown in man, apes and monkeys in the greatest degree). When lobule D_1 has a segment in the hemisphere, this is generally connected with the dorsal paraflocculus. This connection is clearly indicated in the ungulates. In monkeys it seems within the bounds of possibility that the dorsal paraflocculus is replaced by the large portion of lobule D_1 which lies in the hemisphere.

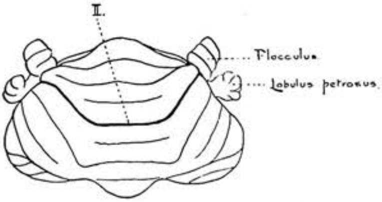
Lobe E is subject to some modifications in size, but the variation is not notably great. Its continuation into the hemisphere is not of common occurrence, but in Cebus and *Viverra civetta* it was found to be so continued; and in Didelphis and Herpestes the continuation of its grey cortex reaches as far out as the flocculus. Like the mesial part of lobe E, the flocculus does not vary to any great extent. It appears to reach its lowest point in some of the carnivora.

The difference in the size of the paraflocculus in different mammals is very striking. In its most highly developed condition it is composed of two rows of folia, to which may, or may not, be added a lobulus petrosus. This lobulus, when present, is generally attached to the posterior end of the ventral paraflocculus, but there are exceptions to this rule. The peculiarity of the paraflocculus in the monkeys has received some detailed attention. In the apes it shows various stages of diminution, and in man it has entirely disappeared in many, if not in most cases.

Although throughout these papers the paraflocculus and flocculus have been described by themselves in the accounts of the various cerebella, this has been done merely for the sake of convenience. It is perhaps well to repeat the assertion that the paraflocculus is an outlying part of lobe D, and the flocculus bears the same relation to lobe E (fig. 75). Both embryology and comparative anatomy demonstrate this. The separation of the paraflocculus and the flocculus, either in part or entirely, from the more mesial portions of the lobes of which they are parts, depends solely on secondary development. They are apparently crowded to one side, and their connections with the vermis weakened or broken down by the growth of the superposed parts of the hemisphere.

EXPLANATION OF THE FIGURES.

Fig. 47. Phoca vitulina. Mesial sagittal section. × 1.
Fig. 48. Hapale jacchus. Superior view. × 2.
Fig. 49. ,, Posterior view. × 2.
Fig. 50. ,, Left lateral view. × 2.
Fig. 51. ,, Mesial sagittal section. × 3½.
Fig. 52. Nyctipithecus trivirgatus. Superior view. × 2.
Fig. 53. ,, ,, Posterior view. × 2.
Fig. 54. ,, ,, Mesial sagittal section.
Fig. 55. Cebus capucinus. Anterior view. × 1.
Fig. 56. ,, Superior view. × 1.
Fig. 57. ,, Posterior view. × 1.
Fig. 58. ,, Inferior view. Left half. × 1.
Fig. 59. ,, Mesial sagittal section.
Fig. 60. Macacus rhesus. Anterior view. × 1.
Fig. 61. ,, Superior view. × 1.
Fig. 62. ,, Posterior view. × 1.
Fig. 63. ,, Mesial sagittal section.
Fig. 64. Cercocebus fuliginosus. Mesial sagittal section.
Fig. 65. Human embryo. No. I. Anterior view. × 2.
Fig. 66. ,, No. I. Superior view. × 2.
Fig. 67. ,, No. I. Posterior view. × 2.
Fig. 68. ,, No. I. Right lateral view. × 2.
Fig. 69. ,, No. I. Mesial sagittal section.
Fig. 70. ,, No. II. Posterior view. × 2.
Fig. 71. ,, No. III. Superior view. × 2.
Fig. 72. ,, No. III. Posterior view. × 2.
Fig. 73. ,, No. III. Left lateral view. × 2.
Fig. 74. ,, No. IV. Mesial sagittal section. × 2.
Fig. 75. Schema of the lobes and lobules of the average mammalian cerebellum arranged in one plane.
Fig. 76. Schema of the mesial sagittal section of the average mammalian cerebellum.



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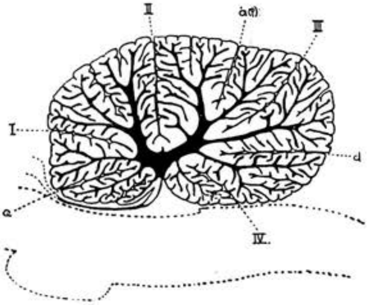

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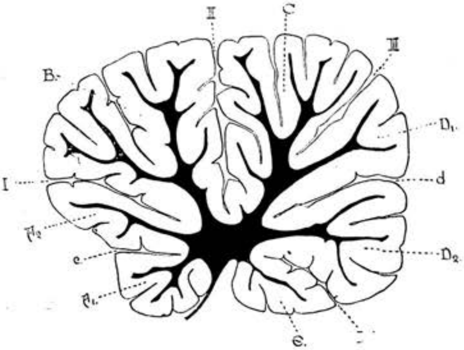

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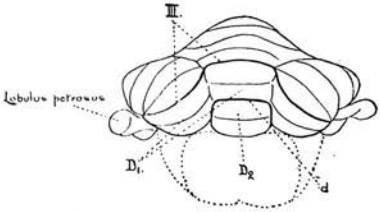

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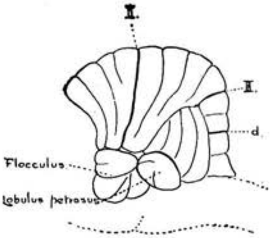

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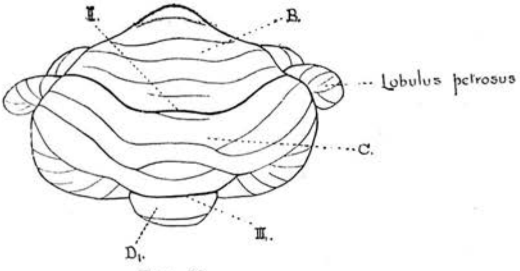

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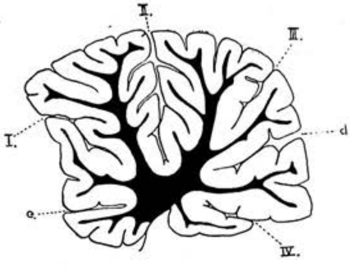

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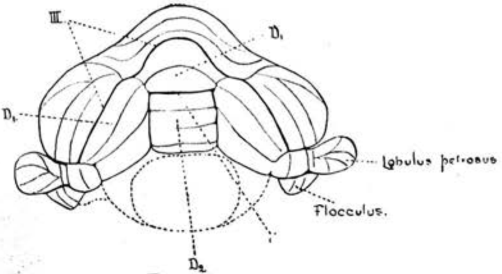
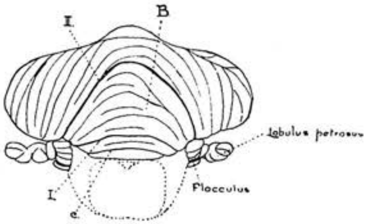


FIG. 53.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.



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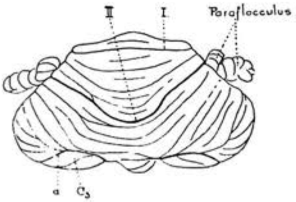

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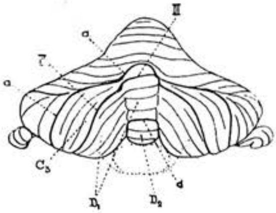

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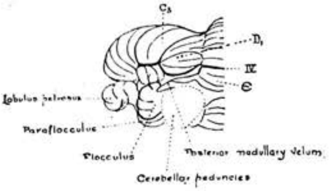

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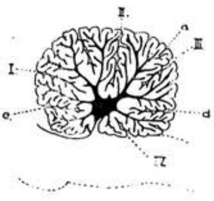

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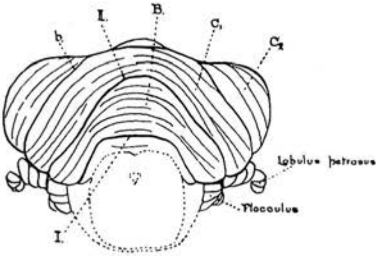

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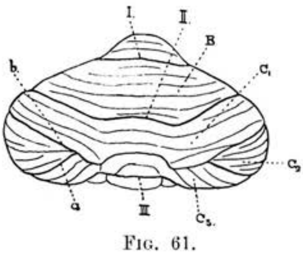

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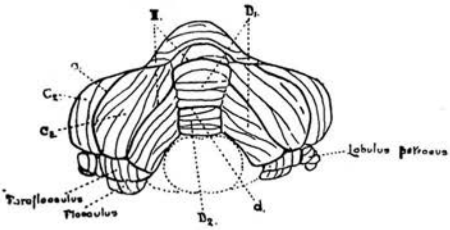
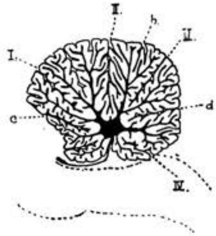


FIG. 62.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.



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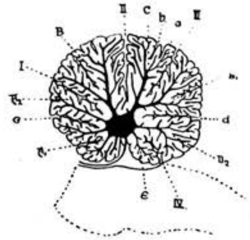

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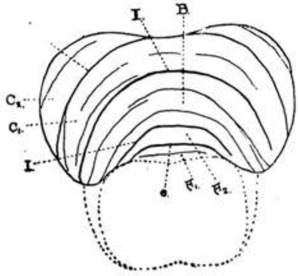

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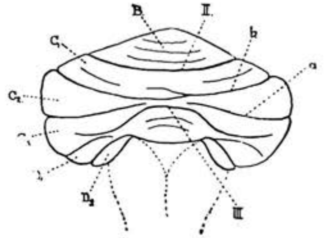

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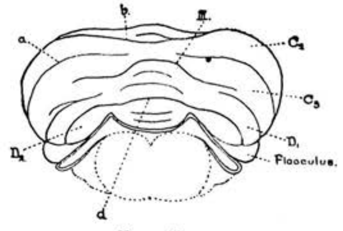

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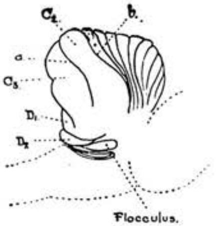

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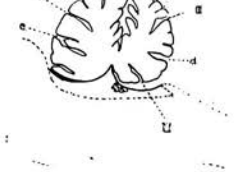

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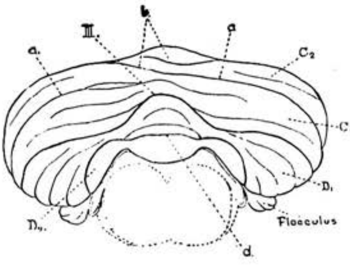
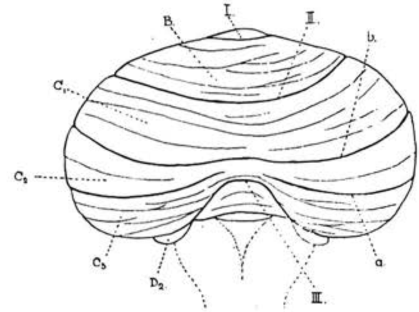


FIG. 70.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.



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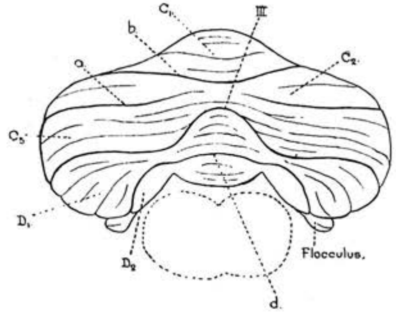

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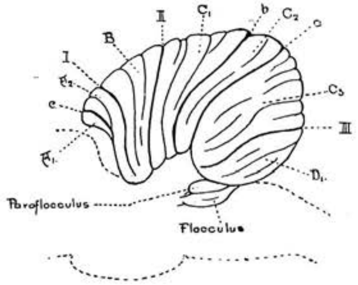

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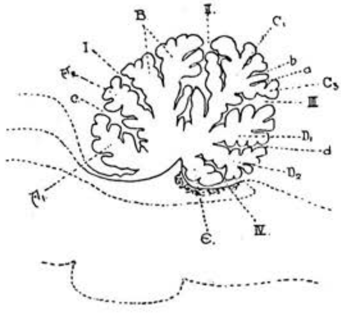

FIG. 74.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum :
its Lobes and Fissures.

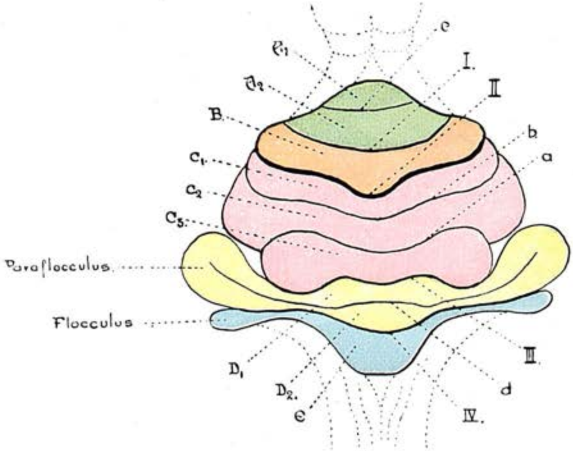

FIG. 75.

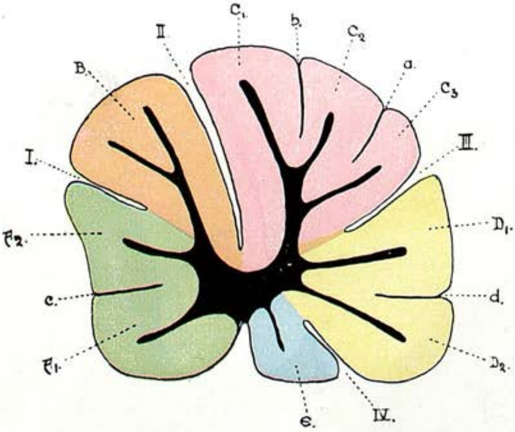

FIG. 76.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.

Original Article

NEUROMERES OF THE RHOMBENCEPHALON OF THE PIG.

By O. CHARNOCK BRADLEY, M.B., F.R.S.E.,
Royal Veterinary College, Edinburgh; Goodsir Fellow, University of Edinburgh.

SINCE 1828, the year in which v. Baer (1) was the first to observe their occurrence, a considerable amount of attention has been directed to those segments of the embryonic neural tube for which Orr (11) suggested the name of "neuromeres." The earlier authors detected neuromeres in the region of the medulla oblongata only; but it has been shown that they are not confined to this particular section of the central nervous system, but that the whole neural tube is divided into segments by constrictions which are indicated on the outer surface by grooves running transversely to the long axis of the tube. It was in 1889 that McClure (16) averred that segments could be distinguished in the embryonic spinal cord, and employed the name of "myelomeres" for these in order to differentiate them from the segments of the brain, which he named "encephalomeres." He was careful to point out that "myelomeres" and "encephalomeres" have common histological characters.

The earlier observers, moreover, attributed no particular significance to this segmentation; indeed, Bischoff (2), in a figure illustrating the median section of a twenty-five days dog embryo, showed seven folds in the wall of the medulla oblongata without making any reference to them in the text.

The following table shows in chronological order the animals in which neuromeres have been observed in the hind-brain, and the number of them which has been counted. Since the present communication is only intended to place on record the consideration of a small number of embryos of one particular mammal, it does not seem justifiable to preface it by a lengthy review of the somewhat numerous papers, both long and short, which have been devoted to the examination of neuromeric segments during the past half-century. Nor would such a proceeding be entirely necessary under any circumstances, for the literature has been very fully reviewed by Hill (28) in 1900, and still more recently by Kupffer (30).

	Year.	Investigator.	Animal.	No. of Neuromeres in Hind-Brain.
2[1]	1842	Bischoff	Dog	7
3	1855	Remak	Chick	5-6
4	1869	Dursy	Calf	6
5	1875	Dohrn	Teleosts	8-9
6	1877	Mihalkovics	Rabbit	5-6
			Chick	
7	1884	Béraneck	Lizard	5
8	1885	Rabl	Chick	7-8
9	1885	Kupffer	Teleosts	5
			Sheep	
			Mouse	
			Man	
10	1887	Béraneck	Chick	6
11	1887	Orr	Anolis	6
12	1887	Scott	Petromyzon	5
13	1889	Prenant	Pig	6
14	1889	Platt	Chick	6
			Salmon	5
15	1889	Hoffmann	Lizard	7
			Tropidonotus	
16	1889	McClure	Chick	6
			Anolis	
			Amblystoma	5
17	1890	Reighard	Stizostedion	6

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[1] The numbers in the first column refer to the list of papers given at the end of the present communication.

	Year.	Investigator.	Animal.	No. of Neuromeres in Hind-Brain.
18	1891	Zimmermann	Rabbit Chick Acanthias Mustelus	8
19	1891	Clarke	Alligator	5
20	1891	Waters	Amblystoma Gadus	5 6
21	1892	Froriep	Mole	7
22	1892	Herrick	Snake	6
23	1893	Kupffer	Acipenser	5
24	1895	Locy	Squalus	6 (9)
25	1895	Broman	Man	7
26	1898	Neal	Squalus	5
27	1899	Neumayer	Sheep	5
28	1900	Hill	Chick Teleosts	6
29	1903	Lewis	Pig	5

From an examination of the above table it is evident that the occurrence of neuromeres in mammalian embryos has not been extensively observed. I have only been able to find two references to neuromeres in the pig, and of these only one is at all a detailed account. Prenant (13) found six folds in the hind-brain of a 14 mm. pig embyro, and noticed that certain cranial nerves were connected with different folds. More recently, Lewis (29), in his description of a model of a 12 mm. pig embryo, says that "the hind-brain possesses three well-marked neuromeres followed posteriorly by a fourth shallow one. In a 9 mm. pig there are five which are distinct."

In view of the fact that little has been written on the neuromeres of the pig, it appears permissible to briefly relate some observations on the hind-brain of three embryos of different ages. It is unfortunate that the youngest of the three is already fairly advanced in development, it having been taken from the uterus nineteen days after coition. In this embryo the pontine flexure has barely begun to form. Looked at from the interior, the hind-brain shows seven grooves of unequal size, but symmetrically disposed. These grooves correspond to bulgings which are easily distinguished on the exterior of the neural tube.[1]

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[1] These descriptions are based upon reconstruction models, made according to Born's method, as well as upon microscopic sections, both sagittal and coronal.

The first neuromere is large, and coincides in position with the, as yet, rudimentary Anlage of the cerebellum (Fig. 1). Its internal groove is not very deep, nor is it, in direction, perfectly transverse to the long axis of the hind-brain. Supposing the rhombencephalon to lie horizontally, the groove runs downwards and forwards. A very considerable external elevation corresponds to this internal groove. The groove and its correlated elevation lie at some distance from the fissura rhombomesencephalica, which circumstance might lead one to question if the neuromere be really the first of the hind-brain. A cursory inspection might give rise to the supposition that a neuromere, previously evident anterior to the one now described, had lost its identity as a consequence of the incipient growth of the cerebellum. It has been shown, however, by Orr (11), Hill (28), and Kupffer (30), that the cerebellum is formed from one neuromere only (*Kleinhirnneuromer* of Kupffer). It may, therefore, be concluded that the position and direction of the groove are due to growth of the cerebellum in its initial stages. Support is lent to this conclusion by the association of the various cranial nerves with the different neuromeres, as will be described later.

The internal groove of the second neuromere is, in this embryo, deeper than any of its fellows. The external constriction between the second and third neuromeral segments is absent, a condition possibly accounted for by the fact that the root of the N. trigeminus is connected mainly with the second neuromere, but also slightly with the third. The two neuromeres, consequently, are associated in the formation of one prominent external elevation, which corresponds in position to the widest part of the rhombencephalon. The fourth neuromere is marked by an internal groove of some depth, and a very prominent external ridge. The internal grooves and the corresponding external prominences of the fifth and sixth neuromeres are not so pronounced as are those immediately in front of them. They are, however, sufficiently distinct to prevent any dubiety as to the extent of these neuromeres.

The seventh segment of the hind-brain differs in some respects from its fellows. In the first place, it is larger than any of the others, with the exception of the first. It has a deep and spacious internal depression, which can hardly be called a groove, and its external eminence is equally extensive. Further-

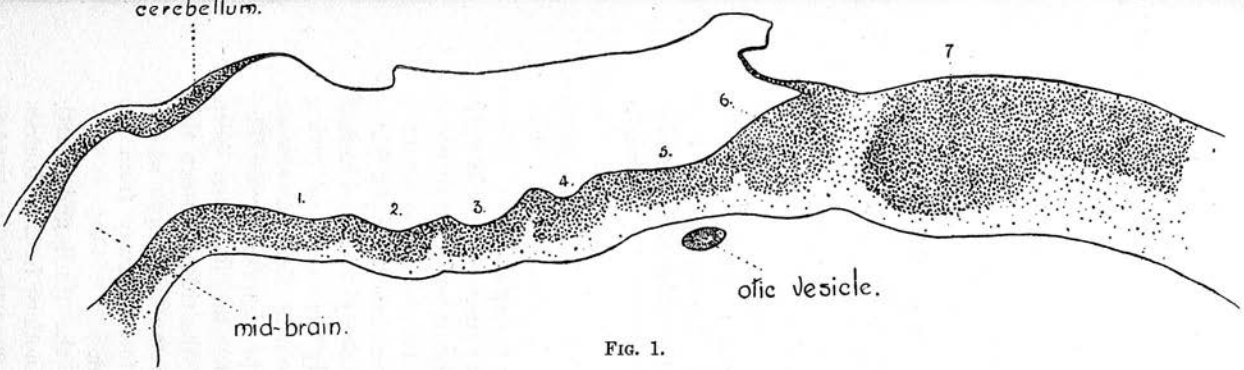


FIG. 1.

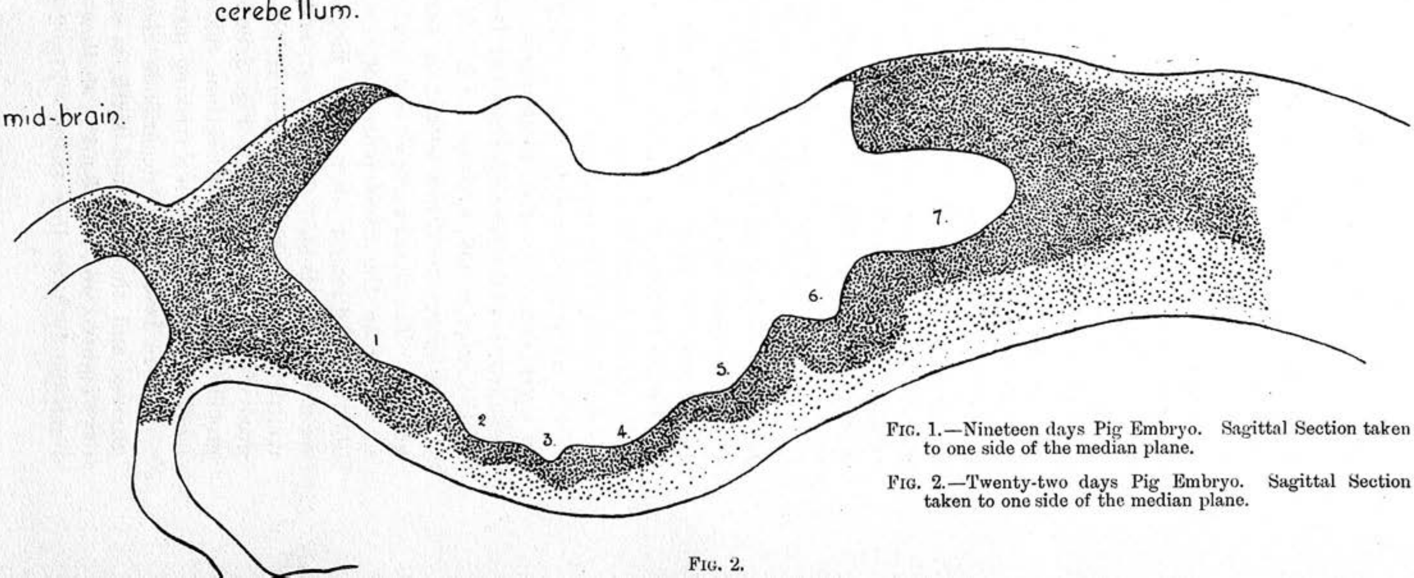


FIG. 2.

FIG. 1.—Nineteen days Pig Embryo. Sagittal Section taken to one side of the median plane.

FIG. 2.—Twenty-two days Pig Embryo. Sagittal Section taken to one side of the median plane.

more, the groove between the alar and basal laminæ is continued forwards into the depression of the neuromere; but, while this is so, the posterior limit of the seventh segment can be determined by noting the greater depth and the more ample vertical dimensions of the neuromeral depression. It may be contended that this is not a hind-brain neuromere at all. Hill (28) has very firmly asserted that there are never more than six neuromeres in the rhombencephalon, and has averred that those who have counted more than six have included "segments caudad to the true sixth." It is, none the less, difficult to say definitely where the limit of the embryonic hind-brain is to be set. If the root-origin of the vagus is included in the hind-brain (Locy), the seventh neuromere, as here described, belongs to the rhombencephalon. If, however, the auditory invagination is taken as occurring on a level with the junction of the head and trunk (Neal and others), then the seventh neuromere does not belong to the brain. However the division of the head and trunk may be finally decided, in the embryo at present under consideration there is a clear cervical flexure which occurs behind the seventh neuromere. The relatively large size of the seventh segment might give origin to a further doubt. It is possible that more than one segment is here represented. This, clearly, could only be decided by the examination of younger material.

In a twenty-two days embryo (Fig. 2) there is no difficulty in again detecting seven neuromeres. The internal depressions are clear, but the constrictions and the intervening prominences on the exterior have become much less pronounced. It is, therefore, necessary to direct attention particularly to the internal grooves. The first groove is now relatively less deep, and, owing no doubt to the development of the pontine flexure, is more oblique in direction than it was in the previous embryo. The second groove is still the deepest, and this has doubtless been contributed to by an increase in height of the ridge between this groove and the first. In Fig. 2 no outstanding depth of the groove is indicated, but sections taken farther away from the median plane show it in a striking manner.

There is nothing remarkable about the third and fourth grooves, and the fifth and sixth, as was noticed in the nineteen days embryo, are, in the main, shallow as compared with the two immediately preceding them. Fig. 2 includes the deepest part of the fifth and sixth grooves. The seventh depression is distinctly shallower, relatively, than in the nineteen days embryo, and the interzonal sulcus (sulcus between the alar and basal laminæ) is continuous with it. But, again (as in the nineteen days specimen), its greater vertical diameter serves to establish its identity. It should be added that the seventh neuromere is still decidedly larger than those immediately in front of it.

In a twenty-five days embryo all external evidence of neuromeres has disappeared, and only five grooves can be distinguished in the interior. There can be no doubt that those which have disappeared are the sixth and seventh. This can be determined by an examination of the connections of the cranial nerves. The interzonal sulcus can now be followed as far forwards as the fifth neuromeral groove; but, it is to be noted, it is much wider on a level with the sixth and seventh neuromeres than it is farther back.

The first groove is now very shallow, but occupies the same relative position as before. If this is indeed the remains of the internal groove of the first neuromere of the hind-brain, and there appears to be little reason to doubt it, then it is clear that this particular neuromere develops differently from those behind it. If we assume that the neuromeral groove lies originally equidistant from the two ends of the segment to which it belongs, then, in the second to seventh neuromeres inclusive, development has been equally vigorous in front of and behind the groove. In the cerebellar neuromere (first *Rautenhirnneuromer* or *Kleinhirnneuromer* of Kupffer), on the other hand, growth has been particularly marked in that part which lies anterior to the groove. Consequently the groove has been gradually removed farther and farther from the fissura rhombomesencephalica. The groove of the second neuromere is now far and away the deepest, and the ridge between it and the first is more prominent than in the younger embryos.

It is not proposed at this time to follow the history of the neuromeral grooves further, but it may be stated that the examination of older embryos leaves little ground for doubting that some of them persist for a much longer time, in the pig at any rate, than is generally supposed.

The idea that the neuromeres are indicative of the primitive segmentation of the head has gained many adherents during the past twenty years. The majority of those who have devoted special attention to these structures appear to be persuaded that they cannot be neglected in formulating a hypothesis as to the constitution of the vertebrate head. On the other hand, there are the utterances of those who have not been convinced of the segmental significance of neuromeres. Mihalkovics (6) looked upon them as being produced mechanically by the pressure of the mesoblast. Hertwig (31) made passing mention of them in the second edition of his text-book on embryology, and considered that their transitory nature was opposed to a conception of their segmental value. Gegenbaur (32) also did not consider neuromeres to be important morphological structures. Froriep appears, from his earlier papers, to have been inclined to attribute metameric value to them, but later (21) he has shown himself to be sceptical. In 1898 Neal (26) published his critical papers on the segmentation of the nervous system of *Squalus acanthias*, in which he stated that the neuromeres are not " segments in the true sense of the word," because, he says, " I find them irregular in size, inconstant in number, bilaterally asymmetrical, and without definite relation to structures known to be segmental."

In seeking to determine how much value should be assigned to neuromeres as affording evidence of the segmentation of the head, their association with cranial nerves has, naturally, received much attention. It would occupy an undue amount of space to detail the various differences in nerve-connection which are to be found in the reports of the different investigators. It will suffice, at this time, to make chief mention of the points upon which the majority are agreed, and incidentally touch upon the disagreements.

The N. acustico-facialis affords the most convenient starting-point, since all observers, with the exception of Locy and Broman, have described it as being associated with the fourth neuromere of the hind-brain. Broman (25) places it one neuromere farther back, *i.e.* in connection with the fifth ; and Locy (24) states that the " roots of the facialis and the auditory arise separately in *Squalus acanthias*," the former from the fourth and the latter from the fifth hind-brain neuromere. In the embryos which form the subject of the present communication, the acustico-facialis root-complex is undoubtedly connected with the fourth neuromere.

The almost complete uniformity in the description of the origin of this particular nerve is of very considerable importance, since it thus forms a definite point from which the neuromeres can be counted.

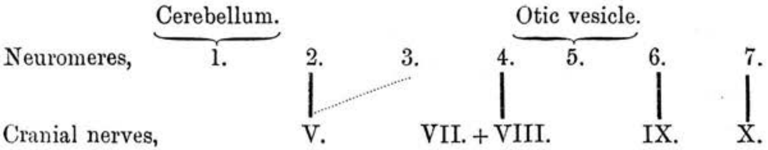
With the exception of Miss Platt and Broman, investigators are agreed that the primary connection of the N. trigeminus is with the second neuromere of the hind-brain. Miss Platt (14) holds that it arises from the constriction between the second and third neuromeres, and Broman (25) associates it with the third neuromere alone. Locy (24) and Hill (28) state that the anterior root of the trigeminus is related to the first neuromere, but the main root, they say, stands connected with the second. As has been previously stated, in the nineteen days pig embryo the N. trigeminus is mainly connected with the second neuromere, but in addition some of its fibres pass to the third. The relationship with the third neuromere is still more evident in the older embryos. It appears likely, therefore, that the third neuromeral connection is a secondary one, a similar arrangement having been noticed by Béraneck (10), Zimmermann (18), and Froriep (21).

It is generally conceded that the otic vesicle lies opposite the fifth neuromere, and in the nineteen days pig embryo this is certainly the case, though it also overlaps a small portion of the sixth neuromere. In the twenty-two days embryo the vesicle still lies opposite the whole of the fifth neuromere, but it now extends farther backwards than in the younger specimen, and so comes to cover a considerable part of the sixth neuromere. A backward movement of the otic vesicle during its development has been noticed by Locy (24) in *Squalus*, an observation supported by Kupffer (30).

The glosso-pharyngeus and vagus nerves were found in the pig embryos to be connected with the sixth and seventh neuromeres respectively. It should be stated that these nerves, as well as the acustico-facialis, have only very slender fibrillar connection with the neural tube in the nineteen days' embryo. In the next older specimen the connections are much stronger.

The precise origin of the N. abducens has offered difficulties to all investigators, it having been variously attributed to the third, fourth, and fifth neuromeres. The pig embryos do not afford any evidence of value.

The relations of the hind-brain neuromeres in the pig may be schematically indicated as follows :—



Prenant (13) is the only writer who has treated of the neuromeral nerve-connection in the pig; and, if we add the cerebellar neuromere to the six which he has described as occurring in a 14 mm. embryo, he is in almost entire agreement with what I have found and noted above. His only point of difference is in assigning an origin for one of the roots of the vagus to the sixth neuromere.

References.

1. v. Baer, K. E. *Ueber Entwicklungsgeschichte der Thiere*, Th. 1, Königsberg, 1828.
2. Bischoff, T. L. W. *Entwicklungsgeschichte der Säugethiere und des Menschen*, Leipzig, 1842.
3. Remak, R. *Untersuchungen über die Entwickelung der Wirbelthiere*, Berlin, 1850-55.
4. Dursy, E. *Zur Entwicklungsgeschichte des Kopfes des Menschen und der höheren Wirbelthiere*, Tübingen, 1869.
5. Dohrn, A. *Der Ursprung der Wirbelthiere und das Princip des Functionwechsels*, Leipzig, 1875.
6. v. Mihalkovics, V. *Entwicklungsgeschichte des Gehirns*, Leipzig, 1877.
7. Béraneck, E. "Recherches sur le développment des nerfs crâniens chez les Lézards," *Recueil Zool. Suisse*, T. 1, 1884.
8. Rabl, C. "Bemerkung über die Segmentirung des Hirnes," *Zool. Anz.*, Bd. 8, 1885.
9. Kupffer, C. "Primäre Metamerie des Neuralrohrs der Vertebraten," *Sitzb. d. Akad. München. Phys.-Math. Cl.*, 1885.
10. Béraneck, E. "Étude sur les replis médullaires du Poulet," *Recueil Zool. Suisse*, T. 4, 1887.
11. Orr, H. B. "Contribution to the Embryology of the Lizard," *Journ. Morph.*, vol. 1, 1887.
12. Scott, W. B. "Notes on the Development of Petromyzon," *Journ. Morph.*, vol. 1, 1887.
13. Prenant, A. "Note sur l'existence des replis médullaires chez l'embryon du porc," *Bull. de la Soc. d. Sc. de Nancy*, Sér. 2, T. 9, 1889.
14. Platt, J. B. "Studies on the Primitive Axial Segmentation of the Chick," *Bull. Mus. Comp. Zool. Harvard,* vol. 17, 1889.
15. Hoffman, C. K. "Ueber die Metamerie des Nachirns und Hinterhirns, und ihre Beziehung zu den segmentalen Kopfnerven bei Reptilienembryonen," *Zool. Anz.*, Bd. 12, 1889.
16. M'Clure, C. T. W. "The Primitive Segmentation of the Vertebrate Brain," *Zool. Anz.*, Bd. 12, 1889.
17. Reighard, J. "Development of the Wall-Eyed Pike, Stizostedion vitreum," *Bull. Michigan Fish Comm.*, 1890.

18. Zimmermann, W. "Ueber die Metamerie des Wirbelthier-Kopfes," *Verhandl. Anat. Gesellsch. (München)*, 5, 1891.

19. Clarke, S. F. "Habits and Embryology of the American Alligator," *Journ. Morph.*, vol. 5, 1891.

20. Waters, B. H. "Primitive Segmentation of the Vertebrate Brain," *Quart. Journ. Micros. Sci.*, vol. 33, 1892.

21. Froriep, A. "Zur Frage des sogenannten Neuromerie," *Verhandl. Anat. Gesellsch. (Wien)*, 6, 1892.

22. Herrick, C. L. "Embryological Notes on the Brain of the Snake," *Journ. Comp. Neurol.*, vol. 2, 1892.

23. Kupffer, C. "Die Entwicklung des Kopfes von Acipenser sturio, an Medianschnitten untersucht," *Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten*, Heft 1, München u. Leipzig, 1893.

24. Locy, W. A. "Metameric Segmentation in the Medullary Folds and Embryonic Rim," *Anat. Anz.*, Bd. 9, 1894.

Ibid. "Contribution to the Structure and Development of the Vertebrate Head," *Journ. Morph.*, vol. 11, 1895.

25. Broman, I. "Beschreibung eines menschlichen Embryos von beinahe 3 mm. Länge, mit speziellen Bemerkung über die bei demselben befindlichen Hirnfalten," *Morph. Arbeiten vom Schwalbe*, Bd. 5, 1895.

26. Neal, H. V. "The Segmentation of the Nervous System in Squalus acanthias," *Bull. Mus. Comp. Zool. Harvard*, vol. 31, 1898.

27. Neumayer, L. "Studie zur Entwicklungsgeschichte des Gehirnes der Säugetiere," *Festschr. z. 70. Geburtstag v. C. v. Kupffer*, 1889.

28. Hill, C. "Developmental History of the Primary Segments of the Vertebrate Head," *Zool. Jahrb. Abth. f. Anat. u. Ontogenie*, Bd. 13, 1900.

29. Lewis, F. T. "The Gross Anatomy of a 12 mm. Pig," *Amer. Journ. Anat.*, vol. 2, 1903.

30. v. Kupffer, C. "Die Morphogenie des Centralnervensystems," *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbelthiere.* Herausgegeben von Dr Oscar Hertwig. Lief 16, Jena, 1903.

31. Hertwig, O. *Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbelthiere*, 2te Aufl., Jena, 1888.

32. Gegenbaur, C. "Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskelettes," *Morph. Jahrb.*, Bd. 13, 1887.