THE ROOF AND LATERAL RECESSES OF THE FOURTH VENTRICLE, CONSIDERED MORPHO- LOGICALLY AND EMBRYOLOGICALLY.

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My investigations on this subject were prompted by the contradictory opinions and the lack of absolute knowledge concerning the nature of the communications between the cavity of the fourth ventricle and the subarachnoid space.

At first my efforts were confined to the study of the morphology of the metapore, or foramen of Magendie, but I soon found that it was necessary to include that of the entire roof of the ventricle, and then naturally followed an elucidation of the problems found in the lateral recesses.

The development of the roof of the ventricle is very closely connected, it is needless to say, with that of the oblongata and cerebellum.

The development of the oblongata in man has been worked out by His, but we need further knowledge of its development in the lower animals. Our knowledge concerning the cerebellum is as yet unsatisfactory.

The lateral recesses have been ably described by Mihalcovics and by Retzius, but the descriptions in our text-books are, as a rule, faulty, if not incorrect.

Their relations to the medulla and cerebellum and their segmental value have not been sufficiently determined.

Hitherto the investigations on the metapore and foramina of Luschka have been chiefly to determine their presence, while their nature has been largely a matter of supposition. The methods employed have been almost entirely those of in-

jection and of inspection by careful dissection or gross sectioning.

A brief résumé of the results of these investigations is as follows: Key and Retzius found the metapore present in 98 out of 100 cases examined. In one of the exceptions there was a continuous tela. They also found the lateral recesses open in all but three. In two brains it was closed on both sides and in one brain on one side. C. Hess examined the brains of 30 adults, 10 new-born children and 7 embryos of different stages, and found the metapore absent in one. In 54 lateral recesses he found all open except two. Others who do not give the number of brains investigated and who found the metapore present are, Wilder, Morton, Kohlmann, Jacobi and others, and its presence is conceded in most of the descriptive anatomies.

On the other hand, Kölliker states that the cavity is originally closed and always remains so, and Reichert that both the metapore and foramina of Luschka are artifacts. Its presence is questioned by Cruveilhier and See. The openings in the lateral recesses, first discovered by Luschka, have been most fully described by Key and Retzius, and later by Retzius, by Hess and by Mihalkovics. Their presence is doubted by Wilder.

In the lower animals most observers agree that the metapore is absent but that the lateral recesses are open. Wilder has found the metapore in the chimpanzee, baboon and several old world monkeys. Hess found openings in the roof of the ventricle of an embryo cat. Jacobi has proved the presence of openings of the lateral recesses in the live dog by injecting methyl blue into the subarachnoid cavity in the lumbar region and having it emerge from a cannula placed in the ventricle of the brain and vice versa.

In the last year articles on the metapore and the foramina of Luschka have appeared by A. Cannieu. His investigations were partially by gross methods and partially histological. By gross methods he found the metapore present in the dog, cat, rabbit, guinea-pig, horse, ox, ass, and in man. He allowed the brains of the lower animals to soften so that they would approximate the condition in which it is usual to obtain human

brains. By histological methods he found it absent in the dog and cat, and concluded that its apparent presence in all animals is due to a poor state of preservation of the brain. Also by histological methods he finds that the lateral recesses are closed in the lower animals.

In regard to the appearance of the metapore, we find that the usual description is that it is a perforation in the roof of ventricle at the region of the calamus, varying in size and with more or less ragged edges.

Henle, Schwalbe and Key and Retzius describe its margins as smooth or rounded, and the latter give its dimensions and boundaries. Hoffman and Rauber describe it as appearing like a short tube and not as a break in a membrane.

C. S. Minot has suggested that it might be the orifice of an evagination of the endyma. But as to whether he thinks the orifice normal or artificial is not stated.

The condition of these openings found in pathological states of the brain vesicles, as hydrocephalus, cysts, etc., is of interest as bearing upon their function and their necessity. The evidence thus obtained, it must be confessed, is fragmental and inconclusive largely on account of the lax methods and observations employed in autopsies.

Absence of the metapore has been reported by O'Carroll in two cases of hydrocephalus, by Neurath in another, and A. Henle attributes hydrocephalus largely to the closure of the ventricular openings. Sutton states that early closure gives rise to ventriculo-meningocele and later closure to localized cysts.

Hydrocephalus is also attributed to the presence of tumors, especially in the regions of the mid- or hind-brain.

Magendie has reported two cases of closure and concomitant hydrocephalus in old people; Martin St. Ange one in an 8-year old child; Virchow a case of closure of lateral recesses with localized cysts. The metapore has been reported open by Morton in seven cases of tubercular meningitis, even where the pia was much thickened. The efficacy of lumbar puncture in hydrocephalus is admitted by many (A. Broca, P. Maudslayi, Quincke, Jacobi), and Quincke has withdrawn 100 cc. of

fluid in one sitting by this method from a case of hydrocephalus due to a tumor, an amount which could hardly have been afforded by the spinal subarachnoid space with its unyielding walls.

The evidence in regard to the function of the communications is more or less negative in these cases, for a hydrocephalus might occur with the openings present and be due to a fault in the absorbents.

But the more numerous the cases of hydrocephalus with closure of the communications, with otherwise normal condition of the structures, the stronger the evidence that they are functional in allowing the passage of the cerebro-spinal fluid.

The present contribution is based upon researches conducted for the greater part microscopically upon both adult and embryonic brains, both of man and the lower mammals. All the objects were cut serially; great difficulties were encountered from the necessity of keeping the membranes intact.

In so far as practicable the entire head was cut; when this was impracticable, either a portion of the head containing the cerebellum and oblongata with the tentorium intact was decalcified and sectioned, or the entire brain was hardened in situ, generally by the intra-arterial injection of formalin, and the cerebellum and oblongata with their surrounding membranes then carefully isolated by cutting away the adjacent structures.

The reagents used for fixation and hardening were generally formalin or a mixture of formalin and bichromate of potash; other usual fixatives were also employed for the embryonic material.

Both celloidin and paraffin were used for embedding, chiefly the latter.

The most valuable stain for adult forms was found to be Van Gieson's, it giving a very clear differentiation between the membranes and epithelium. The usual hæmatoxylin and carmine stains were used for the embryonic material with combination stains.

In the illustration of this paper I am indebted to Mr. E. A. Spitzka who made all the drawings of sections.

NOMENCLATURE.

Inasmuch as there are some apparent inconsistencies in the nomenclature employed, it is well to call attention to them, so that they will not be misunderstood.

As generally accepted, the third cerebral vesicle is divided into two encephalic segments, the epencephal and metencephal, the corresponding cavities being the epicœle and metacœle.

These terms have been used in several of the accompanying drawings, and also the term fourth ventricle—Figs. 12, 13 and 14, for example.

The writer is unable to accept, for reasons that will appear later, the division of this part of the brain into two segments, and has used the terms metacœle and epicœle to emphasize the fact that they cannot be made to apply to a considerable portion of the fourth ventricle.

Objection may be made to the use of secondary rhomboidal lip in figures of advanced embryos and adults, when that structure no longer exists as such. The reason for its employment in these cases is to indicate the derivation of the structure thus designated, its adult name being also added when it seemed necessary.

In order to fully comprehend the conditions found in the adult fourth ventricle, it is necessary to follow the development from early embryonic stages, i. e., before the institution of the pons flexure.

The roof at this period is comparatively simple, but soon complications appear, due to change in the margins of the ventricle or rhomboidal fossæ, as it is generally termed.

Later the involution of vessels to form the choroid plexus appears, together with the pons flexure.

Thus it is convenient to classify the study of the roof as follows :

- I. The line of attachment of the roof.
- II. The choroidal fold.
- III. The roof as a whole.

LINE OF ATTACHMENT OF ROOF.

The attachment of the roof is largely influenced by the changes which take place in the margins of the rhomboidal fossa.

As has been shown by His, the neural tube is divided into four longitudinal laminæ, two dorsal and two ventral (Flügelplatte and Grundplatte).

These laminæ are well marked in the spinal cord and medulla at early stages. The two dorsal laminæ are connected by the roof plate and the ventral laminæ by the floor plate.

The oblongata is characterized by the separation of the dorsal laminæ and consequent widening of the roof plate. Fig. 1.

This separation begins at the calamus region and is most marked at this region of the auditory vesicle and the interval then decreases rapidly and the laminæ meet again caudad to the isthmus where they form the proton or fundament of the cerebellum (His).

In human embryos of the fifth week, ten millimeters long, according to His, a marked folding of the dorsal margins of the dorsal laminæ occurs.

This takes place throughout the whole length of the rhomboidal fossæ and the attachment of the roof is thus further shifted laterad. In a few days this fold fuses to the outer surface of the dorsal laminæ, at the same time its margin of attachment to the roof becomes drawn out into another fold or lip which tapers into the epithelium of the roof. His calls the first fold the Rautenlippe and the second the secondary Rautenlippe; as anglicized by Minot the rhomboidal lip and the secondary rhomboidal lip. Fig. 1.

Hitherto the primary rhomboidal lip has not been demonstrated in the lower mammalia.

Evidences of it appear in several rather advanced embryos I have studied, namely, in the pig, sheep, cat and rat, as a rounding of the dorsal margin of the dorsal lamina and an apparent shifting of the roof attachment which does not proceed

so far as to form a lip but gives rise to what simulates the Flügelwülste of His, i. e., the rounding formed by the growth of the rhomboidal lip.

Its existence in rabbit embryos has been denied by Dexter.

Lately¹ I have been able to demonstrate conclusively its existence in the rat embryo of three millimeters N. B. length. Fig. 1.

Its development does not proceed so far in the lower mammals as in man, especially in the region of the cerebellum. It certainly does not achieve the morphological importance attributed to the rhomboidal lip by His in man, namely, the covering in of the funiculus solitarius and the formation of the raphé and olive, unless we can consider this process to take place by an emigration of the neuroblasts from the lip rather than by an actual folding of the lip around the medulla, which latter seems to me an unsubstantiable proposition.

The existence of a primary rhomboidal lip in a non-fused condition in the lower animals, is probably extremely transitory, which explains its hitherto apparent absence. With the formation and fusion of the rhomboidal lip the secondary rhomboidal lip makes its appearance.

The secondary lip is essentially a transition between the nervous parietes and the roof and it partakes in its constitution of the characters of both. It commences as a lamina of nervous matter and thins away more or less quickly into the roof.

In man it reaches its greatest development, but it was present in all the embryos and adult animals studied.

The primary rhomboidal lip is narrow in the calamus region and then broadens somewhat in the region of greatest width, but reaches its greatest extent in the cerebellar region. Figs. 5, 6, and 8.

His states that in the calamus region it later becomes separated from the sides of the oblongata, but I am inclined to think that what appears as a separation is really the development of the secondary lip. In any case in this region the dis-

¹ Within a few weeks after the reading of this paper.

inction between the two is not marked and is rather one of degree than of absolute limitation.

In my descriptions I designate the portion giving direct origin to the roof plate as the secondary lip and reserve the primary lip for the bending of the substance of the dorsal lamina.

The directions of the two lips are different as a rule, but in the region of the lateral recess they coincide and it is impossible to make a definite separation of them in later stages. Figs. 4, 8, 30, 34, 36, and 38.

In the cerebellum the differentiation of the lips is very evident, the primary consisting of a large portion of the cerebellar plate (dorsal lamina) so that when the folding is completed the attachment of the secondary lip is carried to the vicinity of the isthmus. Figs. 6, 7 and 8.

The primary rhomboidal lips fuse in the calamus region and produce a bridge of nervous matter over the emergence of the myelocœle into the fourth ventricle. This appears as a well marked projection in sagittal sections at the meson. Figs. 24, 25 and 26.

The secondary lips in the same region have a caudal bend over the closed portion of the oblongata and may or may not fuse across the median line. When they do they form the obex, Figs. 16, 17, 24 and 26. The obex appears to be inconstant not only in man but in the lower animals as well. In three adult rabbit brains it appeared once. The obex is entirely intraventricular as is evinced by the attachment of the roof epithelium to its caudal margin. Figs. 24 and 26. In frontal sections advancing cephalad of the obex the secondary lip appears as a well marked rather vascular body which can be readily recognized by the naked eye as staining deeply, especially in advanced embryos. Figs. 28 and 31, human; Fig. 33, cat. It is usually closely fused with the oblongata, but the line of division as a rule can be identified by the entrance of vessels.

In the human foetus at term, Figs. 31 and 32, it bends sharply over into the roof of the ventricle, giving rise to two nervous laminæ which in this region form the major portion of the roof. When the roof is torn away, the margin where the

lip is fused to the oblongata remains and is known as the ligula; compare Fig. 31 with Fig. 2.

In comparing the transections, Figs. 31, 32, 33 and 34, with Fig. 17, the ventricular surface of the lip appears lying between the ala cinerea and the ligula, and is termed by Retzius the area postrema; when followed cephalad it is seen to merge into the area acustica. It is separated from the ala cinerea by a slight ridge called by Retzius the funiculus separans, which appears to be at the point of bending of the lip. According to Retzius the area postrema differs considerably in individuals, which is also characteristic of the secondary lip.

Just before the region of the lateral recess is reached, frontal sections show a commencing reduplication of the lip. Figs. 3 and 7. The lip here is folded laterad, mesad, then again laterad and finally mesad to end in the tela. In other sections these folds are seen to be fused together so that the ventricular surface comes to be narrowed to some extent. At the same time it is evident that the endymal layer is carried laterad and enclosed in the substantial nervous matter of the oblongata.

The foldings of the secondary lip are not so pronounced in the lower animals but are recognizable. In Fig. 9 a frontal section of the brain of a cat embryo ten millimetres N.B. measurement, the folding of the lip may be seen at the margin of the ventricle as a slight thickening. An analysis of this with a higher power shows a condition represented in Fig. 10.

The cells thus transferred to the ectal surface of the oblongata seem to give rise to a group of cells which appear on the sides of the oblongata in many embryos as far cephalad as the trigeminus and which may be connected with the ganglia of some of the nerves. An apparent connection was observed in relation to the auditory and it seemed from their position that they might have a possible connection with the so-called accessory nucleus of that nerve. I have been unable, however, to obtain sufficient evidence to make a positive assertion in regard to them.

At the region of the lateral recess the secondary lip un-

folds and forms an undulating lamella of considerable thickness which forms the entire ventral and mesal wall of the lateral recess. Figs. 4, 8, 29, 33, 35 and 36.

At the cephalic portion of the recess the primary and secondary lips are indistinguishable and are closely fused with the ectal surface of the restis and apparently enter into the formation of the lateral root and ganglion of the auditory. Compare Figs. 30 and 34, human, with Fig. 14, a frontal section of the brain of a pig embryo, twenty-one millimeters long, through the auditory nerve and with Figs. 15, 16 and 38, dog.

Cephalad the rhomboidal lip can be followed beyond the pons flexure, where it becomes very pronounced in the region of the cerebellum and probably gives rise in a large degree to the lateral protuberances of that organ. Figs. 7 and 8.

The connection of the rhomboidal lip with the auditory tract or acusticum seems fairly well proven. The tuberculum acusticum (dorsal nucleus) apparently corresponds to the flügelwülste, i. e., primary bend of the rhomboidal lip, and as just stated the ganglion of the lateral root is carried by the bending of the lip over the restis.

The comparison of this region in early embryos with the acusticum in some fishes, is exceedingly interesting and suggestive. The brain of *Amia* as figured by Kingsbury closely resembles the early embryonic condition of the mammalian brain in this region. The close connection in this form of the cerebellum with this portion of the oblongata is emphasized by him, which is of great interest when we consider that in mammalia, as already pointed out, the lateral portions of the cerebellum and the auditory region are probably formed from a continuous fold of the dorsal lamella, namely the rhomboidal lip.

The excursion of the primary rhomboidal lip in the region of the cerebellum, which is so marked in the human embryos, has not so far been observed in embryos of the lower Mammalia. Compare Figs. 6, 7 and 8 of the human embryos, with Figs. 9, 11, 12, 13 and 14 of the cat and pig.

It is possible that it may be in more advanced embryos of these forms. I have observed indications of it in slightly older

sheep embryos. An investigation of a complete series is needed in regard to this point.

According to His the attachment of the epithelial wall to the secondary rhomboidal lip in the cerebellar region after having been carried dorsad by the folding of the primary rhomboidal lip, becomes shifted again by the fusion of the contiguous surfaces of the two lips.

Stroud states that he is unable to obtain this impression from his observations, but believes that it becomes shifted by a process of unfolding without fusion.

I am inclined to the view of His in the matter, namely, in so far that a certain amount of fusion does take place.

In the sections of a human embryo from which Fig. 7 was drawn, the line of fusion was readily made out and is indicated in the figure. However, the fusion takes place apparently for only a short distance, and the further shifting is due to a greater proportional growth of the ectal portion of the substance of the cerebellar proton to that of the ventricular portion.

The growth of the cerebellum in the later stages is thus the opposite of that of the earlier stages, which are characterized by a greater proportional growth of the ventricular portion.

In the same manner the tent of the cerebellum is formed late in embryonic life by the growth of the ectal portions in a cephalo-caudad direction, thus producing a transverse fold. Fig. 26.

It is out of the province of this paper to enter fully into the discussion of the development of the cerebellum, and besides it would be premature with the information at hand.

But a point which has been brought out in my investigations I wish to record, namely, the existence in the human embryo, at least, of a well marked *ventriculus cerebelli*.

It is to be regretted that the brains from which the frontal sections were made, showing this cavity, had already been cut sagittally to the neighborhood of the meson.

This cavity is well shown in Fig. 7, of an embryo of about the seventh week, twenty-two millimeters N. B. length, and also appears in Fig. 2, of an embryo forty-two millimeters in length.

The cavity lies in the mesal portion of the cerebellum, the part to become the vermis, and while of considerable extent in the younger embryo, has in the older one become comparatively much reduced by the juxtaposition of the opposite walls. Later a fusion between the walls undoubtedly takes place, giving rise to the funnel-shaped depression as figured by Kohlmann. An attempt to homologize this cavity with that in some teleosts and birds would be interesting.

CHOROIDAL FOLD.

During the middle of the second month in the human embryo the pons flexure is instituted. It consists of a bending of the whole nervous tube, so that the extremities of the rhomboidal fossa are approximated dorsally and finally the caudal border of the cerebellum comes to lie in the vicinity of the calamus region of the medulla. Figs. 6, 11, 18, 19 and 20.

A fold in the roof is thus produced into which the mesenchyme insinuates itself and forms the plica choroidalis. Figs. 5, 6 and 11. At the same time the roof is carried laterally over the sides of the medulla forming the lateral recesses. Figs. 13 and 20. (See page 100.)

The villi are at first developed chiefly in the mesal portion of the fold and later appear in the sides of the lateral recess. At first in human embryos they are somewhat scattered over its lateral wall, but are more discreet in embryos of other animals. Compare Figs. 8 and 13. They soon coalesce to form a somewhat crescentic continuous body with its concavity cephalad, reaching from the extremity of one recess to that of the other. Later, two processes are developed, reaching caudad on either side of the median line along the roof of the body of the ventricle. Fig. 28. At the same time the choroid plexus, on account of the non-development of the mesal portion, appears to become divided between the caudal extensions. The picture now presented is that of a choroidal plexus starting in the extremity of each lateral recess, passing to the meson and then extending caudad to the extremity of the ventricle. Fig. 16.

The caudal portions form the paired choroidal plexuses of

the body of the fourth ventricle, the other those of the lateral recesses. In their course they follow that of the arteriæ post-cerebellaris.

In the lower animals the plexus in the lateral recess reaches the greatest development; in man the development in both regions is about the same.

In man, however, the plexus in the body of the ventricle has a greater proportional length and may reach caudad on the vermis as far as the pyramis.

I was at first led to believe that this development of the plexus took place beyond the limits of the ventricular epithelium but am now convinced that it does not.

In the early embryos the lateral extensions of the choroidal plexus are situated a little ventrad to the middle of the caudal and lateral wall of the lateral recess. Figs. 4, 8 and 13. Later because of the greater growth of the portion of the roof situated caudad to the plexus, and possibly partly on account of partial fusion of the roof cephalad of the plexus to the cerebellum, this portion of the roof (*velum medulare posterius*) becomes much abbreviated in comparison with the remainder. This relation holds true throughout life and the plexus is involuted along a line which closely borders the peduncle of the flocculus. Figs. 15, 16 and 29.

That the plexus forms a true part of the roof is evinced by the continuity of the epithelium over it.

Having considered the development of the margins of attachment of the roof and choroid plexus, it becomes necessary to follow the changes which take place in the roof as a whole.

THE ROOF AS A WHOLE.

In early embryos the opening between the body of the ventricle and the lateral recess is relatively wide, Fig. 18, but soon the constriction becomes more marked, so that the description of the ventricular cavity becomes naturally divided into that of the lateral recess and the body of the ventricle.

The constitution of the roof of the body of the ventricle differs considerably in man from the condition found in the lower

mammals. In man, with the exception of the choroid plexus, it consists largely of two distinct medullary laminæ which spring from the ligula on either side. Figs. 31 and 32. These nervous plates extend caudad beyond their direct attachment to the lip over the apex of the ventricle and they are here attached laterally by means of the pia, lined only by a thin epithelial layer. Fig. 31. In five brains of children at term examined especially with this in view essentially the same condition appeared in all. The epithelium continues on from the caudal margin of these plates over the pia of the vicinity for a short distance and then gradually fades away.

This formation of the roof seems to be peculiar to man. In no other animal did the roof appear otherwise than as thin membranous tela consisting of a layer of epithelium lying on the pia.

The reason for this appears in the greater development of the secondary rhomboidal lip in man.

This characteristic appearance of the roof is apparent in human embryos at the beginning of the third month. Compare Figs. 2 and 31.

As will be seen, the differences in the extent of nervous matter are even more pronounced in the lateral recesses.

Although the roof is better developed in man, it seems to be more persistent in the lower animals, and we have to turn to them to find an elucidation of the condition which appears in the caudal portion of the roof in man.

In advanced embryos of dogs, cats, pigs, sheep and also the chick, a marked caudal protrusion of the ventricle appears, which consists of the ventricular epithelium surrounded by a special condensation of the mesenchymatic tissues. This protrusion is completely closed and resembles the finger of a glove. Figs. 21, 22 and 23. The floor of this pocket springs directly from the caudal margin of the secondary rhomboidal lip, which is here folded over backward, while the walls are directly continuous with those of the ventricle. Its lumen at its commencement corresponds to the width of the ventricle and is circular in section. It terminates abruptly in a rounded extremity.

The choroid plexus extends in its roof a short distance caudad of the extremity of the vermis.

In the dog at birth the vermis has not as yet covered in the ventricle, which is still visible a short distance behind it. Transactions through this region appear exactly similar to those of the same region in man. There is the same extension of the choroid plexus along the under surface of the vermis. If the sections are followed back serially, or if a sagittal section is examined, it will be evident that an evagination of the ventricle has been cut, giving rise to the appearance of a break in the roof. Fig. 25. This evagination differs slightly in its relations at this stage from the condition found in the earlier ones, in that the roof of the evagination has become fused to the opposed surface of the vermis.

The floor of the evagination still remains separate from the pia of the oblongata. An explanation of this can be found in the relations of the mesenchymatic tissues which form the pia and arachnoid. In all young embryos this forms a delicate but close meshed network between the brain and the parietes of the cranium. As growth proceeds rarefactions and condensations of this network appear which arrange themselves according to fixed rules, and thus the subarachnoid spaces and the membranes are formed. Fig. 21.

It is out of the province of this paper to treat further of this subject except to state that in the region under consideration the network between the vermis and the evagination of the ventricle becomes condensed, while the other portions about the evagination become rarefied into the postcisterna. The condensed portion dorsal to the evagination forms quite a strong close meshed layer, which has been recognized and described by Hess, who attributed to it the drawing up of the choroid plexus on the vermis. In the horse he states that it is especially well developed, and below is attached to a process of pia shaped like the finger of a glove, which closes in the ventricle. He also implies that it draws out this pocket-shaped process. His impressions are seen to be erroneous from both points of view, inasmuch as the pocket is preformed, and secondly, does not

consist of pia except in its outer covering. He also describes the same glove-finger process in the sheep and in a cat embryo 100 mm. in length.

In the embryos of the animals so far mentioned, the cerebellum has not reached sufficient growth or development to cover in the ventricle and hide it from view. In the dog at birth the vermis only reaches the apex of the ventricle and the evagination of the ventricle is well marked and evident. In the adult dog the vermis reaches over both ventricle and evagination and both are hidden by it. On section, however, the evagination can still be made out, but it is flattened so that its roof and floor are in contact in places. The pia covering the ventral surface of the vermis fuses also in places with that covering the oblongata. No openings were found in the evagination.

The choroid plexus reaches to the end of the evagination but is generally weakly developed. The conditions as found in the dog may be taken as a general type for the majority of the mammalia.

Other adult types sectioned and studied microscopically are as follows :

Marsupialia : *Didelphys virginiana*. The ventricle has a marked protrusion reaching beyond the vermis, and lying in the subarachnoid space, but entirely closed, Fig. 24. The plexus in the body of the ventricle is weakly developed, while the plexus reaches an enormous size in the lateral recesses, studied by transections and sagittal sections in two animals.

Rodentia : *Lepus cuniculus* and *Sciurus carolinensis* both present the same condition, namely, practically no evagination of the ventricle and a continuous roof. In all, the brains of three rabbits were cut and one squirrel.

Primates : In all the primates sectioned, with the exception of the *Anthropoidæ*, a peculiar condition was found in regard to the caudal extension of the ventricular walls. Apparently the pouch becomes compressed between the mesal portion of the vermis and the oblongata and its mesal portion becomes obliterated by the fusion of the roof and floor, while the lateral portions persist along the vallis. Thus the protrusion in their

forms obtains the shape of a Y whose arms project caudally in the vallis, lying between vermis, hemisphere of cerebellum and the oblongata.

Hapalidæ : Hapale. Two brains sectioned. In both the caudal pouch was closed and had lateral extensions, in one extending caudad as far as the caudal extremity of vermis, in the other not so far.

Cercopithecidæ : *Macacus cynomolgus*. Pouch was present with lateral extensions, but closed. In the remaining old-world monkeys sectioned, namely, *Macacus rhesus* (two specimens), *Macacus memestrinus* and *Cynocephalus anubis*, the conditions were the same with the exception that the extremities of the lateral extensions were open. Thus there was a double metapore formation. These openings, however, were very small. Through them the choroid plexus reached into the subarachnoid cavity.

No other adult forms were sectioned microscopically. Several adult brains, however, were examined by gross methods.

As far as could be determined by this method the conditions found in the sheep, ox and cat, resembled those in the dog.

Two brains of the chimpanzee (*T. niger*) were examined. In one there was a metapore formation exactly similar to that found in man, with a caudal extension of the choroid plexus on the vermis. The other exhibited a closed pouch of only moderate extent the choroid plexus being very short, resembling the condition exceptionally found in man.

These observations corroborate those of Wilder who found a metapore in the chimpanzee, gorilla, orang and several old-world monkeys.

In the *Anthropoidæ* the vermis is relatively small as in man and it does not occlude as a rule the caudal extremity of the ventricle.

In the *Cercopithecidæ*, as before stated, the vermis does project caudad to the extremity of the ventricle and its pia fuses more or less with the pia of the oblongata. The caudal protrusion thus becomes compressed, but the tendency to metapore formation is present in the lateral portions of the sac in the ma-

jority. An investigation of embryos of these forms would be very instructive.

In the new world monkeys, so far as examined (*Haplidæ*) there is no absorption of the sac, conforming to what was found in the lower mammalia.

In all these forms, however, the communications between the lateral recesses and the subarachnoid cavity are very large.

If we attribute a functional importance to these communications in equalizing the intra- and extra-cerebral pressure by permitting the flow of *cœliolymph*, we can readily see why they should not be necessary in those forms in which a large portion of the walls of the brain are membranous.

In all forms in which the cerebellum is rudimentary, there is relatively a large expanse of membranous tela in the roof of the fourth ventricle.

In some of these forms, however, there is a tendency to the formation of a sac-like caudal protrusion of the ventricle.

If the fresh elasmobranch brain be tilted so that the *cœliolymph* gravitates to the caudal extremity of the ventricle, a bulging in the roof at this point is produced that is quite suggestive, although no distinct protrusion is found on sectioning. In the *Holostei*, Gage has figured a distinct caudal protrusion with recurvation of the lips of the ventricle in *Amia*.

In the *Dipnoi*, Burckhardt has found a similar protrusion in *Protopterus*.

In *Batrachia* through the kindness of Dr. O. S. Strong I have been able to make an examination of the following urodele forms, *Amblystoma*, *Spelerpes*, *Desmognathus*. In them I have found no evidence of a protrusion or metapore. Gage, however, has found an opening in the caudal portion of the roof in the adult *Diemyctelus viridescens* with the eversion of the lips of the ventricle.

In the *Anura* I have sectioned tadpoles of *Rana catesbiana* and *Rana palustris*, also adults of the same species and *Rana silvatica*, and found no ventricular protrusion. In the *Reptilia* on account of the difficulties experienced in fixation and decalcification, I have so far been unable to obtain satisfactory sec-

tions of this region. I should expect in these forms to probably find a caudal protrusion of the ventricle.

In Aves I have found in embryo chicks of the tenth day and later a very marked caudal protrusion which is received in a special compartment of the skull.

In comparing the conditions in the roof of the body of the ventricle in man, with those found in the lower animals, the similarity is seen to be very striking, except for the difference already mentioned in the development and extension of the secondary rhomboidal lip.

The relation of the vermis is practically the same as is found in advanced embryos of other animals, namely, it does not extend over and cover in the caudal extremity of the ventricle. We have then the conditions which in other animals have been shown to be accompanied with a caudal extension of the roof forming a closed pouch. In the foetus at the beginning of the fifth month frontal sections of this region show the following appearances: if the sections are followed back from where they pass through the cavity of the ventricle in the first sections will be seen the floor of the ventricle, or either side the secondary lip folded laterally and extending from its margin a wall of epithelium with its pial substratum, which passes dorsad toward the cerebellum and meets with its fellow in the roof where the choroid plexus is seen. Thus we have a condition of complete coelian circumscription. Fig. 28. Passing caudad to the apex of the ventricle we find that a complete endymal tube is now cut in whose roof the choroid plexus is still seen, and whose floor is separated from the medulla by a reflexion of the pia. Fig. 27. We have here the same picture as seen in sections of the same region in advanced embryos of the dog, pig, cat, and sheep. Figs. 22 and 23.

The walls of the tube, however, are much thinner and its caliber greater. In following the sections further caudad, the walls soon become lost, but the roof still continues fused to the extension of the pia under the cerebellum. Fig. 26.

Hess describes the brain of a child at term in which he states that the ventricle was closed by a pouch-like fold of the

pia, and remarks on its resemblance to the condition found in the horse.

Judging from his description and figure, it is evidently an instance of the condition found in the lower animals. He also describes a thinning and perforation of the sides of the pouch which throws light on the formation of the aperture.

The hypothesis that there is an evagination of the roof explains the excursion of the choroid plexus on the surface of the worm. The roof of the pouch is here supported by its adhesion to the pia of the cerebellum and consequently persists.

The variations in length of the choroid plexus may depend upon the extent of the evagination of the ventricle or upon the development of the plexus itself.

The supposition that the metapore might be the orifice of an evagination has been advanced by Prof. C. S. Minot in a communication to Prof. B. G. Wilder.¹

In comparing the above described conditions as found in the embryo with those found in the adult or child at term (for there is no material difference between them) we find that the difference exists merely in a more extensive obliteration of the lateral walls and floor of the evagination, so that its characters as a tube are lost. The numerous vessels in this vicinity encroach upon the lumen of the tube, it becomes absorbed between them, and thus arises the ragged appearance of this region.

A suspicion that there is no break in the ventricular epithelium and that the evagination becomes applied to the surface of the arachnoid is refuted not only by the facts revealed by injection but by the mesh-work of arachnoidal fibers that passes between tonsillæ, arachnoid, vermis and oblongata.

In support of the injection method, I would state that the epithelium has been found to persist only when supported by a layer of tissue sufficiently strong to withstand considerable force.

The comparatively few instances of complete closure of the ventricle may be due primarily to a short or incomplete evagination, or to secondary adhesions between the arachnoidal or

¹ B. G. Wilder: The Metapore in Man and Orang. New York Med. News, Oct. 14, 1893.

pial surfaces, the epithelium being absorbed. The evidence in favor of an incomplete evagination as a factor in absence of the metapore is, that in these cases the choroid plexus does not extend back on the vermis.

In any case we must look upon an extension of the choroid plexus into the subarachnoid cavity as evidence as to the presence of the metapore.

The metapore is essentially not an aperture in a roof but rather the disappearance of the end of a structure, so that it can be compared to the opening of a shed. Hence many of the current descriptions are incorrect.

Its boundaries are not definable in all cases since its position depends upon the amount of absorption of the epithelial tube. Its apparent boundaries are those given by Key and Retzius, namely the choroid plexus above, the membranous epithelial walls on either side, and below the posterior margin of the obex if present, otherwise the ligula. The propinquity of vessels and arachnoidal strands may give it the ragged appearance described by some.

Its resemblance to a tube has been recognized by Retzius and emphasized by Hoffman and Rauber and by C. A. Morton.

Of great interest and value as bearing upon the nature of the metapore are the appearances of the ventricular epithelium, especially in the roof and its extensions.

These changes are best followed in embryos, for in them they have not proceeded so far as to entirely obscure its characters.

The epithelium lining the floor of the ventricle is columnar and ciliated, on the secondary lip it becomes lower as it approaches the margin and loses its ciliæ. Where the roof is simply epithelial it is of a low cuboidal character.

In older embryos these changes become more accentuated. Where the roof is membranous the epithelium becomes flattened and the cells much broader, so that they approach closely the appearance of the endothelial cells of the arachnoid. In the evagination of the roof in the lower animals this appearance is marked but the epithelium can be recognized by a slightly closer

arrangement of the cells and by its taking certain stains more readily.

In the extension of the ventricle in the child at term and the adult, which forms the walls of the metapore, the epithelium gradually loses its character and can not be distinguished from the arachnoidal endothelium. There is no abrupt termination.

As to the time of the appearance of the metapore it is difficult to give exact figures. It was found by C. Hess in embryos of 7, 12, 5, 16 and 17 cm., by Retzius in an embryo of 4 mos. and by Gratiolet in one of 14 weeks. There is an element of doubt in regard to these observations, especially in the younger embryos, since the nature of the opening was not recognized. I have found it in two embryos at the end of the fourth month, the others so far studied being at too early stages. In embryos of 22 and 42 mm. the epithelium of this region appears to be very weakly developed and its continuity can only be determined with difficulty.

LATERAL RECESSES.

The lateral recesses are formed by the lateral portions of the roof of the rhomboidal fossæ, when the pons flexure is completed.

The fold in the roof formed by the flexure does not extend across the roof at the region of its greatest breadth, i.e. opposite the bend in the nervous parietes, but at a point caudad to it which later corresponds to the caudal part of the entrance to the lateral recess. Figs. 18 and 19. That is to say, the fold in the roof is essentially not similar to a fold caused by the bending of a flattened tube. Rather, the entire cephalic portion of the roof is carried caudad over the oblongata.

Thus it happens that there is no infolding of the roofs of the lateral recesses since they are carried back with the cerebellar laminæ. A reference to the figures will make the point clear. The choroidal fold does not exist as such in the lateral portions of the ventricle, the involution of the choroidal plexuses in the lateral recesses being a secondary formation and not in a preformed fold. Figs. 4, 8, 9, 13 and 14.

The primary fold which has been called the choroidal fold becomes continuous with the fold between the secondary lip and the oblongata, thus the entire lateral recess is cephalad to it. Fig. 19. If we ascribe a limiting value to this primary fold, we will have to place the lateral recesses entirely in the epencephalic segment. If sagittal sections through the region of the lateral recess are examined in embryos of man, sheep, pig, dog or cat, the cerebellar laminæ will be seen to entirely form its roof. Fig. 20. Its caudal wall, caudal portion of floor and extremity in these stages are the only membranous portions. The major portion of its floor is formed by the oblongata and its lip (rhomboidal lip). Figs. 26, 33, 34, 35 and 36.

As will be seen directly, the enlargement of the membranous portions constitutes the major portion of the lateral recess in adult stages.

As growth proceeds there seems to be a distension of the recesses which is more pronounced in the lateral portions. The walls bulge as if from some internal hydrostatic pressure. Their extremities now approach the cranial walls and come to lie in close relation with the recessus labyrinthi. Figs. 4 and 8. In man, as growth proceeds, they apparently recede from the cranial wall (Figs. 29 and 30) and fold over the sides of the oblongata, where they are finally limited by the roots of the nerves.

In the pig, dog, cat and sheep their extremities seem to fuse with the dura. Fig. 38.

Coincident with their lateral extension they grow caudally. In the lower animals the caudal bulging is not so marked as in man, where their caudal limits extend as far as a point opposite the apex of the ventricle. Fig. 28.

The entrances to the recesses share but little in the general growth, and here the original embryonic condition is nearly preserved, namely, the formation of the roof by the cerebellum. Figs. 33, 34 and 35.

As growth proceeds further the lateral recess loses its distended character and the roof and floor in many cases come in contact, except where separated by the choroid plexus, so that its cavity appears as a slit. Figs. 33, 34 and 35.

Owing to the greater development of the secondary rhomboidal lip in man, the parts of the recess which it forms are as a rule entirely retained, while in the lower mammals these parts consisting from the start only of epithelium, become lost.

In man the floor of the recess is formed chiefly from the secondary lip where it extends from the medulla at the region of greatest width. It here forms a plate of nervous matter peculiarly convoluted, which usually not only extends to the extremity of the recess, but folds on itself both at its caudal and lateral portions and so enters into the formation of the roof. In the instance where it is well developed, it may form a considerable portion of the roof as well as the floor. Fig. 37. In these cases a more or less complete pouch is formed at the extremity of the recess, which Retzius proposes to call the *Marsupium* or *Pera*. Figs. 35, 36 and 37.

In other cases the lip at its extremity does not turn over into the roof but ends as a free rounded margin. Fig. 33. In contrast to the condition found in the lower mammals the caudal part of the recess in man is, as a rule, well developed and the recess is here closed. Exceptionally the condition presented in Figs. 32, 33 and 34 is found, a condition which closely approximates that found in the lower mammals. The caudal and lateral extremity is here lost and the recess opens widely into the subarachnoid cavity. In this brain the metapore was almost completely filled by the choroid plexus (Fig. 31) which may explain the unusual size of the openings in the lateral recesses.

In a large number of brains of adults and children examined, I found the openings in the lateral recesses (foramina of Luschka) present and almost invariably they conformed to the description as given by Retzius, with the single exception figured here.

Sections of this region of the brain of children at term under the microscope show the margins of the foramen as in Figs. 35 and 36. The wall of the recess ends in a smooth rounded margin and the abrupt termination of the epithelium is readily made out.

The wall of the pocket may be more or less fused to the roots of the glossopharyngeus and vagus. The existence of this fusion has given rise to the contention that the foramina here are artifacts. Microscopical sections, however, effectually demonstrate their presence.

The roof the lateral recess caudal to the involution of the choroid plexus along the margin of the posterior medullary velum, consists in all mammals, when it exists, of a simple layer of epithelium unsupported by nervous matter. Figs. 15 and 32. In the lower mammalia there is usually a slight extension of the epithelium of the roof beyond the choroid plexus forming a lateral wall for the recess, Figs. 15 and 16, which is closely applied to the dura, and which closes in the cephalic portion of the recess. Cannieu evidently observed this arrangement and thus led to the conclusion that the recess is completely closed in all mammals.

While his observations are correct for the cephalic portion of the recess, I have found in embryos of cat dog, pig, sheep and rat in their later stages, a complete disappearance of the caudal portion of the recess, and thus a free communication with the subarachnoid cavity. In man there is as a rule no extension of the roof epithelium beyond the choroid plexus in the lateral portion of the recess, thus the dorsal margin of the foramen of Luschka is formed by the choroid plexus. Figs. 29, 32 et. seq.

It is out of the province of this paper to enter into a discussion at length of reasons for and against the division of the third cerebral vesicle into two cephalic segments.

Several of the arguments of those advocating the division have been, it seems to me, successfully refuted by Spitzka and others.

If we divide this portion of the brain into epencephalon and metencephalon there necessarily follows a division of the cavity of the fourth ventricle into epicœlia and metacœlia; and furthermore, if we cannot make this division of the cavity the whole framework of this segmentation falls down.

A successful division of the cavity that would stand criti-

cism has, as far as I am able to ascertain, never been made.

The division into epencephalon and metencephalon has been made by reason of changes of the so-called epencephalic portion which have a late appearance, both ontogenetically and phylogenetically.

The difficulty in dividing the ventricle lies in finding the point where the transverse line should be drawn.

In the division generally accepted, this line falls at the widest portion of the lateral recesses and as the oblongata terminates at the pons flexure the line must be taken as the flexure.

Now the lateral recesses are generally included in the epencephalic segment, as is evinced by their name *parepicœlia* (Wilder).

As has already been shown, the roof of the lateral recesses is formed from cerebellum, both in embryonal and adult stages, yet the floor is formed by oblongata, consequently they can be included in neither segment. Likewise the portion of the ventricle lying between them is equally indivisible.

Reference to Figs. 12, 13, and 14 will help to elucidate this point.

In Fig. 12 the terms *epicœle* and *metacœle* are easily applicable; also they can be applied in Fig. 13, but cannot be in Fig. 14. The same can be seen in comparing Figs. 3 and 7 with Figs. 4 and 8.

The reconstructions also demonstrate the same thing, Figs. 18, 19 and 20.

Sagittal sections at the meson do not help to elucidate this point.

It may be said that we can divide the lateral recesses and relegate a portion to each segment. This, however, seems to be out of the question.

Finally, if one follows the development of the rhomboidal fossa the similarity displayed throughout cannot help but impress him that the division is artificial and needless. While the use of the terms epencephalon and metencephalon is convenient in the description of certain portions, yet it only leads to embarrassment in that of other portions.

Furthermore, it leads to misconception and error. In a recent text-book of anatomy, the author recognizing the necessity of an actual demarcation between these so-called segments, makes the statement that the third encephalic vesicle becomes constricted transversely into the fourth and fifth and that a little of this constriction remains in the adult. A misstatement like this certainly does not help a student to a true understanding of this region.

CONCLUSIONS.

1. That compared with the lower mammals the rhomboidal lips reach a greater development in man.
2. That consequently in man there is a greater development of nervous matter in the roof of the fourth ventricle and in the walls of the lateral recesses.
3. That the disappearance of the walls of the lateral recesses is of greater extent in the lower mammals.
4. That in mammalia and aves a caudal protrusion of the roof of the fourth ventricle is formed at some stage in their embryonic life.
5. That in mammalia there is a tendency to the absorption of the ventricular epithelium unless it is supported by nervous matter or by the pia of neighboring structures.
6. That in man the caudal protrusion becomes lost, giving rise to a metapore.
7. That in all Anthropoidæ there is generally a similar metapore formation.
8. That the Cercopithecidæ represent an intermediate stage between the Anthropoidæ and the lower mammals, in that there is a tendency to metapore formation.
9. That in the lower mammalia the caudal protrusion as a rule remains closed.
10. That the lateral recesses represent an intermediate area shared in equally by cerebellum and oblongata.
11. To call attention to the presence in the human embryo of a well-marked cavity between the protuberances of the vermis.
12. That this cavity becomes obliterated by the fusion of the opposing surfaces, and the tent is of later formation and

due to the greater proportional growth of the ectal portion of the cerebellar mass.

13. To call attention to the considerable part played by the rhomboidal lip in the formation of the acusticum.

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EXPLANATION OF PLATES.

PLATE IV.

Fig. 1. Frontal section through the rhomboidal fossa of the brain of an embryo rat (*Mus decumanus*, var. *alba*) three millimeters long N. B., near the region of the X nerve. $\times 60$. The section is slightly oblique.

Figs. 2, 3 and 4. Frontal sections of a human embryo forty-two millimeters long. The head had previously been partially sectioned sagittally. $\times 6$.

Fig. 5. Sagittal section of the same embryo near the meson. $\times 9$.

Fig. 6. Sagittal section near the meson of a human embryo twenty two millimeters long. $\times 10$.

Figs. 7 and 8. Frontal sections of the same embryo. *Fig. 7* caudad of the X, *Fig. 8* at the X nerve. $\times 11$.

PLATE V.

Fig. 9. Frontal section of an embryo cat ten millimeters long N. B. through the ganglion of the X nerve. $\times 22$.

Fig. 10. Amplification of the region marked Sec. rhomboidal lip in *Fig. 9*. $\times 450$.

Fig. 11. Sagittal mesal section of an embryo pig twenty-one millimeters long. x 9.

Figs. 12, 13 and 14. Frontal sections of an embryo pig twenty-one millimeters long. Fig. 12 through choroidal fold. Fig. 13 cephalad of choroidal fold. Fig. 14 through auditory nerve. x 15.

PLATE VI.

Figs. 15 and 16. Reconstruction of a portion of the brain of a dog at birth. In Fig. 16 the cephalic portion of the reconstruction has been removed. Reconstructed from the series of sections from which Fig. 38 was taken. 9 diameters.

Fig. 17. Floor of the fourth ventricle of an adult man. After Retzius. x 2.

Figs. 18, 19 and 20. Reconstruction of a portion of the brain of an embryo pig twenty-one millimeters long. Reconstructed from the series of sections from which Figs. 12, 13 and 14 were taken. 17 diameters.

PLATE VII.

Figs. 21, 22 and 23. Frontal section of an embryo cat seventy millimeters long. x 9.

Fig. 24. Sagittal mesal section of fourth ventricle of an opossum (*Didelphys virginiana*). x 8.

Fig. 25. Sagittal mesal section of the fourth ventricle of a dog at birth. x 10.

Fig. 26. Sagittal section near the meson of the fourth ventricle of a human embryo of 130 days. x 5.

PLATE VIII.

Figs. 27, 28, 29 and 30. Transections of a human embryo of 125 days. Only the brain and enough of the membranes to show the relations are drawn. The sections are more advanced on the right side. x $7\frac{1}{2}$.

PLATE IX.

Figs. 31, 32, 33 and 34. Transections of the brain of a child at term. Fig. 31 at the calamus region. x 18. Figs. 32, 33 and 34. x 6.

PLATE X.

Figs. 35 and 36. Transections of the lateral recess of a child at term. Fig. 35, region of IX. Fig. 36, region of X. x 9.

Fig. 37. Transection of the lateral recess of a child at term. x 9.

Fig. 38. Transection of the brain of a dog at birth. The section is more advanced on the left side. x 8.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

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Fig. 9

Fig. 10

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Fig. 37

Fig. 38