XIII. *On the Commissures of the Cerebral Hemispheres of the Marsupialia and Monotremata as compared with those of the Placental Mammals.* *By* William Henry Flower, *F.R.S., F.R.C.S., Conservator of the Museum of the Royal College of Surgeons of England.*

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The terms used in describing the anatomy of the vertebrated animals have in most cases been originally bestowed on parts of the human body, being frequently derived from some quality, relation, or real or fancied resemblance to some known object, possessed by the structure in question in Man. It will therefore be most convenient to pass from the best to the least known, and to commence by a short recapitulation of the characters and relations, in the human brain, of those parts to the consideration of which, in the brains of the lower mammalia, this communication is specially devoted.

Plate XXXVI. fig. 1 is a view of the inner surface of one of the hemispheres of the human cerebrum, such parts as pass across the middle line to the other hemisphere having been divided, and those that do not belong to the hemisphere proper being removed. A convenient central point to start from in the description is the part cut through to make the section last referred to. A is the surface of the divided mass of fibres, by which the hemisphere is connected with the inferior parts of the encephalon, and with the spinal cord—the crus or peduncle of the brain. The section is made between the corpus striatum and the thalamus opticus. The thalamus, as not belonging to the hemisphere proper, and interfering with the view of essential parts, is removed.

The upper and posterior portions of the circumference of the part just described are surrounded by the narrow slit-like opening, the "ventricular aperture" (O O), which leads into the great cavity in the interior of the hemisphere, the lateral ventricle. The inferior margin of the ventricular aperture is formed by the "tænia semicircularis," the superior by a stronger and better marked band of white fibres, forming the free edge of the inner wall of the hemisphere, the "fornix." Leaving this for the present, we must next notice as an important landmark, the great or superior commissure, or "corpus callosum" (B), here seen in its entire length, slightly arched, thick and rounded behind (the "splenium" E), and curving downwards in front (the "genu" C), ending in a pointed "rostrum" or beak (D) directed backwards. The hinder edge is also curved upon itself, ending in a rounded edge (N) projecting downwards and forwards and folded under the main body of the corpus callosum, much in the same way, though in a less degree, as the rostrum in front. This part requires special attention in connexion with the present subject, as in the lower mammals it acquires a much greater relative importance.

Through this a portion of the pia mater (afterwards developed into the choroid plexus) enters. The fissure is at first perpendicular in direction. In front of it (at G) the two hemispheres are united across the middle line, immediately behind it (A) they are connected with the parts formed by the second cerebral vesicle, the subsequent optic thalamus and crus cerebri. The last-named point (the *crus* or "*hirnstiel*") forms a pivot around which the whole hemisphere curves itself as development proceeds. The fissure undergoes a corresponding change of form and direction. The anterior edge becomes its upper convex border. The upper end gradually becomes depressed until it is finally the lowest part, and the characteristic form of the ventricular aperture is already recognized at this early age (Plate XXXVI. fig. 3, III). The point of union between the hemispheres is still confined to the part immediately in front of the anterior end of the fissure, the "septal area." About this time the wall of the hemisphere commences to undergo a folding upon itself, producing certain definite grooves or sulci on the outer surface, and corresponding elevations upon the interior. At a very early period an arched sulcus (*bogenfurche*) appears parallel to the upper border of the fissure, marking off an arched convolution or gyrus between it and the fissure, the "marginal arch" (*randbogen*, SCHMIDT). It is the hinder part of this groove which afterwards forms the "hippocampal sulcus." Into the further development of the convolutions and sulci it is unnecessary to enter. A more important subject in connexion with the present communication is the mode of formation of the corpus callosum, the fornix, and adjacent parts. KÖLLIKER* has given so good an abridgement of SCHMIDT's views, that I have thought it best to follow pretty closely his words.

The convolutions of the hemispheres are distinctly seen from the third month to consist of two layers, an external with perpendicular fibres, which at a later period constitutes the grey or cortical substance of the convolutions, and an inner layer with fibres running horizontally. The fibres of the inner layer, constituting the medullary substance of the hemispheres, are found already in the third month, before the corpus callosum exists, to converge towards two points; first, towards the crus (*hirnstiel*, A), where they form the so-called *stabkranz*; and secondly, towards a point situated immediately above the place of union of the two hemispheres. This last arrangement of fibres is the first indication of the radiation of the corpus callosum (*balkenstrahlung*). It is at this spot (B) that in the fourth month the horizontal fibres break through the cortical substance and unite with the corresponding fibres of the opposite hemisphere.

This is the commencement of the corpus callosum, which in its earliest form (see Plate XXXVI. fig. 3, IV) is a very small nearly cylindrical commissure, situated in the "marginal arch" immediately above the most anterior part of the ventricular aperture. In order to indicate more closely the relation of the marginal arch to the corpus callosum, it is to be noticed that the former separates into two parts, a lower division immediately bordering the ventricular aperture, consisting only of horizontal or antero-posterior fibres, without the cortical layer, and an upper division possessing both layers.

* Entwicklungsgeschichte des Menschen und der höheren Thiere, p. 237, Leipzig 1861.

Now the corpus callosum breaks through just at the limit between these two divisions, and by its further growth backwards, the upper division comes to lie on its outer surface and is converted into the stria alba Lancisi and stria obtecta of the corpus callosum, and into the fascia dentata of the hippocampus major; whilst the inferior or inner arch, with its longitudinal fibres, forms the fornix and septum (*scheidewand*). The fornix is thus, as was known to ARNOLD and RETZIUS, a transformation of the upper margin of the transverse fissure. The lower margin of the fissure is formed into the tænia semicircularis or stria cornea, which, as is well known, is connected at each end with the extremities of the fornix. It will be seen from the preceding observations that the anterior perpendicular part of the fornix is originally united with the corresponding part of the other side, and the body of the fornix developes itself out of the uppermost part of this spot, adjoining the primitive corpus callosum. Lower down the parts separate and then resolve themselves into the columnæ fornicis, or anterior crura, and the two halves of the septum lucidum, the ventricle of which is thus no primitive formation. In this part also originates, not by growing together from opposite sides, but by histological differentiation, the anterior commissure (F), which is evident a short time before the corpus callosum. The septum lucidum and body of the fornix, in the beginning very small, gradually increase in extent with the development of the corpus callosum.

According to SCHMIDT, the opinion formerly entertained that the genu of the corpus callosum was the part first formed, and that the hinder part developed afterwards, is not correct. The rudimentary corpus callosum on its first appearance already contains the elements of all its subsequent parts, as from the very first, fibres radiate from it into the hinder and middle, as well as the anterior lobes, and the intimate connexion of the former with the posterior crura of the fornix can already be recognized. It increases, with the rest of the hemisphere, chiefly in longitudinal extent, spreading both backwards and forwards from the point of its first appearance, but principally in the former direction. The curved part in front, called the genu, is not formed until the end of the fifth month, and about a month later, the thickening and extension of the hinder end over the corpora quadrigemina gives the permanent form to this part of the brain.

I will next proceed to trace the modifications of the parts of the brain above indicated, in certain of the placental mammalia. The preparations from which the figures are taken were all made in the same manner as that adopted in the case of the human brain, viz., (I.) a vertical longitudinal section in the middle line, exhibiting the inner surface of a single (the right) hemisphere, the thalamus opticus and crus having been removed so as to show clearly the whole surface with the parts forming the upper boundary of the ventricular aperture; (II.) a vertical transverse section through the middle of the anterior commissure.

The Sheep.—In the longitudinal section of the sheep's brain (Plate XXXVII. fig. 1), the elongated narrow corpus callosum (B) is seen lying in a line nearly horizontal, or corresponding with the long axis of the hemisphere; slightly concave in the middle above, with a thickened posterior end (E) turned somewhat downwards, and a distinct genu (C) and rostrum (D) in front. The latter has a smaller proportional development than in the human brain. On the other hand, the slightly projecting posterior fold observed in the human corpus callosum is prolonged forwards as a thin layer of transverse fibres (N) arching across the under surface of the longitudinal fibres of the fornix, and ending in no abrupt edge in front. The difference in the form and extent of this part of the great transverse commissure may be clearly seen to depend upon the difference in the form, and more extensive proportions of the parts that have to be brought into relation to each other by it, viz. those forming the inner wall of the descending cornu of the lateral ventricle. At a considerable distance below the anterior part of the corpus callosum the small anterior commissure (F) is seen, with the wide septal area (G) in front of and above it. The portion of this part to which the term "septum lucidum" can be applied, is reduced to a small strip beneath the anterior third of the corpus callosum, exactly defined below and in front by the extent of the rostrum of that body. The greater part of the septum is formed by a thick layer, consisting of a great development of the precommissural fibres of the fornix, associated with much grey matter. The small white column (L) of the fornix is seen passing down behind the anterior commissure. The ventricular aperture is less regularly curved than in man, being bent almost at a right angle. Above and behind it is seen a broad corpus fimbriatum (M), behind which the abrupt termination of the cortical substance of the hemisphere in the fascia dentata (P) is very distinctly seen. The regularly curved hippocampal sulcus (Q) ends beneath the hinder end of the corpus callosum, the grey matter of the fascia dentata being continued superficially round its extremity into that of the next succeeding gyrus.

In the transverse section (Plate XXXVII. fig. 2), at the bottom of the deep longitudinal fissure, is seen the corpus callosum (B), a transverse white band of moderate thickness, and slightly arched upwards externally, where its fibres radiate out in the medullary substance of the hemisphere. The anterior commissure (F) is readily recognized near the lower part of the section. The cavities of the lateral ventricles are somewhat triangular in form and bounded above by the under surface of the corpus callosum, towards the middle line by the septum, and externally by the corpora striata. The septum obviously consists of two halves, one belonging to each hemisphere, but more or less joined together in the middle line. The upper part (septum lucidum) is extremely thin, and here the absence of union between the two halves allows the existence of a minute cavity, the fifth ventricle. The lower and larger part is very thick, with rounded outer surface. It contains much grey matter, with white longitudinal fibres externally. Within it, near the middle line, on each side, can be seen two bundles of white fibres, standing nearly perpendicularly and slightly diverging from each other below; they are the upper part of the columns of the fornix.

The most essential deviations in the commissures of this brain from those of Man consist in the reduction of the rostrum of the corpus callosum and the septum lucidum, and the augmentation of the inferior thick part of the septal area and of the psalterial fibres.

The Rabbit.—Plate XXXVII. fig. 3 represents the inner surface of the cerebral hemisphere of a rabbit. The corpus callosum (B) is no longer horizontal in its general direction, but, like the upper margin of the hemisphere, is elevated at the posterior end. In front it is slightly thickened, but the rostrum is scarcely perceptible. Although this commissure in its median section appears elongated from before backwards, it is very thin from above downwards. The inferior layer of transverse (psalterial) fibres are well developed, and, except posteriorly, distinct from the main part of the great transverse commissure. The septal area is large in extent. The anterior commissure is proportionally larger than in man or in the sheep. The hippocampal sulcus, corresponding with the large size of its internal projection into the ventricle, is deep, and prolonged for some distance beneath the hinder end of the corpus callosum. The hollow for the reception of the optic thalamus and corpora quadrigemina is very large, and the fascia dentata (P) lying in it very broad. The smooth inner wall of the hemisphere shows no other sulcus than that of the hippocampus.

The transverse section (Plate XXXVII. fig. 4) shows the corpus collosum at the bottom of the longitudinal fissure, curving up at the two extremities, in consequence of the form of the lateral ventricles. The anterior commissure is of actual greater depth in the section than the corpus callosum. Between the two is the septum, now only represented by the thick lower portion, very considerably increased in development. The thin upper part, together with the fifth ventricle, has entirely disappeared with the rostrum of the corpus callosum.

In the Two-toed Sloth (*Cholœpus didactylus*), Plate XXXVII. fig. 5, the same parts can be recognized, though somewhat changed in proportions. As compared with the sheep especially, the whole hemisphere is greatly shortened in the antero-posterior direction, and a greater shortening still has taken place in the corpus callosum. Instead of bearing, as in the sheep, the proportion to the hemisphere of 53 to 100, it is but as 32 to 100. It rises at the posterior part, where it is slightly enlarged. The anterior end is simple and obtusely pointed, without a trace of the reflected rostrum. The anterior commissure is considerably larger, relatively to the hemisphere, than in the sheep. The ventricular aperture is nearly vertical in general direction. At the posterior edge of the body of the fornix there is a considerable thickening, caused by the transverse psalterial fibres of the corpus callosum. The hippocampal sulcus may be traced upwards to near the hinder end of the corpus callosum; it then makes a sudden curve backwards, and almost immediately after another nearly equally sudden bend forwards, then arches over the end of the corpus callosum, and gradually approaching the upper surface of that body, at about its middle disappears in the lower margin of the callosal gyrus. Thus a thin portion of the dentate gyrus (fascia dentata) is continued over the hinder edge, on to the upper surface of the corpus callosum. In its principal part the gyrus itself is longitudinally grooved by a shallow sulcus, anterior and parallel to the hippocampal sulcus. The characteristic indentations are faintly indicated on the posterior edge.

The transverse section (Plate XXXVII. fig. 6) shows the corpus callosum curving up at the outer extremities owing to the upward development of the lateral ventricles, as in the rabbit, and in the fœtal condition of the higher mammals. The corpora striata (R, R) are very large. The anterior commissure exceeds in vertical depth the corpus callosum. The septum, broad below where it rests on the anterior commissure, diminishes above to a narrow edge, where it touches the under surface of the corpus callosum; but there is no part which can properly be called septum lucidum. On each side of the middle line are seen the vertical white fibres, forming the commencement of the columns of the fornix.

Plate XXXVII. figs. 7 & 8 are taken from the brain of the Common Hedgehog (*Erinaceus europæus*). The transition from the Sloth's brain to this is easy, although it presents a wide difference from that of the Rabbit. The inner surface of the cerebrum shows no trace of any sulcus, except the deep one of the hippocampus (Q), which is placed very near the hinder border of the truncated hemisphere, and terminates a little way behind and below the posterior end of the corpus callosum. The last named body is extremely reduced in size, its length being but one fifth that of the entire hemisphere. Its obliquity is so much increased that its general direction is rather vertical than horizontal. The psalterial fibres form a distinct projection (N) in the section closer to the body of the corpus callosum than in the two previously described brains. The septal area is much reduced, and the anterior commissure increased in bulk. The great size of the olfactory ganglion is very remarkable.

The transverse section shows a corresponding simplicity, and agrees in all its essential characters with that of the Sloth. The oblique position of the corpus callosum gives its section an apparent thickness, which it would not possess if divided, as in the higher mammals, at a right angle to the plane of its upper surface.

These are examples of some of the modifications of the commissural apparatus of the cerebral hemispheres among the placental mammals. They might be considerably multiplied, but they are sufficient for the purpose of affording a basis of comparison with the same parts in the Marsupials and Monotremes.

Before entering upon this part of the subject, it may be desirable to give an outline of the present condition of knowledge upon it. A reference to the works of comparative anatomists who wrote before the year 1837, shows that up to that period no important distinction had been suspected to exist in the cerebral organization of the placental and the implacental mammals. In the Philosophical Transactions of that year, however, appeared the memoir of Professor OWEN "On the Structure of the Brain in Marsupial Animals," in which was announced the absence in these animals, of the "corpus callosum and septum lucidum." A transverse commissure between the hemispheres superior to the anterior commissure is described, but called by Professor OWEN "fornix" or "hippocampal commissure." Of this it is stated, "This commissure may, nevertheless, be regarded as representing, besides the fornix, the rudimental commencement of the corpus callosum; but this determination does not invalidate the fact that the great commissure which unites the supraventricular masses of the hemispheres in the Beaver and all other placentally developed Mammalia, and which exists in addition to the hippocampal commissure, is wanting in the brain of the Wombat: and as the same deficiency exists in the brain of the Great and Bush Kangaroos, the Vulpine Phalanger, the Ursine, and MAUGE's Dasyures, and the Virginian Opossum, it is most probably the characteristic of the marsupial division of Mammalia." The relatively large size of the anterior commissure in the marsupials is referred to in the paper as worthy of notice, as also is the proportionally very large size of the hippocampi majores.

The description given in this important memoir was subsequently reproduced in the Cyclopædia of Anatomy and Physiology, art. Marsupialia, and it was shown that the same peculiarity also existed in the Monotremata, and therefore was characteristic of the whole implacental division. In the paper by the same author "On the Characters, Principles of Division and Primary Groups of the Class Mammalia"*, the Subclass *Lyencephala* ("loose" or "disconnected" brain), equivalent to the Implacentalia, are characterized as having "the cerebral hemispheres but feebly and partially connected together by the 'fornix' and 'anterior commissure,' while in the rest of the class a part called 'corpus callosum' is added, which completes the connecting or commissural apparatus"†. The views of Professor OWEN have been adopted without hesitation or qualification, in this country at least, and have been incorporated in almost every text-book on Anatomy and Physiology subsequently published. The same has been the case to a great extent upon the continent, and what is more important, they have received confirmation apparently from original dissections of several of the marsupials by the editors of the third edition of CUVIER's 'Anatomie Comparée,' MM. F. CUVIER and LAURILLARD (1844), and in the case of the Echidna by MM. EYDOUT and LAURENT (Voyage de la Favorite, 1839).

But expressions of dissent have also been raised. LEURET, speaking of the brain of

* Proc. Linn. Soc. 1858.

† [The necessity of doing full justice to the labours of one who has made this subject so peculiarly his own, will excuse my quoting the following succinct account of the distinctive characteristics of the views of this eminent anatomist, as set forth in his most recent publication bearing upon the question.

"In investigating and studying the value and application of the cerebral characters of Man in the classification of the Mammalia, I have been led to note the relations of equivalent modifications of cerebral structure to the extent of the groups of mammals respectively characterized by such conditions of brain. The Monotremes and Marsupials, which offer numerous extreme modifications of the limbs, all agree in possessing a brain in which there is no connecting or commissural mass of fibres overarching the lateral ventricles of the cerebrum. The surface of this part shows, however, a few symmetrical convolutions in *Echidna* and *Macropus*, especially the largest species; but in the majority of marsupials the hemispheres are smooth. The 'corpus callosum,' or great commissure, makes its appearance abruptly in the Rats, Shrews, Bats, and Sloths, which in general organization and powers are next the 'loose-brained' marsupials or *Lyencephala*: but this commissure is associated with a similarly smooth unconvolute cerebrum, and with so small a size of the cerebrum as leaves uncovered the cerebellum and in most the optic lobes."—Contributions to the Natural History of the Anthropoid Apes, No. VIII., by Professor OWEN, Trans. Zool. Soc. vol. v. part 4, 1865, p. 270.—April 1865.]

the Kangaroo, says,* "J'y ai vu bien manifestement un corps calleux, situé entre les deux lobes cérébraux, comme chez les autres mammifères."

FOVILLE, in a note to p. 172 of his well-known treatise on the Nervous System (1844), says, "M. DE BLAINVILLE a toujours soutenu l'existence du corps calleux chez les didelphes, et me l'a fait voir de la manière la plus manifeste chez plusieurs de ces animaux. Il a si peu de volume qu'on s'explique facilement comment on a pu croire à son absence."

F. J. C. MAYER†, speaking of the brain of the Common Opossum (*Didelphis virginiana*), says, "Das *corpus callosum* betreffend, so ist dasselbe ebenfalls und namentlich bei *Didelphis* vorhanden, nur schmal oder kurz, allerdings etwas schmäler oder kürzer, als bei den Nagern, allein noch kürzer ist das *corpus callosum* beim Igel [hedgehog] wo es ebenfalls nur ein vorderes schmales Markblatt bildet. Aber schon bei den Nagern treten der Eingang in den dritten Ventrikel und der Sehhügel hinter dem *corpus callosum* zu Tage, am meisten aber bei dem Igel, und die Beutelthiere stehen nur zwischen beiden, den Nagern und dem Igel in der Mitte, und es ist somit im Gehirne derselben keine abweichende Organisation wahrzunehmen, welche mit der Geschlechtstheile etwa eine Parallele liefern könnte"‡.

The more detailed description of this structure in the brain of the same animal, given by PAPPENHEIM§ in language remarkable for its precision, deserves to be quoted in full, as it has received little attention from subsequent authors. It agrees in the main with the observations recorded in this paper.

"Mais je crois devoir m'occuper, avant tout, de la nature du *corps calleux*. C'est une opinion très-répandue, que ce corps n'existe pas chez les Marsupiaux. Cependant les dessins et la description de M. OWEN prouvent que ce corps à été très-bien vu par cet anatomiste habile; mais que, d'un coté, il n'a pas reconnu sa marche entière, et que, de l'autre, il à été frappé par la situation de cette commissure, qu'il à considérée plutôt comme un fornix (voûte à trois piliers). Comme cet organe se trouve dessiné en partie dans le paquet cacheté que l'Académie a bien voulu me faire l'honneur d'accepter, je me bornerai aujourd'hui à signaler quelques faits qui, rapprochés de mes observations anciennes, prouveront que le corps en question est bien un corps calleux.

"1°. La commissure dont je parle est située en avant des couches optiques, là où leur

* Anat. Comp. du Système Nerveux, t. i. p. 412 (1839).

† Neue Untersuchungen aus dem Gebiete der Anatomie und Physiologie. Bonn, 1842, p. 24.

‡ Professor OWEN (Annals and Mag. Nat. Hist. vol. xvi. p. 101, 1845), in replying to MAYER's statement, says, "The great transverse band or commissure which unites the two hemispheres, spanning from one to the other *above the lateral ventricle*—which is plainly visible, as such, in the lowest Rodent or other placental mammal, with the smoothest, and, to outward appearance, simplest brain,—this great commissure or corpus callosum, I again affirm, after reiterated dissections, to be absent in all the known genera of Marsupials. If the narrow transverse band, which unites together the hippocampi majores, at the front part of the fornix, be regarded, as I originally stated it might be, a rudiment of the 'corpus callosum,' the comparative anatomist is at liberty to apply that name to it."

§ "Notice préliminaire sur l'anatomie du sarigue femelle (*Didelphis virginiana*)," Comptes Rendus, tom. xxiv. p. 186 (1847).

premier développement s'opère, au-dessus de la commissure antérieure du cerveau. Toutes ses fibres rayonnent au-dessus du corps strié, dans les hémisphères, où elles se terminent en faisceaux parallèles aux fibres des pédoncules cérébraux.

"2°. Elle s'allonge en avant dans un corps genouillé, qui ne peut être comparé aux pédoncules du fornix, lesquels entrent dans les couches optiques, tandis que ce dernier corps rayonne dans les hémisphères.

"3°. Les fibres de cette commissure sont purement transversales, direction qui n'a aucun rapport avec celles des fibres du fornix.

"4°. Les fibres du fornix ne s'étalent jamais dans les parois des ventricules; aussi n'occupent-elles pas toute la longueur du ventricule latéral.

"Cette commissure n'est donc ni un fornix, ni un mélange du fornix avec le corps calleux.

"La partie postérieure est composée de fibres accumulées en un faisceau très-épais, tandis que les fibres antérieures du corps calleux sont étalées dans une couche large, mais extrêmement mince et tellement transparente, que l'on voyait à travers le corps strié. Du reste, quand on écartait les hémisphères, les fibres du corps calleux, étalées, se laissaient détacher facilement de l'autre substance blanche, sous forme de feuillet mince, tapissant, pour ainsi dire, la paroi du ventricule latéral dans chaque hémisphère.

"Les hémisphères étaient composés d'une manière trés-simple, savoir; des fibres des pédoncules cérébraux, qui étaient les plus externes; des fibres de la commissure antérieure, en avant et en dedans, et d'un feuillet appartenant au corps calleux, situé en dedans du rayonnement des fibres du pédoncle; tout autour, enfin, était une couche corticale très-épaisse et peut-être plus considérable que toutes les fibres blanches."

Such are the main results of the researches of those anatomists to whom we are indebted for all that is known upon the cerebral commissure of the Implacental Mammals. I will next give an account of these structures as actually observed in several of the leading types of the group, and afterwards discuss the relation which the conclusions derived from the present examination (differing somewhat in method from those previously used) bear to the opinions most generally received.

Kangaroo.—Several specimens of the brains of both *Macropus major* and *Macropus Bennettii* have been examined. They agree so closely in all essential points that one description will suffice for either, unless otherwise specially stated.

On looking at the upper surface of the brain (Plate XXXVI. fig. 4), the two hemispheres being partly separated, a transverse white band (B) is seen extending across the bottom of the longitudinal fissure, roofing over the anterior portion of the third ventricle, and occupying the same general position as the corpus callosum in the ordinary mammal, but developed to a smaller extent even than in the Hedgehog. In a brain of *Macropus Bennettii* it was found to cover, when still undisturbed by removal from the cranial cavity or contracted by spirit, about half the optic thalamus, and to measure from before backwards in the middle line, a quarter of an inch, or one-sixth of the entire length of the hemisphere. It is situated deeply in the great longitudinal fissure, is thickened and most elevated posteriorly, where the margin, slightly and evenly concave, crosses the cavity of the third ventricle (S), the peduncles of the pineal gland (T), and the optic thalami (U). The anterior margin is also concave, but extremely narrow, the white substance being continued on each side of a longitudinal median cleft for some distance towards the front of the cerebral hemisphere, as if in this anterior part the two lateral halves of the commissure had not been joined together in the middle line. On close examination it is seen to be composed of fibres of which the general direction is transverse, but on its upper surface can be distinguished a longitudinal median raphe, and on each side of this a few longitudinal white fibres, corresponding to the "striæ laterales" of other mammals.

On either side, the transverse fibres are lost beneath the overlapping grey matter constituting the margin of the convolution of the corpus callosum, the "labia cerebri" of some authors. To follow them further, the last named parts must be carefully removed with the handle of a scalpel or some similar instrument, when a delicate broad lamina formed by the lateral expansion of the narrow transverse band will come into view, passing at first horizontally outwards and then curving upwards above the precommissural fibres of the fornix (I), the cavity of the lateral ventricle, and the corpus striatum (R), and finally losing themselves in the medullary substance of the upper part of the cerebral hemispheres. The fibres radiate extensively forwards and backwards but forming a continuous lamina, posteriorly conterminous with those on the surface of the hippocampus major, anteriorly becoming much more delicate, so much so, indeed, that it is not easy to make a complete dissection of them without causing some rents, like that on the left side shown in the figure, through which the cavity of the ventricle below is exposed. This expansion of the transverse commissure in the hemisphere, though described by PAPPENHEIM in the Opossum, appears not to have been observed by OWEN in any of his dissections.

Plate XXXVIII. fig. 1 is a view of the inner surface of the right hemisphere of the Great Kangaroo. The hemisphere is short, and deep from above downwards, obtusely pointed in front and flattened or abruptly truncated behind. The temporal lobe is largely developed. Several well-marked sulci are seen upon the surface of the hemisphere. One of the most striking characteristics presented by this section is the great development of the anterior commissure (F), far exceeding that seen in any placental mammal. The form of its section is oval, with the long diameter nearly vertical, or inclining slightly forwards at the upper end. It consists of firm, white, transverse fibres, distinctly defined from the surrounding part, and forms a good landmark to the adjoining structures, as about its homologies there can be no question. At a very short distance above this is seen the section of the median part of that transverse band before described (B). This is oval, elongated from before backwards, slightly arched on its upper border. Its anterior and posterior extremities are rounded, the former is the narrowest. To the under surface of the latter, a body of transverse fibres (N), almost equal in size to the upper portion of the commissure, is intimately united. Beneath the anterior part of this, close to the middle line, a distinct white cylindrical band of fibres is seen to pass down, behind and in close contact with the anterior commissure, at first directed somewhat backwards and afterwards downwards until it loses itself in the thalamus opticus. This evidently answers to one of the columns of the fornix, its position being somewhat disturbed by the immense development of the anterior commissure. Between the superior transverse commissure (by which name I propose for the present to call the part marked B) and the anterior commissure are some fibres continued forwards from above the anterior end of the ventricular aperture, and mixed in this region with much grey matter, forming the greatly reduced septal area (G). They curve forwards and downwards, encircling the anterior half of the anterior commissure, and represent, doubtless, those designated as "precommissural" fibres in the higher mammals. The ventricular aperture is seen to occupy its ordinary position. Its upper margin is formed by the edge of a broad white band, corpus fimbriatum (M). On tracing this band forwards, it is found to be continuous with the hinder edge of the whole of the upper transverse commissure. The superficial grey layer (P) external to the corpus fimbriatum is readily recognized as the fascia dentata. This is bounded on the outer side by the hippocampal sulcus; but in respect to this sulcus a great peculiarity presents itself. On tracing it forwards, instead of stopping short beneath the projecting posterior rounded end of the corpus callosum, as in most, if not all placental mammals *, it is continued on, passing over the top in close contact with the upper transverse commissure, and is not lost until it reaches the inner surface of the anterior lobe, considerably in advance of both the upper and anterior commissures. The remarkable disposition of this sulcus must be particularly noted in reference to the nature of the commissure in close relation with it.

In the transverse section (Plate XXXVIII. fig. 2) the immense size of the anterior commissure (F) is as conspicuously seen as in the longitudinal section. It occupies one-fourth of the whole height of the brain in the middle line. Its fibres spread themselves outwards, the lower ones sweeping first slightly downwards, then curving up into the white medullary substance of the middle of the hemisphere. The higher fibres, taking a course more directly upwards, penetrate the grey matter of the corpora striata (R R), which they here divide into two distinct masses, and finally reach the medullary substance of the upper part of the hemisphere. Lying immediately upon the anterior commissure, close to the median line, are two bodies, which, taken together, present a surface broad from side to side, slightly concave above, nearly flat below, and rounded off at the outer inferior angles. These consist mostly of grey substance, with some white fibres, especially collected into two bands close to the median line (the roots of the columns of the fornix). These bodies are the two lateral halves of the very much thickened and depressed ventricular septum. Below they are in contact with the anterior commissure, on each side with the cavity of the lateral ventricle, above with a white

* A partial exception was shown in the Two-toed Sloth.

transverse band. This band, lying at the bottom of the great longitudinal fissure of the cerebrum, is the one previously mentioned as the superior transverse commissure. Traced outwards, its fibres, spreading into an extremely thin layer, form the upper and inner boundary of the superior portion of the lateral ventricle. They have a regular curve, outwards, upwards, and finally inwards, losing themselves in the medullary substance of the hemisphere at its upper and inner angle. Their internal concave border is in contact with a fold of cortical grey matter, surrounding a deeply penetrating sulcus, which from the very bottom of the longitudinal fissure runs outwards and then upwards in the hemisphere, and which, as shown in the previous section, is continuous with the hippocampal sulcus in the posterior part of the hemisphere. The lateral ventricle, as seen in this section, is prolonged to a considerable height in the hemisphere, but otherwise its relations are similar to those of the same part in the placental mammals.

Figs. 3 & 4, Plate XXXVIII. are taken from the brain of the Wombat (*Phascolomys vombatus*). In general form the cerebral hemispheres are more depressed and elongated than those of the Kangaroo, and the temporal lobe obtains a comparatively slight development. Corresponding with this general elongation, the ventricular aperture and the surrounding parts have a wider curve backwards. The essential characters are, however, precisely the same. The anterior commissure attains an equal magnitude. The superior transverse commissure has the same form and relations, and the continuation of the hippocampal sulcus extends above it, though it is not prolonged to quite the same extent on the anterior lobe. Seen in transverse section, the septum is narrower from side to side.

The large carnivorous Marsupial, the Thylacine (*Thylacinus cynocephalus*), so widely separated in external characters from both the Kangaroo and Wombat, shows the same general peculiarities of cerebral organization, but attended with a smaller development of the superior transverse commissure, especially of its anterior part, and a greater reduction of the thickness of the interventricular septum (see Plate XXXVIII. figs. 5 & 6).

Dissections of the brains of *Phalangista vulpina* and of *Didelphis virginiana* have yielded similar results, so that it may be presumed that the principle upon which the cerebral commissures are arranged is uniform throughout the Marsupial Order.

Of the two genera of Monotremes, I have only had the opportunity of dissecting the brain of one, the Echidna. This most remarkable brain, with its largely developed and richly convoluted hemispheres, conforms in the main with the Marsupial type in the disposition of the commissures, but in detail presents a still further deviation from the ordinary mammalian form. As seen in Plate XXXVIII. fig. 7, the anterior commissure is as large relatively as in the Marsupials. Above it is seen the section of the superior transverse commissure, very much reduced in extent, and in which the two portions, upper and lower, observed in the Kangaroo are no longer distinguishable. Its relations to the hippocampal sulcus, to the ventricular aperture, to the columns of the fornix, to the precommissural fibres, and to the lateral ventricles are however the same, so that whatever parts of the placental mammalian brain are represented by this commissure in the Kangaroo, are also represented by it, though in a reduced degree, in the Echidna. Perhaps the greatest change is in the extreme reduction of the septum, as best seen in the transverse section (Plate XXXVIII. fig. 8). In dissecting the brain from above, the fibres of the superior commissure are found to spread out into a delicate layer roofing in the ventricles quite to the anterior part of the hemisphere, as described in the Kangaroo.

Having described the actual condition of an important and well-marked region of the cerebrum in several members of the two great groups of the Mammalia, it now remains to trace out the relation that the several structures entering into the formation of this region bear to one another in each of the two groups. It will be necessary also to inquire how far the results brought out by the present method of examination are in accordance with the views generally received.

At the outset a distinct confirmation is afforded by the dissections recorded in this paper, of the great fact, first observed by Professor Owen, that the brains of animals of the orders Marsupialia and Monotremata present certain special and peculiar characters, by which they may be at once distinguished from those of other mammals. The appearance of either a transverse or longitudinal section would leave no doubt whatever as to which group the brain belonged. In the differentiating characters to be enumerated, some members of the higher section present a considerable approximation to the lower; but, as far as is known at present, there is still an interval between them unconnected by any intermediate link.

The differences are manifold, but all have a certain relation to, and even a partial dependence on, each other.

They may be enumerated under the following heads:—

1. The peculiar arrangement of the folding of the inner wall of the cerebral hemisphere. A deep fissure, with corresponding projection within, is continued forwards from the hippocampal fissure, almost the whole length of the inner wall. In other words, the hippocampus major, instead of being confined as it is, at least in the higher forms of placental mammals, to the middle or descending cornu of the lateral ventricle, extends up into the body of the ventricle, constituting its inner wall.

2. The altered relation (consequent upon this disposition of the inner wall) and the very small development of the upper transverse commissural fibres (corpus callosum).

3. The great increase in amount, and probably in function, of the inferior set of transverse commissural fibres (anterior commissure).

These propositions must now be considered a little more closely. Arguing from our knowledge of the development of the brain in placental mammals (for of that of the marsupials we have at present no information), it may be supposed that the first-named is also first in order of time in the gradual evolution of the cerebral structures. Before any trace of the budding out of the fibres which shoot across the chasm separating the two hollow sac-like hemispheres, before the differentiation of a portion of the septal area into the anterior commissure, that remarkable folding of the inner wall, indicated by the deep furrow on the surface and the corresponding rounded projection in the interior, has already become distinctly manifest, and the future form of the ventricular cavity, with its elevations and depressions, has been sketched out. Now the first rudiment of the upper transverse commissure is found undoubtedly at the spot afterwards situated near its middle—that part to which in the lowest placental mammals it is almost entirely confined. This spot is situated a little way above and in front of the anterior end of the ventricular aperture, at the upper edge of the region of adherence of the two hemispheres (the future septal area). In the placental mammals this part is in direct relation to the great mass of the internal medullary substance of the hemispheres, which have to be brought into communication. In the Marsupial, on the other hand, the prolonged internal convolution or hippocampus extending up to and beyond this part, forms the inner wall of the hemisphere from which the fibres pass across, and it is necessarily through the medium of this convolution, and following the circuitous course of its relief in the ventricle, that the upper part of the hemisphere alone can be brought into connexion.

Can this transverse commissure, of which the relation is so disturbed by the disposition of the inner wall of the hemisphere, be regarded as homologous with the entire corpus callosum of the placental mammals? or is it, as has been suggested by Professor OWEN, to be looked upon as only representing the psalterial fibres or transverse commissure of the hippocampi? Undoubtedly a large proportion of its fibres do come under the latter category. But even if they should nominally be all so included, it is important to bear in mind that we have still a disposition in the marsupial brain very different from that which would remain in the brain of any placental mammal after the upper and main part of the corpus callosum had been cut away. In the latter case the commissure of a very small part of the inner wall of the hemisphere alone is left, that part folded into the hippocampus. In the former there is a commissure, feeble it may be, but radiating over *the whole of the inner wall*, from its most anterior to its posterior limits. Granted that only the psalterial fibres are represented in the upper commissure of the marsupial brain, why should the name of "corpus callosum" be refused to it? These fibres are part of the great system of transverse fibres bringing the two hemispheres into connexion with each other; they are inseparably mingled at the points of contact with the fibres of the main body of the corpus callosum, and are only separated from it in consequence of the peculiar form of the special portions of the hemisphere they unite. Indeed, as mentioned before, they are not more distinct than is the part called "rostrum" in front. And although they blend at each extremity with the fibres of the diverging posterior crura of the fornix, they certainly cannot be in any sense confounded with that body, the essential character of which is that it is a longitudinal commissure consisting of two halves closely applied in the middle, but each composed of fibres belonging to a single hemisphere only.

But is the main part of the corpus callosum of the placental mammal not also represented by the upper and anterior part of the transverse band passing between the hemispheres of the marsupial brain? The most important and indeed crucial test in determining this question, is its position in regard to the septum ventriculorum, and especially the precommissural fibres of the fornix. Without any doubt in all marsupial and monotreme animals examined (sufficient to enable us to affirm without much hesitation that it is the character common to all) it lies *above* them, as distinctly seen in the transverse sections. Moreover, passing outwards into the hemispheres, it overarches or forms the roof of the lateral ventricles of the cerebrum. This is precisely the same relationship as that which occurs in Man and all other mammalia.

The defective proportions of the part representing the great transverse commissure of the placental mammal, which appears to me to result from, or, at all events, to be related to the peculiar conformation of the wall of the hemisphere, must not lead to the inference that the great medullary masses of the two halves of the cerebrum are by any means "disconnected." The want of the upper fibres is compensated for in a remarkable manner by the immense size of the anterior commissure, the fibres of which are seen radiating into all parts of the interior of the hemisphere. There can be little doubt but that the development of this commissure is, in a certain measure, complementary to that of the corpus callosum. That it is not simply correspondent with the large size of the olfactory ganglion, as Professor Owen has suggested, is shown by the fact that in the Hedgehog and some other placental mammals this ganglion attains a far greater proportionate volume than in many marsupials, and yet the commissure is very considerably smaller.

In descending the series from Man to the Placental Mammals of lowest cerebral organization, the great change in the condition of the corpus callosum has been seen to be, the disappearance of the rostral portion, and the coincident greater development of the posterior folded or psalterial portion; the latter being connected with the relative increase of the hippocampal region of the cerebrum. In the brain of the marsupial a change of precisely the same nature is carried to an excess. There is, however, as far as my observations show, no structure characteristic of the higher group which is absent in the lower.

The step from the marsupial or monotreme brain to that of an animal belonging to one of the lower vertebrate classes is very great. Indeed it is difficult to see in many of the peculiarities of their brain even an approach in the direction of that of the bird. We may allow that the diminution of the volume of the corpus callosum leads on to its entire absence; but in the great development of the anterior commissure is presented a special characteristic of the lowest group of mammalia, most remarkable because it is entirely lost in the next step of descent in the vertebrate classes. The same may be said of the cerebral folding constituting the hippocampus major.

Plate XXXVI. figs. 5 & 6 are views of the brain of a Goose, corresponding to those given of the various mammals. The smooth, thin, inner wall has no trace of that folding upon itself which gives rise to the hippocampus major in the mammal. In this respect there is a vast difference from the brain of the marsupial. The ventricular aperture (O O) is extremely reduced. Its upper border may be properly compared to the fornix, and the thickened part of the inner wall (G), above and in front of the small anterior commissure (F), evidently corresponds to the lower part of the septal area and precommissural fibres, as well seen in the transverse section. The walls of the hemispheres are in close apposition at this part, as the two lateral halves of the septum are in the mammals; but a distinct band of fibres passing across the middle line from one hemisphere to the other, above the anterior commissure, has never yet been satisfactorily demonstrated. The homology of the minute and delicate transverse lamella of nerve-substance, described by A. MECKEL as situated above the ventricular aperture posterior to the anterior commissure, is very questionable.

Great as is the difference between the placental and implacental mammal in the mode and extent of the connexion between the two lateral hemispheres of the cerebrum, it is not to be compared with that which obtains between the latter and the oviparous vertebrate.

DESCRIPTION OF THE PLATES.

All, except fig. 3, Plate XXXVI., are from original dissections. For convenience of comparison the cerebral hemispheres are reduced to the same absolute length.

PLATE XXXVI.

Fig. 1. Inner surface of the right cerebral hemisphere, Human brain.
Fig. 2. Vertical transverse section (through the anterior commissure), Human brain.
Fig. 3. Development of the Human brain (after F. SCHMIDT). I. Sixth week. II. Eighth week. III. Tenth week. IV. Sixteenth week. V. Sixth month.
Fig. 4. Brain of Kangaroo (*Macropus Bennettii*) dissected from above, natural size. A portion of the extremely delicate great transverse commissure (B) has been removed on the left side to show the structures lying beneath it.
Fig. 5. Brain of Goose. Inner surface of right hemisphere.
Fig. 6. Brain of Goose. Vertical transverse section.

PLATE XXXVII.

Fig. 1. Brain of Sheep. Inner surface of cerebral hemisphere.
Fig. 2. Brain of Sheep. Vertical transverse section.
Figs. 3 & 4. Brain of Rabbit.
Figs. 5 & 6. Brain of Sloth (*Cholœpus didactylus*).
Figs. 7 & 8. Brain of Hedgehog (*Erinaceus europæus*).

PLATE XXXVIII.

Figs. 1 & 2. Brain of Kangaroo (*Macropus major*).
Figs. 3 & 4. Brain of Wombat (*Phascolomys vombatus*).
Figs. 5 & 6. Brain of Thylacine (*Thylacinus cynocephalus*).
Figs. 7 & 8. Brain of Echidna (*Echidna hystrix*).

Explanation of the Letters used in all the Figures.

A. Crus cerebri, divided between thalamus opticus and corpus striatum.
B. Body of corpus callosum.
C. Genu of corpus callosum.
D. Rostrum of corpus callosum.
E. Splenium of corpus callosum.
F. Anterior commissure.
G. Septal area.
H. Septum lucidum.
I. Precommissural fibres.
K. Body of fornix.
L. Columns of fornix.
M. Corpus fimbriatum. Edge of posterior crura of fornix.
N. Psalterial fibres of corpus callosum.
O. Ventricular aperture.
P. Fascia dentata.
Q. Hippocampal sulcus.
R. Corpus striatum.
S. Third ventricle.
T. Peduncles of pineal body.
U. Thalamus opticus.
V. Corpora quadrigemina.

Fig. 1.

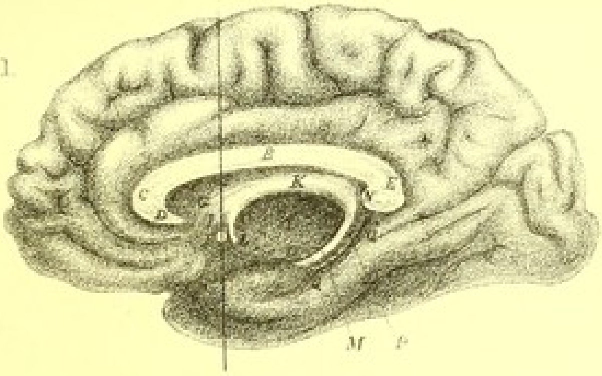
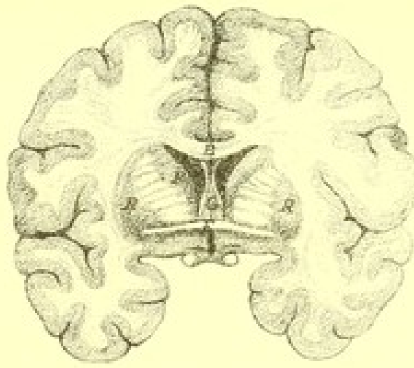


Fig. 2.



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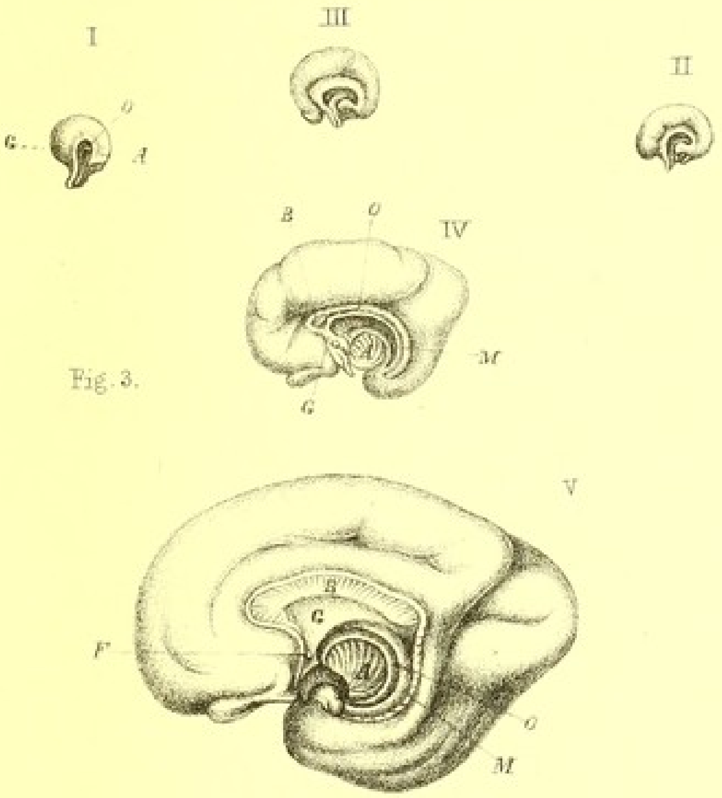

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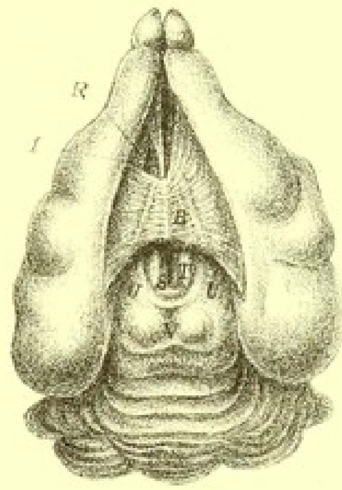

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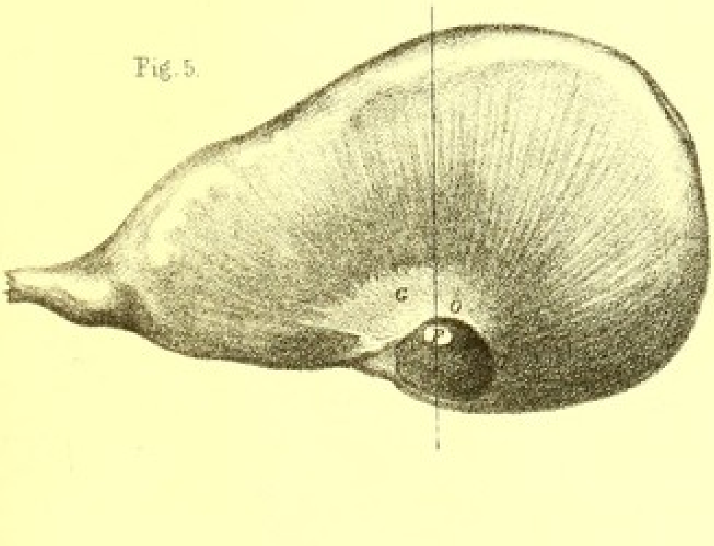
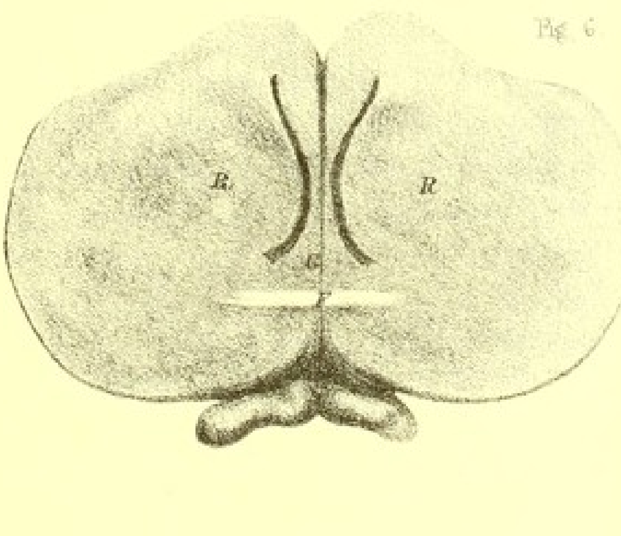
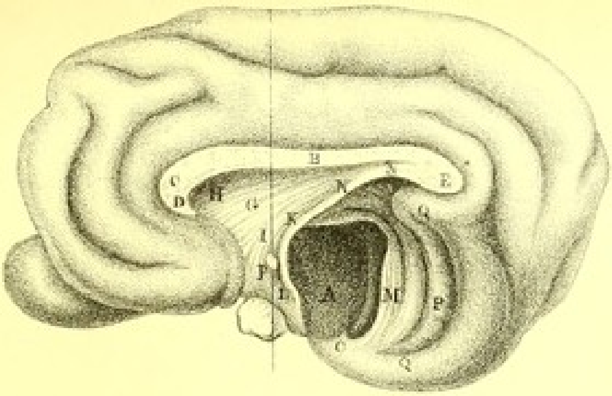


Fig. 6



H.F. ad. nat. del. (except Fig. 3)

Edwin M. Williams



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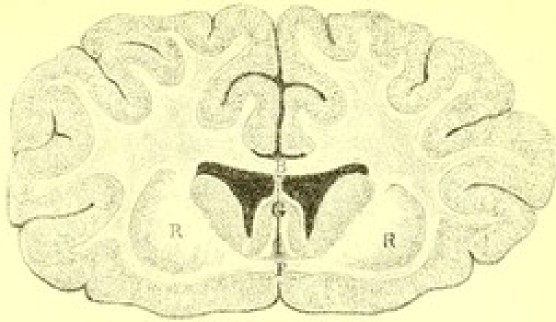

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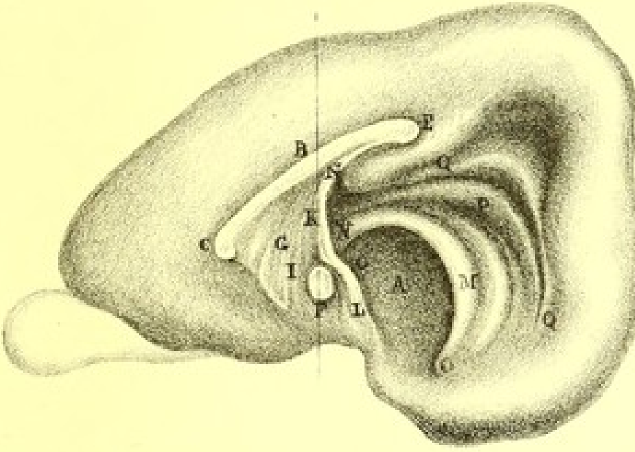

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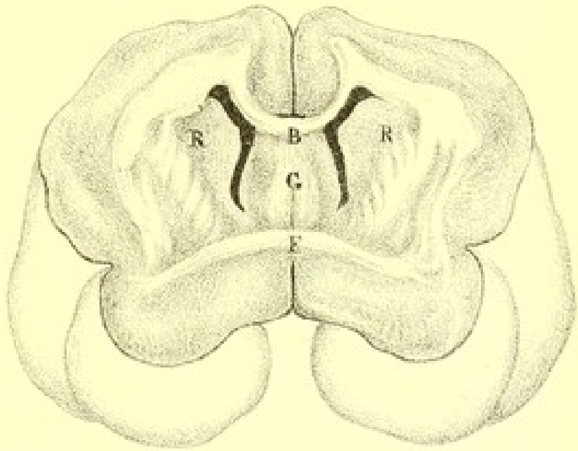

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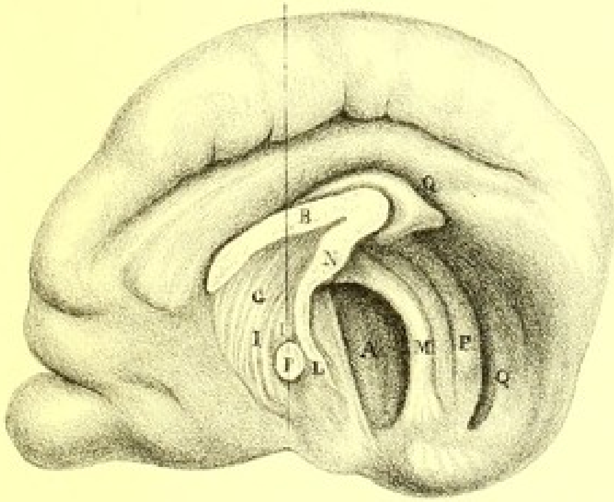

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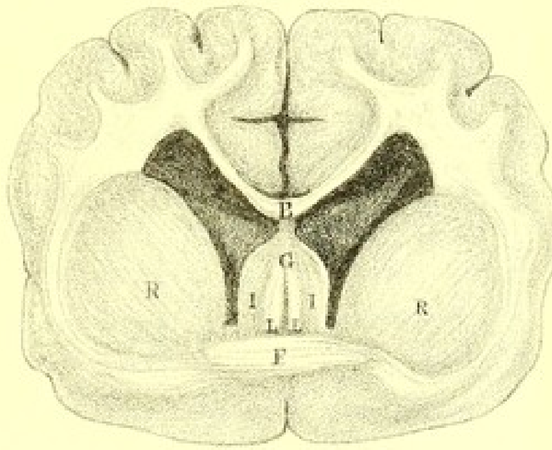
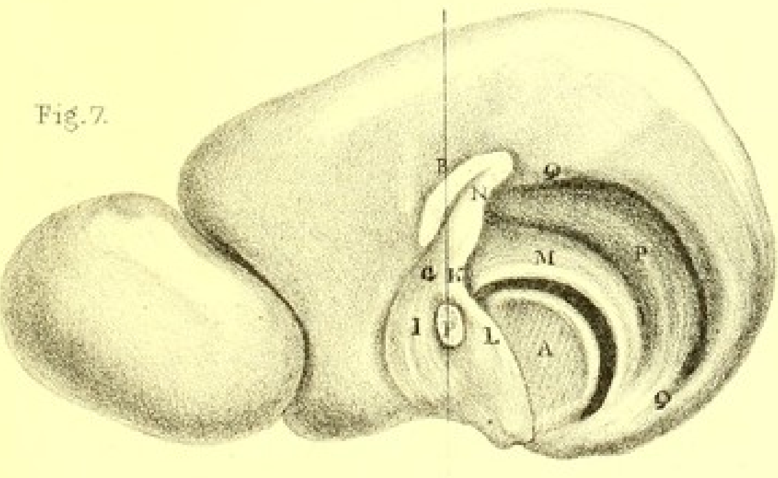


Fig. 6.

Fig.7.



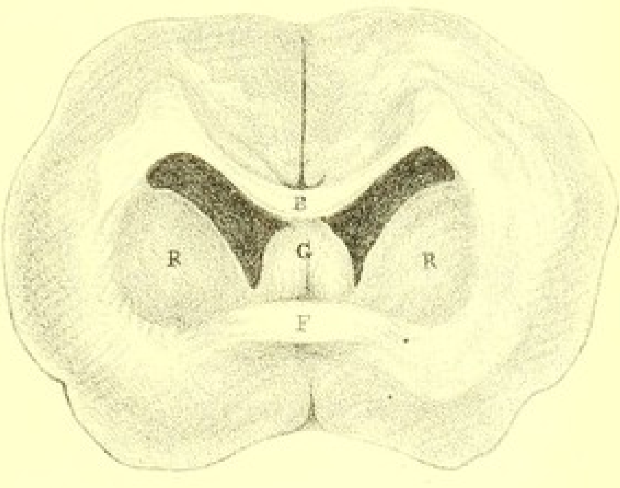
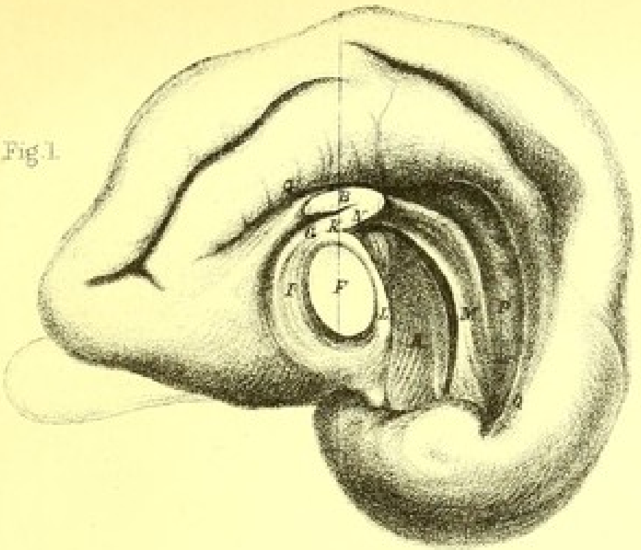


Fig.8

Fig. 1.



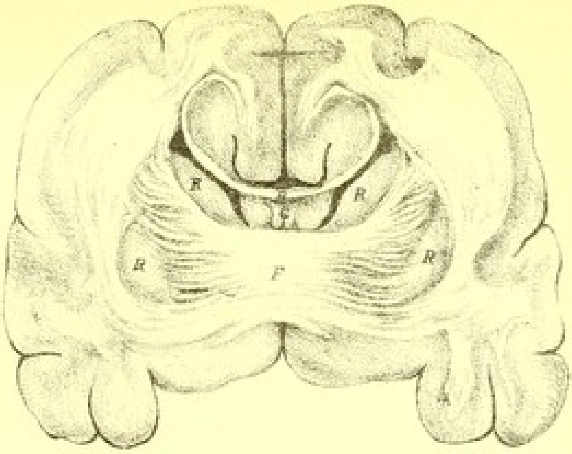
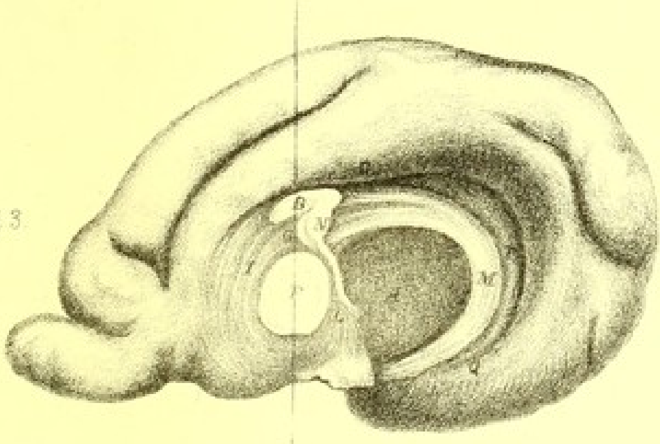


Fig. 2.

Fig. 3



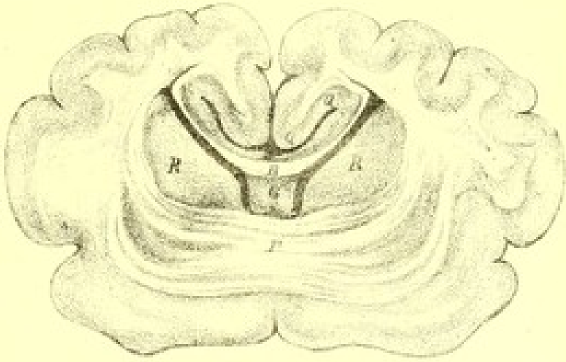
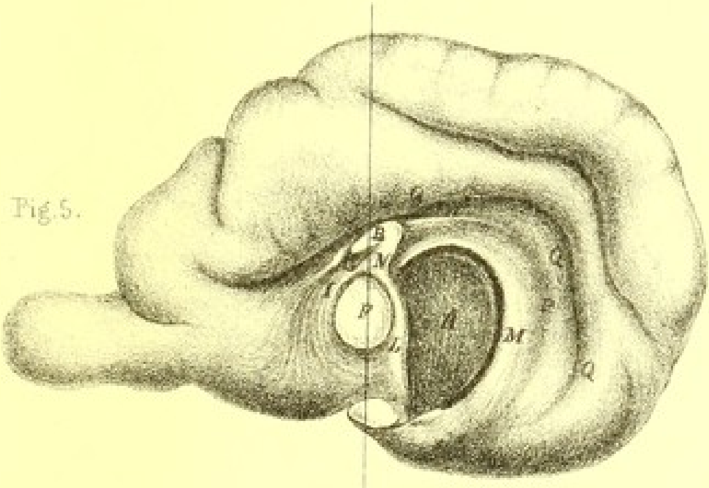


Fig. 4.

Fig. 5.



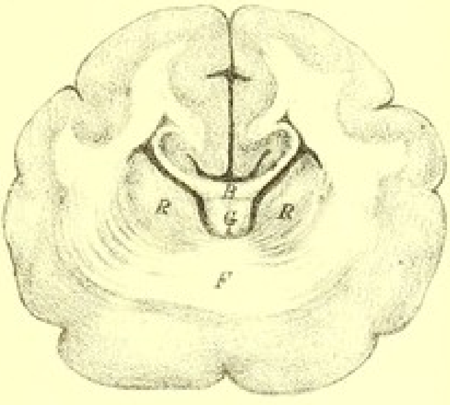
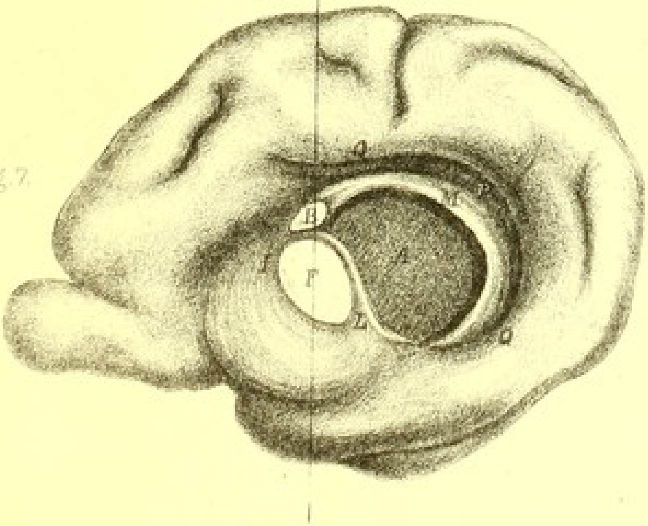


Fig. 6.

Fig. 7.



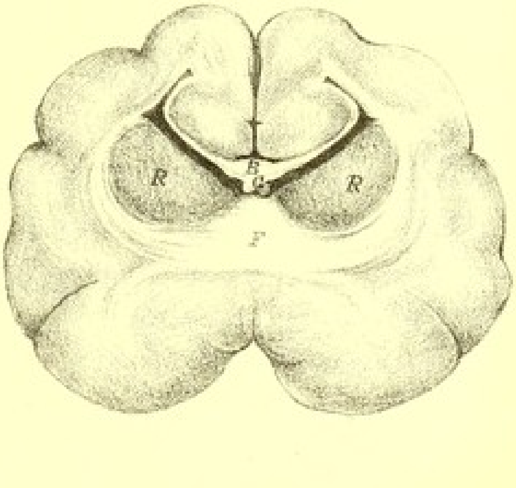


Fig. 8.