III. *The Origin of the Corpus Callosum: a Comparative Study of the Hippocampal Region of the Cerebrum of Marsupialia and certain Cheiroptera.* By G. ELLIOT SMITH, M.D., Ch.M. (Sydney), "James King" Research Scholar of the University of Sydney; St. John's College, Cambridge. (Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

(Plates 15 & 16.)

Read 21st January, 1897.

IT is now a generally recognized fact that the dorsal commissure of the Metatherian is not strictly homologous to the similarly-situated commissure of the Eutherian cerebral hemispheres. For while the dorsal commissure of the Marsupial springs mainly, if not wholly, from that peculiar cortical formation which we know as "*hippocampus*," its topographical representative in the more highly-organized mammal is derived from a much wider cortical area, of which the hippocampus constitutes a part—and in the great majority of cases only a relatively very small part. In other words, the dorsal commissure of the Metatherian is essentially "hippocampal," while that of the Eutherian cerebrum is partly "hippocampal" and partly "non-hippocampal." These "non-hippocampal" fibres of the dorsal commissure of Eutheria are derived from the general or typical cortex which Sir William Turner calls "*pallium*."

It will be found that in higher mammals, such as the Primates, the Cetacea, the Carnivora and Ungulata, the "pallial" element forms the main bulk of the dorsal commissure. But if we compare a large series of mammalian cerebra we find that, speaking generally, there is a rapid decrease in the extent and importance of this "pallial" factor as we descend the Eutherian scale. The "pallial" or "non-hippocampal" factor shows a rapid actual decrease, while the hippocampal factor takes a continually increasing share in the constitution of the dorsal commissure. From such considerations, and from the knowledge that the "pallial" factor was wanting altogether in the Marsupialia, it seemed likely that some Eutherian form might be found in which the newer "non-hippocampal" element might be so slightly developed as not to interfere with or destroy the resemblance of its dorsal commissure to that of the Marsupial. And if such a transitional form could be found we ought to be able to decide the exact relation of the newly-developed "pallial" fibres to the pre-existing "hippocampal" fibres, and hence form some accurate conception of the nature of this new commissure, which in its highly-developed state in man we know as the "*corpus callosum*."

The desired "connecting links" I have had the good fortune to find in certain Cheiroptera—*Nyctophilus Timoriensis* and *Miniopterus Schreibersii*—both of which, but more especially the former, realize the conditions above stated.

In this contribution I propose to compare the commissures and certain neighbouring

cortical areas of these bats with the Marsupial type, in order to find out the distinctive mode of arrangement of the former. Having determined the nature of the dorsal commissure of the bat and its relation to the pre-existing type, I shall attempt, by means of comparison with more highly-developed Eutherian forms, to indicate the true lines along which the evolution of the corpus callosum proceeds in the Mammalia.

For a considerable time I have been aware of the fact that Zuckerkandl, in his remarkable work upon the olfactory centre ('Ueber das Riechcentrum,' 1887), had grouped together the brains of Monotremes, Marsupials, and certain small Cheiroptera on the ground that they presented in common certain features in which they differed from all other mammals.

These distinctive features were stated in the following terms:—(1) that the Randbogen [or Randwindung—*Gyrus marginalis* *] retains its embryonic form; *i. e.* that it is in all parts equally broad, and extends up to the Ammonsfurche *, and is continuous with the mesial wall of the hemisphere anteriorly; (2) that the corpus callosum is rudimentary; and (3) that the Balkenwindung * is wanting.

From the fact that Zuckerkandl uses the term Randbogen instead of hippocampus we might infer that he did not definitely recognize the dorsal part of the Randbogen as hippocampus—an inference which is borne out by his reference to the corpus callosum. If any other evidence were needed to show that Zuckerkandl quite failed to appreciate the most salient features of the Monotreme and Marsupial cerebrum, it is provided in his remarks upon the cerebrum of *Echidna*, where he speaks of the fascia dentata as "der ventrale Schenkel des Randbogens." This clearly indicates that he did not recognize the dorsal limb of the Randbogen as fascia dentata or hippocampus. [It is only right to mention that Zuckerkandl's work appears to have been purely macroscopic.]

Thus Zuckerkandl reduces the cerebrum of the Marsupial and Monotreme to the conventional Eutherian type, possessing a true corpus callosum, and with a hippocampus practically limited to the descending limb of the lateral ventricle. Such being the case, until quite recently I paid little heed to his remarks concerning the resemblance of *Vespertilio murinus* (the bat of which he examined the brain) to the Marsupial type; for, having reduced the Marsupial to conformity with a simple Eutherian type, it seemed very natural to group an actual example of such a type (which the bat provides) with the Marsupial.

But quite recently, upon examining the brain of a common Australian bat (*Nyctophilus Timoriensis*), I was struck by the remarkable resemblance which its hippocampus (Zuckerkandl's Randbogen) and cerebral commissures present to the Metatherian type. It appeared to be a case of reducing the bat to the Metatherian condition rather than advancing it to the Eutherian status, as Zuckerkandl's researches would appear to indicate. In the course of this communication we shall see how far this appearance is justified by the histological examination of *Nyctophilus* and *Miniopterus*.

The object of this paper being to consider phylogenetically the origin of the true corpus callosum (as distinct from the hippocampal commissure), we are solely concerned with the transition from the condition found in the Proto- and Metatheria, in which

* These terms will be explained subsequently.

the true corpus callosum is wanting, to the Eutheria, in which alone that structure is found. This relieves us from the necessity of discussing the writings of Osborn and many others who have based their researches primarily upon the examination of some sub-mammalian form, and from this treacherous standpoint have advanced hypotheses to include the Mammalia.

Since Flower ('Philosophical Transactions,' 1865) compared the cerebral commissures of the Marsupial with those of certain lowly-organized Eutheria, in order to determine the nature of the former, no one, so far as I know, has dealt with the subject from this comparative standpoint. But while Flower compared the two series in order to throw light upon the Marsupial, I am instituting the reverse process of comparing the Cheiroptera with the more distinctly defined Metatherian type.

Within the last three years the labours of Blumenau *, Marchand †, and Paul Martin ‡ have added considerably to our knowledge of the process of development of the corpus callosum in the higher mammals. And it is very instructive to compare the progress of the developing commissure in man or the cat with the stages of its phylogeny with which this contribution deals.

The following statements concerning the ontogenetic process are a free translation of certain of Martin's conclusions (*loc. cit.*):—A thickening takes place in the lamina terminalis, which later disappears; but before the disappearance the first fibres of the corpus callosum appear in the dorsal part of the thickening. [Martin throughout uses the term corpus callosum (Balken) in the sense of the whole dorsal commissure, including the hippocampal commissure. This will be apparent from the next statement.] The first "callosal" fibres spring from the posterior columns of the fornix. The ventral part of the corpus callosum [the psalterium] consists of fibres which run in the inner Randbogen. The splenium is composed of fibres which extend from the inner and outer Randbogen to the other side. The body and genu of the corpus callosum consist of fibres passing through the outer Randbogen. The cavum septi pellucidi is formed during the disappearance of the thickened lamina terminalis, partly in the place of the disappearing thickening, but mainly by the inclusion of a part of the longitudinal fissure of the cerebrum by the corpus callosum. For a long time it is open naso-ventrally. Upon the ventral side of the corpus callosum a gradual "soldering" of the hemisphere-walls takes place in the situation of the cavum septi. The corpus callosum increases by intussusception as well as by apposition of fibres. The striæ longitudinales are formed in part by the upper Randbogen. The thickened lamina terminalis contributes towards the formation of the caudal part of the striæ mediales.

In the subsequent consideration of the results of our comparison we will see the extent to which the ontogenetic process recapitulates the phylogenetic history. At the

* "Zur Entwicklungsgeschichte und feineren Anatomie des Hirnbalkens," Archiv für mikroskopische Anatomie, Bd. xxxvii. 1891, pp. 1-14, Taf. i.

† "Ueber die Entwicklung des Balkens im menschlichen Gehirn," Archiv für mikroskopische Anatomie, Bd. xxxvii. 1891, pp. 298-334, Taf. xv., xvi.

‡ "Bogenfurche und Balkenentwicklung bei der Katze," Jenaische Zeitschrift für Naturwissenschaft, Bd. xxix. 1895, pp. 221-252, Taf. ii. and 13 figures in text.

same time we will see how the latter explains much that is apparently meaningless and purposeless in the ontogenetic process.

From the foregoing remarks concerning the scope of this investigation, it must be evident that we are mainly concerned with the hippocampal region of the two types of cerebrum. In other words, we are going to study and compare the dorsal commissure of the Marsupial, which is "hippocampal," with its topographical representative in the bat, which is mainly "hippocampal." It is therefore necessary to have a clear and definite idea of disposition of the hippocampal region of the Metatherian cerebrum; and we may first of all consider the hippocampus of *Perameles nasuta*, which exhibits very clearly the distinctive features of the Marsupial brain (mainly by means of sections stained by the Weigert method).

I have not yet been fortunate enough to get specimens of the brain of *Nyctophilus* in a condition suitable for the application of the Weigert stain. But the resemblance to the Marsupial type is so great that with the aid of the lithium carmine stain quite sufficient detail can be made out to reveal the distinctive features of the region with which we are concerned. I hope soon to be able to supplement these notes by a fuller paper on the brain of *Nyctophilus*, studied by more specialized neurological methods*.

My friends Mr. James P. Hill and Mr. J. Macpherson, of the University of Sydney, very kindly placed at my disposal four brains of *Nyctophilus* which were in a good state of preservation, though hardened only in alcohol. My friend Dr. R. Broom, who was at Taralga working at the organ of Jacobson in *Miniopterus*, kindly gave me the brain from one of his specimens. Mr. Robert Grant, the able assistant in the Physiological Laboratory at Sydney, stained and cut series of coronal, sagittal, and oblique sections from these specimens. To these gentlemen I acknowledge my deep gratitude and great indebtedness.

This work was done mainly in the Anatomical Department of the University of Sydney, and has been completed—so far as such an unfinished work can be said to be—in Cambridge.

The Hippocampal Region in the Marsupial.

The mesial wall of the descending limb of the lateral ventricle of the cerebrum of the Marsupial presents a marked prominence, which extends in the long axis of the ventricle. This is the *hippocampus*—the homologue of the *hippocampus major* of the Primate brain. In its histological structure and in the disposition of its constituent parts this region of the Metatherian cerebral hemisphere agrees exactly with the corresponding part of the Eutherian, so that in seeking for distinctive features of the two types of brain it may be neglected. We will therefore begin the study of the brains under consideration at a point just in front of the place where the lateral ventricle begins to curve downward to form its descending cornu.

The first figure (Pl. 15. fig. 1) represents a coronal section through the forebrain of

* Since this was written I have confirmed, by means of preparations stained by Weigert's method, all the observations concerning *Nyctophilus* which are here recorded.

Perameles nasuta at about the junction of body and descending limb of the lateral ventricle. This corresponds to a situation almost immediately behind the commissures of the hemispheres, as we shall see later.

In this section the 'tween-brain—a somewhat square-shaped mass with rounded corners—will be seen to occupy the ventral mid-region. The basal part of the thalamic region lies upon the optic tract (*o.tr.*), which may be seen extending into the furrow between the hemisphere (the region of the *nucleus amygdalæ, n.a.*) and the 'tween-brain. The two halves of the optic thalamus are connected by means of a broad bridge of grey matter—the *commissura mollis (c.m.)*—and above and below the latter portions of the third ventricle may be observed. The small recess of the third ventricle lying above the soft commissure is roofed by a somewhat dome-shaped epithelial fold, which is attached on either side to a ridge containing a longitudinal band of medullated fibres—the *stria medullaris thalami (s.m.t.)*.

Upon its lateral aspect the thalamic region fuses with the corpus striatum of the cerebral hemisphere, and a mass of medullated fibres, cut either transversely or obliquely, indicates the place of union. The corpus striatum consists of two parts, which are separated one from another by the internal capsule (*c.i.*). A smaller grey mass, lying above the internal capsule and projecting into the lateral ventricle, is the *nucleus caudatus (n.c.)*. A larger grey mass lying below the internal capsule is the *nucleus lenticularis (n.l.)*. The ventral part of the nucleus lenticularis (*n.a.*) is the homologue of the grey mass known in human anatomy as the *nucleus amygdalæ*. It is directly continuous with a cortical area of distinctive structure known as the *pyriform lobe (py.l.)*, from which the nucleus lenticularis in its upper part is separated by a layer of medullated fibres (the *external capsule, c.e.*).

Along its dorsal border the pyriform lobe is separated from the general cortex (which Turner calls "*pallium*," *p.*) by the shallow *rhinal fissure (f.r.)*. Above the corpus striatum, where the lateral wall and roof of the ventricle are formed by this general cortex or *pallium*, the inner lining of the latter is formed by a mass of medullated fibres—the *corona radiata (c.r.)* of writers. If the cortex be traced in a mesial direction its edge will be found to present those peculiarly distinctive features which we at once recognize as *hippocampus*. Thus if the mesial wall of the hemisphere be traced downward in the section (fig. 1, Pl. 15) we reach a deep indentation—the *hippocampal fissure*, and corresponding to this fissure a marked prominence into the lateral ventricle forming the hippocampus (*hip.*). Below the hippocampal fissure the characteristic features of the *fascia dentata (f.d.)* (which we shall consider subsequently) are immediately recognizable. And extending into the deep depression between the nucleus caudatus (*n.c.*) and optic thalamus is the prominent *fimbria (fi.)*, spur-like in transverse section. [In order to avoid an unnecessary confusion in the figure, the choroidal fold of the lateral ventricle which is attached to the fimbria has not been represented.]

Having thus seen how the "hippocampal formation" constitutes the edge of the cortex cerebri, I propose to carefully examine the series of changes which this peculiar formation undergoes as we trace it forward in a series of coronal sections of the cerebrum of the bandicoot (*Perameles*).

A coronal section through the cerebrum, just in front of that represented in the first figure, presents a marked change in the appearance of the hippocampal region, which is represented upon an enlarged scale in fig. 2. The hippocampus itself, as well as the fascia dentata, have undergone practically no change, but a huge bundle of medullated fibres from the upper part of the fimbria is now exposed in the act of crossing the middle line. This is the posterior extremity of what—to avoid confusion of terms—will for the present be termed the *commissura dorsalis* (C.D.).

It would be foreign to the scope of this work to describe in detail the histology of the hippocampal formation, seeing that the minute structure of the Metatherian hippocampus is identical with that of the Eutherian, which Sala, Schaffer, Ramon y Cajal, and von Kölliker*, among many others, have so carefully and minutely described within recent years. But I wish to call attention to certain features which are intimately associated with the evolution of the structure we are primarily considering.

Lying upon the upper surface of the “*dorsal commissure*” (C.D.) there is a complicated epithelial fold the outline of which is roughly triangular, and which projects upward into the great cleft between the two cerebral hemispheres. The fascia dentata (*f.d.*) lies in contact with this epithelial (choroidal) fold on either side, and may be easily recognized by certain distinctive features. Thus it possesses a very thickly-packed column of small cells—the *stratum granulosum* (*s.gr.*)—the nuclei of which stain very deeply, lying parallel to the surface, from which they are separated by a clear layer almost devoid of cells—the *stratum moleculare*. The fascia dentata—consisting of stratum granulosum and stratum moleculare—is folded in a peculiarly characteristic manner. Its mesial extremity is completely bent upon itself, so that the stratum moleculare or superficial layer rests upon the dorsal aspect of the *dorsal commissure*. The lateral extremity of the fascia dentata undergoes a corresponding bending, the concavity of which is directed toward the mesial plane. It would appear that the fascia dentata had continued to increase in breadth whilst its mesial and lateral extremities were relatively fixed, and, to accommodate itself to these conditions, it had bulged out into a pouch, as it were, and at the same time become flattened by the resistance of the general cortex lying immediately above it. Such factors, in reality, seem to have been at work, as I have recently pointed out†. The fissure which separates the fascia dentata from the general cortex where their respective superficial layers come into contact is the *fissura hippocampi* (*f.h.*).

The concavity of this pouch of fascia dentata is occupied by scattered nerve-cells, many of which give origin to the brush of medullated fibres which are to be seen in the figure, collecting near the inner margin of the fascia dentata, to lose themselves in the huge mass of medullated fibres lying immediately below.

The hippocampus proper projects as a large rounded swelling into the lateral ventricle. This swelling is covered by a thick layer of medullated fibres—the so-called *alveus* (*alv.*). These fibres almost all pursue an oblique course, so that in a coronal section only short pieces of fibre are seen massed together. In the first figure most of the fibres of the

* ‘Gewebelehre des Menschen,’ Bd. ii. zweiter Hälfte, 1896.

† “The Fascia Dentata,” Anatomischer Anzeiger, xii. Bd. Nr. 4 und 5, 1895, p. 119.

alveus are tending towards the fimbria, but in the section under consideration many fibres of the alveus, as well as fibres coming from the "pouch" of the fascia dentata, proceed directly into the *commissura dorsalis* along with many fibres of the fimbria which have come from more caudally situated regions of the hippocampus. It will be noticed, however, in the figure that as yet only the upper part of the fimbria is contributing fibres to the commissure. The tip of the fimbria, which contains fibres coming from the most distant parts (temporal pole) of the hippocampus, is yet undisturbed and has given no contribution to the dorsal commissure. Between the alveus and the curved lateral part of the hippocampal fissure there is a broad, more or less definitely stratified region. Slightly nearer to the alveus there is a very uniform and clear layer (in specimens stained by Weigert's method). This is the layer of "pyramidal cells," and consists of a closely-packed column of large cells, which stain moderately with ordinary stains. Between the layer of pyramids (*pyr.*) and the alveus (*alv.*) there is a stratum containing scattered polymorphous cells and very abundant medullated nerve-fibres—the *layer of polymorphous cells*. The space between the hippocampal fissure and the layer of pyramids is usually divided by writers into three zones—a broad clear layer next to the layer of pyramids (*stratum radiatum, s.r.*), a thin superficial layer (*stratum zonale*), and an intermediate layer very rich in medullated nerve-fibres (*stratum lacunosum, s.l.*).

A large number of fine medullated fibres (*x*) extend from the region of the layer of pyramids through the stratum radiatum into the stratum lacunosum. These fibres are very distinct in the region bordering upon the fascia dentata (*vide fig.*). In the stratum lacunosum many of these fibres end by means of free branching in relation to the processes of the pyramidal cells, which extend through the stratum radiatum into the more superficial regions. But a considerable number of medullated fibres assume a longitudinal direction (*i. e.* in the long axis of the hippocampus) as soon as they reach the stratum lacunosum (*s.l.*). These fibres, which may be called "*longitudinal association fibres of the hippocampus*," appear in transverse section (*s.l.*) as rounded bundles immediately surrounding the lateral or deeper part of the hippocampal fissure.

In the general cortex (*p.*) the cells are scattered throughout the whole thickness of the cortex, whereas in the hippocampus (leaving out of account the fascia dentata) the great majority of the nerve-cells are crowded together into the regular row of pyramids. The transition-region from typical cortex to typical hippocampus is generally known as the *subiculum cornu ammonis* (*sub.*). Whether the "subiculum" ought to be grouped with the general cortex or with the hippocampus is a question to which we shall have to refer subsequently. The deepest layer of the general cortex consists of a mass of medullated fibres—the *corona radiata*. It will be noticed at a glance that while the fibres derived from the hippocampus and "subiculum" proceed into the alveus, those derived from the general cortex proceed away from the alveus, *i. e.* towards the external capsule. At the point of meeting of alveus and corona radiata there is obviously a commingling of fibres, but it is equally clear that any passage of fibres from the alveus into the "corona" or *vice versa* is either non-existent or extremely slight and practically negligible. In the adjoining regions there are groups of longitudinal fibres belonging respectively to the two distinct formations, and it is quite possible that an interchange between these two

series *may* take place. The longitudinal series belonging to the margin of the general cortex or pallium is the so-called *cingulum* of higher forms (figs. 6 & 11, *cing.*, *cing.*¹). There are, however, definite bonds of union between hippocampus and general cortex which are found in their junction. Thus from the stratum zonale and stratum lacunosum of the hippocampus fibres extend not only into the "neutral ground," so to speak, of the "subiculum cornu ammonis" but well into the molecular layer of undoubtedly true cortex. This is a definite association bundle between hippocampus and pallium, which may be called *tractus hippocampi ad pallium* (fig. 2, *y*).

As the hippocampal region is successively examined in a series of coronal sections, the main features of the hippocampal formation itself remain unchanged for some time, but its commissure—the *commissura dorsalis*—undergoes marked changes.

Thus the depth of the commissure rapidly increases at the same time that the prominence of the fimbriæ is diminishing (fig. 3). The meaning of this is that an increased number of fibres from the fimbria are crossing in the dorsal commissure. The scheme (fig. 4) of the commissures as they are seen in sagittal section explains the meaning of these changes.

In figure 5 a new factor for the first time becomes evident. Upon the lateral aspects of the commissure, more especially upon the right side of the figure, a mass of grey matter (*s*) will be observed to enclose the dorsal commissure and to become continuous ventrally with a mass enclosing a second commissure—the *commissura ventralis*. This grey mass enclosing the two commissures will for the present be distinguished as the "*commissure-bed*." On either side it will be noticed to become continuous by a narrow bridge of grey matter with the *corpus striatum* (*c.st.*). In this narrow bridge there are a number of longitudinally-coursing nerve-fibres (*s.t.*). These are the uncrossed fibres of the *stria terminalis*, the other fibres of which may be seen entering the ventral commissure (*s.t.*) in figure 3 to cross to the other side. In figure 5 the dorsal commissure has reached its greatest depth.

Figure 6 shows the appearance which is presented by a section after all the commissural fibres of the fimbria have crossed. The thin *commissura dorsalis* (*c.d.*) is derived from the corresponding region of the hippocampal formation. The huge *commissura ventralis* (*c.v.*) appears to become continuous with the *capsula externa* (*c.e.*), which, after being joined by fibres of the *capsula interna* (*c.i.*), becomes the *corona radiata*. The dorsal and ventral commissures lie in the large mass of grey matter which forms the *commissure-bed*. A thin lamina (*i*) of this grey mass may sometimes be distinguished upon the dorsal aspect of the *commissura dorsalis*. This may be distinguished as the "*indusium verum*."

The "*commissure-bed*" (*s*) contains large numbers of uncrossed fibres (*d.f.*), which are derived from the alveus of the hippocampus (which is situated above them) and from the fimbria. These fibres are divided into two groups by the ventral commissure. The *postcommissural fibres* (*columna fornicis*, *c.f.*) collect upon the dorsal aspect of the ventral commissure and incline backward and downward to enter the thalamic region. The *precommissural fibres* proceed downward and forward in front of the ventral commissure.

As we proceed forward in the examination of coronal sections, the dorsal commissure will be found to become gradually thinner and finally disappear altogether, while the *descending fornix-fibres* remain unchanged. The ventral commissure disappears in about the same coronal plane. The "*commissure-bed*" extends a slight distance further forward before the hemispheres become separated one from another.

Figure 7 represents (about four times the natural size) the appearance of a coronal section immediately in front of the place where the hemispheres become separated from each other.

In this figure the hippocampus is again easily recognizable, although its conformation has become greatly simplified. The *fissura hippocampi* (*f.h.*) is much shallower, and the hippocampal projection into the ventricle less prominent. The fascia dentata is much narrower, and consequently much less folded. The thin alveus may be seen proceeding directly into the mass of *descending fornix-fibres* which occupy the superficial portions of the grey mass which we may call the "*corpus præcommissurale*"*, but which is really only the anterior continuation and homologue of the grey mass which further back has been called "*commissure-bed*." The other features of the section do not concern us in considering the hippocampal formation. The only other point to which I wish to call attention is that the "*corpus præcommissurale*" is directly continuous below the lateral ventricle with the corpus striatum, where the latter is capped by the peculiar cortex which Ganser calls the "*cortex of the head of the corpus striatum*," and which corresponds to the "*tuberculum olfactorium*" (*t.o.*)—such a prominent feature upon the ventral aspect of this brain.

If we were to trace these various structures forward in a series of coronal sections, we should find that the hippocampal fissure would become gradually shallower until it eventually disappeared, the prominence in the ventricle disappearing *pari passu*. The fascia dentata, now placed entirely upon the surface, becomes narrower and less clearly differentiated, until at last we fail to recognize any distinguishing feature of a hippocampus. But by the time this has occurred we have arrived almost at the olfactory peduncle. In certain Marsupial brains (*Dasyurus viverrinus*) it is even possible to distinguish the hippocampal formation as far forward as the olfactory peduncle, so that here we have the "*precommissural area*" completely cut off from the general cortex or pallium (*p.*) by a hippocampal band, as semi-schematically represented in figure 8 (*hip.*" & *f.d.*). This is the primitive condition of the hippocampus, which is found (although recognized with difficulty) in the Reptile, and which I have already described in the foetal *Ornithorhynchus* (Qu. Jour. Mier. Sci. vol. xxxix. pp. 181–206).

Figure 9 represents the appearance which this region presents in *Perameles* when viewed from its mesial aspect.

In this figure the optic nerve (*opt.*) is seen extending towards the lamina terminalis, at the inferior extremity of which is the oval section of the optic tract (*o.tr.*). Extending upward from the optic tract is the thin ventral portion of the lamina terminalis—the *lamina cinerea* (*l.c.*). At its upper part this lamina expands to enclose the large

* By "*corpus præcommissurale*" is meant that grey mass the mesial surface of which is the "*precommissural area*" (*p.a.*).

commissura ventralis (c.v.), oval in section and placed obliquely. Extending upward from the ventral commissure there is a thick mass of grey matter—the “*commissure-bed*” (*s*)—which contains in its upper part the *commissura dorsalis* (c.d.), shaped somewhat like an inverted obliquely placed V with the dorsal limb nearly horizontal.

Above the dorsal commissure the *fascia dentata* (*f.d.*) is easily recognizable and is separated from the general cortex (*p.*) by the *fissura hippocampi* (*f.h.*). Anteriorly the hippocampal fissure gradually becomes shallower until it can no longer be traced, so that the fascia dentata, the stratum zonale of the hippocampus, which now of course lies upon the surface (compare figure 8, *hip.*"), and general cortex (*p.*) are indistinguishable. Upon its ventral side the fascia dentata becomes directly continuous with the extensive pale region which constitutes the “*precommissural area*” (*p.a.*). In the forward direction the “*precommissural area*” is directly continuous with the mesial wall of the extremely short olfactory peduncle, which connects the hemisphere with the olfactory bulb (*o.b.*). Upon its ventral side the “*precommissural area*” becomes continuous with the grey boss generally known as the “*tuberculum olfactorium*” (*t.o.*).

By means of this representation of the anterior portion of the mesial wall of the hemisphere of *Perameles* (fig. 9), and the semi-schematic representation of the corresponding region in *Dasyurus* (fig. 8), we obtain a good general idea of the anatomy of the commissural region.

In *Dasyurus* it will be observed that the *dorsal commissure* is not so distinctly bilaminar as it is in *Perameles*; and in *Phascolarctos* (Pl. 16. fig. 10) it can hardly be called bilaminar. Thus we have in the Marsupial all the intermediate stages between the rounded dorsal commissure of *Ornithorhynchus* and *Echidna* and the distinctly bilaminar form found in most mammals. There are certain important features of this region which can only be demonstrated by sagittal section, which we will consider almost immediately. But before leaving the consideration of figure 8, I wish to call attention to the possible consequences of elongation of the *commissura dorsalis*.

The “*commissura dorsalis*” is contained in the mass of grey matter which I have called the “*commissure-bed*,” the separate anterior prolongations of which in the two hemispheres are formed by the “*corpora præcommissuralia*”—the grey masses corresponding to the surface-region of each hemisphere, which is distinguished as “*precommissural area*.” Now this combined grey mass—“*commissure-bed*” and “*corpus præcommissurale*”—is separated from the general cortex (pallium) above it by the hippocampus; and the dorsal limb of the commissure separates the “*commissure-bed*” from what we may call the “*supracommissural hippocampus*,” while the “*corpus præcommissurale*” becomes directly continuous with what we may call the “*precommissural hippocampus*.” Now it is clear that if the dorsal commissure elongates in the forward direction it must cut off part of this “*precommissural*” body from the *precommissural hippocampus*, which becomes “*supracommissural*.” The structure lying upon the ventral aspect of such an elongated dorsal limb of the *commissura dorsalis* must be either “*commissure-bed*” or “*corpus præcommissurale*.”

Figure 10 represents the appearance of a sagittal section through the corresponding region in the brain of *Phascolarctos cinereus*, after staining by the Weigert method. Between the small *commissura dorsalis* (c.d.) and the large elliptical *commissura ventralis* (c.v.) a large number of non-crossing fibres will be noticed in the "commissure-bed" and "precommissural area." Of these the postcommissural form the *columna fornicis* (c.f.). The precommissural area contains various sets of fibres. The largest group (α) connect the alveus hippocampi and the basal region of the brain just behind the tuberculum olfactorium (t.o.). In *Ornithorhynchus* I distinguished these fibres as the "hippocampo-basal association bundle" *. Other fibres (β) pass backward below the ventral commissure to enter the subthalamie region, where they become lost. Fibres entering into the constitution of these two series may be seen in the precommissural area (in the region marked *p.a.*), proceeding from the most anterior part of the hippocampus. Fibres may also be seen proceeding directly from the olfactory peduncle (and probably bulb) to enter the fascia dentata (*f.d.*). This is the *olfactory bundle of the fascia dentata* (γ). Other fibres belonging to the same series (δ) may be seen proceeding backward above the dorsal commissure as a well-defined tract, probably homologous with the nerve-fibres of the *stria medialis Lancisii* of the higher mammalian brain.

In the Marsupial, a typical hippocampal formation lies upon the dorsal aspect of the commissura dorsalis. In this hippocampal formation there are two important series of longitudinal fibres, which are displayed most clearly in a horizontal section. Such a section of the cerebral hemisphere of *Trichosurus vulpecula* is represented in fig. 11. In this figure (as also in fig. 2) a large series of longitudinal association bundles are visible in the *stratum lacunosum*. Secondly, in the region of the subiculum (and possibly in other regions of the hippocampus) large numbers of longitudinal fibres are contained in the alveus, but in transverse section are not recognizable in the mass of oblique fibres.

Upon the ventral aspect of the hippocampus in its anterior part we have had occasion to refer to a large mass of grey matter, the anterior paired region of which we have known as the "corpus præcommissurale," and its posterior region as the "commissure-bed." This region has been the great source of confusion to comparative anatomists, more especially those working at reptilian and amphibian forms, and it therefore demands a very careful study. Most writers call the whole mass the "septum."

A study of figs. 5, 6, and 9, which are all from *Perameles*, shows that the "commissure-bed," or matrix of the commissures, extends across the median plane uninterruptedly, becomes continuous upon its dorsal aspect with the hippocampus of both sides, and upon its ventral aspect with that thin band (*l.c.*) of the lamina terminalis which extends from the ventral commissure to the optic tract (*o.tr.*). It is connected also in the median line above with the thin epithelial roof of the third ventricle (a structure not shown in the figures). It is clear, therefore, that this matrix, which includes the two commissures, occupies the situation of the dorsal part of the lamina terminalis, and in part bounds the third ventricle anteriorly.

* Journal of Anatomy and Physiology, vol. xxx. p. 480.

If we examine a series of transverse and sagittal sections of a reptilian brain, it will be found that both ventral and dorsal commissures lie *in* the easily recognizable lamina terminalis. This lamina contains in the median plane a minimal amount of grey matter. But on either side of the median plane this thin bridge of grey matter becomes continuous with a huge mass of grey matter which we readily recognize as the backward continuation of the "precommissural body." Thus in the Reptile the "commissure-bed" consists of the posterior extremities of the "precommissural area" united by the thin grey lamina formed by the lamina terminalis.

In the mammal it is evident that either the grey mass of the "precommissural area" has invaded, and thus thickened, the lamina terminalis, which becomes a continuous grey mass across the mesial plane, or, on the other hand, the mesial surfaces of the two posterior regions of the precommissural area may have become "glued" together. One or other event must have occurred; and the evidence, I believe, points to a gradual thickening of the lamina terminalis by the invasion of grey matter from the adjacent "precommissural area." However the thickening is brought about, we know that the two cerebral commissures of the Marsupial lie *in* the "commissure-bed," which is morphologically a thickening of the lamina terminalis. Yet we are equally sure, both from its topographical relations to surrounding structures and from its minute structure, that the "commissure-bed" is morphologically part of the same sheet of grey matter as the "precommissural area."

If the hippocampal region be studied where it bulges in the descending limb of the lateral ventricle in any Eutherian brain, a considerable variety of the form and relative sizes of its constituent parts will be apparent. In the Marsupial brain equally great variations are found in the corresponding region of the hippocampus. But if we examine the supracommissural part of the hippocampus in a series of Marsupials, the greatest variety and most varied degrees of complexity are demonstrated. In *Notoryctes*, and less markedly in *Dasyurus*, the formation is very simple. In *Macropus* it is much more complex. *Perameles* is an example of a highly-developed type. Both Monotremes present in the supracommissural region a more complicated form of hippocampus than is found in any other mammal. But the anterior extremity of the hippocampus undergoes the same process of unfolding and simplification in all Marsupials and Monotremes which I have so briefly described in *Perameles*. Hence, should we find a difference in the relative degree of development of various parts of the hippocampal formation in the brains of two different animals, we must not lay much weight upon such differences as an indication of the systemic position of their possessor.

The Hippocampal Region in the Bat.

The cerebrum of the bat may now be studied in the same manner as that of the bandicoot. Beginning with a coronal section through the hippocampal region of *Miniopterus* immediately behind the region of the commissures, one cannot fail to notice the great similarity between the two forms (figs. 12 and 1). What differences do occur, apart from those of absolute size, point to a less complex form of structure in *Miniopterus* (fig. 12) than in *Perameles* (fig. 1). This simplification consists of a diminished depth of

the hippocampal fissure (*f.h.*), a less prominent hippocampal eminence in the lateral ventricle, and a less broad and slightly less convoluted fascia dentata (*f.d.*). These variations in the *form* of the hippocampus are of little moment, for, as I have before remarked, great variations are found in any order. Moreover, it is noteworthy that in very small Marsupials like *Notoryctes* one finds a simplicity of hippocampal formation similar to that which the minute *Miniopterus* presents (compare fig. 6 of my paper on *Notoryctes* *).

In the next section, which passes through the posterior extremity or *splenium* of the dorsal commissure (Pl. 16. fig. 13), we have a condition which recalls that presented by the corresponding section through the brain of *Perameles* (Pl. 15. fig. 2).

But if we compare the hippocampus in figs. 12 and 13, a distinct simplification will be noticed in the foremost section (fig. 13). The fascia dentata (*f.d.*) is narrower, the layer of pyramidal cells (*pyr.*) is shorter, and the hippocampus as a whole is distinctly flatter. In fig. 12 there is a very sharp angle between the alveus and the corona radiata, while in fig. 13 the angle has become rounded off. It is possible that fibres coming from a wider cortical field may round off the angle, but the carmine stain does not permit us to definitely decide this. But in the next section (fig. 14) there is no question, even with the carmine stain, of the much wider field of origin of the dorsal commissure.

If we are undecided whether any fibres other than hippocampal are passing to the dorsal commissure in fig. 13, we have in fig. 14 a very distinct demonstration of the existence of a very considerable bundle of fibres arising from the general cortex and forming part of the superior commissure. In fact, the insignificant flattened band of grey matter which now represents the hippocampus can contribute but a very small share towards the formation of the thick commissural tract (*c.d.*) upon which it lies. The hippocampus is now much more insignificant and more flattened than it was in the last figure. The regular row of nuclei immediately above the dorsal commissure belongs to the layer of pyramidal cells of the hippocampus (*pyr.*), and the group of closely-aggregated smaller nuclei which cap the mesial end of the layer of pyramids represents the stratum granulosum of the fascia dentata. In fig. 15 the region of the fascia dentata from fig. 14 has been represented upon a larger scale, and in figs. 12, 13, 14, and 15 the stratum moleculare of the fascia dentata has been shaded in order to render its recognition more easy.

It will be noticed, if we compare figs. 13 and 14, that the commissural fibres of the general cortex pursue their new course through the alveus of the hippocampus. In other words, the alveus of the "dorsal hippocampus" of the bat consists of a mixture of fibres derived from the hippocampus, which we might call "true alveus," and commissural fibres derived from the general cortex—"false alveus." Our "false alveus" is the corpus callosum proper. From the examination of this series, therefore, we may infer that *the fibres of the corpus callosum proper reach the mesial plane by passing through the alveus of the dorsal part of the hippocampus.*

* "The Cerebrum of *Notoryctes typhlops*," Transactions of the Royal Society of South Australia, vol. xix. pl. viii. (1895).

As we proceed forward the supracommissural hippocampus becomes more and more rudimentary. Had we not been tracing these structures in a series of sections, we should never recognize in the few cells situated above the commissures in fig. 16 the representatives of the fascia dentata (*f.d.*) and the rest of the hippocampus (*pyr.*).

If we were to examine a series of sections further forward we should find, after the anterior extremity of the dorsal commissure had been passed, that at the junction of the precommissural area and general cortex (pallium) a few small cells would be found to represent the hippocampus which is present in the marsupial (fig. 7).

Now that we have seen how the hippocampus is disposed in transverse sections, it will complete our ideas concerning the commissural region if we study its disposition in sagittal section. The transverse sections which I have figured were those of *Miniopterus*. The two series of sections of the brain of *Nyctophilus*, which would have served our purpose even better, were not exactly transverse, and therefore might be confusing. It may be remarked, however, that the "non-hippocampal" element in the dorsal commissure is even less developed in *Nyctophilus* than it is in the single specimen of *Miniopterus* which I have examined. I have made several series of sagittal sections of the brain of *Nyctophilus*, and, for illustration, a section slightly to the side of the middle line has been chosen in order to show the relation of the hippocampus to the "*splenium*" of the dorsal commissure. A section passing through the mesial plane presents no difference in the appearance of the commissures from that presented in fig. 17.

In this section (fig. 17) we cannot fail to be struck with the resemblance to the Marsupial. The relatively enormous size of the ventral commissure (c.v.) and the shape and proportions of the dorsal commissure (c.d.) are strongly suggestive of the Metatherian structures. Yet in no Marsupial are the two limbs of the commissure so broadly expanded. For the ventral limb (c.v.) is nearly vertical, and the dorsal limb (c.d.) nearly horizontal, so that the angle included between the two limbs is not far short of 90°. Of the two limbs the ventral is the larger. Both limbs become thicker as they are traced towards their place of union, where they form a massive "*splenium*." Immediately behind the splenium in this section we see the fascia dentata (*f.d.*) cut very obliquely, and extending forward from the concavity of the pouch formed by the stratum granulosum the layer of pyramidal cells of the hippocampus (*hip.*) immediately above the dorsal commissure.

The "commissure-bed" (*s*) enclosing both commissures fills up the great interval between the two limbs of the commissura dorsalis and the commissura ventralis.

In the dorsal limb of the commissura dorsalis (c.d.) I have represented by means of dots the position which a study of transverse sections leads me to regard as approximately those occupied by the commissural fibres which do not spring from the hippocampal formation, *i. e.* by the fibres of the corpus callosum proper. From this we see that the anterior extremity of the dorsal limb is almost purely "callosal"—if we may use such a term. The transition from purely "callosal" to purely "hippocampal" parts of the commissure is a very gradual one, "hippocampal" and "non-hippocampal" fibres being intimately mixed one with another at the place of junction.

Thus it would appear that in this bat commissural fibres arising from a very restricted area of the dorso-mesial cortex above the supracommissural region of hippocampus, instead of passing by the circuitous route viâ the external capsule and through the central commissure, pass through the alveus of the supracommissural hippocampus to reach the opposite hemisphere through the dorsal limb of the dorsal commissure. In other words, fibres which do not arise in the hippocampal formation pass through the alveus of the hippocampus to become commissural, and, as a result of the consequent atrophy of the invaded region of hippocampus, the invading fibres usurp the place previously occupied by the anterior part of the hippocampal commissure.

The "usurping fibres" are the "corpus callosum," and the atrophic hippocampus forms part of the "indusium" and "striae Lancisii."

The relation of the rudimentary corpus callosum to the hippocampus, to the "commissure-bed," and to all the surrounding structures is identical in every respect with that which the corresponding part of the hippocampal commissure presents in the Marsupial. We have no reason to regard the "commissure-bed" in the bat in any other light than as the strict homologue of the structure which we have designated by that name in the bandicoot. For even though the large mass of hippocampal cortex is wanting upon the dorsal aspect of the commissure, it cannot have been absorbed into and swell the mass of the "commissure-bed," for its vestiges are clearly and indubitably present, as we have just seen, upon the *dorsal* aspect of the "commissura dorsalis." Since our new commissure or corpus callosum lies entirely upon the ventral aspect of the hippocampus, it must be still contained in the "commissure-bed" (or possibly the "corpus præ-commissurale") just as in the Marsupial.

General Considerations.

We have now contrasted the hippocampal region of a typical Marsupial cerebrum with that of certain Cheiroptera as types of an extremely low grade of Eutherian organization. I propose now to briefly discuss the significance of the differences observed, and their special bearing upon the question of the origin of the corpus callosum.

Fig. 1 (p. 63) represents in a schematic manner the position which the hippocampus occupies in the mesial wall of the hemisphere of a Marsupial. This hippocampus may be roughly divided into three segments:—(a) a "precommissural segment" (*hip''*), which lies in front of the commissures and separates the precommissural area (*p.a.*) from the general cortex (*p*); (b) a "supracommissural segment" (*hip'*), which lies above the dorsal commissure, whose dorsal limb separates it from the "commissure-bed" (*s*); and (c) a "postcommissural segment," which constitutes the greater part of the hippocampal formation and possesses a true fimbria (*fi*).

These three segments of the hippocampus form an extensive arc, reaching from the olfactory bulb (*o.b.*) in front to the tip of the temporal pole (*t*) behind and below. The "commissura dorsalis" derives its fibres from this extensive arc. [The few fibres springing from the precommissural body which probably enter into the constitution of the dorsal commissure may be disregarded in this discussion.] The commissural fibres

derived from the precommissural and supracommissural segments form the dorsal limb, and those derived from the postcommissural segment form the splenium and ventral limb of the "commissura dorsalis."

Now, we have seen that in the brain of the bat commissural fibres arise from a small area of the mesial cortex, which is distinctly not hippocampal, but which is placed above the hippocampus, and that, after passing through the alveus of the supracommissural hippocampus, they cross the mesial plane intimately intermingled with the hippocampal fibres of the dorsal limb of the "commissura dorsalis." Coincidentally with this invasion of the alveus, and possibly as a direct result of it, retrogressive changes occur from before backward in the "precommissural" and "supracommissural" segments of the hippocampus. So that soon these parts of the hippocampus (*hip'* and *hip''*) are reduced to mere vestiges, which, however, may still retain their characteristic histological elements. These vestiges are the so-called striæ Lancisii (mesial and lateral) and the associated film of grey substance. It is natural to suppose that with the retrogressive changes in the supracommissural hippocampus the hippocampal factor in the dorsal limb of the dorsal commissure wanes, so that the usurping pallial fibres remain practically if not actually unmixed with hippocampal fibres, to constitute the dorsal limb of the dorsal commissure.

This change is so gradual, and the pallial invasion so insidious, that at first the appearance of the commissures is unchanged, as in *Nyctophilus*, from our Marsupial type, and we are apt to overlook the fact that there has been thus introduced "the greatest modification exhibited by the brain in the whole series of vertebrated animals," as Huxley has said. It is unnecessary to discuss the question of the homology of these pallial fibres in the dorsal commissure; for, in the 'Transactions of the Linnean Society of New South Wales,' I have already (October 1894) called attention to the fact that while in the Marsupial the whole pallium is bound to its fellow of the opposite hemisphere by means of fibres of the ventral commissure, in the Eutherian hemisphere part of the homologous pallium sends its commissural fibres by the much shorter route which the commissura dorsalis provides. Therefore we cannot regard the corpus callosum as an entirely new group of commissural fibres, but rather *as fibres the undoubted homologues of which are found in the ventral commissure of the Metatherian cerebrum*. The passage of these pallial fibres through the dorsal commissure is an adaptive feature which is obviously advantageous to the organism, since the new route provides a very considerably shorter and more direct path for the commissural fibres of the rapidly-increasing dorsal part of the pallium. It is not at all surprising, therefore, to find a great and rapidly-growing demand upon this advantageous pathway *viâ* the dorsal limb of the dorsal commissure. Thus quite early this dorsal limb becomes completely transformed from a practically purely "hippocampal" to a practically purely "pallial" structure. (In fig. 1, p. 63, this reconstructed limb of the commissure has been darkly shaded.) But the continued crowding in or intussusception of new commissural fibres soon expands the bulk of the dorsal limb not only in thickness, but also in length. At first the increase in length is most noticeable in the caudal direction, in correspondence with the rapid backward growth of the hemisphere. This backward extension of the commissure takes place in the

plane in which the dorsal limb already lies. Now this plane is directed backwards and upwards, as indicated by an arrow in fig. 1.

What are the effects of such a backward extension upon the hippocampus? The

Fig. 1.—Scheme to show the arrangement of the hippocampus in the mesial wall of the hemisphere of a Marsupial.

The darkly-shaded part represents the first corpus callosum, such as is found in *Miniopterus*, and the arrow indicates the line of its backward extension in the higher Mammals.

Fig. 2.—Scheme of the corresponding region of a more highly developed cerebrum, such as that of *Pteropus*.

Fig. 3.—The "spherical" region from fig. 2 on a larger scale.

remains of the hippocampus which cover the dorsal aspect of the corpus callosum are stretched, and thus further attenuated, by the lengthening commissure. The backward growth of the commissure, owing to its obliquity, soon indents the hippocampal formation just at the junction of the atrophic "supracommissural" segment with the

unaltered "postcommissural" segment. This indentation soon increases and becomes a very extensive bend, the portion of the hippocampus which surrounds the posterior extremity of the dorsal commissure being carried backward and greatly stretched (fig. 2). In this way the obliquely-directed commissure first of all pushes upward and backward the hippocampus at the junction of supra- and postcommissural parts, stretching and carrying back the part of hippocampus that invests it *above the rest of the postcommissural hippocampus*. The "postcommissural hippocampus" (fig. 3, *hip*) thus appears to become subcallosal and to be separated in the vertical plane from the splenium of the dorsal commissure (*spl*) and the circumsplenic portion of the hippocampus (*hip'*) by a process of pallium (figs. 2 and 3, *) upon which Zuckerkandl has laid so much stress under the confusing name "Balkenwindung." (It will be remembered that it was the lack of this feature which, in part, led him to group a bat with Marsupials and Monotremes).

As a result of the operation of the above-mentioned factors, therefore, a somewhat reversed S-shaped bending is produced in the hippocampus at the junction of its middle and posterior segments. The upper part of the S with its concavity looking forward is formed by the attenuated hippocampus (fig. 3, *hip'*) surrounding the splenium (fig. 3, *spl*), while the lower part of the S, which is convex in front, is formed by a "subsplenic" bending of a plumper hippocampal region, which I have distinguished as the "*hippocampal flexure*" (*flw*).

Throughout all these changes the main mass of the ventral limb of the dorsal commissure (C.D.) has remained unchanged.

In the Marsupial and in a large number of lowlier Eutheria the plump ventral limb extends obliquely upwards to meet the dorsal limb in a thick splenium. But when the dorsal limb extends further backward, the main mass of the ventral limb is left in its old position (fig. 2, C.D.), its postero-superior extremity becoming greatly stretched and correspondingly thinned by the backwardly-extending corpus callosum.

The fimbria maintains its position unchanged (figs. 1 and 2, *f*) and always lies upon the posterior or inferior aspect of the corpus callosum. In its backward growth the corpus callosum carries back its matrix or "commissure-bed," in which it always lies.

But although the elongation of the corpus callosum is most obvious in the backward direction, it also grows forward towards the anterior extremity of the brain.

In the Amphibia and certain Reptiles, where the olfactory bulb is placed in front and is not overlapped by the hemisphere, the "corpus præcommissurale" extends forward as a horizontal band from the lamina terminalis to the mesial wall of the olfactory peduncle. It is bounded upon its dorsal aspect by the homologue of the hippocampus. In the Marsupials with small pallia the upper margin of the precommissural body is slightly oblique (Pl. 15. figs. 8 and 9). As the pallium increases in extent it bulges over the olfactory bulb (figs. 1 and 2, p. 63) more and more, and consequently the "precommissural" hippocampus (*hip''*) becomes more and more oblique, because it always extends towards the olfactory peduncle. Thus the hippocampus comes to bend downward in front of the commissures. Now it is obvious that the dorsal limb of the commissura dorsalis (fig. 1), if it extends forward, must indent this precommissural segment of the

hippocampus as I have represented in fig. 2. This anterior portion of indented hippocampus is the "*gyrus geniculi*" of Zuckerkandl.

It is apparent from this that *the dorsal commissure, which in the Marsupial lies within a well-defined arc formed by the hippocampus* (fig. 1), *never breaks through this hippocampal arc even in its much more extended and reconstructed form as a corpus callosum, but pushes the dorsal part of the arc before it as it elongates in both directions* (fig. 2).

We have seen that in the Marsupial a large mass of grey substance, containing both commissures and formed by the "corpus præcommissurale" and "commissure-bed," is situated upon the ventral aspect of this hippocampal arc. Since the hippocampal formation may be recognized surrounding the corpus callosum even in the brains of the ox, the monkey, and man, it is clear that the matrix of this commissure can be formed of no other structure than the "precommissural body" and the "commissure-bed." This introduces us to the problem of the nature of the "septum pellucidum."

We have already seen that the first "callosal" fibres replace the hippocampal fibres of the dorsal limb of the "commissura dorsalis," and in every respect present the same relations as the fibres, the places of which they usurp. The first "callosal" fibres, therefore, must lie in the structure which is exactly homologous to what we have called, in the Marsupial, the "commissure-bed."

In discussing the nature of the "commissure-bed" we came to the conclusion that with the increasing dimensions of the commissures the dorsal part of the lamina terminalis became thickened or invaded by the posterior parts of the "corpora præcommissuralia," so that a bridge of grey matter—the "commissure-bed"—was formed, connecting the two hemispheres, and forming a matrix for the two cerebral commissures. This secondary thickening appears to take place gradually in the ontogeny of each individual, and cannot be regarded as a mere mechanical fusion of the precommissural areas of the two hemispheres. We may therefore safely say that the dorsal commissure of the Metatherian and (for the reasons stated above) of the early Eutherian cerebrum is contained in a matrix which is formed by a thickening of the dorsal part of the lamina terminalis at the expense of the "corpora præcommissuralia." As new commissural fibres crowd in and the commissure increases in length and depth, this matrix becomes extended, but I believe it always continues to enclose the dorsal commissure, even in its most extended form.

Paul Martin says that in the cat the cephalic extremity of the corpus callosum or genu is formed by the apposition of fibres in front of those which are situated in the thickened lamina terminalis. It must be evident (if we glance at fig. 1) that if these apposed fibres grow in a "secondary fusion of the walls of the hemisphere," such a fusion must consist of a "soldering" of the two "precommissural hippocampi" (*hip*). But such a "soldering" does *not* take place, because in the *gyrus geniculi* we have seen the representative of the "precommissural" hippocampus pushed before the advancing corpus callosum. There seems to be no other alternative which could be for a moment maintained but that the corpus callosum is contained in its original matrix or "commissure-bed," which has become enormously but gradually elongated. This conclusion is strongly forced upon us by comparison, in the order mentioned, of such a series of

cerebra as those of the *Iguana*, *Ornithorhynchus*, *Phascogale*, *Perameles*, *Nyctophilus*, *Dasypus*, and *Talpa*, with more highly-developed forms.

In this process of forward extension the dorsal commissure has carried forward its own matrix, derived from the original "commissure-bed." It is obvious that if this takes place without a corresponding growth of the bridge of grey matter (*s*) which lies between the dorsal and ventral commissures, we shall have part of the great longitudinal fissure (bounded on either side by the precommissural area) roofed in by the corpus callosum (contained, of course, in its proper matrix). This roofed space will be bounded posteriorly by the ventral limb of the "commissura dorsalis." This enclosed part of the great longitudinal fissure is the so-called "*fifth ventricle*," or "*cavum septi pellucidi*."

By means of the accompanying five schemes (in which the commissure-bed is shaded) I have graphically represented different stages in this process. From these schemes it will be readily recognized how the backward extension of the dorsal commissure (fig. 8) stretches not only the matrix in which it lies but also the sheet of the "precommissural body" (*p.a.*) which fills up the large angle between the two limbs of this commissure. Thus a portion of the precommissural body of each hemisphere becomes one of the leaves of the septum pellucidum. In his valuable memoir Paul Martin speaks of a fusion taking place (in the brain of the cat) between the opposed walls of the hemisphere on the ventral side of the corpus callosum. In this manner, in the more highly-developed macrosmatic Eutherian cerebra, the massive corpora præcommissuralia below the corpus callosum may meet and fuse in the median plane so as to obliterate the cavum septi. But the commissure itself is *not* situated in any such secondary fusion of the hemisphere walls, so that it does *not* affect the main argument advanced above.

But though the corpus præcommissurale thus takes an important share in the formation of the septum pellucidum, part of it always remains distinct in the higher mammalian cerebrum as a vertical band, lying parallel to the lamina terminalis and separating the latter from the general pallium. This band is the "gyrus subcallosus" of Zuckerkandl. In order to show the last stage which this process reaches, I have represented in Pl. 16. fig. 18 this region of the cerebrum

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

FIG. 8.

Figs. 4-8.—Schemes to explain the evolution of the "septum pellucidum."

Fig. 4 is a type of a Reptile.

" 5 " " Monotreme.

" 6 " " Marsupial.

of an adult man. The anterior extremity of the corpus callosum has become so bent that its rostrum (*r.*) becomes continuous with the remains of the "commissure-bed," which still surrounds the ventral commissure (*c.v.*). In this way the septum pellucidum (*sept.*) becomes surrounded by a complete ring of the matrix of the commissures and cut off from the gyrus subcallosus, which is the remainder of the precommissural area. This gyrus subcallosus extends down to the base of the cerebrum immediately in front of the ventral commissure and lamina cinerea (*l.c.*). Its line of separation from the pallium is indicated in the figure by a dotted line (*a.l.*). The gyrus subcallosus is traversed by a well-marked vertical depression—the *fissura prima* (*fiss.pr.*),—which has no important morphological significance.

With the knowledge which we have acquired of the process of phylogenetic development of the region of the commissures, it is extremely instructive to study the beautiful figures with which Marchand, in man, and Paul Martin, in the cat, represent (*op. cit.*) the process of ontogenetic development.

In the Marsupial we have a *fissura arcuata* or *hippocampi*, extending from the tip of the temporal pole right round the mesial wall of the hemisphere towards the olfactory peduncle; so, in the foetal child or kitten, we find the Bogenfurche (which we might, with Mihalkovics, appropriately call "Ammonsfurche") following a similar course and shading away towards the cephalic pole of the hemisphere. And it is necessary to remark, in passing, that the so-called part of the "vordere Bogenfurche," which His calls "fissura prima," has nothing whatever to do with the true Bogenfurche or fissura arcuata, if we regard the latter as the primitive fissura hippocampi.

In the early stages of the cat, the lamina terminalis becomes thickened and invaded by the commissural fibres of the fornix (Paul Martin), so in phylogeny we have the corresponding stages in the adult Monotremes and Marsupials.

Then, as the commissural fibres increase in number, the grey mass or thickening of the lamina terminalis is invaded by so many white fibres that the grey substance seems to disappear, but it is in reality being gradually extended by the swelling commissure.

The backwardly-extending commissure produces exactly the same series of changes—the same hippocampal flexure—in our phylogenetic series as it does in the developing brain of the cat and man (see Martin and Marchand's figures).

Thus, for all the stages in the developing brain of the cat, we can find almost exact prototypes among the more lowly-developed mammals.

The great feature which far more than any other distinguishes the mammalian brain from that of all submammalia is the possession of a definite pallium—distinct alike in its histological features and its morphological relations—giving rise to a definite internal capsule of projection-fibres and well-defined and fully-medullated commissural fibres. At first, in the Monotremata and Marsupialia, this pallium (like the parent mass of the basal ganglion from which it appears to have sprung) is united to its homologue of the opposite hemisphere by means of the "commissura ventralis"—"the commissure of the cerebral hemisphere" *par excellence*.

But the rapid growth in extent and complexity of this general cortex or pallium is accompanied by a richer and more abundant commissural system. This growing commissural system from the dorsal part of the enormous pallium not only finds in the

"commissura dorsalis" a shorter path, but a clearer scope for longitudinal extension than the ventral commissure provides. And thus we have pallial fibres invading and subsequently superseding the dorsal limb of what was previously the hippocampal commissure.

"Pallial" commissural fibres probably first make their appearance in Reptiles and form a very insignificant constituent of the ventral commissure. In Monotremes and Marsupials these fibres become extremely abundant, and swell the proportions of the ventral commissure enormously. But in Eutheria a rapidly increasing proportion of these fibres forsake the commissura ventralis and form the new "dorsal commissure of the pallium"—the corpus callosum,—which throws the "parent" commissure into insignificance. The remnant of the commissura ventralis is known in man by the somewhat misleading name "anterior commissure."

EXPLANATION OF PLATES 15 & 16.

- Fig. 1. Coronal section through the forebrain of *Perameles nasuta*. Stained by Weigert's method. $\times 4$. The section passes just behind the commissures.
2. Coronal section through the hippocampal formation and the posterior extremity of the "*commissura dorsalis*" in *Perameles*. Weigert stain. Fascia dentata represented as it appears after nuclear staining. $\times 20$.
- Figs. 3 & 5. Coronal sections of the "*commissura dorsalis*" of *Perameles*, a short distance in front of fig. 2. $\times$ about 6.
- Fig. 4. Representation of the commissures of *Perameles* (as seen in a mesial sagittal section) to show the planes in which the sections represented in figs. 2 (a), 3 (b), 5 (c), and 6 (d) were cut.
6. A coronal section of the cerebral hemispheres of *Perameles*, to show the general arrangement of the commissures. Weigert stain. $\times$ about 6.
7. Coronal section of the right cerebral hemisphere of *Perameles* immediately in front of the cerebral commissures. Weigert-Pal and carmine stains. $\times 4$.
8. Semi-schematic representation of the anterior part of the mesial wall of the cerebral hemisphere of *Dasyurus viverrinus*. $\times$ about 4. To show that, as a result of the unrolling of the hippocampus anteriorly, the whole of its *morphologically* superficial layer now *actually* forms part of the visible surface. Thus the surface of the hippocampus proper (*hip.*''') appears above the fascia dentata (*f.d.*!).
9. Anterior portion of the forebrain of *Perameles*, exposed in a mesial sagittal section. $\times 4\frac{1}{2}$. The bulbus olfactorius only represented in part and in outline.
10. Sagittal section through part of the anterior portion of the mesial wall of the cerebral hemisphere of *Phascogalea cinerea*. Weigert stain. $\times 6$.
11. Horizontal section through the left hemisphere of *Trichosurus vulpecula*, a short distance above the commissures. $\times 2$. *ant.mes.*, the antero-mesial angle.
12. Coronal section through the right hippocampal formation of a bat (*Miniopterus Schreibersii*), to compare with the hippocampal region of fig. 1. Lithium-carmine stain. $\times$ about 20.
13. Coronal section of *Miniopterus*. Compare fig. 2.
14. Coronal section of right hemisphere of *Miniopterus*. $\times$ about 20. Compare with fig. 6.
15. The fascia dentata and adjacent parts. Enlarged from fig. 14.
16. Coronal section of the hippocampal region of *Miniopterus*, a short distance in front of fig. 14.
17. Sagittal section of the commissures and adjacent parts of brain of *Nyctophilus* near the mesial plane. $\times$ about 40.
18. Drawing of the "gyrus subcallosus" of a human brain.

Explanation of reference-letters in the figures.

The significance of the reference-letters *a, b, c, d, α, β, γ, δ* is explained in the text.

<p><i>a.l.</i> Anterior limit of the "gyrus subcallosus."
 <i>alv.</i> Alveus hippocampi.
 <i>cing.</i> Cingulum.
 <i>cing^l.</i> Longitudinal fibres in the alveus hippocampi adjacent to the cingulum.
 <i>c.d.</i> "<i>Commissura dorsalis</i>."
 <i>c.d.^l</i> Dorsal limb of the "<i>commissura dorsalis</i>."
 <i>c.d.^v</i> Ventral limb of the Metatherian type of "<i>commissura dorsalis</i>."
 <i>c.e.</i> Capsula externa.
 <i>c.f.</i> Columna fornicis.
 <i>c.i.</i> Capsula interna.
 <i>c.m.</i> Commissura mollis.
 <i>c.r.</i> Corona radiata.
 <i>c.st.</i> Corpus striatum.
 <i>c.v.</i> "<i>Commissura ventralis</i>."
 <i>d.f.</i> Descending hippocampal or fornix-fibres.
 <i>e.</i> Epithelial fold roofing the third ventricle.
 <i>e.o.t.</i> External olfactory tract.
 <i>f.d.</i> Fascia dentata.
 <i>f.h.</i> Fissura hippocampi.
 <i>fi.</i> Fimbria.
 <i>fi^l.</i> The remains of the fimbria intermingled with fibres of the commissura dorsalis.
 <i>fx.</i> The "subsplenial hippocampal flexure."
 <i>f.r.</i> Fissura rhinalis.
 <i>g.h.</i> Ganglion habenulæ (and stria medullaris thalami).
 <i>hip.</i> Hippocampus.
 <i>hip^l.</i> "Supracommissural hippocampus."
 <i>hip^u.</i> "Precommissural hippocampus."
 <i>hip^m.</i> Stratum zonale of the "precommissural hippocampus" lying upon the surface immediately above the stratum zonale (<i>vel</i> molecularæ) of the fascia dentata (<i>f.d.^l</i>).
 <i>i.</i> "<i>Indusium verum</i>."
 <i>i.l.s.</i> Internal limiting sulcus of the tuberculum olfactorium (<i>t.o.</i>).</p> | <p><i>l.</i> "Longitudinal association bundles" of the hippocampus.
 <i>l.c.</i> Lamina cinerea.
 <i>l.v.</i> Lateral ventricle.
 <i>n.a.</i> Nucleus amygdalæ.
 <i>n.c.</i> Nucleus caudatus.
 <i>n.f.d.</i> Nucleus fasciæ dentatæ.
 <i>n.l.</i> Nucleus lenticularis.
 <i>o.b.</i> Olfactory bulb.
 <i>opt.</i> Optic nerve.
 <i>o.tr.</i> Optic tract.
 <i>p.</i> General cortex or pallium.
 <i>p.a.</i> "<i>Precommissural area</i>" or "<i>corpus præ-commissurale</i>."
 <i>py.l.</i> Pyriform lobe.
 <i>pyr.</i> Layer of pyramidal cells of the hippocampus.
 <i>r.o.</i> Recessus opticus.
 <i>s.</i> "Commissure-bed."
 <i>sept.</i> "Septum pellucidum."
 <i>s.gr.</i> Stratum granulosum of the fascia dentata.
 <i>s.l.</i> Stratum lacunosum of the hippocampus.
 <i>s.m.t.</i> Stria medullaris thalami.
 <i>spl.</i> Splenium of the corpus callosum.
 <i>s.r.</i> Stratum radiatum of the hippocampus.
 <i>s.t.</i> Stria terminalis.
 <i>s.t^l.</i> The crossing fibres of the stria terminalis entering the "<i>commissura ventralis</i>."
 <i>s.t^u.</i> The uncrossed part of the stria terminalis.
 <i>sub.</i> Subiculum cornu ammonis.
 <i>t.</i> "Temporal pole" of the cerebral hemisphere.
 <i>t.o.</i> Tuberculum olfactorium.
 <i>v.3.</i> Third ventricle.
 <i>x.</i> Medullated nerve-fibres going to the stratum lacunosum.
 <i>y.</i> "<i>Tractus hippocampi ad pallium</i>."</p> |
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Fig. 1.

Fig. 3.

Fig. 2.

Fig. 5.

Fig. 7.

Fig. 9.

Fig. 4.

Fig. 6.

Fig. 8.

Fig. 13.

Fig. 12.

Fig. 17.

Fig. 15.

Fig. 14.

Fig. 16.

Fig. 18.