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NOTES UPON THE NATURAL SUBDIVISION OF THE CEREBRAL HEMISPHERE. By G. ELLIOT SMITH, M.D.,  
*Fellow of St John's College, Cambridge ; Professor of Anatomy, Cairo.*

IT is a peculiar fact, significant not only of the imperfections of the current nomenclature, but even to a greater extent of the unsatisfactory state of the present teaching in cerebral morphology, that there is no term generally accepted or acceptable among the multitude of names now employed in Descriptive Anatomy which can be applied exclusively and without confusion to the most characteristic and distinctive feature of the mammalian brain; to that part, in fact, which is the dominant organ of the whole body, and in the more highly placed Eutheria, constitutes the great bulk of the whole nervous system. I refer to that area of the cerebral cortex, with its associated medullary matter, which, in a series of earlier memoirs,<sup>1</sup> I have wrongly called the "pallium." But it is only one of the three histological formations which constitute the true pallium; and, as it is the latest of these to reach the height of its development, we may call it the "new pallium," or, if the hybrid term be permissible, "neopallium," in contradistinction to the "old pallium" of the Sauropsida and the earlier Vertebrata, which is *chiefly* formed of the other two pallial areas.

If a cerebral hemisphere of any mammal be submitted to careful examination, it will be found to be composed of a number of distinct regions, each of which exhibits well-defined and unmistakable histological features peculiar to itself. Thus

<sup>1</sup> See "The Brain in the Edentata," *Trans. Linn. Soc.*, 2nd series,—Zoology,—vol. vii., 1899, p. 324.

the hemisphere readily lends itself to a natural subdivision, which, strange to relate, is not adequately recognised in any one of the many accounts found in current Descriptive Anatomy.

These regions are demonstrable with much more readiness in some brains than in others, although their arrangement is essentially the same in all mammals; and in no case can they

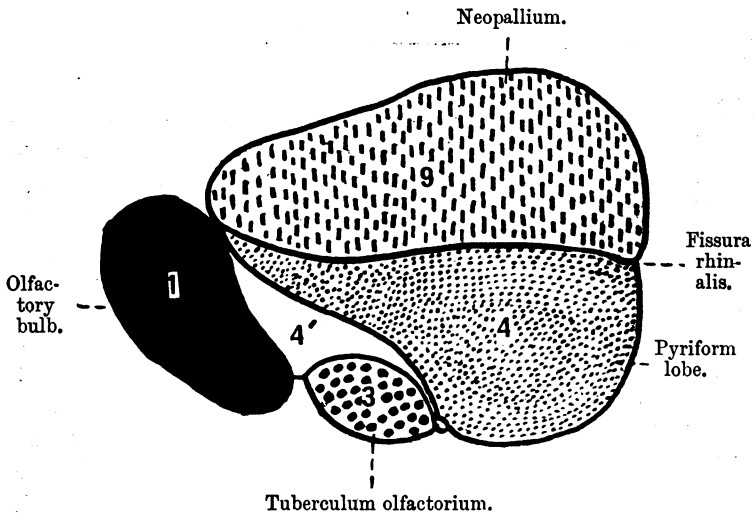


FIG. 1.—Diagram representing the lateral aspect of the left cerebral hemisphere of the typical brain.

be shown more clearly than in the Hedgehog (*Erinaceus*), which we may take as a type for the whole Mammalia.

In such a hemisphere the following distinct histological formations may be readily recognised, in addition to the epithelial structures:—

- (1) The olfactory bulb.
- (2) The olfactory peduncle.
- (3) The olfactory tubercle (*tuberculum olfactorium*).
- (4) The pyriform lobe.
- (5) The "paraterminal body."
- (6) The anterior perforated space.

These numbers are employed in the various diagrams to indicate the respective regions.

- (7) The hippocampal formation, sharply differentiated into (a) the hippocampus (*sensu stricto*), and (b) the fascia dentata.
- (8) The corpus striatum; and
- (9) The rest of the hemisphere, consisting of a dorsal cap which is the "neopallium."

(1) The olfactory bulb calls for no description, because no one can dispute the fact of its peculiarly distinctive histological structure.

(2) The olfactory peduncle is merely the prolongation backward of the innermost layers of the olfactory bulb.

(3) The olfactory tubercle (figs. 1, 2, 3, and 4) is a peculiar cortex, which forms a cap upon the ventral aspect of the head of the corpus striatum. Its structure is well known from the descriptions of Ganser, Calleja, and others (see Kölliker, *Gewebelehre*, Bd. ii., 1896, p. 725).

(4) The pyriform lobe is a mantle or "pallium" of a structure so peculiarly distinctive that it may be recognised in sections of the brain of any mammal, even when coloured by ordinary nuclear stains. Its features have been well described by Kölliker (*op. cit.*, 1896, p. 723). The exact extent and relations of this "mantle" (I use this term advisedly) are not generally recognised. Its anterior portion is closely applied and attached to the lateral aspect of the corpus striatum (fig. 5), and extends forward so as to pass into direct continuity with the olfactory peduncle, its peculiar structure undergoing a gradual transition into the somewhat indefinite "peduncular" formation; its antero-ventral part is covered by the thick mass of the tractus olfactorius [lateralis] (fig. 1, 4'), radiating fibres of which are spread over the whole of the pyriform lobe. In its caudal part the pyriform lobe becomes free from the corpus striatum, and becomes a real "mantle" (fig. 5), which extends in the caudo-mesial direction to become continuous with the hippocampus.<sup>1</sup>

<sup>1</sup> Waldeyer (Merkel and Bonnet's *Ergebnisse der Anat. u. Entwick.*, Bd. viii. for 1898, pp. 372 and 380) objects to my spelling of the word "pyriformis," on the ground that a word derived from the Latin "*pirum*" ought not to be spelled with the letter "y." This undoubted philological error, however, is not only shared by most writers of all nationalities, but is so fixed by long usage (at any rate in England), in such terms as "*musculus pyriformis*," that it would be pedantic at this late hour to attempt to rectify the spelling.

(5) The peculiar histological formation which I shall call "paraterminal body," is a structure of great morphological interest and importance, the essential unity of the various parts of which has not hitherto been recognised by other writers. It consists of a large ganglionic mass (figs. 3 and 4), which is directly continuous in front with the olfactory peduncle (2). It extends backward as far as the lamina terminalis, and extends upward to fill up the gap between the corpus callosum and the hippo-

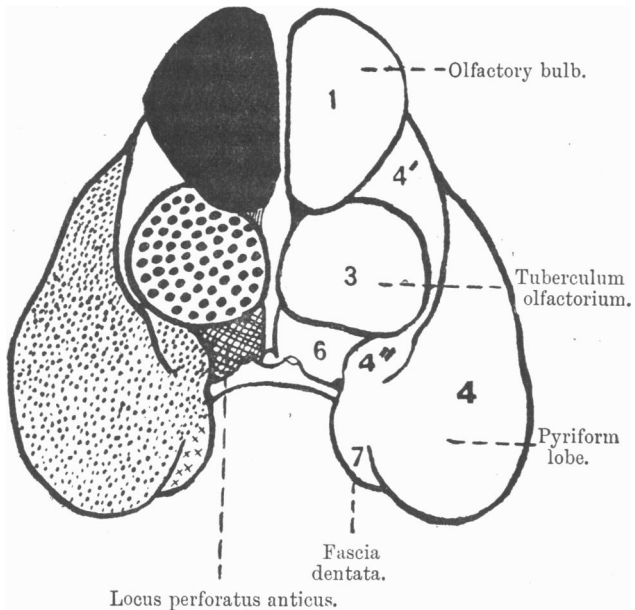


FIG. 2.—Diagram representing the ventral surfaces of the cerebral hemispheres of the typical brain.

campal commissure (psalterium). This part of the body becomes greatly stretched in many mammals by a large corpus callosum, and is then known as a folium of the septum lucidum.

The surface of this paraterminal body I have distinguished in several earlier memoirs as the precommissural area, and the ganglionic mass itself was referred to at different times as the "corpus præcommissurale" and "corpus paracommissurale." For these unwieldy terms I propose to substitute the name "paraterminale," not only because it is less cumbrous, but

because this hybrid term more aptly describes its relation to the lamina terminalis in many of the lower vertebrates. (For a fuller account of this body, see "The Relation of the Fornix to the Margin of the Cerebral Cortex," *this Journal*, vol. xxxii.)

(6) The locus perforatus anticus calls for no special mention.

(7) The hippocampal formation presents the well-known peculiar structure which is quite distinctive. Under this heading we include not only the hippocampus (*sensu stricto*), but also the fascia dentata, the *hippocampus nudus* (Zuckerkandl's "Balkenwindung"), the supra- and pre-callosal vestiges of the hippocampus and the fornix (fimbria) (figs. 3 and 4). Vide *Jour. of Anat. and Phys.*, vol. xxxii., *op. cit.*

(8) The corpus striatum is a ganglionic mass, which is excluded from participation in the surface of the hemisphere by the tuberculum olfactorium below, and by part of the pyriform lobe, and part of the neopallium upon its lateral aspect.

(9) The region which I have called "neopallium" presents a structure which is different from that of any of the eight other histological formations in the cerebral hemisphere. It presents, in fact, those peculiar characters, that distinctive gradation of pyramidal cells, which one generally associates with the idea of the typical cortex and its medulla. And although different parts of this neopallium exhibit undoubted specialisations of structure, especially in the more highly organised mammalian brains, these differences in texture are so slight in comparison, say, to those which distinguish the pyriform lobe or the hippocampus from the neopallium, that they may be neglected in a primary subdivision of the hemisphere into its fundamental parts.

More than forty years ago Reichert came to the conclusion (in a work<sup>1</sup> dealing more especially with the development of the human brain) that it would facilitate the accurate description of the cerebral hemisphere if the thin upper part of the walls of the embryonic cerebral vesicle, which he termed "pallium" (*mantle*), were distinguished from the thicker basal mass which he called the "*Stammlappen*." The latter expression was so employed as to include the locus perforatus anticus;

<sup>1</sup> *Der Bau d. mensch. Gehirns*, Berlin, 1859.

the corpus striatum (together with the nucleus amygdalæ) and the floor of the fossa Sylvii, *i.e.*, the insula Reilii. It did *not* include what Reichert calls the "tractus olfactorius" (the bulbus and pedunculus olfactorius), although he recognised that this is attached to the "Stammlappen."

It will be observed that the term "pallium" was thus originally employed to designate that cortical area (with its associated medullary layer) which is free from (*i.e.*, is not adherent to the surface of) the corpus striatum. As such the

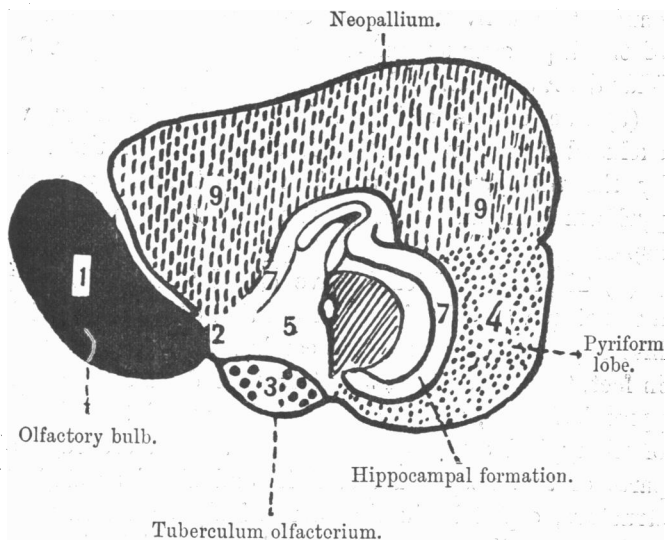


FIG. 3.—Diagram representing the mesial aspect of the right cerebral hemisphere of the typical brain.

name is of little morphological value, for while it groups together the greater part of the neopallium with the whole of the hippocampus and a small part of the pyriform lobe, it excludes a small area of the neopallium (the insula Reilii of Human Anatomy) and the greater part of the pyriform lobe from the "mantle," and includes them with the corpus striatum in the "Stammlappen." If any part of the pyriform lobe constitutes a part of the "pallium," there can be no valid reason (*i.e.*, if the proposed subdivision is to be natural and based upon sound morphological grounds) for excluding the rest of the same histological formation, simply because it does not happen to be

in contact with (or fused to) the surface of the corpus striatum; nor, for similar reasons, should the "island of Reil" be separated from the rest of the neopallium.

In spite of these obvious defects, Reichert's terminology became almost universally adopted; and the name "pallium" was, without any more precise definition, very generally applied to the thinner portions of the walls of the cerebral hemispheres in all Vertebrates. Even at the present day the term "mantle" may be used to designate the epithelial roof of the hemisphere

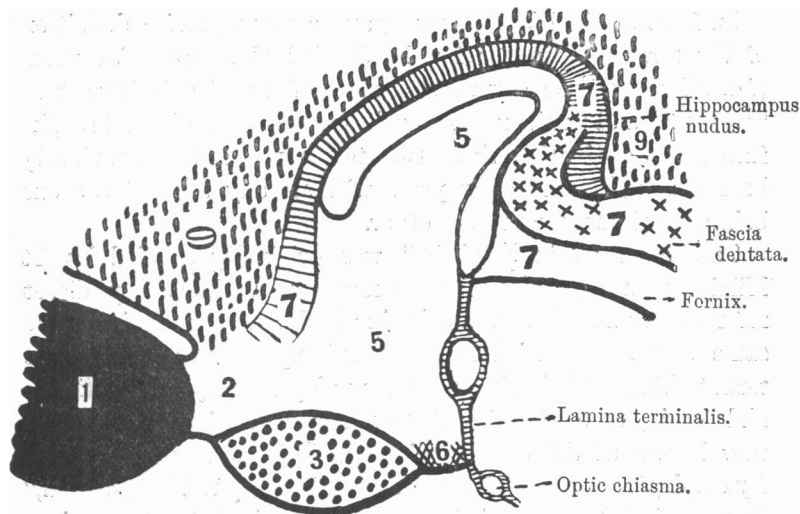


FIG. 4.—Diagram representing a part of figure 3 on an enlarged scale.

of a Teleostean, or the thinner parts of the hemisphere in Reptiles, without any attempt to determine whether or not this thin portion is in any way comparable to a cortical formation; or, granting that it is so, that it may not be partly represented in the mammalian brain by those cortical areas which are placed in contact with the corpus striatum; and as such belong, not to Reichert's "pallium," but to the "Stammlappen."

It is true, however, that some writers have slightly modified Reichert's conception by expressing the main idea of his teaching in the more accurate language of modern Anatomy in such a way as to avoid the obvious inconsistencies indicated in the

above remarks. Thus Minot<sup>1</sup> says, "the mantle comprises all that part of the hemispheres which enters into the formation of neither the olfactory lobes (*rhinencephalon*) nor basal ganglia." This slight change of expression gives to the "pallium" a significance very different from that of Reichert, for it includes the whole cerebral cortex, excepting only "the olfactory lobes." What Minot may mean by the latter expression is not altogether clear; but, judging from a footnote (p. 691), his "pallium" includes the "lobus hippocampi" (*i.e.*, the caudal expanded part of the pyriform lobe).

In 1890 Sir William Turner<sup>2</sup> gave a more precise definition of the term "pallium"; for he divided the superficial parts (*i.e.*, all except the corpus striatum) of the hemisphere into "pallium" and "rhinencephalon." Such a subdivision brought into contradistinction these two terms which had previously been employed for many years without any idea of the one being complementary to the other.

The term "rhinencephale" was originally applied by St Hilaire to a type of unioocular monsters without any direct reference to a region of the brain; Robin also used it in the same sense. But Richard Owen subsequently introduced the term "rhinencephalon," apparently independently of St Hilaire and Robin, to distinguish those parts of the brain which are now known as the olfactory bulb and the olfactory peduncle. By employing the same term as complementary to his "pallium," Turner (1890) extended its meaning to include the regions which in these notes are called tuberculum olfactorium, locus perforatus anticus, and pyriform lobe.

Now the term "lobus olfactorius" (or some equivalent expression, the word "rhinencephalon" being sometimes used) had long been employed by writers upon cerebral anatomy with a variety of different meanings. After Turner's memoir of 1890, the old term "rhinencephalon" attained a much greater vogue than it had previously enjoyed, and many anatomists, especially in Germany and America, adopted this expression and used it in the same sense in which they had been using the term "lobus olfactorius." It is unnecessary to cite instances of this,

<sup>1</sup> *Human Embryology*, 1890, p. 694.

<sup>2</sup> "Convolutions of the Brain," *Jour. of Anat. and Phys.*, vol. xxv.



because the example (that of His) which has gained the widest currency is discussed below. Others again (and especially those who employ the French language) began to employ the term "rhinencephalon" as a synonym for the "lobus limbicus" of Broca.

As the result of all this diversity of application of the term which is now found in anatomical literature, the greatest confusion reigns; and as the name in question is most generally employed as the complement of the "pallium," the latter also loses an exact significance.

If the curious reader will take the trouble to examine the most recent literature of this subject, he will find each of these terms being employed at the present time in half a dozen different senses, and it is by no means rare to find two and sometimes three meanings attached to each of these expressions in one work. It would serve no useful purpose to enumerate and discuss all these vagaries of interpretation of the terminology in question. But there are three important applications of the terms, which it is necessary (simply because they are so widely prevalent) to consider and seek wherein they fail as natural subdivisions of the hemisphere.

The first is naturally that of Sir William Turner, who first placed the two expressions in juxtaposition; secondly, there is the interpretation of His, who, as the reporter of the German Nomenclature Commission, as well as by his own reputation as a sound anatomist, exerts a singularly wide-spread influence; and in the third place, there is Broca's theory of a "limbic lobe," which still exercises a strange fascination over the minds of many writers.

The consideration of these views lends itself best to intelligent discussion if we examine the views of His first. The facts observed during the development of the human brain form the basis of the teaching of His; the data of comparative anatomy do not enter into his consideration of the limits of the "rhinencephalon" whatsoever; and hence it is not surprising that the fatal defects of his subdivision are most clearly demonstrated by the comparative method. His himself<sup>1</sup> does not apply his

<sup>1</sup> "Die Formentwick. d. mensch. Vorderhirns," etc., *Abhandl. d. königl. Sächs Gesell. d. Wissensch.*, Bd. xxvi., Math. Phys. Classe xv., 1889, p. 714.

definition of a "rhinencephalon" to other mammalian brains, but many of his followers have attempted to do so:<sup>1</sup>

His includes in the "Riechlappen" the "bulbus," "tractus" (i.e., *pedunculus*) and "trigonum olfactorium," the "area parolfactoria Brocæ," the "gyrus subcallosus," and the *locus perforatus anticus*. The last two of these regions are separated, upon supposed embryological grounds,<sup>2</sup> as a *lobus olfactorius posterior* from the rest, which constitute a *lobus olfactorius anterior*. If we examine this grouping of cerebral areas in the light of Com-

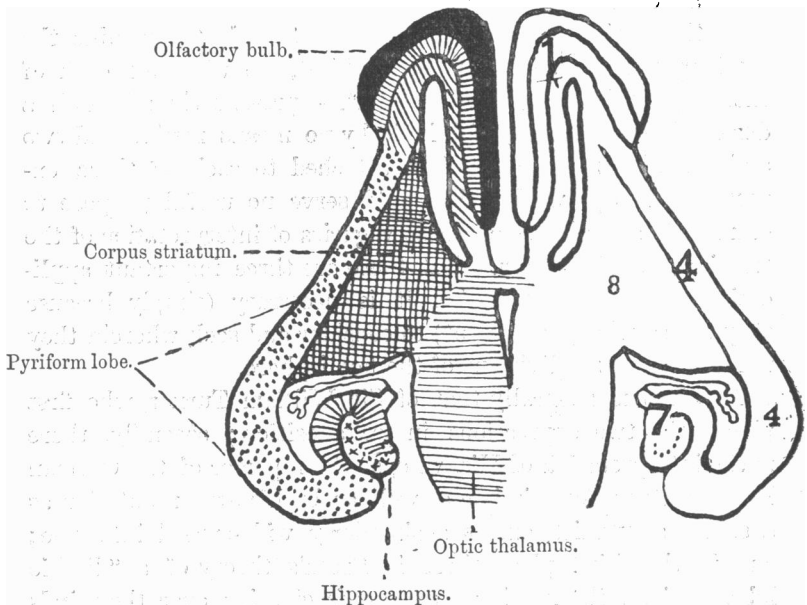


FIG. 5.—Diagram representing a horizontal section through the two cerebral hemispheres of the typical brain, on a plane ventral to the rhinal fissure.

parative Anatomy, its value as a natural division is found to be very slight. In the first place, it includes the *gyrus subcallosus* of Zuckerkandl, and excludes the septum lucidum, both of which are parts of one and the same histological formation, the paraterminal body, which forms a natural and indivisible area

<sup>1</sup> A typical example of such an attempt is afforded by a recent work by Flatau and Jacobsohn, to which Professor Waldeyer has given his countenance.

<sup>2</sup> In regard to this point, see Hochstetter's masterly exposure of the nature of so-called "transitory fissures," *Bibliotheca Medica*, A. Heft 2, 1898.

of the cerebral surface. He also includes in his "olfactory lobe" the so-called "outer root of the olfactory nerve." Now, if this so-called "root" in the human brain be compared with that of a macrosomatic mammal, or even with the condition found in the early human embryo,<sup>1</sup> it will be found to consist of the cephalic extremity of the pyriform lobe upon which the olfactory tract is spread as its superficial medullary layer. A "lobe" of the brain cannot be partly formed of a layer of nerve fibres without also including the cortical area of which this layer forms an integral constituent.<sup>2</sup> Now, if the anterior part of the pyriform lobe be included in the "Riechlappen," there can be no legitimate reason (provided, of course, that the lobe is to be a natural division) for excluding its posterior part—the so-called "hippocampal lobule."

Upon these grounds alone His's suggestions will not stand the test of comparative anatomy, because they introduce purely arbitrary lines of demarcation between regions which, in a natural classification of cerebral areas, should not be separated.

The German Anatomical Nomenclature Commission adopted the teaching of His in this matter in its entirety, and called his "lobus olfactorius" the "*rhinencephalon*," under the mistaken idea that it represented the region so-called by Turner.<sup>3</sup>

As His adopts the subdivision of the surface-areas of the hemisphere into pallium and rhinencephalon, and excludes from the latter the septum lucidum, the posterior part of the pyriform lobe, and the whole hippocampal formation, it, of necessity, follows that these regions form constituent parts of his "pallium." His statements concerning the subdivision of the mesial surface of the hemisphere are, however, too vague to indicate this peculiar grouping of surface-areas in a specific manner; nor in his list of terms does he include either Broca's "limbic lobe" nor Schwalbe's "falciiform lobe"; nor, again, does he define the mesial limits of the frontal and parietal lobes of

<sup>1</sup> See G. Retzius, *Menschenhirn*, 1896.

<sup>2</sup> Moreover, His states that his "olfactory lobe" includes the pyriform lobe. *Vide infra*.

<sup>3</sup> W. His, "Die Anatomische Nomenclatur," *Arch. f. Anat. u. Phys.*, 1895, Suppl. Bd., pp. 174-176, note especially the footnote *v.* on p. 174, in which His says that he is using the terms in the same sense as Turner.

the brain. So that he thus spares himself the inconsistency of some of his less cautious followers, who at one and the same time adopt the views of His, Turner, and Broca, apparently without appreciating the fundamental distinctions between the three teachings.

There are much wider grounds for objection to the subdivision suggested by His than the comparatively minor reasons just urged; but as these major considerations apply equally to all the current opinions, they will be best discussed after the views of Turner and Broca have been considered.

One of the two minor inconsistencies of His's subdivision, which were indicated in the above remarks, calls for further mention in order to clinch the matter. I refer to the separation of the so-called "stria olfactoria lateralis" (which is really part of the anterior extension of the pyriform lobe) and the "lobulus hippocampi" (which is merely the caudal extremity of the same histological formation).

This error is one which the human anatomist is very liable to commit when his observations are not checked by comparative studies, because the cephalic part of the pyriform lobe has dwindled to such insignificant proportions that the name *stria olfactoria*, which is thus applied to it, is not altogether inappropriate. But in the early human fœtus and in macromammals, in which the anterior part of the pyriform lobe has not undergone such an atrophic change (see fig. 1), it requires no argument to demonstrate that any definition which includes the anterior part of the pyriform lobe in the rhinencephalon must be not only arbitrary but also morphologically unnatural if it excludes the rest of the pyriform lobe. Now, the natural division between the pyriform lobe and the neopallium is the rhinal fissure (fig. 1). And His, inconsistent though it may seem with the above-quoted statements,<sup>1</sup> freely admits that the rhinal fissure is the line of demarcation between the "pallium" and the "rhinencephalon." But he appears to entertain a misconception as to the identity of the rhinal fissure. There can

<sup>1</sup> His does not deliberately exclude the pyriform lobe from his rhinencephalon, in fact, he seems to imagine that he has included it; but in his list of parts of the "olfactory lobe" he makes no mention of the tip of the uncinate convolution (the pyriform lobe). In other words, his "rhinencephalon" is nothing else than the "lobus olfactorius" of the older German writers.

be no doubt that the depression he refers to in the embryonic human brain as the "*fissura rhinica*" of Turner (*op. cit.*, "*die Anat. Nomenclatur*," p. 176) is not the true rhinal fissure. For Retzius has clearly shown (*Das Menschenhirn*, 1896) that the rhinal fissure in the early human foetus is exactly analogous to that of other mammals, and cuts *into* the temporal region [witness the incisura temporalis of the adult] instead of marking the cephalic limit of the temporal pole. In other words, the rhinal fissure marks off a part of the temporal pole which belongs to the pyriform lobe.

Sir William Turner approached the consideration of this subject from the comparative standpoint, and therefore avoided the error regarding the pyriform lobe which His committed, and still persists in committing, although apparently unconsciously and unintentionally. Turner, therefore, includes in his "rhinencephalon" the whole, and not merely the anterior part, of the pyriform lobe. It "consists," to use his own words, "of an olfactory bulb, a crus or peduncle, and a lobus hippocampi" ("The Convolution of the Brain," *Jour. of Anat. and Phys.*, vol. xxv., 1890, p. 107). He says nothing concerning the gyrus subcallosus, Broca's "carrefour," or the septum lucidum, so that presumably these structures are excluded from the "rhinencephalon," which means that they form part of the "pallium."

By this not unnatural process of extending Owen's term to include not only the olfactory bulb but also its obvious appendage, so to speak, the pyriform lobe, Turner has incidentally introduced a paradoxical nomenclature. The terms "pallium" and "rhinencephalon" are now used as complementary expressions, so that the pyriform lobe, being regarded as rhinencephalic, cannot be "pallium"; and yet the posterior portion of this "lobe" fulfils all the conditions which had hitherto been regarded as distinctive of pallium or mantle; in other words, it is a complex or cortex and medullary layer quite free from the corpus striatum (*vide* fig. 5). In the strict meaning of the term, the posterior part of the pyriform lobe is "pallium" in the sense of Reichert.

The genesis of such a conception of a rhinencephalon may be indirectly attributed to Broca's suggestion of a "limbic

lobe." Upon supposed morphological grounds Broca separated the olfactory bulb and its peduncle, the locus perforatus anticus, the uncinatus gyrus, and the callosal gyrus as a great cortical ring completely surrounding the hilum of the hemisphere. He supposed these regions to be still further united physiologically as all appertaining to the sense of smell. With various modifications proposed by different anatomists, the main idea of this "limbic" or "falciform lobe," as Schwalbe calls it, has met with a very wide acceptance. As at present most usually interpreted it includes the gyrus fornicatus, the gyrus uncinatus, hippocampus and septum lucidum, in addition to the basal structures already enumerated.

But to such a subdivision there is an unsurmountable objection. Even granting, for the sake of argument, that the gyrus fornicatus and gyrus uncinatus were exclusively olfactory in function—which is very far from the truth—this would not justify us in separating this strip of the neopallium<sup>1</sup> from the whole of the rest of the same histological formation, in defiance of the most obvious morphological principles.

Turner adopted the ideas of Broca only so far as to include in his "rhinencephalon" those parts of the hemisphere which he regarded as indubitable connections of the olfactory apparatus; and to institute a contrast to which Turner gave a concrete form in the shape of complementary terms, between the olfactory and the non-olfactory parts of the hemisphere.

The idea of subdividing the mesial surface of the hemisphere into a series of concentric areas seems to exert some strange fascination over the minds of morphologists within recent years, thanks very largely to the writings of Zuckerkandl. What exactly is gained when the mesial surface has been thus arbitrarily split up into "Randwindungen" is not very evident, unless it be the fact that Broca's ideas of a "limbic lobe" and Schmidt's conception of "Bogenwindungen" both find expression in this exercise of the imagination, generally so futile and meaningless.

The chief fallacy in Broca's great morphological excursus I

<sup>1</sup> For the whole of the gyrus fornicatus and the greater part of the gyrus uncinatus of Human Anatomy are neopallium. Exclude this strip of neopallium from Schwalbe's "falciform lobe," and we have the "rhinencephalon" or "*pars limbica hemispherii*" of these notes.

have exposed in the above notes; and Hochstetter<sup>1</sup> has recently shown how fallacious must be the conclusions drawn from a belief in the genuineness of "Bogenwindungen."

Arguing from the comparative standpoint, I attempted in 1897 to expose the futility of such efforts,<sup>2</sup> and this criticism called forth an instructive rejoinder,<sup>3</sup> to which the reader is referred.

It is now necessary to discuss the relationship which the hippocampal formation presents to the main subdivisions of the hemisphere. Both Turner and His exclude it from the rhinencephalon, and, *ipso facto*, regard it as part of the pallium. Schwalbe includes it in his falciform lobe. His includes part of the paraterminal body (Broca's area and Zuckerkandl's gyrus subcallosus) in the rhinencephalon, and excludes the rest (septum lucidum), whereas Turner mentions none of these bodies, and presumably includes them in his pallium.

An examination of the brain in the Monotremata and the lower Vertebrata shows that the paraterminal body is merely a connecting link between the olfactory bulb and the hippocampus. This body is intimately connected on the one side with the hippocampus and on the other with the olfactory peduncle, into which it merges anteriorly. A study of the progressive evolution of this region in the lowlier Vertebrates, and especially the Amphibia, shows that the hippocampus and the paraterminal body are essentially specialised parts of one ganglionic mass; and that the latter retains its primitive structure and its original relations to the olfactory peduncle and bulb, and forms the connecting link to the progressively-specialised hippocampus. Therefore any method of subdividing the cerebral hemisphere which ignores this interdependence and separates these two histological formations must, *ipso facto*, be arbitrary and unnatural.

Although these two structures appear to become separated

<sup>1</sup> F. Hochstetter, "Beiträge zur Entwick. d. Gehirns," *Bibliotheca Medica*, Stuttgart, 1898.

<sup>2</sup> "The Relation of the Fornix to the Margin of the Cerebral Cortex," *Jour. of Anat. and Phys.*, vol. xxxii. pp. 56-57.

<sup>3</sup> G. Retzius, "Zur Morphologie der Fascia Dentata und Ihrer Umgebungen," *Biologisch. Untersuchungen*, Bd. viii., 1898, No. 3. Compare also "Zur Auseren Morphologie des Riechhirns," etc. *Op. cit.*, No. 2, p. 25, regarding the terms "*pallium*" and "*rhinencephalon*."

the one from the other in the Eutheria, they are still closely linked together, not only by the fornix and septum lucidum, but also by the vestiges of the anterior part of the hippocampal arc, which remain as a testimony to the intimacy of the relationship between these two bodies. If physiological reasons had any weight in this argument, the hippocampus should, beyond all question, be regarded as part of the rhinencephalon or "smell-brain." But the question at issue is not a problem of function, but one that must be settled upon purely morphological grounds. The relations which a study of the brain in the Sauropsida and Monotremata shows to exist between the olfactory peduncle, the corpus paraterminale, and the hippocampus, establish a claim for the two latter bodies at least equal to that of the pyriform lobe and tuberculum olfactorium in the constitution of a rhinencephalon. The point at issue is this:— that the term "rhinencephalon" can logically be applied only to the olfactory bulb and its peduncle (*i.e.*, in its original application by Owen), or it should also include *all* those specially modified parts of the cerebral hemisphere the fate of which is linked inseparably with that of the olfactory bulb. If the latter course is followed, we must include the whole pyriform lobe, as well as the paraterminal body and the whole hippocampal formation. For if we exclude the latter, where can we rationally draw the line between the hippocampus and the olfactory peduncle? Even His and the German Nomenclature Commission include the gyrus subcallosus, *i.e.*, part of the paraterminal body. But to be logical we must also include the rest of this body, *i.e.*, the septum lucidum. And we cannot draw the line of division between the paraterminal body and the hippocampus, between two structures the fate of each of which is so intimately bound up in that of the other.<sup>1</sup>

Upon these grounds alone, even if there were no other reasons, the hippocampus has an unquestionable right to be grouped along with the paraterminal body and olfactory apparatus in the "smell-brain," whether we call such a complex "rhinencephalon" or not. But there are more potent reasons than these for such a grouping.

<sup>1</sup> For further information concerning the intimacy of the connections of these bodies see "The Relation of the Fornix," etc., *this Journal*, vol. xxxii.



Upon histological grounds the hippocampus and the neopallium ought not to be regarded as one formation. But even if their structure were similar, the behaviour of the two regions, as their evolution is traced through the Vertebrate series, stands in such marked contrast that their inclusion under the one term "pallium" (Turner, His, and others) in the higher Mammalia can hardly be regarded as a happy grouping, or one conducive to accurate comparison.<sup>1</sup>

The pyriform lobe shares far more in common with the neopallium in structure, in its phylogenetic history, in its behaviour in relation to the ganglionic masses and the fibre systems of the hemisphere, than the hippocampus does; and yet one cannot hesitate to acknowledge the wisdom of separating the pyriform lobe from the neopallium in a primary subdivision of the hemisphere. But if the pyriform lobe is thus separated from the "pallium" of Turner and His (as Turner has separated it and as His believed he had done), the hippocampal formation should, *à fortiori*, be similarly excluded; for is it not the earliest cortical formation to be elaborated; a formation which throughout the whole Vertebrate series retains its own peculiar fibre-system—the fornix—separate from the other fibre-systems of the hemisphere; a cortex, moreover, which attains the height of its morphological importance in the Vertebrata when the neopallium is yet an altogether insignificant area? Furthermore, in the Mammalian series, in which for the first time the neopallium attains to any noteworthy functional significance or anatomical importance, the hippocampus steadily declines in relative proportions as this non-hippocampal pallium increases. For the hippocampus does not share in the progressive greatness of the mammalian brain. What legitimate reason, then, can there be for harnessing together as "pallium" these two regions, the behaviour of which contrasts so markedly that it might almost with truth be said that they vary inversely in size and importance? If it be justifiable to separate the pyriform lobe from the "pallium," how much greater reason is there for also excluding the hippocampus! If any critic objects (as he has good reason

<sup>1</sup> I have elsewhere pointed out the inevitable confusion which results from this usage in Comparative Anatomy (*this Journal*, vol. xxxii. pp. 243-246).

to object)<sup>1</sup> to such an abuse of the word "pallium," I would remind him that he should with equal vigour, if he be logical, oppose the exclusion of the pyriform lobe (which is a true "mantle," *vide* fig. 5) from the "pallium."

But the most potent reason that can be advanced for thus separating the hippocampus and the pyriform lobe from the neopallium is not so much the constitution of a logically correct "rhinencephalon" (if we be permitted the use of this much-abused term in such a sense), but rather that such a procedure gives due recognition and a distinguishing name to a morphologically well-defined cortical area, which is the most important feature of the whole brain, or, for that matter, of the whole body in the higher Eutheria. Hitherto the strange irony of a confused morphology has denied a name out of the plethora of cerebral nomenclature to be the exclusive property of this the dominant organ of the nervous system, and the master-structure of the whole body; for it has been linked with the hippocampus, which does not share these high attributes, but has long since reached the height of its importance, and is now on the wane in those mammals in which the neopallium reaches its supreme development. A distinctive name—*corpus callosum*—is now very generally admitted for the commissural fibres of this neopallium, in contradistinction to those of the hippocampus—*psalterium*. Why, then, should not a like distinction be conferred on the cortical areas from which the commissures ultimately spring?

When we come to consider an appropriate name for this culminating feature of the mammalian brain, we are faced by many difficulties. On the one hand, anatomists are very chary of accepting an entirely new term for a well-known structure; and on the other hand, it is confusing to use an old term in a new sense. For there is no term in the whole range of anatomical literature which has been applied to just that part of the cerebral hemisphere which is responsible for the greatness of the mammalian brain, and overshadows in its greatness and usurps many of the functions of all the other regions of the nervous system. In these notes I have spoken of this body as the "neopallium," and in a series of memoirs on cerebral morphology I have been accustomed since 1894 to speak of it as

<sup>1</sup> C. L. Herrick, *Jour. Comp. Neurology*, 1896, p. xvii.

the "pallium." I began using the latter term in this peculiar sense as the result of a misreading of Turner's memoir of 1890. Equipped with only that superficial knowledge of the nervous system which the average medical student possesses, I commenced the study of what is perhaps the most generalised and ideally simple brain—that of *Perameles*—in the whole Mammalian series. Under such circumstances it was only natural to recognise in the area called here the "neopallium" a region eminently worthy of separate and distinctive recognition; and I, unconsciously, "read into" Turner's memoir my own views on morphology, which are the same now in regard to this matter as they were then.<sup>1</sup> So that when he spoke of the rhinal *and hippocampal* fissures as being the limits of the "pallium," I somewhat hastily concluded that he did *not* include the hippocampus in his "pallium"—a view for which, of course, there is no warrant in his memoir. But although I have thus for more than six years been using the term "pallium" in a sense which is different from that of other writers, and altogether foreign to the idea of Reichert, I must in justice point out that such a usage implies an important morphological fact not hitherto duly recognised. At the same time, I took a liberty with the term "pallium" which is no greater than that of Turner and His in their employment of the same expression.

It must be obvious, from the preceding discussion, that the terms "rhinencephalon" and "pallium" cannot be employed as complements the one of the other without considerable distortion of the original meaning of one or both of the terms.

The pallium, in the strict sense, is composed of three distinct structural elements: a ventral part, or pyriform lobe, the "*basipallium*,"<sup>2</sup> the marginal pallium or hippocampus, and lastly that large dorsal cap the "*dorsipallium*" or *neopallium*. If now we regard this term "neopallium" as the complement of "rhinencephalon," it will involve a new definition of the latter, which would then include the whole pyriform lobe, the whole hippocampal formation and paraterminal body, in addition to

<sup>1</sup> *Proc. Linn. Soc. New South Wales*, vol. ix. (2nd ser.), part 4, 1894, p. 648.

<sup>2</sup> G. Retzius ["Zur äusseren Morphologie des Riechhirns," *Biologisch. Untersuch.*, Bd. viii., No. 2, 1898, p. 25] employs this term in an analogous but somewhat different sense.

the olfactory bulb, peduncle and tubercle, and the locus perforatus. Far from such an employment of the term proving awkward, it expresses the obvious relationship of both the hippocampus and the pyriform lobe to the olfactory apparatus in so natural a manner as to afford the last convincing link in the chain of evidence for this rational basis of division into neopallium and rhinencephalon.

It is a matter of common knowledge that the olfactory peduncle passes into direct continuity with, and in addition exhibits further most intimate links with, the paraterminal body and hippocampus (mesially), and with the tuberculum olfactorium and pyriform lobe (laterally). And there is ample proof that all these parts of the brain are pre-eminently, if not wholly, olfactory in function. In anosmatic animals (*e.g.*, *Phocæna*) the hippocampus dwindles, the paraterminal body almost completely vanishes, and the typical elements in the tuberculum olfactorium and pyriform lobe practically disappear. All these regions are, therefore, eminently worthy of the name "rhinencephalon."

Ziehen<sup>1</sup> objects to this term, because the pyriform lobe does not wholly vanish in anosmatic mammals, and he refers to the superficially apparent paradox of a smell-less animal possessing a "smell-brain" (rhinencephalon). One might with more justice object to the term "optic thalamus" because the greater part of this body persists in eyeless animals, or to the term "trigonum acusticum" because the lateral regions of the floor of the fourth ventricle still remain in deaf mammals! But the fact that other terms are not perfect is not a sufficient reason for retaining the name "rhinencephalon" if a better can be found. Unfortunately this name is not new, and no amount of writing is likely to rid the Science of Anatomy of the term, even if this were desirable. And no one acquainted with recent literature can pretend that the term has any precise meaning at present. Therefore we should endeavour to attach to it the most natural and useful meaning.

So far as I understand the question at issue, there are two, and only two, alternative meanings logically open to us for

<sup>1</sup> *Das Centralnervensystem der Monotremen und Marsupialier*, 1897, p. 23.

adoption.<sup>1</sup> It may be employed to designate the olfactory bulb and peduncle as Owen used it, and as such is unnecessary, and therefore superfluous; or it may be used to include all those regions which are pre-eminently olfactory in function, and have become definitely specialised in structure in consequence. Such a definition will include the olfactory bulb, its peduncle, the tuberculum olfactorium and locus perforatus, the pyriform lobe, the paraterminal body, and the whole hippocampal formation. The paradoxical statement that "if this definition be adopted, a smell-less animal will possess a rhinencephalon," is no argument and only a very "partial truth." For though the brain of an anosmatic Cetacean apparently possesses a tuberculum olfactorium, a pyriform lobe, and a small hippocampus, histological examination will show that the two former present little else than the areas corresponding to the tuberculum olfactorium and pyriform lobe from which most of the typical elements have vanished, and that the hippocampus is a mere wreck of "its former self," as exhibited in osmatic mammals. Ziehen's objection is therefore little else than a verbal quibble. We might evade the difficulty of using these terms "rhinencephalon" and "neopallium" by coining such expressions as "*pars limbica [hemisphaerii]*" and "*pars crescens [hemisphaerii]*" respectively.

It is a curious and instructive fact that many writers who, in name at least, adopt the teaching of Turner and His, are driven by force of circumstances to include (apparently unconsciously) the hippocampus in their "rhinencephalon." Several of the most prolific writers on Comparative Neurology of recent years fail to draw a sharp line of distinction between the hippocampus (which they sometimes erroneously call the "hippocampal convolution") and the uncinate [or hippocampal] gyrus (which they often call the "hippocampus" or "cornu ammonis"). Under such circumstances it is not surprising that having recognised the pyriform lobe (which forms the cephalic extremity of the human uncinate gyrus) as part of the "rhinencephalon" of Turner, they also include the hippocampal formation. In other

<sup>1</sup> There does not seem to me to be any evidence to substantiate the views of several writers, more especially in America, that this term may be given a segmental significance.

words, they virtually adopt a definition of the "rhinencephalon" such as I have suggested in these notes.

Others, again, reach the same end without confusing the hippocampus and the so-called "hippocampal gyrus." Thus, in a recent work,<sup>1</sup> the writers commence with a tabulation of the teaching of His and the Nomenclature Commission (page 1); they then describe the brain of the Chimpanzee, and exclude from their rhinencephalon not only the hippocampus, but also the pyriform lobe (p. 45). In other words, they follow the tabulated list of the Nomenclature Commission, but appear to forget that this same Commission also stated (*vide supra*) that the rhinal fissure ("*fissura rhinica*" of Turner) is the line of demarcation between pallium and rhinencephalon. Toward the end of the work, however (p. 550), the authors include both the pyriform lobe and the hippocampus in the rhinencephalon!

#### *Conclusion.*

In these fragmentary notes my principal object has been not so much to seek for a more logical interpretation of the term "rhinencephalon" as to call attention to the exact limits of the neopallium. For if we retain the term "pallium" in its present sense as a complex of neopallium and hippocampus, the greatest confusion will be perpetuated in the language of Comparative Anatomy. Thus, a writer on the Sauropsidan brain will speak of the "pallium" of a lizard or bird when he refers to what is chiefly hippocampus; and the unwary reader may imagine that it is the same "pallium" as that of Man, which, however, is chiefly "neopallium."<sup>2</sup> But it is high time that some distinctive name should be found for that great progressive cortical field, the high development of which becomes in the Mammalia the great fundamental condition of their survival. At every epoch in the history of the mammal this part of the brain shows a

<sup>1</sup> Flatau and Jacobsohn, *Vergl. Anat. d. Centralnervensystems*, 1899.

<sup>2</sup> This confusion is nowhere more pronounced than it is in the writings of certain anatomists who call the hippocampal commissure of Reptiles and Birds the "*commissura pallii*." Boyce and Warrington even call other hippocampal tracts "*pallial*" (*Phil. Trans.*, 1899, p. 296).

progressive increase in size, whereas the other superficial parts of the hemisphere become relatively or actually smaller, and may even disappear almost entirely without any vital injury to the individual (e.g., as in the anomatic Cetacea).

This neopallium is a great unlimited area (far removed from the disturbing influences of the purely "administrative" parts of the nervous system), where "impulses of diverse nature," coming from all regions of the body and from all the sense organs, "may meet and play upon each other."

It is, in fact, that *sensorium commune* for which the ancient philosophers sought in vain for so many ages, and which Aristotle called at various times the *πρῶτον αἰσθητήριον*, as well as the *ἡγεμονικόν* (*caput humanæ substantiæ*), the *κύριον*, the *ἐπικρῖνον*, and the *ἀρχή*, among many other names. These ancient writers recognised that there must be somewhere in the body some distinct organ where all the sensory impulses of the body might meet and react one upon the rest, so as to produce that consciousness of the various properties of one object which everyone recognises. And many of these writers recognised that this organ must at the same time be the "storehouse" of impressions, and the dominant organ of the body, with the power to quicken or restrain the activities of each and every part of the whole organism in response, either directly or indirectly, to the impressions from the outside world which are constantly pouring into this common sensorium.

Such an organ is the neopallium, and these special attributes it does not equally share with any other cortical formation, or any other part of the nervous system.

It is therefore a region of the hemisphere which is in a greater degree than any other part "the organ of the mind," and as such is surely worthy of a distinctive name. It might be called the "*pars crescens*" [*hemisphærii*], in reference to the peculiar characteristic of its rapid expansion in the Mammalia; and in that case we might distinguish the rest of the hemisphere (exclusive of the corpus striatum) as the "*pars limbica*" [*hemisphærii*], because its various parts are grouped around the hilum of the hemisphere.

But instead of selecting a new phrase, such as "*pars crescens*," I prefer to use the term *neopallium*, because the basis of this

hybrid, conveys some idea as to the meaning of the expression. No one is more conscious than the writer of the many obvious defects of such terminology, which he will be quite willing to sacrifice if some one will suggest a happier phrase to indicate that region which is, in reality, the ultimate product of the evolution of the vertebrate fabric.