# THE CEREBRAL HEMISPHERES OF *LACERTA VIRIDIS*

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In a survey of the literature dealing with the anatomy of the reptilian fore-brain, one is struck not only by the wealth of descriptive detail, but also by the confusion in the terminology employed and the variety in the homologies which have been suggested. The descriptive detail is no doubt accurate so far as the technical methods in use allow. That the interpretations of this detail are so varied suggests that the methods themselves may be at fault, and have failed to reveal certain essential facts.

The method commonly used has been the microscopical examination of serial sections stained by toluidin blue for cells, or by the Weigert-Pal or a silver impregnation method for nerve fibres. In this work these same methods have been used on the brain of *Lacerta viridis*, and after each region of the hemisphere has been described, the findings are discussed in relation to those of other workers and in other reptiles. In this way a general view may be obtained of the facts which have been elicited by these or similar methods throughout the reptilian class. Such a general view will form the basis of a discussion of homologies in which the limitations inherent in the methods can be taken into account. It will help to show where disagreement between different workers has been due to gaps in our knowledge resulting from these limitations, and what lines of investigation should be followed in order to fill them. It will also be of value in suggesting a more uniform terminology, for there is no doubt that much of the confusion which exists in fore-brain morphology is due to the number of ill-defined terms which have been used in incompatible ways by different workers.

Certain difficulties peculiar to fore-brain morphology may be stressed at the outset. The structural analysis of the nervous system cannot be carried further than the neurone, so that morphological comparisons must ultimately be made between neurones and groups of neurones. Now the simpler methods of neurological histology which have been used here, and by most workers in this field, do not show two of the essential parts of a neurone, the cell body and the axon, in one and the same preparation. It follows that the relation between the two is often left in doubt, or, in other words, that whether an axon carries an impulse from another cell body to the one in question, or *vice versa*, cannot be clearly demonstrated. This is obviously a technical limitation of very great importance.

Secondly, in an investigation of this kind, the data must be almost all microscopical. The structures under consideration are groups of neurones which must be distinguished from adjacent groups, all of which have a very similar histological structure. Boundaries are consequently often ill-defined, and sometimes invisible. This is not entirely the fault of the methods, but an inherent characteristic of a correlating mechanism like the fore-brain.

A third difficulty is implied in the principle of neurobiotaxis which has been elaborated by Kappers and his school. A group of neurones is liable to migrate from its original position under the influence of repeated stimulation. It follows that even where such a group can be delimited accurately, care must be exercised in comparing it with a similar group in another species, since position and relations may have been altered considerably by neurobiotactic migrations. The fibre connections will form a constant criterion for comparison in cases like these, but, as has been pointed out already, the methods in common use do not reveal them as clearly as could be desired.

It is clear then, that both the nature of the material and the technical methods employed provide a tempting field for the application of preconceived homologies, which are very difficult to prove or disprove. It is unfortunate that practically none of them can be checked by palaeontological investigation. In this paper the attempt will be made to discuss them critically, and, bearing in mind the technical limitations, to reaffirm those which are reasonably sure, to state clearly where doubt still exists, and possibly to indicate the lines along which this doubt may be removed.

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## MATERIALS AND METHODS

The material available consisted of twelve brains of *Lacerta viridis*. They were all obtained immediately after death, and except when the technique required a different fixative, fixed at once in 10 per cent. formalin. Both Golgi and Cox-Golgi methods were tried, but each was a failure. Ranson's and Weigert's methods were also unsatisfactory, the latter as medullated fibres seem to be comparatively few in this brain. Bielschowsky's silver impregnation method was found to be the best for fibres, and the toluidin-blue method for cells. All brains were embedded in celloidin and paraffin before being cut. Complete series were made in each case, and those on which this work is actually based are as follows:

| Series no. | Stain | Plane of section | Thickness |
|---|---|---|---|
| B 87 | Toluidin blue | Transverse | 12$\mu$ |
| B 97 | ,, | ,, | 12$\mu$ |
| B 99 | ,, | Sagittal | 12$\mu$ |
| B 120 | ,,<br>(Huber's technique) | ,, | 25$\mu$ |
| B 98 | Toluidin blue | Horizontal | 12$\mu$ |
| B 86 | Bielschowsky | Transverse | 12$\mu$ |
| B 102 | ,, | ,, | 12$\mu$ |
| B 109 | ,, | Sagittal | 15$\mu$ |

The most satisfactory series were B 87, B 99, B 102 and B 109, and most of the observations and figures were made from them. Figs. 2*a* and 2*b* indicate the approximate plane of section for series B 87 and B 102, from which figs. 3–10 and 12–16 were drawn respectively.

## EXTERNAL FEATURES AND MAIN SUBDIVISIONS OF THE TELENCEPHALON

In its general features the telencephalon of *Lacerta viridis* does not differ greatly from that of most lacertilia and *Sphenodon.* It is of the macrosmatic type, with a well-developed olfactory bulb joined to the hemisphere by a peduncle of moderate length. Fig. 1, an outline drawing from a photograph, shows the main features. The accessory bulb forms a visible swelling behind the main bulb. In sections it can be seen on the dorso-medial aspect of the peduncle, where it receives the division of the olfactory nerve from the vomeronasal organ. An accessory olfactory bulb has been described in a comparable position in many other Reptiles. It was not mentioned by Cairney in *Sphenodon.*

The term "olfactory peduncle" will be used only for the part of the olfactory apparatus which joins the bulb and accessory bulb to the anterior pole of the hemisphere. It is distinguishable from both regions by the absence of bulbar formation on the one hand, and of cortical formation on the other. Externally there is nothing to mark the junction between the peduncle and the hemisphere.

The general shape of the hemispheres can be seen from the drawing, fig. 1, and the sections, figs. 3–10. Laterally a fairly well-marked longitudinal depression forms the endorhinal fissure, Edinger's "fovea limbica externa." This fissure does not show well in the sections but can be seen in figs. 7 and 12. It lies along the ventral edge of the pyriform cortex and separates it anteriorly from a part of the corpus striatum, posteriorly from the amygdaloid. This posterior part of the fissure corresponds with the "amygdaloid fissure" of Johnston. Medially a slight depression can be seen along the ventral edge of the hippocampal cortex, as is shown in section in figs. 7–9. It begins anteriorly about the middle of the paraterminal body, and ends posteriorly at the level of the posterior pallial commissure. This fissure is very constantly present in Reptiles, and has been given many names. It is the "fimbrio-dentate sulcus" (Johnston, 1915), the "fissura arcuata" (Herrick, 1910), the "fissura hippocampi" (Hines, 1923), the "fissura septo-corticalis" (de Lange, 1911; Kappers, 1921) and so on. As Elliot Smith has pointed out (1903), it lies below the hippocampal cortex, and therefore cannot be homologous with the hippocampal fissure of Mammals. Johnston (1913) has suggested that the part of the brain in Reptiles which lies below the fissure in question really belongs to the hippocampal formation, but that it does not differentiate into definitive hippocampal cortex except in Mammals. He calls this region "primordium hippocampi" and homologises the fissure with the hippocampal fissure of Mammals. The evidence on which these suggestions are based is not satisfactory, and the term first used in 1903 by Elliot Smith for this fissure in *Sphenodon*, the "fissura limitans hippocampi," is the most appropriate. It is unfortunate that even more confusion has been introduced by the application of the term "fissura limitans hippocampi" to a different and inconstant fissure in Reptiles (not represented in *Lacerta*) by Johnston and other American workers. This question will be discussed more fully later when the structure of the paraterminal body is described. There is no representative of the sulcus lobaris, the sulcus coronalis, and the sulcus longitudinalis, described by de Lange (1911). The fissura limitans medially, and the endorhinal fissure laterally, appear to be the only ones constant enough to be of comparative morphological value in the various orders of Reptiles.

For descriptive and comparative purposes it is necessary that the telencephalon should be divided into regions which can be treated separately. Any such division must, *ipso facto*, be artificial, and can only be justified in so far as it separates regions which have some anatomical, embryological, or functional claims to be considered apart from one another. Many such divisions have been suggested (e.g. by Elliot Smith, Johnston, Herrick, Kappers, etc.), which differ more or less according to the criteria which have been used in making them. Since the fore-brain was first differentiated for the reception and correlation of olfactory impulses, and since in the Reptile it is still dominated by olfactory impulses, the arrangement and connections of the olfactory apparatus might make a convenient basis for subdivision. This basis will be used here, but considerably modified for the sake of descriptive convenience. Its main lines were mapped out by Elliot Smith in 1901, and his terminology will be followed.

Anteriorly the individuality of the olfactory bulb and peduncle is obvious. Where the peduncle broadens to join the hemisphere it is surrounded by an undifferentiated layer of cells (fig. 3) which forms a secondary olfactory nucleus. This has been called by Edinger the "lobus olfactorius" and by Herrick (1924) the "nucleus olfactorius anterior." Herrick's term will be adopted here. These three structures, the bulb, the peduncle, the nucleus olfactorius anterior, can be grouped together as the first subdivision of the olfactory apparatus. From them impulses are transmitted to more highly differentiated regions of the hemisphere.

Laterally and ventrally are a series of structures which Johnston (1922) has suggested are concerned primarily with the correlation of olfactory and thalamic impulses. They include the corpus striatum, the amygdaloid nuclei, the pyriform cortex, and the nucleus of the lateral olfactory tract. The group is not very homogeneous since, although the pyriform cortex and amygdaloid nuclei are dominated by olfactory impulses, the striatum is dominated by thalamic and hypothalamic impulses, and in Reptiles has comparatively few olfactory connections. From a descriptive point of view, however, it is undoubtedly convenient to group these structures together, and there is some theoretical support for doing so, since there is evidence that, whatever may be its connections in Reptiles and higher Vertebrates, the oldest part of the striatum is primarily a centre for giving effect to olfactory impulses.

Ventrally, lying between the paraterminal body medially and the endorhinal fissure laterally, behind the anterior olfactory nucleus and in front of the amygdaloid nuclei, is an area called the tuberculum olfactorium (figs. 1, 4–7, 20). It is poorly differentiated in *Lacerta* and is closely related to the striatum and to the paraterminal body, but cannot easily be grouped with either. It will be described as a separate subdivision of the hemisphere.

Medially the wall of the hemisphere is occupied by a well-developed mass of tissue, which appears to serve chiefly as a relay station for impulses coming to or going from the hippocampal cortex. Many of these impulses are olfactory. This region has been given various names; here Elliot Smith's name, "paraterminal body," will be used.

There remains only the dorsal part of the hemisphere. This shows a well-differentiated medial part, the hippocampal cortex. Dorsally there is an area of cortex, clearly differentiated, the morphology of which is obscure. It has been called "parahippocampal" by Elliot Smith, "general cortex" by most American workers, and "cortex ammonis" by Kappers and his school. Here the non-committal term "dorsal cortex" will be used. Dorso-laterally the pyriform cortex can be seen. This has already been grouped with the structures in the ventro-lateral hemisphere wall following Johnston's suggestions (1922). This seems morphologically satisfactory, but for descriptive purposes it will be convenient to follow common usage by classifying it with the other two cortical areas.

Clearly this subdivision and grouping of parts of the hemisphere is a compromise, and receives its chief justification on the grounds of descriptive convenience. As was stated above, many attempts have been made to subdivide on morphological or functional grounds in such a way that the subdivision should be applicable throughout the vertebrate phylum. All of them, as one would expect, are open to criticism.

The various parts of the fore-brain are interdependent functionally. Although one part may be in a state of greater functional activity at any one time than another, the fore-brain works as a whole. This may no doubt be said of any part of the body, or indeed of the whole body, but it is particularly true of the fore-brain, which is essentially a correlating mechanism. It follows, since structure and function go hand in hand, that the attempt to make rigid morphological subdivisions in such an organ is likely to be of no avail.

A rough subdivision into "basal" and "pallial" regions has frequently been made, although accepted and implied more often than specifically stated and defined. Edinger (1908) made such a subdivision into "episphaerium" and "hyposphaerium," the former being pallial and the latter basal. It is a little difficult to see exactly what parts of the brain he means to be included in each of these subdivisions, but it appears that the hippocampal cortex, the pyriform cortex and the dorsal cortex are included in the pallial part or episphaerium; the corpus striatum, amygdaloid, olfactory bulb and tracts, and paraterminal body in the basal part or hyposphaerium. It is obvious that structures which are very different functionally and morphologically are included in both these groups. Moreover, in the case of the pyriform cortex, there is some evidence at least that it is developed from the basal area (Johnston, 1916*b*), or that it is derived from Johnston's "lateral olfactory area" in Selachians (Johnston, 1922), and certainly its most obvious connection is with the lateral olfactory tract. On the medial side, the paraterminal body is very closely related to the hippocampus, so much so that Johnston, on embryological grounds, has been led to include part of it in the hippocampal formation as "primordium hippocampi" (Johnston, 1913). Whether one agrees with his view or not, it at least indicates the difficulty in making a rigid distinction between the two parts, a difficulty which was recognised by Elliot Smith (1903). Similar difficulties apply to the subdivisions which go even further, e.g. Herrick (1910), who divides the hemisphere into four quadrants, dorso-medial, dorso-lateral, etc. In this he has been followed by Kappers (1921). In the adult brain it is clearly impossible to fit the differentiated parts into these sectors without making obviously unnatural divisions, while in the embryo the names merely indicate certain topographical regions of the fore-brain vesicle which have not differentiated far enough to have clearly defined boundaries.

It remains true that, in a general way, the dorsal part of the hemisphere vesicle develops into a "pallial" area, a correlation centre of a high order, and that the ventral part develops into a large ganglionic mass under the influence of fibres which enter it from the cerebral peduncle, which may be called "basal." Both medially and laterally the two regions overlap in such a way as to make strict definition impossible.

The attempt at a subdivision on functional grounds has met with rather more success. Broadly, it is justifiable to distinguish: (i) a rhinencephalon, including the bulb, peduncle, anterior olfactory nucleus, pyriform cortex, amygdaloid nuclei, tuberculum olfactorium, paraterminal body, and hippocampal cortex; (ii) a corpus striatum connected predominantly with the thalamus and hypothalamus; (iii) the dorsal cortex. There is still doubt whether the dorsal cortex should be included in the rhinencephalon as parahippocampal cortex, or whether it should be looked on as the forerunner of the mammalian neopallium. Provisionally it is best kept separate. On the comparative morphological side this division has received considerable support and elaboration from Johnston (1922). Using his terminology, the rhinencephalon would consist of the medial, lateral, and basal olfactory areas of Selachians, together with the primordium hippocampi. To the corpus striatum he assigns a threefold origin: (i) a large part of what has been called the palaeostriatum (the "olfacto-striatum" of Cairney, Herrick, etc.) from the basal olfactory area, under the name of "bed of stria terminalis"; (ii) the remaining part (the so-called "somatic" striatum of Cairney, Herrick, etc.) from the area to which he applies the name "somatic" in the telencephalon medium of Selachians, as globus pallidus and putamen; (iii) the greater part of the caudate nucleus as a new addition in the Reptiles from the lateral edge of the dorsal (his "general") cortex. This would leave an important overlap between the rhinencephalon and the striatum, since his stria terminalis bed is on these grounds primitively an olfactory centre. The amygdaloid nuclei he derives in part from the stria terminalis bed, and in part from an infolding of the superficial parts of the lateral olfactory area. It would therefore remain in the rhinencephalon. It is not quite clear whether the "primordium neopallii," which he distinguishes in Selachians, is looked upon already as a fundamental division of the fore-brain, or simply a differentiated part of the "somatic" area of the telencephalon medium. He obviously considers it to be homologous with the dorsal ("general") cortex of Reptiles. Enough can be seen from this very brief sketch of an elaborate and careful attempt to make consistent morphological subdivisions in the fore-brain to show that a great deal of overlap between the main functional division suggested above (e.g. between rhinencephalon and striatum, and between dorsal cortex and striatum), is inevitable, and becomes more marked as one ascends the scale from the fairly primitive Selachians.

It may be pointed out here that the term "somatic," as used by Johnston and many other comparative neurologists to contrast with "olfactory," will be avoided. There seems no reason why the olfactory sense should be any less "somatic" than, for instance, the visual or auditory senses. The essential difference between the olfactory and other sensory impulses which reach the hemispheres is that the latter are relayed in the thalamus and the former are not. In most cases the word "thalamic" can be substituted for "somatic" in fore-brain morphology. It has the advantage of being a term with a definite anatomical basis, and has no doubtful theoretical implications.

Any thorough-going criticism of Johnston's views in the basis of the work to be described in this paper will obviously be impossible, if only because of the complete lack of embryological data. It will, however, be useful to point out where in the adult anatomy observations appear to be consistent with his view, and where apparent difficulties arise.

## THE OLFACTORY BULB, PEDUNCLE, NUCLEUS OLFACTORIUS ANTERIOR, AND OLFACTORY TRACTS

The olfactory bulb is an oval swelling about 1 mm. in length. It has the characteristic structure, already well described in several reptilian forms (e.g. Crosby, 1917). Glomeruli lie superficially, succeeded by a layer of mitral cells, and then by the fibres of the olfactory tracts, presumably axons of mitral cells and the granule cells which form the next layer. Inside the granule cells comes the ependyma of the olfactory ventricle, which is continuous through the peduncle with the lateral ventricle. The accessory olfactory bulb (fig. 1) extends posteriorly on the dorso-medial aspect of the peduncle for a further millimetre or slightly more. Its structure resembles that of the olfactory bulb. In this region the tract fibres are grouped laterally and ventrally. The vomero-nasal nerves can be seen entering the accessory bulb on its medial side. Posterior to the accessory bulb is a short length of peduncle, about 0·3 mm., which contains only a ring of olfactory tract fibres superficially, a few scattered granule cells beneath them, and the olfactory ventricle.

Where it joins the hemisphere the peduncle swells out to form the nucleus olfactorius anterior (fig. 3). It is characteristically a complete ring of cells surrounding the olfactory ventricle. The cells are of medium size, and cannot be followed anteriorly into the layer of granule cells. The ring shows no differentiation at first, except that dorso-laterally the cells are rather more numerous and slightly larger, and that a little posterior to this level a similar but smaller and less definite ventro-medial accumulation can be seen. Further posteriorly this ring of cells is found to pass gradually into the various regions differentiated in the superficial parts of the hemisphere (fig. 4). Dorso-laterally it passes backwards into the pyriform cortex; dorso-medially and dorsally into the hippocampal and dorsal cortex; medially it gives place to the comparatively cell-free anterior part of the paraterminal body, while ventrally it passes into the tubercular cortex and possibly the palaeostriatum. These last two structures are too poorly differentiated from each other for this statement to be made more precise.

The fate of the olfactory tract fibres is difficult to determine, and from this material cannot be described with complete certainty. The appearances seem best interpreted in the following way. At first, in a transverse section of the peduncle, the tract fibres form a uniform superficial ring. As the nucleus olfactorius anterior is approached they accumulate among the cells in a dorsolateral position, lying more deeply, but showing a tendency to stream towards the surface. These fibres will form the lateral olfactory tract (figs. 6, 12) superficially placed below the ventral edge of the pyriform cortex. Dorsally the fibres persist in a superficial position (fig. 18). They are least numerous here, and probably enter the dorsal part of the nucleus olfactorius anterior, although some may continue onwards to the superficial aspect of the hippocampal and dorsal cortex. Ventrally and ventro-medially fibres are fairly numerous. Many remain superficial (figs. 17, 18), and the most ventrally placed probably run on to enter the superficial surface of the tuberculum. Others become diffused among the cells of the nucleus olfactorius anterior. As the tubercular cortex and palaeostriatum begin to differentiate, fibres can be seen arranged in three zones (fig. 12): (i) superficial (fig. 12, *G*), probably tract fibres running to the tuberculum; (ii) intermediate (fig. 12, *F*), among the cells of the tuberculum, and consisting probably of tract fibres and fibres relayed in the tuberculum and on their way to the paraterminal body; (iii) deep, between the tuberculum and the palaeostriatum. This is a very mixed group of fibres and it has not been possible to analyse them with complete certainty. Some of them, probably most, are fore-brain bundle fibres on their way to or from the striatum. These can be seen in the sagittal series (fig. 18). A few are probably either tract fibres, or tract fibres which have been relayed in the nucleus olfactorius anterior or the tuberculum. They are on their way to the paraterminal body, to the palaeostriatum, and also to an olfactory component of the anterior commissure (fig. 17), a conspicuous bundle in the lateral part of this group of fibres.

Medially the olfactory tract fibres of the peduncle preserve their superficial position. Some ascend dorsally to enter either the superficial dorso-medial surface of the nucleus olfactorius anterior or the extreme anterior end of the hippocampal cortex. Others run more directly posteriorly, are related to the nucleus olfactorius medialis (figs. 4, 20) in the anterior part of the paraterminal body, and probably end in the ventro-medial nucleus of the paraterminal body. They may reach as far as the nucleus of the diagonal band.

The lateral olfactory tract was described as coming from the dorso-lateral accumulation of cells and fibres in the nucleus olfactorius anterior. A little further posteriorly fibres can be seen entering and leaving it to and from the anterior part of the deep surface of the pyriform cortex. Its further course to the amygdaloid region will be discussed later.

This description of the olfactory tracts may be summarised as follows. After forming a complete and uniform layer round the peduncle, most of the fibres concentrate dorso-laterally, where many are no doubt relayed in the nucleus olfactorius anterior. These form the lateral olfactory tract which gives fibres to and receives them from the pyriform cortex, and connects posteriorly with the amygdaloid nuclei. Most of the remaining fibres are relayed in the nucleus olfactorius anterior which they enter superficially. They are not clearly differentiated into medial and intermediate tracts. The former is represented by fibres which run through the nucleus olfactorius medialis to the paraterminal body and possibly (but not certainly) directly to the hippocampus; the latter by fibres which run to the tuberculum, the anterior commissure (its olfactory component), and possibly to the palaeostriatum. It seems probable that the anterior part of the dorsal cortex may receive a few olfactory fibres from the dorsal aspect of the peduncle.

### *Discussion*

It is noteworthy that the nucleus olfactorius anterior corresponds very closely with the same structure described by Herrick (1924), and the appearances fit well with his suggestions that it is a "residual undifferentiated part of a much larger area." It is clearly a secondary olfactory nucleus and many olfactory tract fibres are relayed there, although it probably serves as a correlation as well as a relay centre. Its correspondence with what Edinger, de Lange, Kappers, etc., call the "cortex of the lobus olfactorius" is obvious. In some Reptiles it is separated from the rest of the hemisphere by a "sulcus coronalis" (*Chelone imbricata*, de Lange, 1911). Commonly it extends far forwards into intimate relation with the bulbar formation (opossum, Herrick; *Sphenodon*, Cairney), but in *Lacerta* it is separated by the comparatively cell-free peduncle. Johnston (1915), in the turtle, describes a "nucleus olfactorius anterior" which appears to be only a part of what he there calls the caudate nucleus, later (1922), the bed of the stria terminalis. As Herrick pointed out, this seems unjustified. Johnston (1915) states that both the pyriform and hippocampal formations reach forwards into close contact with the "olfactory formation," and in doing so he is probably referring to Herrick's nucleus olfactorius anterior. Crosby (1917) describes an anterior olfactory nucleus in the alligator. In her fig. 3 (p. 390) this appears as a collection of cells lying ventrally in the peduncle and forming part of a cortical ring similar to that described here for *Lacerta*. The ring shows more differentiation, so that she is able to distinguish the hippocampal from the pyriform part of it. It is possible that here is a nucleus olfactorius anterior which differs from that of *Lacerta* only in its degree of differentiation, or that sections a little further forward would have shown a condition quite like that in *Lacerta*. It appears then, that a nucleus olfactorius anterior is very generally present in Reptiles, and that it is very like the same structure described in the lower Mammals by Herrick (1924), Le Gros Clark (1928), and others.

In *Lacerta* the lateral olfactory tract is much the largest and most definite of the olfactory tracts. In this it agrees with the descriptions published of other forms. Its connections with the nucleus olfactorius anterior, the pyriform cortex, the nucleus of the lateral olfactory tract, and the amygdaloid nuclei are remarkably constant throughout the class. How much of the tract is relayed in the nucleus olfactorius anterior it is impossible to say. It is certain that, as the tract runs posteriorly, it comes to contain fewer secondary and more tertiary fibres. It seems best, nevertheless, to keep the term "lateral olfactory tract," remembering this constant loss of secondary and gain of tertiary fibres, rather than the terms "tractus bulbo-corticalis" and "tractus cortico-epistriaticus" introduced by Edinger, since both the latter involve assumptions which cannot yet be proved.

The medial and intermediate tracts are small and difficult to follow. There appears to be no doubt about their connection in all the described forms with the tuberculum and paraterminal body, or about the presence of a connection in the anterior commissure from the intermediate tract, although the last is not mentioned by Cairney for *Sphenodon*. A direct connection with the anterior part of the hippocampal cortex is described by P. Ramón y Cajal (1917). The evidence from my material is not definite. The presence of an olfactory tract connection with the medial part of the palaeostriatum (called by Johnston the nucleus caudatus in 1915 and bed of the stria terminalis in 1923, and by Cairney, Herrick and others olfacto-striatum) is also suggested but not definitely proved by my material. Cairney describes it definitely in *Sphenodon*. This is a point of some importance since the justification of the name "olfacto-striatum," a useful one in many respects, depends upon it. It is a point which deserves further investigation. Another question which remains to be decided is whether intermediate olfactory tract fibres run down with the mediate fore-brain bundle to the hypothalamus and mid-brain, as Herrick (1924) says they do in the opossum.

## TUBERCULUM OLFACTORIUM

In *Lacerta* this structure is characterised by its poor differentiation and its lack of clear boundaries. It lies (figs. 1, 20) in the base of the brain between the nucleus olfactorius anterior in front and the fibres of the diagonal band behind. Medially it reaches up to the paraterminal body (figs. 5, 6), and laterally to the lateral olfactory tract and the endorhinal fissure. It lies superficial to the palaeostriatum.

It consists of small cells among which are scattered a few fairly large polygonal cells. Their arrangement is hardly definite enough to merit the term "cortex." It is only distinguishable as such where it is separated from the palaeostriatum by fibres of the medial fore-brain bundle, the olfactory tracts, and the olfactory component of the anterior commissure. This region is shown in fig. 6 as a cell-free zone between the tuberculum and the palaeostriatum. Anteriorly it blends with the nucleus olfactorius anterior. Laterally it is indistinguishable from the underlying palaeostriatum (fig. 6), and it is indeed doubtful whether this lateral part should be included in the tuberculum at all. It contains fibres of the lateral fore-brain bundle (fig. 12), and may represent the region which Johnston (1922) calls the anterior perforated space. It also lies in the position of the nucleus of the lateral olfactory tract (turtle, Johnston, 1915), but appears to receive no, or very few, olfactory tract fibres.

Medially and anteriorly there is a small nucleus of round cells in the anterior part of the medial hemisphere wall, which will be called the nucleus olfactorius medialis (figs. 4, 20); some of the fibres of the medial olfactory tract pass through it. As it is probably a cell station in the path of fibres afferent to the hippocampus, it is best included in the paraterminal body, although, as olfactory fibres are also relayed in the tuberculum on their way to the hippocampus, there are as good reasons for calling it a specialised part of the tuberculum.

The fibres related to the tuberculum are very diffusely arranged, so that an exact analysis is not possible in this material. Olfactory tract fibres appear to enter it superficially (figs. 12, *G*, 17). In its substance numerous fibres can be seen, all with a dorso-medial inclination, probably running to the paraterminal body and hippocampus (fig. 12, *F*).

Other fibre tracts related to the tuberculum may of course be connected with it. Such tracts are: the diagonal band posteriorly, the anterior olfacto-habenular tract superficial to it (fig. 12) and the fore-brain bundles and olfactory component of the anterior commissure (fig. 12) deep to it. Definite evidence of connections with these tracts cannot be obtained from my material.

### *Discussion*

The area which has been described here as the tuberculum olfactorium corresponds with the basal olfactory area of Selachians (see Johnston, 1922). In this area in Reptiles and Mammals Johnston differentiates not only a tuberculum, but also an "anterior perforated space." The degree of differentiation in *Lacerta* does not seem to justify such a subdivision of the area in question, although it is possible that its lateral part, where it is practically indistinguishable from the underlying palaeostriatum (fig. 6), represents Johnston's anterior perforated space. Differentiation of a cortex in the tuberculum appears to be much more definite in some other reptilian forms. Johnston (1915), for the turtle, describes a double cortical layer in the deep part of which islets of Calleja can be seen. Crosby (1917), in the alligator, also describes a deep and superficial part, while Durward (1930), in his figures of *Sphenodon*, shows a much more clearly differentiated cortex than is present in *Lacerta*.

A considerable amount of confusion in the terminology of this region has been introduced by the use of such terms as "area olfactoria" and "area parolfactoria," chiefly by Edinger and other continental writers. With regard to the term "parolfactory" Prof. Elliot Smith has kindly allowed me to see some notes of his own about its history. It was first used by His as a substitute for "Broca's area," when eponymous terms were being eliminated in the development of the B.N.A. terminology. Unfortunately he applied it to a small area of neopallium anterior to the paraterminal body, the area defined by Broca in the donkey's brain. Edinger introduced more confusion by including the tuberculum olfactorium in his "area parolfactoria." Most subsequent writers have used the term without any strict definition, and it seems needless to say more than this as a justification for dropping it altogether.

Descriptions of the connections of the tuberculum for different forms agree very well among themselves and with the observations recorded here. The fibres running from it to the paraterminal body and hippocampus have been variously described as "tuberculo-cortical," "tuberculo-septal," "septo-parolfactory," etc. The anterior olfacto-habenular tract has been very generally described (e.g. Cairney, *Sphenodon*; de Lange, *Varanus*, etc.) as connected to the tuberculum and also the olfactory component of the anterior commissure. Although these connections very possibly exist in *Lacerta*, the evidence for their presence is not conclusive.

## VENTRO-LATERAL REGION

### *General*

This is a well-developed and important region in the reptilian fore-brain. It includes the corpus striatum and the amygdaloid nuclei, both "basal" structures. The pyriform cortex, because of its connection to the lateral olfactory tract, its relation to the amygdaloid nuclei (Johnston, 1922), and its development and position below a zona limitans lateralis (Johnston, 1916 *b*), might reasonably be included as well. This is Johnston's view. The embryological findings on which it is based are not extensive and not entirely convincing, and other observers, e.g. Herrick (1910), have come to different conclusions. The pyriform cortex seems to be a structure which has relationships to both the ill-defined "pallial" and "basal" regions of the hemisphere wall, and it is impossible to place it completely in one or the other. While recognising its relationship to "basal" structures, it will be described here with the other cortical or pallial areas.

Owing to the complexity of this region and the difficulty in finding obvious homologies for its differentiated parts, a large and confusing nomenclature has grown up around it. It cannot easily be delimited on the outer surface of the brain because its most characteristic feature is its growth into the ventricular cavity, but it corresponds roughly with the region below the endorhinal fissure (fig. 1), deep to the tuberculum olfactorium. It is seen best in transverse section (figs. 4–10) and also in a parasagittal section (fig. 11), as an enormously thickened part of the hemisphere wall, which forms a very conspicuous prominence in the lateral ventricle. This prominence has been given various names. It is not a simple structure, so that names like "hypopallial ridge," "epistriatum," and so on, which have been applied to it, should not be used for the prominence as a whole. Johnston's term, "dorsal ventricular ridge," applies only to a part of it. Elliot Smith (1919) pointed out that it was first observed and noted by John Hunter, and in one of his figures (fig. 14, p. 282) he labels it "Hunter's eminence." This seems a very appropriate term to use for the structure as a whole.

The main constituents of this ventro-lateral region and of Hunter's eminence are shown clearly in figs. 5 and 6, which are transverse sections of the hemisphere nearer its anterior than its posterior end. The greater part of Hunter's eminence is occupied by the "hypopallium" (Elliot Smith, 1919). Beneath the hypopallium and in the basal part of the ridge is a large mass of cells, the palaeostriatum. It surrounds the ventral angle of the ventricle and abuts on the paraterminal body medially. Laterally it is separated from the hypopallium by a cell-free zone in which many blood vessels can be seen (lateral striate arteries, Elliot Smith, 1919) (fig. 5). It is covered ventrally by the ill-defined cortex of the tuberculum. Posteriorly the ventro-lateral region is rather differently constituted, and the main features can best be seen in the parasagittal section (fig. 11). The hypopallium occupies the whole of the ventricular surface of Hunter's eminence, but its posterior part is sharply differentiated from the anterior at the point *B*. This differentiation of anterior and posterior parts in the hypopallium was noted by Dart (1920), who called them hypopallium anterior and posterior respectively. These terms were adopted by Cairney and Durward for *Sphenodon*, and will be used here, although it seems doubtful if the two parts are as closely related as the terms imply. The hypopallium posterior corresponds with Kappers' "archistriatum," and in part at least with Edinger's "epistriatum," but neither of these terms is appropriate. For various reasons, the chief of which is its connection with the lateral olfactory tract, it should be included in the amygdaloid and not in the striatal complex.

The remaining part of the amygdaloid complex occupies the basal part of Hunter's eminence, corresponding in position to the palaeostriatum which lies in front of it. It can be seen in fig. 11 (*Amy.*), lying just behind the palaeostriatum, from which it is not very clearly differentiated.

The most conspicuous and characteristic fibre tracts of the ventro-lateral region are the fore-brain bundles, the lateral olfactory tract, and the anterior commissure. The fore-brain bundles connect predominantly with the palaeostriatum and the hypopallium anterior, and the lateral olfactory tract with the amygdaloid complex (including the hypopallium posterior). The anterior commissure contains fibres which connect with all the parts of this region.

### *The palaeostriatum*

This is a mass of cells which extends from between the planes of figs. 4 and 5 anteriorly, where it is hardly distinguishable from the deep part of the tuberculum and the nucleus olfactorius anterior, back to the level of the commissures (fig. 9), where it ends in some scattered cells around the anterior commissure, among the fibres of the fore-brain bundles (fig. 14), and by blending to some extent with the amygdaloid complex dorsal to the fore-brain bundles (fig. 9, *C*). It is covered ventrally and anteriorly by the tubercular cortex, and posteriorly by the fibres of the diagonal band (fig. 13).

The main relations of the palaeostriatum to the other cell masses can be seen in figs. 5–8. That part which encroaches on the medial hemisphere wall below the paraterminal body (well seen in fig. 5) has frequently been given a separate name, the "nucleus accumbens" (Ziehen, Herrick, etc.). There is some indication of a division of the palaeostriatum into medial and lateral parts (figs. 5, 6), the lateral consisting of rather larger cells than the medial. These parts clearly correspond with the olfacto-striatum (medial) and the so-called "somatic-striatum" (lateral) of Cairney, Durward and others. For a short part of its extent the palaeostriatum is separated by rather indefinite ventricular sulci from the paraterminal body medially and the hypopallium laterally (figs. 5, 6).

About the level of the commissures a few cells of fairly large size can be seen among the fibres of the stria terminalis. They are shown in fig. 11 between the palaeostriatum and the amygdaloid and less definitely in fig. 9, *C*, dorsal to the fore-brain bundle. It is difficult to say whether these belong to the amygdaloid or to the palaeostriatum.

The chief connections of the palaeostriatum are with the fore-brain bundles. Anteriorly, between it and the tuberculum, fibres of the medial fore-brain bundle can be seen (figs. 12, 18). Some of these appear to begin or end in the medial part of the palaeostriatum (olfacto-striatum) although most are connected to the paraterminal body. In the same region olfactory tract fibres and the olfactory component of the anterior commissure may connect with the palaeostriatum. Laterally it is occupied by the dense network of fibres of the lateral fore-brain bundle (fig. 12). Many of these are on their way to the hypopallium anterior or dorsal cortex, but many no doubt end or begin in the lateral part of the palaeostriatum. Through the fore-brain bundles the palaeostriatum is connected with the thalamus, hypothalamus, mid-brain, and possibly lower levels of the nervous system, and both bundles probably contain ascending and descending fibres.

### *The hypopallium anterior*

This structure can be seen in figs. 4–7 in the transverse series, and throughout its whole antero-posterior extent in fig. 11. It forms the greater part of the ventricular surface of Hunter's eminence, and consists of a fairly definite layer of cells beneath the ventricular ependyma, limited ventrally and medially by a sulcus which separates it from the palaeostriatum. This layer is particularly definite medially and anteriorly, but everywhere there is a marked tendency to the formation of clumps of cells. Laterally and anteriorly (fig. 4) it is continuous for a short distance with the dorsal cortex, underneath the pyriform cortex. Behind the level it is in intimate contact with the ventral edge of the pyriform (figs. 5, 6), and in most sections appears to be continuous with it. Inside the cup formed by the cell layer beneath the ependyma is a core containing fewer and smaller cells. Posteriorly cells of the hypopallium anterior extend back on either side of the hypopallium posterior. These two extensions can be seen in figs. 8 and 9 (*Hyp. ant.*).

Its dorsal limit posteriorly is marked by a very slight depression (fig. 11, *B*) on the ventricular surface of Hunter's eminence. The notch marked *A* in the same figure is probably an artefact. It can be seen only in about six consecutive sections and only in the one series. The ill-defined sulcus *B* corresponds with Kappers' "sulcus neo-archistriaticus" or de Lange's "sulcus striato-epistriaticus," which is apparently very well marked in *Varanus* and some snakes.

The main connection of the hypopallium anterior is with the lateral fore-brain bundle. Its fibres radiate in the core of the hypopallium to all parts of the layer of cells beneath the ependyma (fig. 12). These fibres connect it with the thalamus, and possibly the hypothalamus and mid-brain. Among them may be short fibres between the hypopallium and palaeostriatum as well. Fibres from the hypopallium anterior also form a large component of the anterior commissure (fig. 14). They appear to connect with the hypopallium and amygdaloid complex of the opposite side.

### *The amygdaloid complex*

This is a region of the reptilian brain which it is exceedingly difficult to describe clearly and in such terms as facilitate comparison with the published descriptions of other forms. These descriptions all show a general agreement in that they place the region in question in the hinder part of the ventro-lateral area, and describe its main connections with the lateral olfactory tract, the anterior commissure and the stria terminalis. In terminology there is practically no agreement between any two workers, and the more detailed the analysis, the greater the confusion has become. Johnston's attempt (1922) to reduce this confusion to some sort of order is the most thoroughgoing and consistent, but suffers from the defect, as far as Reptiles are concerned, that it depends for this class on a detailed description of only two forms, the turtle, investigated by himself in 1915, and the alligator, described by Crosby in 1917. It is difficult to compare the condition in *Lacerta* directly either with the turtle or the alligator, so that one is left in the dilemma of adding to an already too complicated terminology or of using terms which imply uncertain homologies, and have been used in many different ways. As a compromise as few specific terms as possible will be used, and only those implying general homologies which are reasonably certain.

The amygdaloid complex of *Lacerta* consists of two main parts, the hypopallium posterior, and a less well-defined structure, which will be called the "central amygdaloid mass." This latter term is not meant to imply an homology with Johnston's "central amygdaloid nucleus," although it is probable that in other animals the central and other amygdaloid nuclei described by Johnston have differentiated in the region of my "central mass." The two parts can be seen in fig. 11. The central mass (*Amy.*) lies behind the palaeostriatum, with which it is more or less continuous, below the hypopallium anterior. It is superficial ventro-laterally behind the tuberculum olfactorium. The hypopallium posterior lies behind the central mass, and its general relations can be seen in the figure.

In fig. 6 a few cells scattered among the fibres of the lateral olfactory tract can be seen (*Tr. olf. lat.*). These probably represent the nucleus of the lateral olfactory tract. They are continuous with the central amygdaloid mass behind, and their degree of differentiation in *Lacerta* does not seem to justify a separate name. In fig. 7 the central mass can be seen below the endorhinal fissure and above the lateral fore-brain bundle, separated from the latter by a blood vessel. The lateral olfactory tract lies in the middle of it. It reaches its maximum development about the level of the commissures (figs. 8, 9). In these figures, on account of the obliquity of the sections (see fig. 2 *a*), the hypopallium posterior has begun to appear above the central mass. It is not clearly differentiated from the central mass ventrally.

The hypopallium posterior has a very characteristic cup-like form, the mouth of the cup being open ventrally and anteriorly, and the rim more or less fused with the central amygdaloid mass. Its general form and relations can be seen in figs. 8–11. Its continuity with the pyriform cortex laterally can be seen in fig. 10.

The principal connections of the amygdaloid complex can be classified in three groups: olfactory, commissural, and hypothalamic. With the latter may be included preoptic connections. There are in addition important but less conspicuous connections with the diagonal band and the stria medullaris.

Olfactory impulses arrive *via* the lateral olfactory tract from the bulb, nucleus olfactorius anterior, and probably the pyriform cortex. The tract is at first superficial, just below the endorhinal fissure (figs. 6, 12). It soon leaves the surface and runs through the central amygdaloid mass (figs. 7, 13–15), becoming a much less compact bundle. No doubt many of its fibres end here. Other fibres leave the main tract and turn ventrally into the basal part of the central amygdaloid mass (figs. 9, 11, and 15, *C*). The remaining fibres can be traced onwards as a very diffuse bundle into the concavity of the cup-like hypopallium posterior (fig. 16).

*Hypothalamic connections* (the olfactory projection tract of Cajal). These are a well-developed but rather diffuse bundle of fibres seen best in fig. 15 (*St. term.*). They arise for the most part in the medial and ventral parts of the central amygdaloid mass, and sweep medially and ventrally over the fore-brain bundles into the hypothalamus. Some join the fore-brain bundles and probably reach the hypothalamus at a more posterior level. Scattered among their fibres are the cells mentioned above (p. 170) and seen in fig. 9, *C*.

*Preoptic connections.* There is another bundle (fig. 13, *Amy. preop.*) which connects the anterior end of the central amygdaloid mass with the preoptic nucleus. It runs outside and below the fore-brain bundles, and it is possible that some of its fibres run on to the paraterminal body and the hippocampus. They appear to end in the preoptic region however.

*Commissural connections.* These all run in the anterior commissure, chiefly in what is called here its amygdaloid component. This arises as a large bundle of fibres from the central mass of the amygdaloid (best seen in fig. 14). It is joined by the olfactory component (fig. 17) and crosses in the anterior part of the commissure (fig. 18). It appears to be distributed to the hippocampus and the hypopallium anterior and posterior of the opposite side, but this cannot be stated with certainty from this material. Commissural fibres from the posterior part of the central amygdaloid mass and from the hypopallium posterior join what is called here the hypopallial component of the anterior commissure. This can be seen in figs. 14–16, and in transverse section in figs. 17 and 18. It forms the dorsal and posterior part of the anterior commissure. It is possible that some of the fibres which run forwards from the posterior parts of the amygdaloid in this component are not commissural, but connect with the paraterminal body above and below the commissure (cf. Johnston, 1922, p. 397). The commissural fibres appear to connect with the same regions of the opposite side.

The diagonal band is seen in fig. 13 (*D.B.*) and again in figs. 17–19. Its fibres arise chiefly from the anterior part of the central amygdaloid mass and superficial to the lateral olfactory tract. A few probably originate in the pyriform cortex. They run ventrally and then turn medially below the fore-brain bundles and behind the tuberculum (fig. 13). They then ascend through the nucleus of the diagonal band (figs. 8, 20, *N.D.B.*), where they are perhaps relayed, and sweep dorsally anterior to the commissures and turn posteriorly above them (fig. 19). They are cut transversely as they run posteriorly in figs. 13–15. Some of these fibres enter the tangential system of fibres superficial to the hippocampus (fig. 14) and probably the bundle as a whole is afferent to the hippocampus. Some of its fibres may connect with the cells of the nucleus of the hippocampal commissure (fig. 20, *N. com. hip.*), most enter the supraforaminal part of the paraterminal body, while others may connect with the ventro-medial nucleus of the paraterminal body further forwards.

The connection to the habenula consists of a few fibres from the ventral part of the central mass which join the stria medullaris lateralis as it lies in the angle between the optic tract and the fore-brain bundles (fig. 15, *St. med. lat.*); the actual amygdaloid connection was not visible in the section from which this figure was drawn. A few fibres from the medial part of the central mass run to the medial cortico-habenular tract (fig. 17, *Amy. hab.*).

It would be well at this point to summarise the main facts about the amygdaloid complex and its connections.

The amygdaloid consists of two main parts, a central mass and the hypopallium posterior. The central mass shows a fairly well-marked ventral condensation of cells which extends back beneath the hypopallium posterior (fig. 11, *C*). This ventral condensation receives a special bundle from the lateral olfactory tract, gives rise to the greater part of the olfactory projection tract to the hypothalamus, and is not easily distinguishable from the palaeostriatum which lies in front of it. It has a small habenular connection.

Commissural fibres run from or to all parts of the amygdaloid; anteriorly these fibres form a large "amygdaloid component" of the anterior commissure, while posteriorly they join the "hypopallial component."

Besides giving the special bundle mentioned above, the lateral olfactory tract brings olfactory impulses to all parts of the amygdaloid.

The diagonal band connects the anterior and lateral part of the central mass with the medial olfactory centres, and this same region of the amygdaloid has a small bundle of fibres running below the fore-brain bundles to the preoptic region. It is probable that this anterior and lateral part of the central mass is the representative of the nucleus of the lateral olfactory tract which is better differentiated in other reptilian orders.

## *Discussion*

Herrick (1921) has described the main features of the ventro-lateral region of the brain wall in Amphibia. In the urodeles there is an undifferentiated strio-amygdaloid mass, having many of the connections typical of the striatum and amygdaloïd, but not yet clearly marked off as separate tracts. Differentiation has proceeded much further in the Anura which show a condition in many ways comparable to the Reptiles. Anteriorly is a corpus striatum (or palaeostriatum), while posteriorly and bulging into the ventricle at the level of the foramen of Monro is the amygdaloid nucleus. This amygdaloid nucleus receives a separate division of the lateral olfactory tract (Herrick's ventrolateral olfactory tract) from the vomero-nasal organ of Jacobson. A dorsolateral division of the tract runs to the rudimentary pyriform cortex. The corpus striatum, Herrick states, is dominated by somaesthetic impulses from the thalamus, and has been almost entirely freed from olfactory connections. He derives the whole lateral wall of the amphibian hemisphere from the lateral olfactory area of lower Vertebrates, and divides it in Amphibia into dorso-lateral (pyriform) and ventro-lateral (strio-amygdaloid) regions. These two divisions are separated by his zona limitans lateralis. In this he disagrees with Johnston (1922), who places his zona limitans above the pyriform cortex. The modern Amphibia are very specialised animals, and it seems possible that the clear subdivision of the lateral region of the amphibian hemisphere into dorso-lateral and ventro-lateral parts, each with its own division of the lateral olfactory tract, may be a specialisation, and not of fundamental importance in fore-brain morphology. The facts suggest that the attempt to find a definite zona limitans, valid for all groups and separating "pallial" from "basal" areas, is vain, especially, as Herrick points out, in the absence of precise definition of the terms "pallial" and "basal."

There is, however, no doubt that the palaeostriatum and amygdaloid nucleus of Anura correspond very closely to the structures given those names here in *Lacerta*. That the correspondence applies to fibre connections as well as to topographical position can be verified by reference to Herrick's paper (1921).

Among the Reptiles themselves the first point for discussion concerns the medial part of the palaeostriatum, which lies beneath the paraterminal body in the medial hemisphere wall. This cell mass has been included in the paraterminal body or "septum" by several authors, notably Herrick, under the name of "nucleus accumbens." It has been pointed out many times (e.g. by Johnston, Kappers, Cairney) that this nucleus accumbens is far more closely related to the palaeostriatum than to the paraterminal body. In fact, the only reason for separating it seems to be an adherence to an artificially rigid subdivision of the hemisphere into ventro-medial and ventro-lateral parts. From its cell type and fibre connections it appears to belong to the striatum, and, as this is generally recognised, it seems best to include it under the term "palaeostriatum" and to drop the term "nucleus accumbens" altogether. For the palaeostriatum to be indented from above by the lateral ventricle seems to be typical not only of Reptiles, but of Amphibia and Mammalia as well.

An important point is the division of the palaeostriatum into medial and lateral parts. The evidence of this from cell-stained preparations alone is not very good in *Lacerta*. In the fibre-stained series, however, it is conspicuous that the medial part is connected mainly with the hypothalamus by the medial fore-brain bundle, and possibly with the olfactory tracts, and that the lateral part has strong thalamic connections *via* the lateral fore-brain bundle. These parts clearly correspond with the olfacto-striatum and "somatic" striatum of Cairney and Durward, and with the bed of the stria terminalis and the putamen of Johnston (1922). Johnston looks upon the bed of the stria terminalis as primarily an olfactory centre derived from the deep or ventricular part of the lateral olfactory area of Selachians. The term "olfacto-striatum" also implies an olfactory origin. Unfortunately, no very clear evidence of olfactory connections in this region was obtained in *Lacerta.* Herrick, too, in Amphibia, states that direct olfactory connections to the palaeostriatum are few or absent. In *Sphenodon* Cairney has described olfactory tract fibres running to the olfacto-striatum, so that in view of the equivocal evidence of *Lacerta,* the point deserves further investigation. The study of degeneration following experimental lesions probably offers the best hope of definite results.

Johnston's term, "bed of the stria terminalis," for this structure seems to have no particular advantage over "olfacto-striatum," and in some ways is less appropriate. The greater part of it lies anteriorly in the hemisphere where there are no fibres of the stria terminalis, unless those fibres of the medial fore-brain bundle which connect it with the hypothalamus are included in that system. In Reptiles at least it is a primary division of the palaeostriatum and as such is well described by the term "olfacto-striatum."

The identity of the lateral part of the palaeostriatum of *Lacerta* with the "somatic" striatum in *Sphenodon* (Cairney, Durward) and with the putamen in the turtle (Johnston, 1922), seems to be quite clear. In *Lacerta* it is pierced by fibres connecting the thalamus with the lateral edge of the dorsal cortex similar to those Johnston has described for the turtle. From Crosby's (1917) description of the alligator there again seems no doubt that the palaeostriatum is divided into the same two parts, medial and lateral, called by her ventrolateral small- and large-celled areas respectively. It may be said then, that a palaeostriatum divided into medial and lateral parts is characteristic of the Reptiles as a whole, that the medial part is primarily concerned with olfactory impulses, and the lateral with sensory impulses which reach it by way of the thalamus.

Johnston, in describing the olfacto-striatum as the bed of the stria terminalis, states that posteriorly it runs more or less indistinguishably into the central and medial amygdaloid nuclei, and that it forms the bed of the anterior commissure. In *Lacerta* the distinction between this part of the palaeostriatum and the central mass of the amygdaloid is certainly difficult to make out, and it appears that the few cells scattered around the anterior commissure belong rather to the striatal than to the paraterminal region. Cairney and Durward both describe the olfacto-striatum as distinguishable from the amygdaloid nuclei. So far as it goes, my material supports Johnston's view.

## THE HYPOPALLIUM ANTERIOR AND POSTERIOR

Although these two structures are essentially distinct, at least in *Lacerta*, they have been very generally described together. The term "hypopallium" was introduced in 1919 by Elliot Smith to describe the whole of the cortex-like arrangement of cells on the ventricular surface of Hunter's eminence, or the "hypopallial eminence" of his paper. This ridge, as is shown in his fig. 5, p. 275, extends "from the extreme anterior end to the posterior inferior recess of the hemisphere." In the sections which he shows (*ibid.* fig. 6, p. 276) it can be seen that the layer of cells in the extreme posterior end of the ridge is broken into clumps, a fact noted by Dart (1920), who consequently divided the hypopallium into hypopallium anterior and hypopallium posterior. Cairney (1926) further noted that the hypopallium posterior had connections with the lateral olfactory tract. Durward (1930) divided the hypopallium differently. According to him, only that part which is in contact with the dorsal cortex should be called hypopallium anterior, while all the rest, in contact with the pyriform cortex, is hypopallium posterior. The morphological value of these apparent connections between cortical and hypopallial areas has been questioned (Hines, 1923); the difference in the fibre connections anteriorly and posteriorly is quite definite and is a much more fundamental distinction, and one about the value of which there is no disagreement. It seems therefore best to keep the term "hypopallium posterior" for that part of the hypopallium which has connections to the lateral olfactory tract. Crosby found similar olfactory connections for the posterior part of the hypopallium, her "dorsolateral area." Johnston looks upon the whole of his dorsal ventricular ridge as hypopallial, presumably hypopallium anterior. The hypopallium posterior is the "amygdaloid ridge" of Johnston's paper (1922) or the posterior end of the "dorsal ventricular ridge" (1915). It is well shown by Elliot Smith in his fig. 14 (1919).

It appears then, that at the posterior end of Hunter's eminence there is a region connected with the lateral olfactory tract. In *Sphenodon* and the alligator this region is not well developed and not very clearly differentiated from the anterior part of the eminence. In the turtle it is still small, but can be clearly differentiated. In *Lacerta* it forms a well-developed and clearly differentiated structure, the hypopallium posterior. In *Varanus* and some snakes (de Lange, 1911) it is even more conspicuous and may be separated from the anterior part of Hunter's eminence by a sulcus, the "sulcus neo-archistriaticus" of Kappers. In addition to the names already mentioned for this structure, it has been called the "nucleus sphaericus" (Meyer) and the "nucleus occipito-basalis" (C. L. Herrick). Because of its connection with the lateral olfactory tract and its position in the hemisphere wall, it is now generally agreed that the hypopallium posterior should be included in the amygdaloid complex. Because it reaches its greatest development in such specialised orders as the Lacertilia and Ophidia, it seems possible that it is a structure which is peculiar to the Reptiles and that no exact homologue will be found in the mammalian amygdala. Dart (1920) homologises it very confidently, but on little concrete evidence, with what he calls the "element C" of the mammalian amygdaloid complex. This "element C" is the "nucleus amygdalae" of Winkler and Potter, and appears to be the lateral amygdaloid nucleus of Johnston (1922). The position under the ependyma of the lateral ventricle (well shown in some of Johnston's figures) does suggest a comparison with the hypopallium posterior of Reptiles, but more detailed knowledge of fibre connections and development is necessary before definite statements can be made on this point. Dart says (p. 21) that this hypopallium posterior discharges by a tractus hypopallio-habenularis to the habenula. Cairney does not mention this connection, and there is no sign of it in *Lacerta viridis*. Possibly he is referring to the connection between the central mass of the amygdaloid and the habenula. Dart's one figure which shows this tract is not clear enough to help in deciding this.

The relationship of the hypopallium anterior and posterior to the dorsal cortex and pyriform cortex is striking and important. So far as adult appearances go, in *Lacerta viridis* one can say that the extreme anterior end of the hypopallium is in intimate contact with the dorsal cortex where it bends ventrally under the pyriform, a region called by Elliot Smith (1919) the "primordium neopallii." For the greater part of its extent, however, the hypopallium anterior is apparently continuous with the ventral edge of the pyriform cortex, as is also the hypopallium posterior. These appearances suggest, as Elliot Smith pointed out, that the hypopallium (both anterior and posterior parts) has been formed by a growth inwards from, or an involution of, the ventral edge of the pyriform cortex. In Chelonia, however, there is a more extensive relationship between the dorsal cortex and the anterior part of the hypopallium anterior than in Lacertilia or in *Sphenodon*. A study of the adult relationships (1915) and of the embryology (1916 *b*) of this region in turtles led Johnston to the conclusion that the dorsal ventricular ridge or hypopallium anterior developed in this animal from the ventral edge of the dorsal cortex. He suggests further (1922) that only the posterior end of Hunter's eminence, the hypopallium posterior or the amygdaloid ridge, develops from the ventral edge of the pyriform, although he has not been able to observe the steps in this development owing to a lack of embryos of a suitable age. In short, the hypopallium anterior is developed from the ventral edge of the dorsal cortex, the hypopallium posterior from the ventral edge of the pyriform, and any connection between the hypopallium anterior and pyriform seen in the adult must be secondary. Hines (1923), working on *Sphenodon*, concluded that the hypopallium developed *in situ* and that all adult cortical connections were secondary. Hines' material was admittedly not entirely satisfactory, and an important part of Johnston's account is hypothetical. It is also clear that an apparent cellular continuity between the hypopallium and a cortical area in the adult is not sufficient evidence for deriving one part with certainty from the other. From what is known of the embryology in *Sphenodon* and the turtle, it seems likely that a considerable part of the hypopallium is not derived ontogenetically from the pyriform, and that it may be derived from the dorsal cortex, or may develop *in situ.* Obviously a very much more detailed knowledge of the embryology of this region in the different orders of Reptiles is necessary before more positive statements can be made.

There remains the central mass of the amygdaloid. Its main characteristics are that it lies behind the palaeostriatum, from which it is poorly differentiated, and that it gives rise to the greater part of the amygdalo-hypothalamic fibres (olfactory projection tract of Cajal, "bundle 2" of stria terminalis of Johnston). Although differentiation in this mass is not clear enough for it to be possible to subdivide it with any certainty, in the characteristics mentioned it corresponds very closely with Johnston's medial and central amygdaloid nuclei. For the same reasons it corresponds with Durward's and Cairney's anterior amygdaloid nucleus in *Sphenodon*, and with Crosby's nucleus ventromedialis in the alligator. Several related nuclei have been described by these workers. The nucleus of the lateral olfactory tract has been described by Johnston, Crosby, Cairney and Durward as closely related to or continuous with the amygdaloid nucleus in question. So far as there is a nucleus of the lateral olfactory tract in *Lacerta*, it is the anterior prolongation of the central mass along the lateral olfactory tract, which corresponds in every way to the nucleus described by the above-mentioned workers.

There is a nucleus in the turtle which Johnston described in 1915 as the "medial amygdaloid nucleus" and in 1922 as the "basal amygdaloid nucleus." This Cairney (1926) homologises with the posterior amygdaloid nucleus of *Sphenodon.* A clearly differentiated comparable region does not exist in *Lacerta*, but it may be represented by the condensation of cells beneath the hypopallium posterior (fig. 11).

Crosby mentions an "intermedio-lateral area," closely related to the nucleus of the lateral olfactory tract and to the posterior part of the hypopallium (dorso-lateral area, Crosby). There is no representative of this area in *Lacerta*, and apparently none in Chelonia or in *Sphenodon.* From Crosby's account it would be reasonable to include it in the amygdaloid complex together with the hypopallium posterior, but the available facts do not justify a more definite statement. Shanklin (1930) describes a similar area in the chameleon, but classes it with the palaeostriatal centres.

The terminology which has been used so far is chiefly that of Elliot Smith, but is not very different from that used by most American workers. The continental workers, led by Edinger and Kappers, have used different terms, about which a word must be said. Edinger (1908) describes this ventro-lateral region of the fore-brain as the "Stamm-lappen," and includes in it an "epistriatum" and a "palaeostriatum," present from Fishes upwards. He states that the epistriatum is characterised by its lateral olfactory connection, the tractus cortico-epistriaticus, and by olfactory connections *via* the anterior commissure, and that it is also connected with the stria terminalis and is homologous with the amygdala of Mammals. From this it follows that his epistriatum must include the hypopallium posterior and also the central amygdaloid mass. From his figures, however (e.g. fig. 247, p. 277), it is clear that he includes the hypopallium anterior in the epistriatum. The objections to this are obvious. The hypopallium anterior has none of the connections which Edinger himself mentions as characteristic of the epistriatum. Two figures which he gives of sections through the chelonian brain complicate the account still more (fig. 247, p. 277; fig. 279, p. 309). Above a basal striatum (=palaeostriatum) are two ventricular ridges, labelled "mesostriatum" and "epistriatum" respectively. De Lange (1911) states that these two structures are both epistriatal, but comparison with Johnston's fig. 22 (1915, p. 445) suggests that the upper is the "pallial thickening" (Elliot Smith's "primordium neopallii") and the lower, Edinger's "mesostriatum," only the anterior end of the dorsal ventricular ridge or hypopallium anterior. De Lange (1911) has further confused the matter by using the term "epistriatum" for both anterior and posterior parts of the hypopallium in Chelonia, and for the posterior hypopallium alone in Lacertilia and Ophidia, although he has not been quite consistent even in this. His fig. 43, from *Lacerta*, labels what is clearly hypopallium anterior as "epistriatum." More detailed criticism of de Lange's terminology, and particularly his misuse of the term "neostriatum," is given by Elliot Smith (1919) and Johnston (1922), and is unnecessary here. The use of the term "epistriatum" has, however, been continued by Kappers (1929). He applies it to an ill-defined part of the strio-amygdaloid complex of fishes and Amphibia which receives secondary olfactory fibres, and to the nucleus of the lateral olfactory tract of Reptiles. The justification for this use of a term which has already had several different meanings attached to it does not seem to be very great. The figures which de Lange and Kappers give of the "epistriatum" in Amphibia do not show it as a structure at all clearly differentiated. The only structure clearly differentiated in the ventro-lateral hemisphere wall, and receiving olfactory tract fibres, is the amygdaloid nucleus described and figured by Herrick (1921) for the frog. From its position and connections, this amygdaloid would correspond very closely with the central amygdaloid mass, and is probably the representative of the whole amygdaloid complex. The nucleus of the lateral olfactory tract in Reptiles is a collection of cells which retains a simple connection with and arrangement among the fibres of the lateral olfactory tract. There seems no reason why it should be considered to be the representative of all that part of the ventro-lateral brain wall which receives impulses from the lateral olfactory tract in Amphibia. To the hypopallium anterior and posterior Kappers has given the names "neostriatum" and "archistriatum." Since very little is known of the relative phylogenetic age of these two parts, and since what evidence there is points rather to a pallial than striatal origin, it seems better to keep to the non-committal terms, hypopallium anterior and posterior.

*The stria terminalis.* Some confusion has arisen in the use of this term and of the term "olfactory projection tract." Johnston (1922) includes in the stria terminalis all fibres which run medially from the amygdaloid complex, dorsal to the fore-brain bundles. Since there is no general agreement about a more restricted use of the term, this seems the most satisfactory definition. Johnston gives a detailed analysis of these fibres in which the amygdalo-hypothalamic fibres or olfactory projection tract are included as "bundle 2." Crosby (1917) differentiates the stria terminalis from the olfactory projection tract, the former running between the pyriform cortex and nucleus of the lateral olfactory tract on the one hand, and the preoptic nucleus on the other; and the latter between the amygdala (her ventro-medial nucleus) and the hypothalamus. In this she has been followed by Herrick (1921). There does not seem to be any reason why so fundamental a distinction should be made between the preoptic and the hypothalamic connections of the amygdala, so that until more is known of the function and comparative anatomy of these tracts, it seems best to class them all as components of the stria terminalis. These can be described (following Johnston) according to their destination. On this basis the following components can be recognised in *Lacerta*:

(i) A hypothalamic bundle (Johnston's "bundle 2," the "olfactory projection tract" of S. Ramón y Cajal).

(ii) A large commissural bundle (Johnston's "bundle 1").

(iii) A small bundle running medially into the stria medullaris (Johnston's "bundle 5").

(iv) A small bundle to the preoptic region. This may be Johnston's infra-commissural "bundle 3." It is not very clearly defined from the hypothalamic bundle in *Lacerta.*

These components were all described by Crosby for the alligator, the hypothalamic bundle from her ventro-medial nucleus and the others chiefly from the nucleus of the lateral olfactory tract. They were also described, with minor differences, by Johnston in the turtle, although he also found a bundle connecting the amygdala with the parolfactory area (paraterminal body) which seems to be lacking in *Lacerta.* Cairney describes preoptic and hypothalamic connections, but no commissural or habenular connections.

All these components of the stria terminalis arise in *Lacerta* from the central mass of the amygdaloid with the exception of some of the commissural fibres, which arise from the hypopallium posterior and run in the hypopallial component of the commissure. It follows that the central mass represents the nucleus of the lateral olfactory tract combined with Johnston's central and medial amygdaloid nuclei, or Cairney's and Durward's anterior amygdaloid nucleus, or Crosby's ventro-medial nucleus.

If the term "olfactory projection tract" is to be used at all, it would seem best to accept Crosby's definition of it, as including those fibres which connect the lateral olfactory centres of the hemisphere wall with the hypothalamus. Crosby differentiates a dorsal and ventral olfactory projection tract. The former is clearly Johnston's "bundle 2" (cf. above). The latter is mentioned by Johnston, who suggests that it is homologous with the tractus pallii of Selachians. It is described and figured by Herrick for the frog, and clearly corresponds with the amygdalo-peroptic connection (fig. 13, *Amy. preop.*, and p. 173) of *Lacerta.*

The amygdaloid complex of *Lacerta* can be said to agree very closely in all its main characteristics with that of the other orders of Reptiles. It is chiefly remarkable for the great development and differentiation of the hypopallium posterior and the lack of differentiation in the remaining part, the central mass. Of the many outstanding problems in the morphology of this region, one of the most important concerns the development of the hypopallium posterior and its possible relation to cortical areas like the pyriform.

## THE PARATERMINAL BODY

This region is well-developed in *Lacerta viridis* and can be defined in much the same terms as were used by Elliot Smith in 1901 to define the same region in Mammals. Its boundaries and the structures differentiated within it are shown in the reconstruction (fig. 20), and in the transverse sections (figs. 4–10).

It forms the whole thickness of the medial hemisphere wall between the ventral edge of the hippocampal cortex above the tuberculum olfactorium and palaeostriatum below. Posteriorly it extends to the lamina terminalis with the hippocampal and anterior commissures in it, and also above the hippocampal commissure and foramen of Monro to a point in the medial hemisphere wall just behind the posterior pallial commissure[1], or commissura aberrans of Elliot Smith (1903). Anteriorly it is bounded by the nucleus olfactorius anterior. The ventral boundary is the least definite, particularly just anterior to the lamina terminalis where the diagonal band fibres are entering (figs. 7, 8). Here it is practically indistinguishable from the posterior part of the palaeostriatum and the central amygdaloid mass.

Anteriorly the paraterminal body is characterised by the fewness of its cells (fig. 5). It does not bulge into the ventricle here, and shows no differentiation except the nucleus olfactorius medialis which has already been described (figs. 4, 20, *N. olf. med.*, and p. 167).

In its middle part (figs. 6–8) its most characteristic differentiation can be seen. It forms a marked prominence into the cavity of the lateral ventricle, and contains many more cells. These are arranged as a dorso-lateral nucleus of large irregularly pyramidal cells, rather loosely packed, and a ventro-medial nucleus of smaller rounder cells considerably more numerous than the dorso-lateral large cells. Very soon, going posteriorly, this differentiation becomes less clear (fig. 8), and the two nuclei, so far as they can be recognised at all,

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[1] Since there is now no doubt that the "posterior pallial commissure" is a commissure of the posterior part of the hippocampal formation, "hippocampal" would be a more accurate term to apply to it than "pallial," and would avoid the vagueness associated with that word. The term "posterior hippocampal commissure" will be used throughout this paper.

become dorsal and ventral and are differentiable only by the size of cell. The ventral nucleus shows a tendency to divide into medial and lateral parts, but this apparent division is due to the fibres of the medial fore-brain bundle, which are passing through it here. The next definite differentiation can be called the nucleus of the diagonal band (figs. 8, 20). It extends up into the medial part of the paraterminal body from the region just in front of the preoptic recess, and back over the commissure among the fibres of the diagonal band as far as the level of the foramen of Monro. In fig. 9 the commissures appear, and the paraterminal body is seen dorsal to the hippocampal commissure and lateral to the descending fibres of the alveus system. It is this part of the paraterminal body which extends back to the posterior hippocampal commissure. It can be called the supraforaminal part because of its relation to the foramen of Monro. It contains the nuclei of the hippocampal and posterior hippocampal commissures (figs. 9, 10), but beyond this differentiation is indefinite. Medially and dorsally its cells are larger and are related to the alveus fibres. Ventro-laterally they are smaller. These two regions may represent the dorso-lateral and ventro-medial nuclei seen anterior to the lamina terminalis.

The nucleus of the hippocampal commissure is situated between the descending alveus fibres of both sides (figs. 9, 20). It lies dorsal to the commissure, and is closely related above to the diagonal band and its nucleus. The part of the nucleus in actual contact with the commissure consists of slightly smaller cells than the dorsal part.

The nucleus of the posterior hippocampal commissure (figs. 10, 20) consists of two parts, a medial, containing comparatively few cells of medium size, scattered among the fibres of the commissure itself, and a lateral, made up of small round cells, fairly tightly packed and lying immediately beneath the ependyma of the ventricle, and just above the membranous part of its medial wall.

The connections of the paraterminal body are numerous and difficult to unravel. Speaking generally, it may be said that it is connected dorsally with the hippocampal cortex, ventrally with the tuberculum olfactorium, diagonal band and medial fore-brain bundle, and anteriorly with the olfactory tracts, so that it lies in the path of most of the impulses passing to or from the hippocampus. In addition, it forms a bed in which the hippocampal and posterior hippocampal commissures lie. The large size of this body in Reptiles suggests that it is an important correlation centre.

Very few fibres enter the paraterminal body directly from the olfactory tracts in the olfactory peduncle. Most of them are relayed in the nucleus olfactorius anterior, the tuberculum olfactorium or the nucleus olfactorius medialis, although the latter may be regarded as a part of the paraterminal body. Fibres from the tuberculum olfactorium are particularly numerous (fig. 12, *F*). Most of these afferent olfactory fibres seem to go to the ventromedial nucleus.

The diagonal band connects medial and lateral olfactory centres. It begins in the lateral part of the central amygdaloid mass, sweeps ventrally behind the tuberculum olfactorium and ascends through its nucleus anterior and a little lateral to the preoptic recess (fig. 13). The fibres then turn back over the hippocampal commissure (fig. 19), probably making connection with its nucleus, and end by being distributed to the supraforaminal part of the paraterminal body and to the superficial aspect of the hippocampal cortex among the tangential fibres (figs. 13–15). The termination of some of the diagonal band fibres can be seen in fig. 18 (*D.B.*) just in front of the posterior hippocampal commissure. They are cut transversely in figs. 13–15, lying medial to the descending alveus fibres, through which they must penetrate to reach the paraterminal body.

The medial fore-brain bundle is the largest single tract connected with the paraterminal body. Its fibres enter in that region in front of the commissures where the dorso-lateral and ventro-medial nuclei are particularly well developed, and most of them run into the dorso-lateral nucleus (figs. 12–14, 18, 19). A few appear to be continuous with alveus fibres (fig. 13), a few enter the medial part of the paraterminal body, while others sweep back over the commissures to its supraforaminal part. These fibres lie lateral to the alveus fibres, while the diagonal band fibres, which have a similar distribution, lie medial (fig. 14). Those fibres of the medial fore-brain bundle which reach farthest anteriorly appear to end in the palaeostriatum. A few enter the anterior end of the paraterminal body, and appearances suggest that there is a connection between the palaeostriatum and the paraterminal body. This last point is not certain.

The medial fore-brain bundle carries impulses in both directions between the paraterminal body and the hypothalamus, mid-brain and possibly thalamus.

The largest dorsal connection of the paraterminal body is with the alveus system of fibres which arises on the ventricular surface of the hippocampal cortex. It extends beyond the lateral margin of the hippocampus underneath the dorsal cortex, but whether it carries fibres from the dorsal cortex as far as the paraterminal body and hippocampal commissures is not certain. Probably it does. Fibres which appear to belong to this system begin anteriorly where the hippocampus merges with the nucleus olfactorius anterior. They run caudally in the dorsal part of the paraterminal body (fig. 19), lying lateral to a superficial bundle from the tangential system which has a similar direction just under the pia (fig. 12). Some of these fibres probably end in the dorsal part of the paraterminal body, but most run back to enter the hippocampal commissure. The rest of the alveus system can be described in two parts, anterior and posterior to the posterior hippocampal commissure.

Most of the anterior fibres converge to the hippocampal commissure. Some run straight into the medial fore-brain bundle anterior to the anterior commissure, while others descend either through or behind the commissure to the hypothalamus (columns of fornix, fig. 14, *C.F.*) or into the stria medullaris as the medial cortico-habenular tract. As far as the paraterminal body is concerned, there is no doubt that many alveus fibres connect with its dorso-lateral nucleus, although most are situated actually in the dorso-medial part of the body. Perhaps some fibres run into the ventro-medial nucleus, but this is not certain, for these medial fibres become very mixed with the fibres of the tangential system and it is not possible to differentiate them clearly.

The posterior part of the alveus system falls into three subdivisions:

(i) Fibres which arise from the ventricular surface of the hippocampus and run forwards above the posterior hippocampal commissure to connect with the paraterminal body (supraforaminal part) (fig. 17, *Alv.* (*i*)), but mostly to run into the hippocampal commissure. These fibres have no connection with the nucleus of the posterior hippocampal commissure.

(ii) Fibres which arise also from the ventricular surface of the hippocampal cortex, effect connections with the nucleus of the posterior hippocampal commissure and then run above the commissure, turn ventrally in front of it, and join the medial cortico-habenular component of the stria medullaris (fig. 17, *Alv.* (*ii*)).

(iii) Fibres which appear to arise from both surfaces of the hippocampal cortex, make connection with the nucleus of the posterior hippocampal commissure and then cross in the commissure (fig. 17, *Alv.* (*iii*)).

The alveus connections, so far as they concern the paraterminal body, can be summarised as follows. They connect the hippocampal cortex with the dorso-lateral nucleus and with the supraforaminal part of the paraterminal body. Some fibres run apparently without interruption through the paraterminal body into the medial fore-brain bundle, probably on their way to the hypothalamus. The rest are concentrated in the hippocampal commissure, where they effect connections with the nucleus of the commissure, or are connected to the nucleus of the posterior hippocampal commissure. From here they are relayed to the commissure itself or to the stria medullaris.

The tangential system of fibres superficial to the cortex is also connected to the paraterminal body. Anteriorly the system is continuous with the plexus of fibres superficial to the nucleus olfactorius anterior, which probably receives olfactory tract fibres. In this region it gives rise to the anterior olfacto-habenular tract (figs. 12–14) which runs ventrally over the anterior part of the paraterminal body and sweeps laterally under the tuberculum olfactorium. Other fibres from the tangential system enter the dorsal part of the paraterminal body and run ventro-posteriorly medial to the alveus fibres. They probably end in this part of the paraterminal body for they cannot be traced far, and soon become indistinguishably mixed with the alveus fibres; they may run as far ventrally as the ventro-medial nucleus. More posteriorly there is an obvious connection between the tangential system and the diagonal band fibres. It seems probable that these connections are efferent from the medial part of the paraterminal body and diagonal band to the superficial surface of the hippocampus.

It would be well at this point to recapitulate the connections of the nucleus of the hippocampal commissure. It is connected to the central mass of amygdaloid by the diagonal band fibres, to the hippocampus by alveus fibres, and to the strio-amygdaloid complex by a few fibres which enter it from the anterior commissure. Posteriorly it may be connected to the medial cortico-habenular tract. This is probable, but not quite certain.

The position of the paraterminal body was defined at the beginning of this section. Its chief differentiations appear to be: a large-celled dorso-lateral and a small-celled ventro-medial nucleus, both best developed in its middle part; a nucleus of the diagonal band, and nuclei of the hippocampal and posterior hippocampal commissures, all consisting of small cells; and a nucleus of the medial olfactory tract which can only doubtfully be included in this region. There is also an anterior part containing comparatively few cells and showing no differentiation.

It receives olfactory fibres from the olfactory tracts anteriorly and from the diagonal band posteriorly. It is probable that these are transmitted on to the hippocampus by the tangential system. Some, and particularly those of the diagonal band, do not appear to get further than the paraterminal body itself, which, in these animals, is an important correlation centre. The alveus fibres carry impulses from the hippocampus and possibly the dorsal cortex as well, chiefly to the dorso-lateral part of the body, whence they appear to be relayed to the hypothalamus *via* the medial fore-brain bundle. Whether this bundle carries ascending impulses as well must at present be left an open question; it seems probable that it does, but there is no evidence in this material to decide the point. The most important connections of the nuclei of the commissures, apart from their connections with the commissural fibres themselves, appear to be with the habenular ganglion *via* the medial cortico-habenular tract. The significance of the possible striatal and amygdaloid connections of the nucleus of the hippocampal commissures is obscure. It is disappointing that more definite differences in the connections of the dorso-lateral and ventro-medial nuclei of the body cannot be made out from the fibre-stained series, for the differentiation in cell-stained series is very distinct.

### *Discussion*

A survey of the literature shows a very large measure of agreement concerning the cell masses and fibre connections of the paraterminal body, but once more the agreement is obscured by the varieties of terminology which have been used.

The name "paraterminal body" was introduced by Elliot Smith (1901). He defined it, and pointed out that the structures included in it form an essential unity in that they all serve as relay stations in the course of fibres going to or coming from the hippocampal cortex. The name "paraterminal body" implies no doubtful homologies and is topographically appropriate. It has the additional advantage that it was from the first precisely defined, and that the same definition is applicable to this region, with minor variations, in all the vertebrate classes. The other two terms commonly used, "septum" and "parolfactory area," are unsatisfactory, because the first implies human homologies which cannot be substantiated, and the second has no precise definition and has been used in different senses by different writers (p. 168). Against this it may of course be urged that the word "septum" has the advantage of brevity, that it has become generally accepted by European and American workers, and that the misconceptions underlying its first use have been forgotten and no longer deceive anyone. It is also a convenient word from which compound terms, e.g. "tractus septo-corticalis," can be built.

The cellular differentiation of the paraterminal body has been investigated chiefly by Americans. Medial and lateral nuclei have been very generally recognised (e.g. Herrick, 1910). Johnston (1913) distinguished the upper part as "primordium hippocampi" and Herrick (1910) included in the lower part the "nucleus accumbens," grouping all these structures in the ventro-medial section of the hemisphere wall. It is now generally agreed that the nucleus accumbens should be excluded from the paraterminal body (septum) and placed with the palaeostriatum (Cairney, 1926; Durward, 1930; Kappers, 1921; Johnston, 1922). No further discussion of this point is necessary.

The term "primordium hippocampi" was introduced by Elliot Smith (1903) and applied by him to that area of the brain of Fishes and Amphibia which is homologous with the hippocampal formation of Reptiles and Mammals, but does not show the histological characteristics which are distinctive of the higher groups. He distinguished this primordium hippocampi from the part of the paraterminal body which extends back above the hippocampus in the frog. Herrick appears to have used the term in the same way for Amphibia in 1910, and again in the figures of his later paper (1921) which is not primarily concerned with this particular region.

Confusion has arisen in the description of Reptiles. Many Reptiles show a well-developed posterior extension of the paraterminal body above the commissures and the foramen of Monro, the supraforaminal part. Johnston calls the dorsal part of the paraterminal body, including the supraforaminal part, "primordium hippocampi." His chief reason for this is embryological. He locates the point of closure of the neuroporic recess between the anterior and hippocampal commissures, and states that all the hemisphere wall above this point is "pallial" and all below "basal." This appears to be a purely arbitrary division, for there seems no reason why the point of closure of the neuropore should be a morphological boundary between these regions. Assuming, however, that it is, it does not follow that any part of the brain wall above it must be hippocampus, or primordium hippocampi, unless it can be shown that it does in some Vertebrate develop into a definitive hippocampal formation. There is no reason why a "pallial" part of the brain wall should not contribute to the adult paraterminal body just as it appears to contribute to the corpus striatum on the lateral side. Now there is no evidence that the supraforaminal part of the paraterminal body of Reptiles ever does differentiate into a true hippocampal cortex, so that the justification for calling it a "primordium hippocampi," as Johnston does, seems very slight indeed. All one can say is that it develops in a part of the brain wall above the level of the neuroporic recess. Whether it should therefore be called "pallial" must remain a matter of opinion, and will depend upon the reliance one is inclined to place on the position of the neuroporic recess as a fundamental morphological landmark in the brain. The question still remains whether, in the adult, there is any other reason for separating the dorsal part of the paraterminal body and for giving it a distinct name. Its chief characteristic is that it contains a large number of alveus fibres crowded together and mixed with fibres from the tangential system superficial to the hippocampus. On this account it has been called the "pars fimbrialis septi" by Kappers. There can be no morphological objection to this term, for it includes the part in question in the paraterminal body or septum, but it seems a little unnecessary to have a separate name for a region which is distinguished only by a crowding together of fibres in it. Both Cairney and Durward found it convenient to describe the paraterminal body of *Sphenodon* without the separation of a part corresponding to Johnston's primordium hippocampi. Their description agrees very closely with the condition in *Lacerta*. Shanklin (1930), in the chameleon, describes similar findings. Neither Herrick's figures (1910) nor Johnston's (1915) for the turtle, nor Crosby's (1917) for the alligator, in which the primordium hippocampi is indicated, show it as a clearly differentiated region in the adult. They give rather the impression that the condition in both turtle and alligator may be essentially similar to that in *Lacerta* and *Sphenodon*, and that the similarity has been obscured by the terminology used. It is impossible to say more without a first-hand knowledge of the animals in question, but the evidence suggests that the description of the paraterminal body or septum in Reptiles would be considerably simplified by the dropping of this term "primordium hippocampi," at least until more substantial evidence either from embryology or adult anatomy can be adduced in its favour.

The relationship between the anterior commissure and the paraterminal body has already been discussed (p. 176). Since the anterior commissure contains only a few fibres which run to or from the hippocampus, it seems reasonable that the cells which surround it should be excluded from the paraterminal body, and this is what the material suggests.

Obviously many of the suggestions which have been made concerning the interpretation and terminology of the paraterminal body are provisional, but the evidence as it stands justifies a preliminary statement of the general cellular structure of the reptilian paraterminal body in the following terms.

The definition given by Elliot Smith in 1901 is applicable to the reptilian paraterminal body, but with the exclusion of the bed of the anterior commissure. It contains medial and lateral nuclei (ventro-medial and dorso-lateral in *Lacerta*) which are respectively afferent to and efferent from the hippocampus. It contains the bed and nucleus of the hippocampal commissure and of the posterior hippocampal commissure when present, and the nucleus of the diagonal band.

The fibre connections do not vary much in the different forms described, but certain variations in terminology may be mentioned. The diagonal band was seen and figured by Unger in the gecko and by de Lange in *Varanus*, and given the name "tractus cortico-parolfactorius," its connection with the amygdala being overlooked. Various workers, chiefly in the European schools, have used such terms as "tractus cortico-septalis," "tractus cortico-olfactorius septi," etc., for tracts connecting the cortex, paraterminal body and tuberculum. Sometimes "parolfactory" is substituted for "septal" in these compound terms, but all of them, provided Edinger's use of the term "parolfactory area" to include the medial part of the tuberculum and the grey matter beneath it is remembered, are self-explanatory and unlikely to lead to confusion. Johnston describes a connection between the amygdala and the paraterminal body *via* the stria terminalis in the turtle. Whether this connection is generally present in other forms or not cannot be decided from the literature, and it seems a point worthy of more attention. I cannot find definite evidence of it in *Lacerta*. The habenular connections *via* the stria medullaris also do not appear to have been completely unravelled. In the literature they are represented by "septo-habenular" fibres (Herrick, 1910; Cairney, 1926), while the medial cortico-habenular fibres are probably relayed to some extent in the nuclei of the hippocampal or posterior hippocampal commissures. I do not find definite evidence in *Lacerta* for habenular connections with the paraterminal body except for the connections to the nuclei of the commissures. The "anterior olfacto-habenular" tract was described by Herrick (1921) in the frog, and by Meyer, de Lange, and Cairney, in different reptilian orders. Herrick (frog) and de Lange (*Varanus*) describe it as connected with the paraterminal body, Cairney (*Sphenodon*) with the tuberculum olfactorium. In *Lacerta* it appears to run up to the anterior end of the hippocampal formation or nucleus olfactorius anterior. It seems probable that the fibres running from the paraterminal body to the habenular ganglion all carry impulses relayed from the hippocampus. Most of them come from the nuclei of the hippocampal and posterior hippocampal commissures. A few may come from other parts of the paraterminal body (Herrick, Cairney) but it is not yet possible to say precisely what part. Most of them run medially direct to the habenula, but a few from the anterior end of the paraterminal body may run laterally under the forebrain bundles to join the stria medullaris from the lateral side. With the latter may be some fibres from the nucleus of the diagonal band.

## THE PALLIUM

The pallial area of the lacertilian hemisphere is situated dorsally, dorsomedially, and laterally. It stretches from the nucleus olfactorius anterior back to the posterior pole of the hemisphere. The nucleus olfactorius anterior is particularly closely related to the three main divisions of the pallium since where it is traced posteriorly it is found to blend with each of them. These areas (e.g. fig. 5) are: dorso-medially, the hippocampal cortex; laterally, the pyriform cortex; and in between the two an area, which can be called the "dorsal cortex." All these areas blend posteriorly in an undifferentiated cap of cortex over the posterior pole of the hemisphere.

### *The pyriform cortex*

This begins anteriorly in the dorso-lateral region of the nucleus olfactorius anterior (fig. 3, *D*), where there is an accumulation of cells among which the fibres of the lateral olfactory tract are scattered. Soon it becomes separate (fig. 4), and the lateral olfactory tract takes up its position close to the endorhinal fissure between it and the tuberculum olfactorium. Dorsally it overlaps the dorsal cortex (fig. 4). Figs. 5 and 6 show the typical appearance in the anterior part of the hemisphere: a fairly clearly defined cell layer, superficial to the dorsal cortex above, and continuous with the hypopallium anterior below. This continuity is not clear in every section, but is sufficiently marked at least to suggest an inrolling of the ventral edge of the pyriform to form the hypopallium anterior. Posteriorly (figs. 7, 8), this appearance is lost, and the whole pyriform cortex is smaller. At the posterior end of the hemisphere (fig. 10) it loses its individuality, forms a continuous layer with the dorsal cortex above, and joins the hypopallium posterior below.

Throughout its extent the pyriform cortex shows a rather indefinite division into dorsal and ventral parts, the former consisting of larger cells than the latter (fig. 9).

### *The hippocampal cortex*

The first break to occur in the undifferentiated cortical ring of the nucleus olfactorius anterior is that between the pyriform and the dorsal cortex. Next, just posterior to it, a break appears medially (fig. 4) in the region of the anterior end of the paraterminal body. A cap of cells is now to be seen over the dorsal wall of the ventricle, tucking under the pyriform laterally to come into continuity with the anterior end of the hypopallium, and extending medially into the dorsal part of the medial hemisphere wall above the paraterminal body. It consists at first of rather diffusely arranged cells of irregular shape and medium size. Very soon the medial part of this region takes on the appearance typical of the hippocampal cortex in the posterior parts of the hemisphere. It becomes compact, very sharply defined from the white matter on either side of it and the paraterminal body ventral to it. It extends just on to the dorsal surface of the hemisphere round the dorso-medial angle and passes at first without any break into the dorsal cortex. Soon a kink appears, so that at the point of transition the hippocampus comes to overlap the dorsal cortex slightly. Just behind this level it breaks off from the dorsal cortex (fig. 5). It now consists of medial and lateral parts. The medial part is made up of small pyramidal cells, closely packed into a very clearly defined plate, and the lateral of a thin tail of cells, pyramidal in shape but much larger and less regularly arranged than the cells of the medial part. These parts will be called the small- and large-celled parts of the hippocampal cortex respectively (fig. 6, *Cx. hip. s. c.* and *Cx. hip. l. c.*). The large-celled part is at first fairly thick (3 or 4 cells) and of short extent medio-laterally. It becomes progressively more extensive, and thinner (1 or 2 cells thick). Behind the posterior hippocampal commissure it extends as far as the lateral aspect of the hemisphere. It remains distinct from the dorsal cortex until just in front of the posterior pole of the hemisphere, where it blends with it. The small-celled medial part of the hippocampus also increases in extent from before backwards, so that the greater part of the cap of cells over the posterior pole is formed by it. It bulges slightly into the cavity of the lateral ventricle on its medial wall, except at the anterior and posterior ends.

There are two sulci related to the hippocampal cortex. One, on the medial hemisphere wall, the fissura limitans hippocampi, has already been discussed (p. 159). The other, a ventricular sulcus, is situated just above the level of the ventral edge of the hippocampus and lies between the paraterminal body and the alveus system of fibres (figs. 6–9). It seems to be caused by the bulging of the paraterminal body into the ventricle and is not well marked till a definite dorso-lateral nucleus has developed. It becomes shallower behind the level of the hippocampal commissure, and has disappeared before the posterior hippocampal commissure is reached. This is Johnston's "fimbrio-dentate sulcus," but he applies this same name to the fissura limitans hippocampi.

### *The dorsal cortex*

The origin of the dorsal cortex anteriorly in the nucleus olfactorius anterior has already been described. It soon becomes broken off from the pyriform cortex and is then for about ½ mm. or less continuous laterally under the pyriform cortex with the hypopallium anterior (fig. 4). The hemisphere wall is naturally thick in this region, since both pyriform and dorsal cortex lie between the pia and the ventricle, but no ventricular ridge is produced as described by Elliot Smith and Johnston in the turtle. At first continuous medially with the hippocampus, the dorsal cortex soon separates and is then overlapped medially by the large-celled part of the hippocampus as it is laterally by the pyriform (fig. 5). These relationships are preserved back to the posterior pole of the hemisphere, where the dorsal cortex becomes continuous with the pyriform laterally and the hippocampus medially, and loses its individuality.

The cells of the dorsal cortex begin anteriorly by being fairly large and rounded, resembling those of the hypopallium with which it is continuous. As it breaks away from the hippocampus its medial part is seen to be made up of slightly smaller, irregularly pyramidal cells (resembling those of the large-celled hippocampus, but smaller), and gradually the whole dorsal cortex takes on a similar cell type. The medial part, however, rather more than just the area overlapped by the hippocampus, is differentiated from the lateral almost to the posterior pole of the hemisphere by the slightly looser and more irregular arrangement of its cells, and by its greater thickness. The dorsal cortex can be described then as a rather irregular and not very well-defined cortical sheet, in which there is a tendency for a medial strip to differentiate from the rest. It is continuous anteriorly with the nucleus olfactorius anterior and the hypopallium anterior and is overlapped medially and laterally by the hippocampal and pyriform cortex respectively.

The fibre connections of the pallial areas can be classified as follows.

*The tangential system.* This is common to all three pallial areas, and consists of a network of fibres lying superficial to them. Anteriorly it is continuous with a similar network over the nucleus olfactorius anterior, which probably receives olfactory tract fibres. It is best developed over the hippocampal cortex. Here it receives olfactory tract fibres anteriorly and gives rise to a small but compact bundle, the anterior olfacto-habenular tract. Behind this level the tangential fibres are connected with the upper part of the paraterminal body and with the fibres of the diagonal band (figs. 12–15). Behind the posterior hippocampal commissure there are many bundles of fibres which pierce through the hippocampal cortex joining the tangential system to the alveus system. Laterally, on the pyriform, the tangential system is not well developed, although it is fairly conspicuous anteriorly. Here it may also receive olfactory tract fibres, and probably sends fibres from the pyriform cortex into the diagonal band and the stria medullaris to the lateral part of the amygdaloid mass (fig. 13), and possibly to the amygdaloid component of the anterior commissure. Over the dorsal cortex the tangential system is less compact. No definite connections can be found for it, except possibly with olfactory tract fibres anteriorly. It probably consists of association fibres between the dorsal, hippocampal and pyriform cortex.

*The alveus system.* These fibres lie just outside the ependyma of the ventricle beneath the hippocampal formation, and it can at once be said of them that the majority from the anterior two-thirds of the hemisphere converge to the hippocampal commissure, and from the posterior third to the posterior hippocampal commissure. The fibres which enter the hippocampal commissure mostly join the hippocampal formations of the two sides. Some appear to pass into the amygdaloid component of the anterior commissure (fig. 14) to join the central amygdaloid mass of the opposite side. The posterior hippocampal commissure not only links the posterior third of the hippocampus of one side to that of the other, but also conducts fibres from the hippocampus to the medial cortico-habenular tract of the opposite side. There are many additional connections. Anteriorly alveus fibres enter the upper part of the paraterminal body (fig. 12). Their course and destination have already been described (p. 184). It is enough to say here that they connect with the dorso-lateral nucleus of the paraterminal body itself, with the hypothalamus through the medial fore-brain bundle and the columns of the fornix, with the nuclei of both hippocampal and posterior hippocampal commissures, and with the habenular ganglia through the medial cortico-habenular tract. It is noteworthy that fibres descending to the hypothalamus pass both anterior to, through, and posterior to the anterior commissure. In fig. 14 the most lateral of these descending fibres (*C.F.*) run into the medial cortico-habenular tract.

In view of the doubt over the homologies of the dorsal cortex, the extent of its connection with the alveus system is important. At the extreme anterior end of the hemisphere, where the hippocampal and dorsal cortex are not clearly differentiated, the alveus system extends laterally under what is continuous posteriorly with the dorsal cortex. Behind this level the alveus is connected with the medial part of the dorsal cortex and, at the level of the hippocampal commissure, this connection extends laterally until it includes all the dorsal cortex except its extreme lateral edge. Whether these fibres actually have similar connections to those described above for the alveus system, or whether they are only associational between the dorsal cortex and the hippocampus, it is impossible to say with complete certainty. The appearances are strongly in favour of the first of these alternatives. This connection of the medial part of the dorsal cortex with the alveus seems to correspond with the cellular differentiation described above.

The remaining pallial connections concern the dorsal and the pyriform cortex. Anteriorly where the dorsal cortex turns in beneath the pyriform to join the hypopallium anterior several fasciculi leave it and run ventro-caudally to join the olfactory component of the anterior commissure (fig. 17). The same region receives a few fasciculi from the lateral fore-brain bundle. Posterior to this region fasciculi can be seen collecting on the ventricular surface of the lateral part of the dorsal cortex (fig. 12), in the same plane as the medially placed alveus fibres. They run ventrally and posteriorly to join the hypopallial component of the anterior commissure (fig. 14).

Finally, there is the connection of the lateral olfactory tract with the pyriform cortex. Anteriorly the deep surface of the pyriform gives fibres to and receives them from the lateral olfactory tract, and it is possible that a further interchange occurs along the ventral edge of the pyriform before the lateral olfactory tract has entered the amygdaloid region.

The cortical fibre connections can be summarised as follows. All three cortical areas are connected by association fibres which probably run in the tangential system. Medially the hippocampus receives olfactory tract fibres anteriorly, diagonal band fibres from the central amygdaloid mass and possibly pyriform cortex, fibres from the paraterminal body (probably the ventromedial nucleus), the tuberculum olfactorium, and the medial fore-brain bundle. Many of these fibres enter the tangential system and they are probably mostly afferent. Its main efferent tract is the alveus, which connects it with the hippocampus and the amygdaloid complex of the opposite side, with the paraterminal body (dorso-lateral nucleus), with the hypothalamus *via* the columns of the fornix and the medial fore-brain bundle, and with the habenular ganglion of the same and the opposite sides. The dorsal cortex is connected in its medial part anteriorly, and posteriorly for almost its whole medio-lateral extent, with the alveus system. Laterally and anteriorly it gives commissural fibres to both olfactory and hypopallial components of the anterior commissure, and is connected with the lateral fore-brain bundle. The pyriform cortex receives fibres from and gives them to the lateral olfactory tract, and probably gives fibres to the amygdaloid complex (lateral part), to the diagonal band, and to the stria medullaris (habenula). It may provide some fibres for the amygdaloid component of the anterior commissure.

### *Discussion*

It is clear that the division of the cortex into the three areas to which the terms "hippocampal," "dorsal," and "pyriform" have been applied, is a very uniform condition throughout the reptilian class. There is some variation in the degree to which the areas are differentiated from one another. In *Sphenodon* they are practically continuous, although there is a tendency for the dorsal edge of the pyriform to overlap the dorsal cortex (Durward, 1930). The continuity is rather more marked in the alligator (Crosby). In the turtle the pyriform is distinct from the dorsal cortex, while in Lacertilia all three areas are discontinuous for the greater part of their extent. In Ophidia the pyriform does not appear to be so clearly differentiated from the dorsal cortex, but otherwise the condition is similar to the Lacertilia (Edinger, Meyer). It is characteristic that when the dorsal cortex is a differentiated area, it tends to be overlapped by the hippocampus medially and the pyriform laterally (the medial and lateral superposition of de Lange). It is also characteristic that when the lateral edge of the hippocampus is separate from the dorsal cortex, it consists of a tail of large pyramidal cells, rather irregularly arranged, which can be called the "large-celled" to contrast with the "small-celled" part of the hippocampus (cf. Unger).

An anterior thickening of the dorsal cortex, where it bends round laterally to come into contact with the anterior end of the hypopallium anterior, has been described in most orders. This thickening sometimes produces a ridge projecting into the lateral ventricle, e.g. in the turtle (Elliot Smith, Johnston), and is connected to the thalamus by fibres of the lateral fore-brain bundle.

The only cortical area which shows a uniform and characteristic type of differentiation is the medial (small-celled) part of the hippocampus. The other areas usually consist of a single more or less well-defined layer of cells. Unger, for the gecko, has described a distinct double layer in the dorsal cortex.

So far as they have been described here, the fibre connections of the cortical areas in *Lacerta* agree for the most part with those described in other forms. There are differences in detail, particularly concerning the cortico-habenular connections, but these are not more than one would expect to find, and probably have no great morphological importance.

The connections of the dorsal cortex have naturally claimed a great deal of attention. There seems now very little doubt that at least its medial part sends fibres into the alveus system (S. Ramón y Cajal, Crosby, Unger, etc.), but the ultimate fate of these fibres deserves further investigation. Anteriorly and laterally the connection between the dorsal cortex and the thalamus *via* the lateral fore-brain bundle has been noted in all the types described. The fibres which run from the lateral part of the dorsal cortex into the anterior commissure, which are very definite in *Lacerta*, are not mentioned in the literature, although a remark by Kappers (1929, p. 141) implies a knowledge of them. In 1921 (p. 1033) he denied their presence.

The interpretations of these facts show many variations, most of which centre round the dorsal cortex. Kappers includes the dorsal cortex with the hippocampus in his "archi-cortex," saying that the small-celled hippocampus is fascia dentata, the large-celled, intermediate, and the dorsal cortex, cortex ammonis. Johnston maintains that the dorsal cortex is neopallial and that fibres from it which run to the hippocampal commissure are callosal fibres. Elliot Smith compromises between these two extremes by calling the dorsal cortex "parahippocampal" and comparing it with the subicular region of Mammals. He finds the homologue of the mammalian neopallium in the antero-lateral thickening of the dorsal cortex, his "primordium neopallii."

As has been stated more than once, our knowledge of the fibre connections of these cortical areas is not detailed enough to make it possible to decide certainly between these different interpretations. Kappers appears to depend for his justification chiefly on the similarity between the "medial superposition" of Reptiles (the overlapping of the dorsal cortex by the large-celled hippocampus) and the relationship between the fascia dentata and cortex ammonis of Mammals. He states further that the hippocampus (medio-dorsal cortex, or small-celled hippocampus) is receptive, and the dorsal cortex efferent to the alveus. In a general way this is perhaps true, but the appearances suggest strongly that many, if not most, of the efferent alveus fibres have their origin in the small-celled hippocampus, and certainly a considerable part of the dorsal cortex in *Lacerta* has its commissural fibres in the anterior commissure. Much more definite evidence than these general resemblances is needed to support a definite homology.

The view that the whole dorsal cortex is neopallial seems also to lack support. The neopallium of Mammals is a correlating mechanism of a high order, receiving ascending sensory impulses from the thalamus and giving descending motor impulses to the brain stem and lower spinal centres. When it first appears in monotremes its commissural fibres run in the anterior commissure. Only a comparatively small part of the dorsal cortex of Reptiles possesses these characteristics. This part is the anterior part of its lateral border, Elliot Smith's "primordium neopallii" and Johnston's "pallial thickening."

Fibres from the thalamus *via* the lateral fore-brain bundle to the dorsal cortex are definite, although in *Lacerta* they are scanty. Whether descending motor fibres are present as well is still very doubtful, although Crosby has produced some histological evidence in their favour from Golgi preparations of the alligator brain. Johnston's experimental evidence (1916 *a*) is suggestive, but needs extension and confirmation. By the courtesy of Prof. Elliot Smith I have been able to see the unpublished description of an extensive series of experiments performed by Dr W. H. Wilson on the brain of *Varanus* and *Uromastyx*. These experiments were done primarily to investigate the electrical excitability of the optic lobes, but in every one the cortex of the hemispheres was stimulated. It was found that there was never a motor response from stimulation of the hemisphere by means of a current which was effective in producing a response from the mid-brain. This suggests that Johnston's results may have been due to a diffusion of the stimulus to neighbouring parts of the brain. Wilson's series included at least forty separate experiments.

That the commissural fibres of the lateral part of the dorsal cortex run in the anterior commissure is certain in *Lacerta*. It would be interesting to know whether this occurs in other Reptiles as well. That part of the dorsal cortex which receives these commissural fibres, or gives rise to them, corresponds very closely with Johnston's electrically excitable area (1916 *a*), and is more extensive than Elliot Smith's primordium neopallii (1919), that is, than the area receiving thalamic fibres. It diminishes in medio-lateral extent from before backwards, while in the same direction the area served by the alveus system increases. This suggests that the anterior and lateral part of the dorsal cortex is neopallial, with commissural fibres in the anterior commissure and the posterior and medial part "parahippocampal" with commissural fibres in the hippocampal commissure.

The presence or absence of callosal fibres in Reptiles will clearly depend upon the extent of the alveus system. If fibres enter it from the neopallial part of the dorsal cortex, and can be traced into the hippocampal commissure, they constitute the rudiments of a corpus callosum. In *Lacerta* the greatest area of dorsal cortex which could be called neopallial, using the criteria enumerated above, is that area served by fibres of the anterior commissure. Alveus fibres do not appear to extend into it, so that the evidence seems to be against the presence of callosal fibres, at least in *Lacerta*. At the same time it is impossible to make a rigid separation of the dorsal cortex into parahippocampal and neopallial parts, so that the question is bound to remain to some extent an open one.

The probable course of events in the evolution of the dorsal cortex can be stated provisionally in the following way. At first there is an area, comparatively undifferentiated, intermediate between the hippocampus and the pyriform cortex, and probably dominated by olfactory impulses from both of them. It may have discharged entirely through the alveus system, although the connection laterally with the anterior commissure may be equally primitive and indicate a relationship with the pyriform, just as the alveus connections indicate a relationship with the hippocampus. The intrusion of somatic impulses from the thalamus into its lateral part is the first step in the development of a cortex primarily concerned with the correlation of non-olfactory impulses, i.e. the first step in the development of a neopallium. This step has been taken by the Reptiles. Whether in addition they have developed descending motor fibres is still doubtful. It is quite possible that in some Reptiles alveus fibres do extend laterally into this area connected with the thalamus, but a clear demonstration of them is so far lacking. If present it would be reasonable to describe them as callosal, since by their increase in the eutherian Mammals a definite corpus callosum would be differentiated from the hippocampal commissure. The medial part of the dorsal cortex which has retained its connection with the alveus system without acquiring thalamic connections seems, as Elliot Smith has suggested, to be comparable with the subicular cortex of Mammals. The latter is a narrow strip of cortex between the hippocampal and neopallial areas. It shows the typical histological structure of neither, but appears to send efferent fibres into the alveus system (the fornix longus, Kölliker, 1889, p. 780).

The views set out here correspond very closely with those of Crosby (1917) and Cairney (1926).

## LARGE FIBRE TRACTS

So far all the different parts of the hemisphere have been described together with their fibre connections. It will make the structure of the brain clearer if certain large fibre tracts, the different components of which have already been mentioned separately, are now briefly described in their entirety.

### *The anterior commissure*

The anterior commissure lies in the lamina terminalis, ventral and slightly anterior to the hippocampal commissure (fig. 20). Anteriorly it is related to the nucleus of the diagonal band, to the diagonal band fibres, and to fibres of the medial fore-brain bundle which run up in front of it (fig. 18). Ventral to it is the preoptic recess and preoptic nucleus. Posteriorly, and close to the medial plane is a comparatively cell-free region which separates it from the anterior end of the thalamus, while more laterally descending fibres of the alveus system (fig. 14, *C.F.*) and the tractus cortico-habenularis medialis (fig. 18) are found. Its bed is formed by a part of the brain which should probably be classed with the strio-amygdaloid complex rather than the paraterminal body. It contains no nucleus of the anterior commissure.

The commissure contains two chief components, which from the origin or destination of most of the fibres composing them, can be named hypopallial and amygdaloid components respectively (figs. 14 and 18, *Com. ant. hyp.*; *Com. ant. amy.*).

The amygdaloid component (figs. 14, 17, 18) lies in the anterior and ventral part of the commissure and collects fibres from the whole of the central amygdaloid mass and possibly the ventral edge of the pyriform cortex. It is joined anteriorly by a compact fasciculus which can be called an olfactory component (figs. 12, 13, 17). It appears at the extreme anterior end of the hemisphere where it collects fibres from the dorsal cortex where it is rolled in under the pyriform cortex to come into contact with the hypopallium, and from the olfactory tracts, either directly or after a relay in the nucleus olfactorius anterior. It runs back among the fibres of the fore-brain bundles between the palaeostriatum and tuberculum, so that it may receive fibres from either of these structures, although this is not certain. It crosses in the upper and anterior part of the amygdaloid component. Most of its fibres come from the dorsal cortex in the region of the "primordium neopallii."

After crossing, some fibres leave the dorsal surface of the amygdaloid component to enter the alveus of the opposite side. These may contain the olfactory component. The rest connect either with the opposite amygdaloid, or the opposite hypopallium. Probably most of them go to the hypopallium.

The hypopallial component lies dorsally and posteriorly in the commissure. It contains fibres from: (i) the dorsal cortex; (ii) the hypopallium anterior; (iii) the hypopallium posterior; and (iv) parts of the central amygdaloid mass.

(i) This contribution consists of several fasciculi which collect from the lateral part of the dorsal cortex anterior to the level of the commissures (figs. 12–14). They run posteriorly, medially and ventrally to cross in the commissure.

(ii) Comparatively few diffusely arranged fibres which collect in the core of the hypopallium anterior at about the level of the commissures (fig. 14). The anterior part of the hypopallium anterior has no commissural fibres, or very few. Behind the commissures these fibres are joined by many fairly large fasciculi which arise from the posterior part of the hypopallium anterior, but from its ventricular surface.

(iii) A large number of fibres which arise from the ventricular surface of the hypopallium posterior. They are seen running anteriorly in fig. 16 (*Com. ant. hyp.*).

(iv) A few fibres which join (iii) from the ventral part of the central amygdaloid mass (fig. 16, *E*).

Many of the fibres of the hypopallial component of the commissure run between the same regions of opposite sides. Some appear to cross obliquely and to run to the central amygdaloid mass on the opposite side (fig. 14). No connection was apparent between this component and the alveus system. Naturally the fate of any of the fibres which enter the anterior commissure is very difficult to determine, as they are all mixed in a compact bundle as they cross the medial plane.

Components corresponding approximately to the hypopallial, amygdaloid and olfactory components of *Lacerta* (the latter joining the amygdaloid component) have been described under various names throughout the literature.

The hypopallial component has usually been named the "pars epistriatica," or "inter-epistriatica" (de Lange, Edinger, Kappers, etc.). In the alligator it appears to be small and to join the amygdaloid component (Crosby's "stria terminalis component"). It is well developed in a snake (*Callopeltis aesculapii*, Meyer, 1893, "markloses Theil der Commissura anterior") and has been described in other Lacertilia (de Lange, 1911; Shanklin, 1930, etc.). In the alligator it appears to consist of only a few fibres from the extreme ventro-lateral part of the dorso-lateral area (hypopallium) (Crosby, 1917).

The amygdaloid component corresponds undoubtedly with the "stria terminalis component" of American writers. This is described by Crosby as being connected to the pyriform cortex and the nucleus of the lateral olfactory tract, and by Johnston (1922) as essentially a commissure of the nucleus of the lateral olfactory tract. Shanklin (1930), in the chameleon, finds the same as Crosby in the alligator. In *Lacerta* its chief connection is with the central mass of the amygdaloid complex. It is probable that this central mass includes the greater part of the nucleus of the lateral olfactory tract which is a much more clearly differentiated structure in other forms.

A different terminology is used by the European writers, e.g. Edinger, Kappers, de Lange, Unger, etc. They distinguish a component of the commissure by the terms "pars corticalis" (Edinger), "tractus cortico-olfactorius cruciatus" (Kappers), or similar terms, all of which stress the connection of this component with the lateral (pyriform) cortex. This is almost certainly the same as my amygdaloid component and the stria terminalis component of the Americans. My findings are to some extent at variance with those of both European and American schools, in that the pyriform connections of this component are certainly few and possibly absent in *Lacerta*, while the amygdaloid connections (to the central mass) are conspicuous. It is possible that poor silver impregnation may account for this.

It should be noted that although the nucleus of the lateral olfactory tract is included in the central mass, the latter must represent other parts of the amygdaloid complex as well because of its connection with other components of the stria terminalis.

The olfactory component of *Lacerta* is apparently like that of other forms, except for its strong connection to the anterior and lateral part of the dorsal cortex (primordium neopallii). It is usually described as receiving fibres from the intermediate olfactory tract (Crosby), from the tuberculum olfactorium (Kappers' "anterior basal olfactory centres"), and from the nucleus olfactorius anterior (Edinger's "lobus olfactorius"). Unger (in the gecko) describes many of its fibres as running up to the hippocampal cortex after crossing in the commissure. In all these respects *Lacerta viridis* is probably like other Reptiles, although it is difficult to get completely convincing evidence in every case.

Kappers (1921) describes a bundle of fibres, the "radiatio frontalis commissurae anterioris." These, he says, arise in the septum (paraterminal body) and run ventro-posteriorly to cross anterior to the commissura pallii anterior (hippocampal commissure). His fig. 532, p. 1030, a sagittal section through the brain of *Varanus*, in which these fibres are shown, is very like my fig. 19. The fibres he labels "rad. front." clearly correspond with my alveus fibres, sweeping back from the anterior end of the hippocampus to join the hippocampal commissure. Until there is clearer evidence available to show that there are fibres in this portion which come from the paraterminal body and do not belong to the alveus system, the question of the presence of such a component in the anterior commissure must be left an open one.

It is clear that there are a great many details in which our knowledge of the connections of the anterior commissure is incomplete. A careful investigation of the condition in Chelonia and in *Sphenodon* might be illuminating. Experimental lesions, with a study of the resulting degenerations, might be useful too, particularly for sorting out the connections of the olfactory component and for tracing fibres from one side of the brain to the other.

### *Stria medullaris*

Under this term are included those fibres which connect various parts of the telencephalon with the habenular ganglia (epithalamus). It can be divided into medial and lateral parts which will be called for convenience "stria medullaris medialis" and "lateralis".

The fibres which run into the stria medullaris lateralis are collected from many different parts of the hemisphere and, following the common usage, can be described according to their origin in the following terms.

*Lateral cortico-habenular fibres.* These arise from the lower edge of the pyriform cortex and the outer part of the central amygdaloid mass (a part probably corresponding to the nucleus of the lateral olfactory tract), at about the level of the commissures. They can be seen running down beneath the pia mater to join the tractus olfacto-habenularis anterior in fig. 14.

*Lateral olfacto-habenular fibres.* These have a more widespread origin. Posteriorly they arise from the preoptic nucleus and perhaps the supra-optic nucleus. They can be seen in fig. 14 running laterally between the fore-brain bundles and the optic tract. Anteriorly they arise as a compact bundle of fibres, the anterior olfacto-habenular tract (Herrick, 1921) (figs. 12–14, *Tr. olf. hab. ant.*). In fig. 13 it crosses superficial to the diagonal band fibres, and is to some extent mingled with them (see also fig. 17). Some of the diagonal band fibres may enter it. Further anteriorly it sweeps round the ventral surface of the tuberculum (figs. 12, 18) and ascends under the pia mater in the anterior part of the paraterminal body to reach the hippocampal formation and perhaps the nucleus olfactorius anterior (fig. 19). It may of course receive fibres from both the anterior part of the paraterminal body and tuberculum as well as from the regions already mentioned.

*Stria medullaris medialis.* This consists of two divisions which are clearly seen in fig. 16, the median cortico-habenular and median olfacto-habenular tracts.

The medial cortico-habenular tract starts in a tangled network of fibres well seen in figs. 17 and 18 behind and slightly above the anterior commissure.

It is connected by crossed and uncrossed fibres with the anterior and posterior parts of the alveus system. Anteriorly (fig. 15) alveus fibres which are descending in the lateral part of the fornix columns run into this network. Posteriorly fibres enter it from the posterior hippocampal commissure (fig. 18) and directly from the posterior part of the alveus system (fig. 17). It receives also some fibres from the medial part of the central amygdaloid mass (fig. 17, *Amy. hab.*).

The medial olfacto-habenular fibres can be seen in figs. 16 and 17. They run ventrally and fork into a large posterior and a small anterior bundle. The posterior bundle joins the medial fore-brain bundle and goes to the hypothalamus. The anterior bundle runs across the fibres of the medial fore-brain bundle to the preoptic nucleus. Since the hypothalamus belongs to the diencephalon, the posterior bundle should be excluded from the stria medullaris if the definition of the latter is adhered to strictly. From the point of view of the anatomy of the adult brain, this exclusion seems an unnatural one.

This description agrees, except in comparatively minor details, with descriptions of the stria medullaris (the "taenia thalami" of continental writers) in other reptilian orders. Some differences have already been mentioned in the discussion of the paraterminal body (p. 189). It is noteworthy that Cairney failed to find direct cortico-habenular fibres in *Sphenodon*.

The use of the term "tract" for the various medial and lateral cortico- and olfacto-habenular connections seems a little inappropriate since only in a few cases (e.g. the tractus olfacto-habenularis anterior) are there fibres collected into definite tracts. The connections are for the most part diffuse and reach nearly all the medial and lateral cortical and olfactory centres of the hemisphere.

### *The fore-brain bundles*

The fore-brain bundles are large tracts of fibres which connect the telencephalon with the diencephalon and also probably with the mid-brain and perhaps lower centres. Most of their connections have been mentioned already, but it will be convenient here to summarise them, and to consider the tracts as a whole.

In the anterior part of the hemisphere medial and lateral fore-brain bundles can be recognised (fig. 12, *M.F.B.*, *L.F.B.*). The medial bundle lies between the palaeostriatum and the tuberculum. It gives fibres to or receives them from the palaeostriatum and the paraterminal body, and possibly the tuberculum olfactorium. It appears to be connected with all parts of the paraterminal body, some of its fibres sweeping up in front of the commissures (fig. 18) and then back into its supraforaminal part. Others appear to run into direct continuity with the alveus fibres (fig. 13). It would appear to be mainly an efferent tract from the hippocampal cortex and paraterminal body to diencephalic and mid-brain centres, but probably contains ascending fibres as well. It runs back underneath the anterior commissure, where it becomes closely applied to the lateral fore-brain bundle and lies lateral to the preoptic and hypothalamic nuclei and above the optic tract (fig. 14). Most of its fibres run ventrally as well as caudally (fig. 18), and end in the hypothalamus, together with many fibres from the lateral fore-brain bundle. In this region it is difficult to distinguish medial and lateral bundles (figs. 15, 16). They are very closely applied to one another, and the only differentiation is due to the denser packing of the fibres laterally. Here it would be most accurate to speak of a single fore-brain bundle which, as Cairney has described it in *Sphenodon*, divides into a dorsal and a ventral peduncle (fig. 17, *Ped. dor.*, *Ped. vent.*). The dorsal peduncle consists of rather coarse fasciculi, probably wholly and certainly mostly derived from the lateral fore-brain bundle. It runs to the thalamus. The ventral peduncle consists probably of all the medial fore-brain bundle and quite a large contribution from the lateral, and runs caudally as well as ventrally. Many fibres undoubtedly end in the hypothalamus, while others run in to the ventral part of the mid-brain and perhaps to lower centres.

The medial fore-brain bundle receives contributions from several other fibre tracts, mostly running to the hypothalamus. These are: (i) alveus fibres anterior to the commissures which have been mentioned already. Other alveus fibres descend between the components of the anterior commissure and still more posterior to them (columns of fornix), and all run with the bundle towards the hypothalamus (figs. 13–15). (ii) The stria terminalis fibres from the amygdaloid complex which arch over the fore-brain bundle and descend with the medial bundle to the hypothalamus (fig. 15). (iii) A strong contribution from the tractus olfacto-habenularis medialis (p. 201 and fig. 17).

The lateral fore-brain bundle consists of coarser fasciculi than the medial and begins a little further forward. It collects fibres from the anterior two-thirds of the hypopallium anterior, from the edge of the dorsal cortex where it bends round to join the hypopallium (the "primordium neopallii") and from the lateral part of the palaeostriatum (the "somatic striatum") through which it runs. Anteriorly (figs. 12, 13) it is fairly clearly distinguishable from the medial fore-brain bundle, and between them the olfactory component of the anterior commissure lies. Its ultimate fate has already been mentioned in describing the dorsal and ventral peduncles. Which particular fibres go to the thalamus and which to the hypothalamus and lower centres it is impossible to say.

It is clear then, that the medial fore-brain bundle is chiefly a tract connecting olfactory centres, the hippocampus and paraterminal body with the hypothalamus. It has also connections with the medial part of the palaeostriatum which may be an olfactory centre (the "olfacto-striatum"). The lateral fore-brain bundle is a link between the thalamus, the hypopallium anterior, and a small part of the dorsal cortex and the lateral part of the palaeostriatum. It has hypothalamic connections as well, and probably both bundles are connected to the mid-brain and perhaps lower centres.

It is very difficult to assess the functional importance of these bundles because of the lack of knowledge of the direction of conduction in them. There is reason to suppose that the alveus is efferent from the hippocampus, which makes it probable, but not certain, that the medial fore-brain bundle contains mostly descending fibres. It would seem likely too, that the lateral fore-brain bundle should contain mostly ascending sensory fibres from the thalamus to the striatum, hypopallium, and cortex, but again the possibility that many fibres are descending to the hypothalamus and mid-brain cannot yet be affirmed or denied.

Very similar descriptions of the fore-brain bundles have been published by American writers, who have used this same terminology. Edinger has used the term "basal fore-brain bundle" for the lateral bundle alone, with the alternative term "tractus strio-thalamicus." In the continental literature the medial bundle is commonly referred to as the "tractus septo-mesencephalicus." The terms "medial" or "lateral" fore-brain bundle seem more satisfactory, since the connections of each are too varied for an accurate and convenient term to be coined which can indicate them. The term "tractus septo-mesencephalicus," for example, is applicable only to some of the fibres which run in the medial fore-brain bundle.

A connection between the thalamus and the antero-lateral part of the dorsal cortex (primordium neopallii) seems to be very general. It has been described in the turtle (Johnston), chameleon (Shanklin), alligator (Crosby), gecko (Unger), *Varanus* (de Lange). The last two writers use the term "tractus fronto-thalamicus" for these fibres. De Lange suggests that the connection is rather with the dorsal part of the pyriform cortex than with the dorsal cortex (his "cortex ammonis"), but his figures do not support this contention.

In *Lacerta* the division of both bundles into dorsal and ventral peduncles is similar to that described by Kappers (1921) and Cairney (1926). Shanklin (1930) states that in the chameleon it is only the lateral bundle which divides in this way. He described mid-brain connections for the lateral bundle (ventral peduncle) in considerable detail. In general my findings agree with his, but the material is not adequate for the investigation of mid-brain connections in detail.

The direction of conduction in these bundles is clearly a matter of importance. Probably it occurs in both directions, with the medial bundle mainly descending and the lateral mainly ascending. Crosby, on the strength of Golgi preparations, finds evidence for conduction in both directions in both bundles in the alligator. This applies also to the cortical connections of the lateral bundle, although it appears that the descending fibres from the dorsal (general) cortex are relayed in the striatum. In view of the possibility that this region of the dorsal cortex is a "primordium neopallii," the presence and destination of these descending fibres is of considerable interest and worthy of further investigation. Experimental lesions with a study of the tract degenerations resulting from them would appear to be the best means of attacking this problem.

## CONCLUSION

A discussion and summary of findings in a paper of this kind cannot be of much value, since the work is mainly concerned with the investigation and correlation of detail. On the whole my observations in *Lacerta* agree very closely with those of others in different members of the same order and in the other different orders of reptiles. The agreement with Cairney's and Durward's descriptions of *Sphenodon* is particularly close.

One of the most striking features of the lacertilian brain is the characteristic development of the hypopallium posterior. In this it is unlike the Rhyncocephalia, Crocodilia, or Chelonia, but like the Ophidia. It appears to be associated with a comparative lack of differentiation in the remaining part of the amygdaloid complex in which Johnston, Crosby and Durward have described definite nuclear masses in the turtle, alligator, and *Sphenodon* respectively.

For a Reptile, cortical differentiation has reached a fairly high level in the Lacertilia, and the presence of commissural fibres from the dorsal cortex in the anterior commissure is a fresh point which suggests the comparison of this cortical region with the neopallium of prototherian Mammals. The question of the presence or absence of these fibres in other Reptiles deserves investigation.

The corpus striatum is typically reptilian. It does not reach the high degree of development seen in the alligator. Compared with the other reptilian orders, the differences are not great, and their significance is obscure.

It seems probable that the structure of the paraterminal body is very uniform throughout the whole class, the most striking difference being due to the presence or absence of a posterior hippocampal commissure with the concomitant presence or absence of a well-developed supraforaminal part of the paraterminal body. The paraterminal body of the opossum (Loo, 1931), and of the Macroscelididae (Le Gros Clark, 1928), appears to be built on the same plan. A re-investigation of the paraterminal body in the Chelonia and Crocodilia with a view to revision of terminology is desirable.

Detail, such as the methods used here can disclose, is still rather meagre concerning the fibre connections in the fore-brain of the Chelonia, and concerning the general anatomy of the ophidian brain. Further investigation in these fields and by these methods may therefore be expected to yield interesting results. Some of the differences between Cairney's description of fibre connections in *Sphenodon* and descriptions in other forms, may be due to his lack of good silver preparations. Further embryological investigations in all orders, and particularly in the region of the corpus striatum and amygdaloid, are clearly needed. The work which has been done already leaves one with the impression that the embryological method may not throw much light on the outstanding morphological problems, but obviously it needs application in a wider field before its limitations can be assessed. The experimental method, or the study of the degenerations resulting from controlled injuries, seems to offer more hope of definite information, particularly so far as the olfactory and cortical connections are concerned. Its findings might usefully be controlled, particularly in the region of the cortex, by a detailed study of Golgi and Cox-Golgi preparations, or by any method which renders both the cell body, axon and dendrites visible in one and the same preparation.

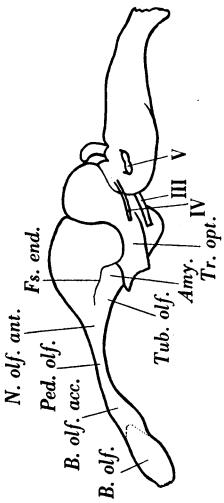


Fig. 1.

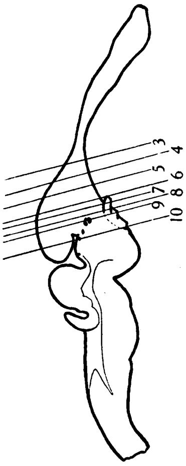


Fig. 2*a*.

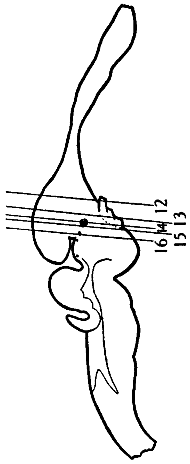
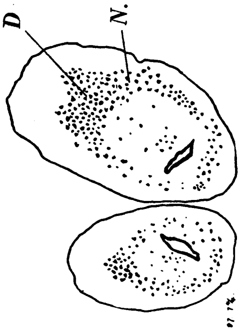


Fig. 2*b*.



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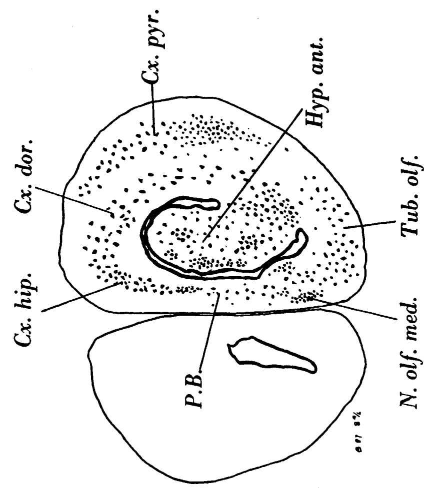
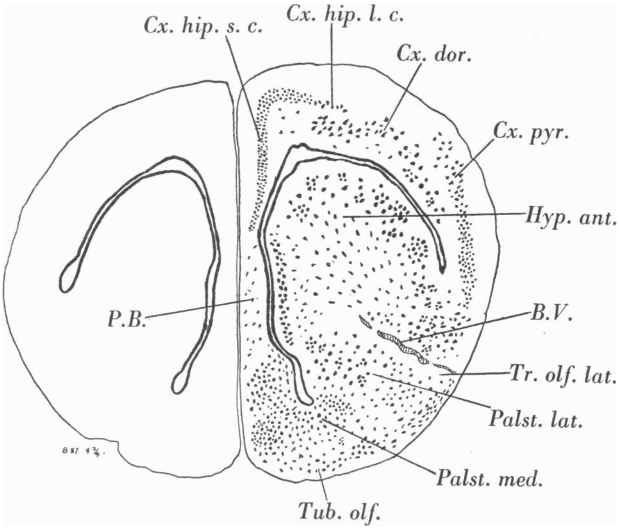


Fig. 4.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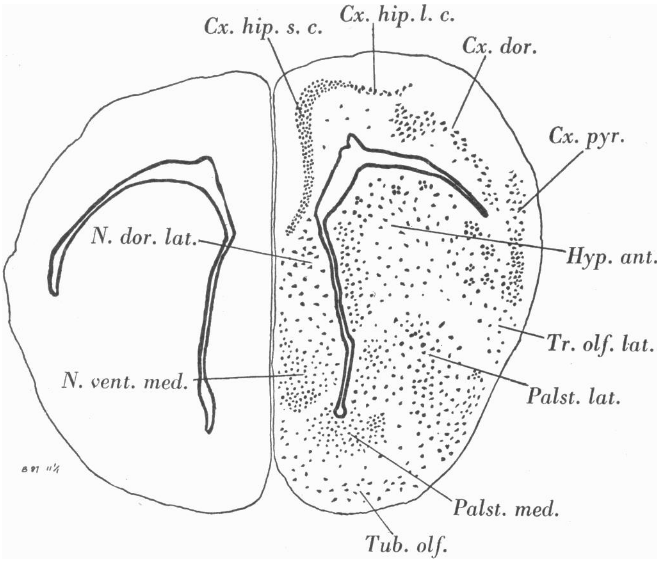
Cx. hip. l. c.
Cx. dor.
Cx. pyr.
Hyp. ant.
P.B.
B.V.
Tr. olf. lat.
Palst. lat.
Palst. med.
Tub. olf.
B87 9¾.

Fig. 5.


Cx. hip. s. c.
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Cx. pyr.
N. dor. lat.
Hyp. ant.
Tr. olf. lat.
N. vent. med.
Palst. lat.
Palst. med.
Tub. olf.
B87 11¼

Fig. 6.

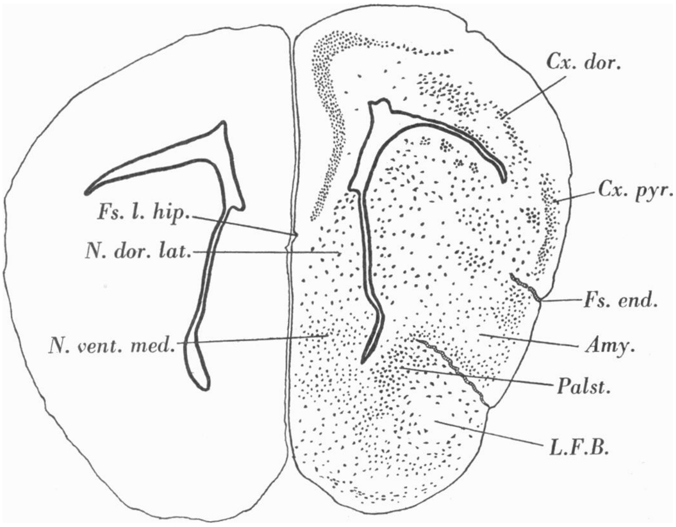

Cx. dor.
Cx. pyr.
Fs. l. hip.
N. dor. lat.
Fs. end.
N. vent. med.
Amy.
Palst.
L.F.B.

Fig. 7.

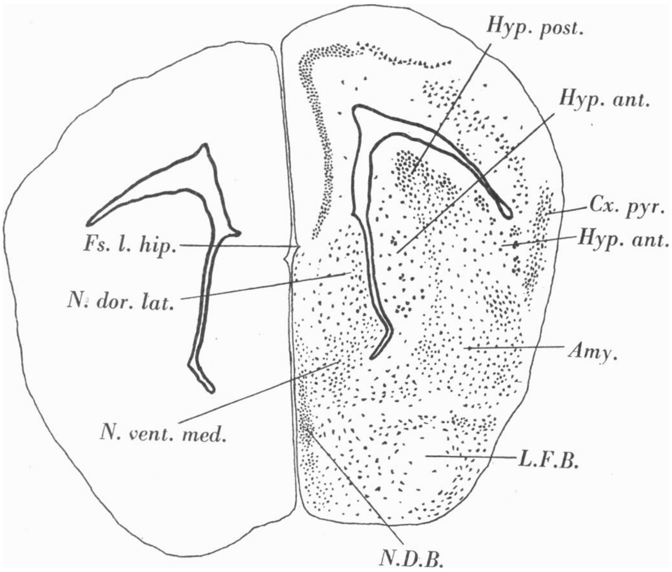
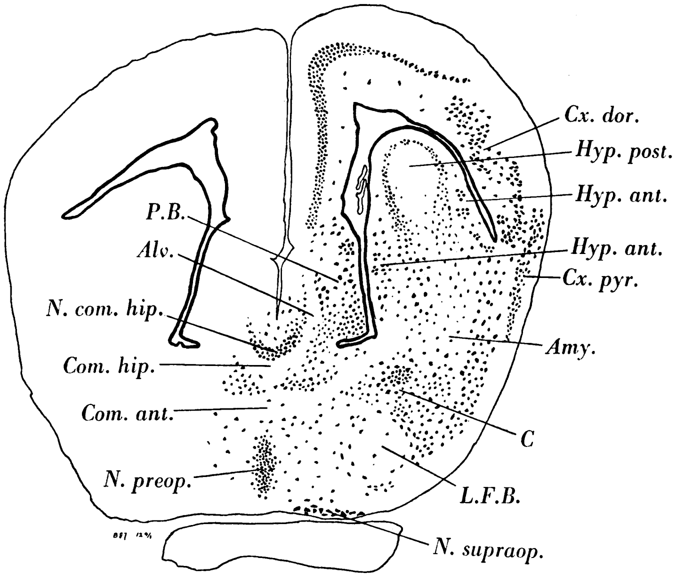

Hyp. post.
Hyp. ant.
Cx. pyr.
Hyp. ant.
Fs. l. hip.
N. dor. lat.
Amy.
N. vent. med.
L.F.B.
N.D.B.

Fig. 8.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Hyp. post.
Hyp. ant.
P.B.
Hyp. ant.
Alv.
Cx. pyr.
N. com. hip.
Amy.
Com. hip.
Com. ant.
C
N. preop.
L.F.B.
N. supraop.

Fig. 9.

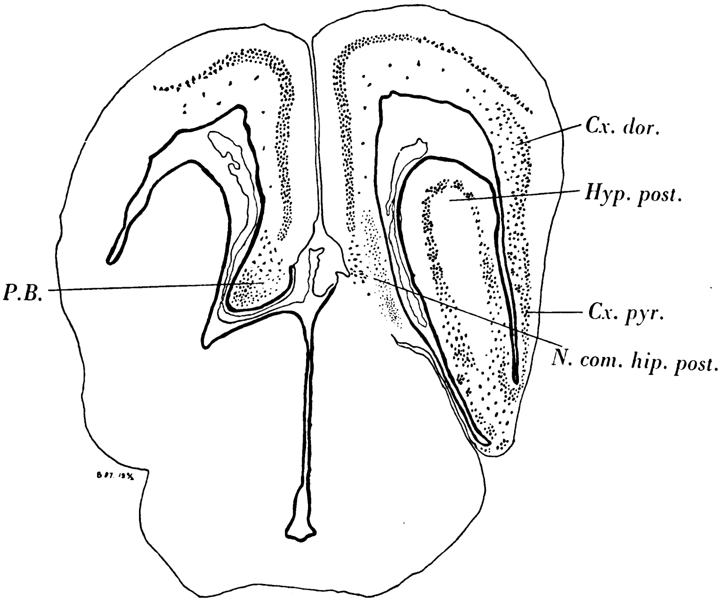

Cx. dor.
Hyp. post.
P.B.
Cx. pyr.
N. com. hip. post.

Fig. 10.

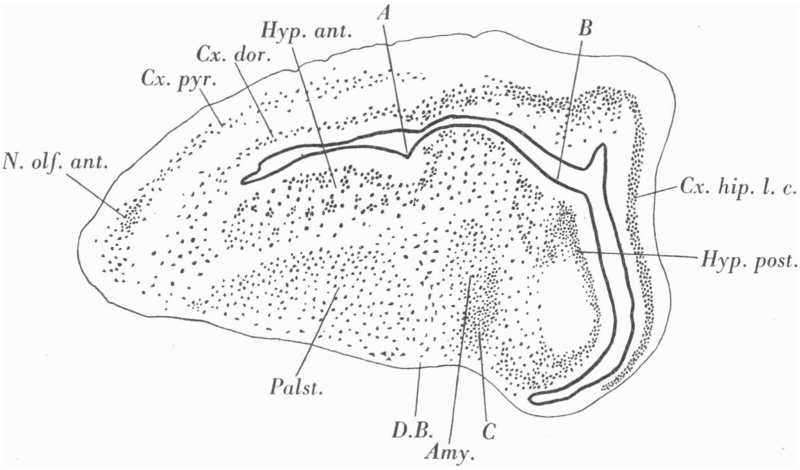
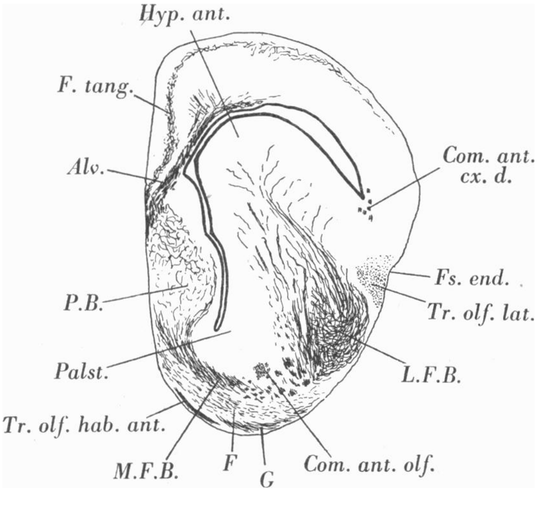

A
Hyp. ant.
B
Cx. dor.
Cx. pyr.
N. olf. ant.
Cx. hip. l. c.
Hyp. post.
Palst.
D.B.
C
Amy.

Fig. 11.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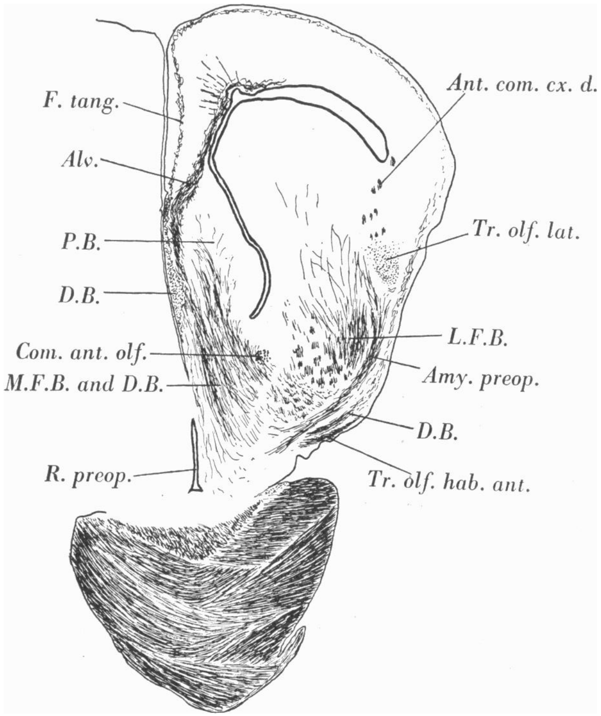
F. tang.
Alv.
Com. ant.
cx. d.
Fs. end.
Tr. olf. lat.
P.B.
Palst.
L.F.B.
Tr. olf. hab. ant.
M.F.B.
F
G
Com. ant. olf.

Fig. 12.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Alv.
P.B.
D.B.
Com. ant. olf.
M.F.B. and D.B.
R. preop.
Ant. com. cx. d.
Tr. olf. lat.
L.F.B.
Amy. preop.
D.B.
Tr. olf. hab. ant.

Fig. 13.

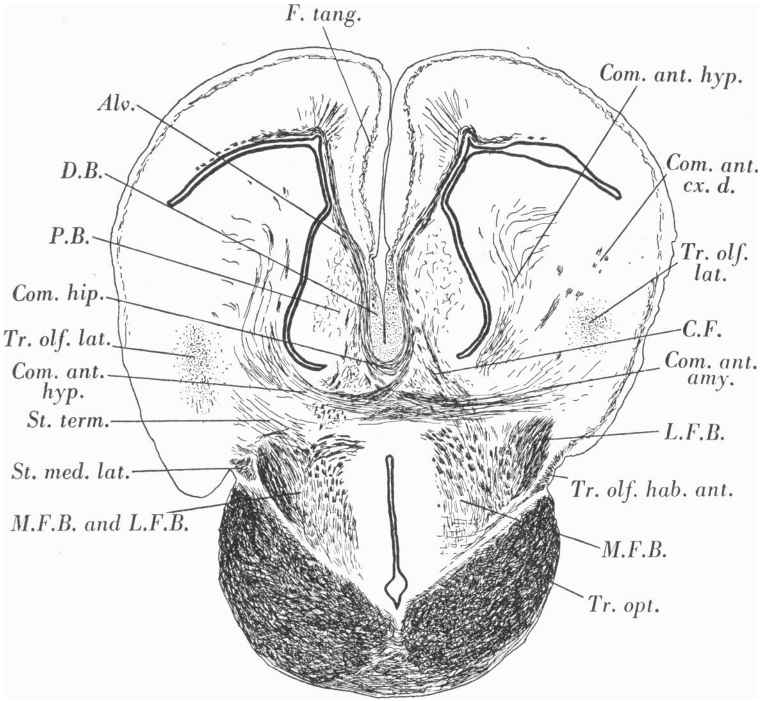

F. tang.
Alv.
D.B.
P.B.
Com. hip.
Tr. olf. lat.
Com. ant. hyp.
St. term.
St. med. lat.
M.F.B. and L.F.B.
Com. ant. hyp.
Com. ant. cx. d.
Tr. olf. lat.
C.F.
Com. ant. amy.
L.F.B.
Tr. olf. hab. ant.
M.F.B.
Tr. opt.

Fig. 14.

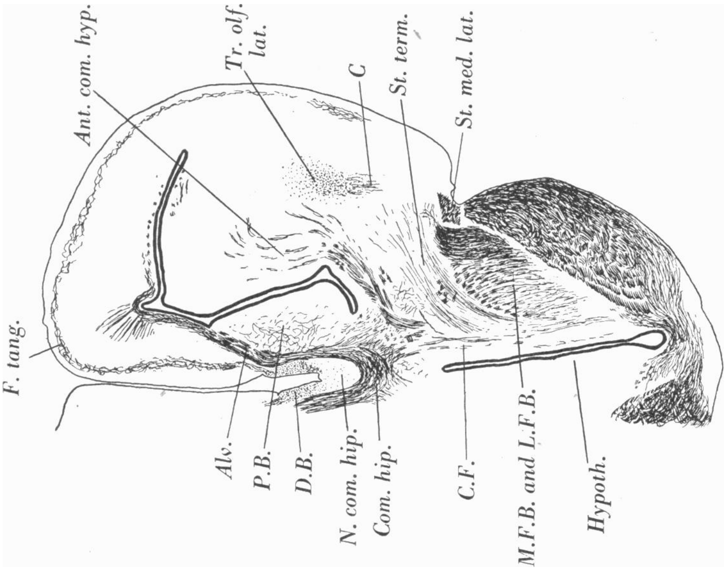

Ant. com. hyp.
Tr. olf. lat.
C
St. term.
St. med. lat.
F. tang.
Alv.
P.B.
D.B.
N. com. hip.
Com. hip.
C.F.
M.F.B. and L.F.B.
Hypoth.

**Fig. 15.**

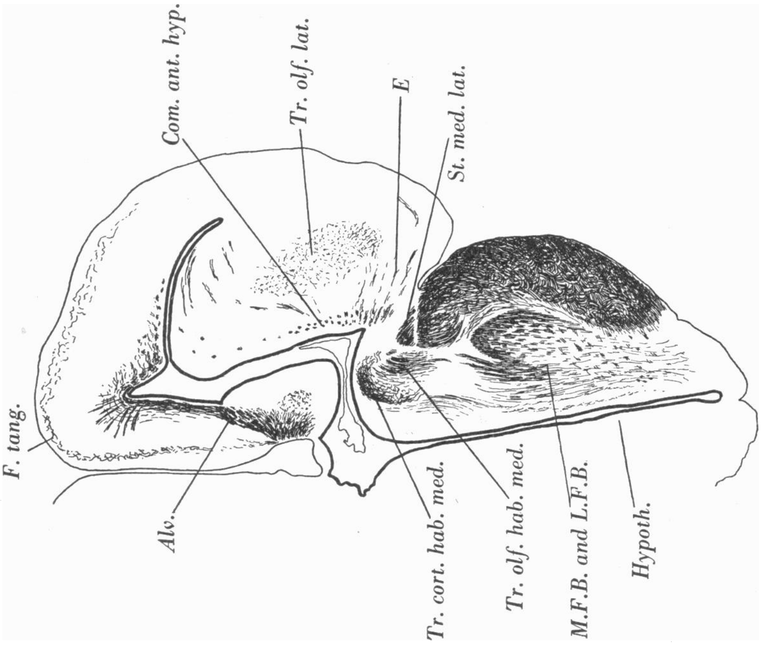

Com. ant. hyp.
Tr. olf. lat.
E
St. med. lat.
F. tang.
Alv.
Tr. cort. hab. med.
Tr. olf. hab. med.
M.F.B. and L.F.B.
Hypoth.

**Fig. 16.**

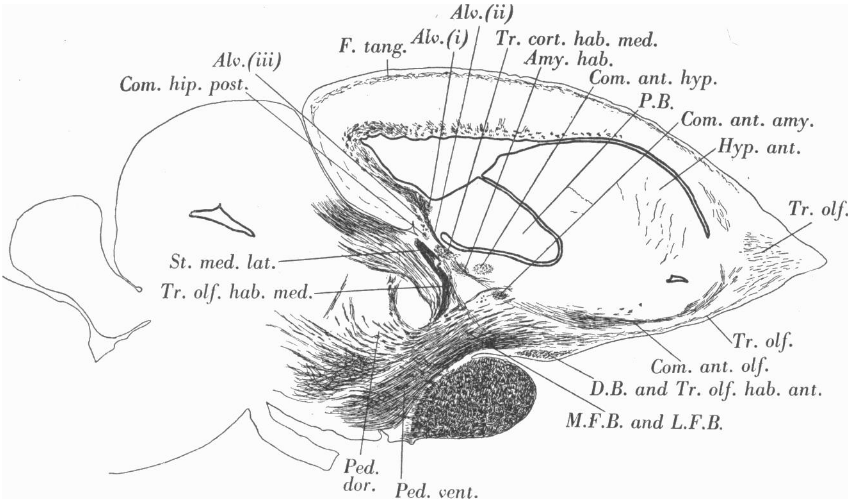
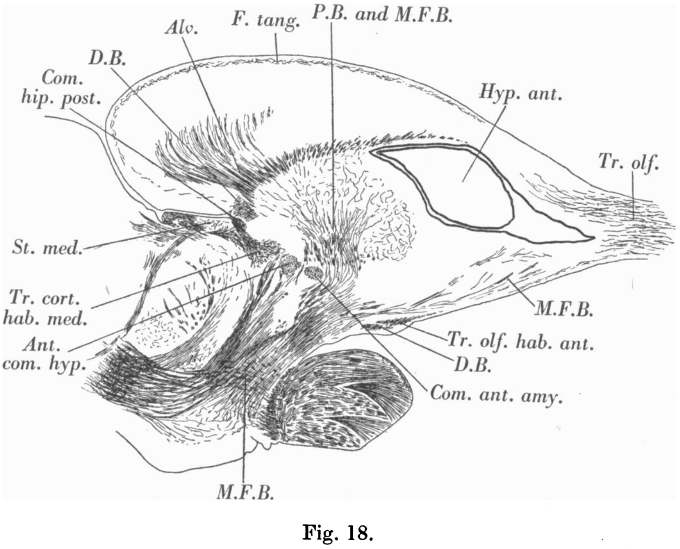

Alv.(ii)
Alv.(i)
F. tang.
Tr. cort. hab. med.
Alv.(iii)
Amy. hab.
Com. hip. post.
Com. ant. hyp.
P.B.
Com. ant. amy.
Hyp. ant.
Tr. olf.
St. med. lat.
Tr. olf. hab. med.
Tr. olf.
Com. ant. olf.
D.B. and Tr. olf. hab. ant.
M.F.B. and L.F.B.
Ped. dor.
Ped. vent.

Fig. 17.


F. tang.
P.B. and M.F.B.
Alv.
D.B.
Com. hip. post.
Hyp. ant.
Tr. olf.
St. med.
M.F.B.
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Tr. olf. hab. ant.
Ant. com. hyp.
D.B.
Com. ant. amy.
M.F.B.

Fig. 18.

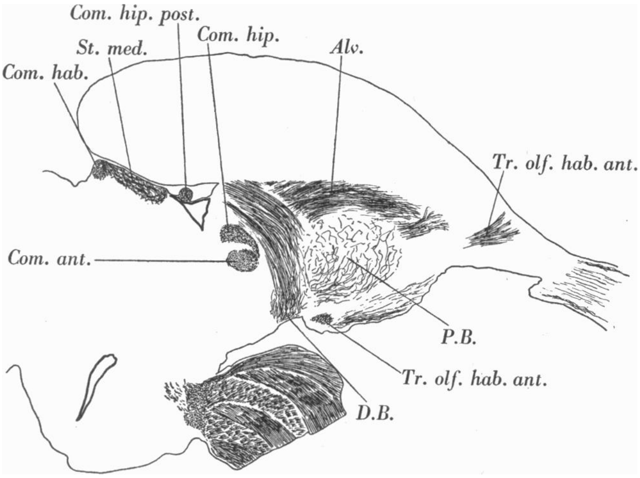

**Fig. 19.**

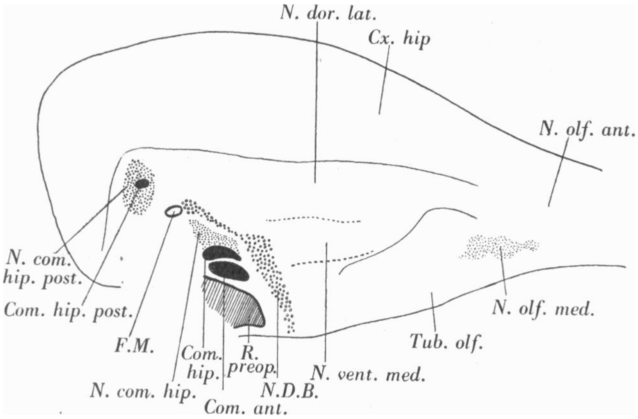

**Fig. 20.**

**All the figures, with the exception of figs. 1 and 2*a* and *b*, which were traced from photographs, and fig. 20, which is a graphical reconstruction, were drawn in outline from the sections with Edinger's projection apparatus. Detail was added afterwards with the aid of a microscope. The magnifications of figs. 1 and 2*a* and *b* are × 5, of figs. 3–16, × 35 and of figs. 17–20, × 23.**

## LEGENDS TO TEXT-FIGURES

Fig. 1. Sketch of lateral aspect of brain of *Lacerta viridis*.

Figs. 2 *a* and *b*. Sketch of a medial sagittal section of the same brain. In *a* the approximate position and plane of the sections from which figs. 3–10 were drawn is indicated. The same is done in *b* for figs. 12–16.

Figs. 3–10. Drawings made from a transverse series stained with toluidin blue (series B 87). The indication of relative sizes of cells is only approximate and the number of cells is very much larger in the actual specimen. Owing to the obliquity of the sections, the left-hand side of the figure (partly completed only in fig. 10) is slightly anterior to the right.

Fig. 11. Parasagittal section drawn from a specimen stained with toluidin blue (series B 99).

Figs. 12–16. Transverse sections drawn from the Bielschowsky series B 102. In these figures the left-hand side (completed in fig. 14) is posterior to the right. The relative thickness of fibres is not indicated accurately.

Figs. 17–19. Parasagittal sections from the Bielschowsky series B 109.

Fig. 20. A graphical reconstruction showing the position of structures in relation to the medial hemisphere wall. Made from series B 87.

## ABBREVIATIONS USED IN FIGURES

| | |
|---|---|
| *Alv.* | Alveus. |
| *Amy.* | Amygdala (central mass). |
| *Amy. hab.* | Amygdalo-habenular fibres. |
| *Amy. preop.* | Amygdalo-preoptic fibres. |
| *Ant. com. cx. d.* | See *Com. ant. cx. d.* |
| *Ant. com. hyp.* | See *Com. ant. hyp.* |
| *B. olf.* | Bulbus olfactorius. |
| *B. olf. acc.* | Bulbus olfactorius accessorius. |
| *B.V.* | Blood vessel. |
| *C.F.* | Columna fornicis. |
| *Com. ant.* | Commissura anterior. |
| *Com. ant. amy.* | Commissura anterior, amygdaloid component. |
| *Com. ant. cx. d.* | Fibres from the dorsal cortex to the anterior commissure. |
| *Com. ant. hyp.* | Commissura anterior, hypopallial component. |
| *Com. ant. olf.* | Commissura anterior, olfactory component. |
| *Com. hab.* | Commissura habenularis. |
| *Com. hip.* | Commissura hippocampi. |
| *Com. hip. post.* | Commissura hippocampi posterior. |
| *Cx. dor.* | Cortex dorsalis. |
| *Cx. hip.* | Cortex hippocampi. |
| *Cx. hip. l. c.* | Cortex hippocampi, large-celled part. |
| *Cx. hip. s. c.* | Cortex hippocampi, small-celled part. |
| *Cx. pyr.* | Cortex pyriformis. |
| *D.B.* | Diagonal band. |
| *F.M.* | Foramen of Monro. |
| *Fs. end.* | Fissura endorhinalis. |
| *Fs. l. hip.* | Fissura limitans hippocampi. |
| *F. tang.* | Fibrae tangentiales. |
| *Hyp. ant.* | Hypopallium anterior. |
| *Hyp. post.* | Hypopallium posterior. |
| *Hypoth.* | Hypothalamus. |
| *L.F.B.* | Lateral fore-brain bundle. |
| *M.F.B.* | Medial fore-brain bundle. |
| *N. com. hip.* | Nucleus commissurae hippocampi. |
| *N. com. hip. post.* | Nucleus commissurae hippocampi posterior. |
| *N.D.B.* | Nucleus of the diagonal band. |
| *N. dor. lat.* | Nucleus dorso-lateralis of paraterminal body. |
| *N. olf. ant.* | Nucleus olfactorius anterior. |

| | |
|---|---|
| *N. olf. med.* | Nucleus olfactorius medialis. |
| *N. preop.* | Nucleus preopticus. |
| *N. supraop.* | Nucleus supraopticus. |
| *N. vent. med.* | Nucleus ventro-medialis of paraterminal body. |
| *Palst.* | Palaeostriatum. |
| *Palst. lat.* | Palaeostriatum, lateral part. |
| *Palst. med.* | Palaeostriatum, medial part. |
| *P.B.* | Paraterminal body. |
| *Ped. dor.* | Pedunculus dorsalis. |
| *Ped. olf.* | Pedunculus olfactorius. |
| *Ped. vent.* | Pedunculus ventralis. |
| *R. preop.* | Recessus preopticus. |
| *St. med.* | Stria medullaris. |
| *St. med. lat.* | Stria medullaris lateralis. |
| *St. term.* | Stria terminalis. |
| *Tr. cort. hab. med.* | Tractus cortico-habenularis medialis. |
| *Tr. olf.* | Tractus olfactorius. |
| *Tr. olf. hab. ant.* | Tractus olfacto-habenularis anterior. |
| *Tr. olf. hab. med.* | Tractus olfacto-habenularis medialis. |
| *Tr. olf. lat.* | Tractus olfactorius lateralis. |
| *Tr. opt.* | Tractus opticus. |
| *Tub. olf.* | Tuberculum olfactorium. |

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