THE CELL MASSES IN THE FOREBRAIN OF *SPHENODON PUNCTATUM*

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INTRODUCTION

So far back as 1897 Elliot Smith made observations on the cell masses in the brain of *Sphenodon* which gave this reptile a unique interest. Various writers since that date have cited his remarks and used his figures; some have had access to fresh material, but up to the present time no paper has appeared dealing with the detailed anatomy of the adult brain stained electively by modern methods to show cell masses.

Hines has given a brief account of the cell masses, but her paper was chiefly concerned with the development of the forebrain. Cairney as recently as 1926, working in the laboratory of Prof. C. Judson Herrick of Chicago, gave a lucid survey of the forebrain, but here again the study of cell masses was hampered by the paucity of material suitably stained for that purpose. Since that date more material has come to hand in this laboratory and has been prepared specially for the study of cell masses.

In the present paper the aim has been to present a complete and detailed account of the cell masses in the forebrain of *Sphenodon* rather than to determine the homologies of the various component nuclei. I have not been able to add anything further to Cairney's account of the olfactory bulb and peduncle; a description of these parts is, therefore, not included in the present paper. A nomenclature corresponding largely with that adopted by Cairney has been used where possible; but in certain regions, e.g. the septum and thalamus, where this writer due to lack of suitable material was unable to unravel completely the nuclear arrangement, the usage of Huber and Crosby (1926) has been adopted where homologies seemed at all certain.

A definite drawback to the practical study of comparative neurology in New Zealand has been the inability of access to many of the more important papers dealing with the reptilian brain. For this reason the scope of the present paper has been largely confined to a pure description of the cell masses.

MATERIAL AND TECHNIQUE

The observations incorporated in this paper have been made on numerous series of adult brains stained by toluidin blue. The technique was one kindly proposed by Prof. G. Carl Huber, University of Michigan, Ann Arbor, and has in all cases given the utmost satisfaction. Six brains were cut transversely, one horizontally, and four in a sagittal plane. Besides this adult material several foetal brains were prepared by Huber's toluidin blue technique and cut in various planes. These, however, were not sufficiently early to add anything to what has already been so clearly described by Hines (1923) and Wyeth (1924).

In addition to such material electively stained by toluidin blue, I have had at my disposal numerous series stained by Weigert, Cajal, Ranson and Gurdjian methods and cut in all three planes. Although the study was not made on such fibre material, it was invaluable at times for confirmation of what was shown in cell preparations.

This study of the forebrain of *Sphenodon* is a continuation of the research programme instituted in the Anatomy Department of the University of Otago by Prof. W. P. Gowland. It is hoped ultimately to provide a complete description of the brain of this reptile and also of the brain of the New Zealand kiwi (*Apteryx australis*).

I have to acknowledge a just debt of gratitude to Dr Gowland, at whose suggestion I undertook this work and whose advice and encouragement I have at all times received.

CENTRES OF THE HEMISPHERE

THE CORTEX CEREBRI

The cerebral cortex of *Sphenodon* is demonstrated with diagrammatic clarity in toluidin blue preparations, and in the figures accompanying this paper the cortex is shown in all its aspects. It forms a continuous sheet over the dorsal aspect of the hemisphere throughout its whole extent from the peduncular base rostrally back to the caudal pole. It also descends on both medial and lateral aspects of the hemisphere for varying distances in different regions.

Three cortical sheets are identifiable on the evidence of cell arrangement, viz. a medial hippocampal cortex, a lateral pyriform cortex, and an intervening one, the general cortex. Cell size, which apparently has been of use in other forms in distinguishing the three sheets of cortex, has not been found to lend any assistance in *Sphenodon*; nevertheless each sheet has quite distinctive features, which will be detailed under the appropriate headings.

Hippocampal cortex

Undoubtedly this is structurally the best organised and the most highly developed portion of the cortex cerebri, and presents remarkable constancy in appearance when traced throughout the length of the brain wall. It is composed of a continuous sheet of cells bent upon itself and lying in the adjacent portions of the medial and dorsal walls of the hemisphere. The longer limb generally occupies the medial wall, whilst the part bending over into the dorsal wall is shorter, particularly in the rostral part of the hemisphere.

The cells composing the hippocampal cortex are of medium size, are densely packed, and in general do not show much scattering into the adjacent white matter. At its ventral extremity the hippocampus becomes more slender and here, as a rule, the cells show some scattering towards the septum. There is no marked difference in cell size in different parts of the hippocampus; those at its ventral extremity are, if anything, slightly smaller than in the rest of the sheet, but the difference is so slight that one cannot fairly divide the hippocampus into dorsal and ventral portions on this criterion, as suggested by Elliot Smith (1910).

The position of the sheet in the brain wall is uniformly about midway between pial and ventricular surfaces, but ventrally it inclines towards the pia. Its ventral extremity coincides with the level of the fissura hippocampi (figs. 1–10).

As the hippocampal cortex is traced rostrally in transverse series it does not diminish so rapidly as does the cross-section of the hemisphere; thus this cortical sheet appears more conspicuous and of greater relative extent in the more rostral sections. The characteristic features of the column are, however, preserved well forwards towards the peduncle, although some loosening of its structure—a loss of compactness—is observable here (fig. 1). The vertical limb is decidedly the longer in the rostral part of the hemisphere.

Caudally from the level of the foramen of Monro the hippocampal cortex becomes reduced in extent and, as was the case in the most rostral sections, loses some of its sharp definition.

The general features of this cortical layer are well seen in horizontal sections. It is then seen to be most clearly defined about its middle, and to become somewhat more bulky and less sharply circumscribed in its most rostral and caudal portions.

Johnston (1915) found in the case of the turtle that the cells of the hippocampal cortex became smaller when traced caudally; this is certainly the case in *Sphenodon*; but the striking difference in size between the cells of the hippocampus and of the general cortex mentioned by Johnston cannot be defined.

The dorso-ventral extent of the vertical portion of the hippocampus gradually decreases from before back, a feature well evidenced by comparing figs. 5 and 9 which belong to the same series and are drawn to the same scale. Rostrally it stretches almost as far ventrally as the level of the sulcus septo-striaticus (fig. 4) but, followed caudally, the ventral border is seen to recede dorsally till it coincides with the level of the sulcus fimbrio-dentatus (fig. 7). This upward recession of the hippocampal cortex coincides with the appearance and gradual increase of the septal nuclei.

The relationship of the hippocampal cortex to the general cortex will be discussed under the heading of the latter.

General cortex

In *Sphenodon* the general cortex extends from the base of the peduncle backwards over the dorsal aspect and caudal pole of the hemisphere. Medially it meets the hippocampal cortex along its whole length, whilst laterally it lies in apposition in front with the hypopallium and behind with the pyriform cortex—relationships which will be discussed more fully below.

In his account of the general cortex of *Cistudo*, Johnston (1915) figures this cell mass as coming to a somewhat tapered anterior extremity (see Johnston's fig. 7), and in the text describes how hippocampal and pyriform cortices meet rostral to the general cortex. In *Sphenodon* the general cortex certainly narrows rostrally in conformity with the diminishing size of the hemisphere, but not in so marked a manner as in *Cistudo*, and certainly no evidence of the meeting of the hippocampal and pyriform cortices is found. At the peduncular base the general and hippocampal cortices lose their identity at practically the same level; the pyriform cortex, however, continues on into the peduncle.

The general cortex possesses several distinctive features, which readily determine its identity from the hippocampal cortex. Its distinction from the pyriform cortex in cell preparations is not so striking.

As hippocampal cortex merges into general cortex the most striking change is the alteration of the texture of the whole cell mass, which gradually becomes more open. The hippocampal cortex, indeed, commences to show some evidence of this change before the general cortex is reached, and in the latter field the scattering of cells throughout the brain wall is its most characteristic feature. The scattering is chiefly towards the pia and this is most evident caudally (compare figs. 4 and 9). Despite such broadcasting of the cells, however, there may generally be detected some semblance of a column of cells running laterally from the undoubted hippocampal cortex and forming the basis of the general cortex. Nowhere does the general cortex show such a well-organised column of cells as the hippocampus; at its best it is composed of clumps of more or less densely packed cells, welded into some semblance of a column by more scattered cells.

At its medial border the general cortex, like the hippocampus with which it is here continuous, lies about midway between the pial and ventricular surfaces, but it gradually inclines towards the ependyma and at its lateral border lies closely upon it.

Laterally the general cortex presents a feature which has been noted by Johnston (1915) in the turtle, viz. a thickening of its lateral border. This thickening is well shown in all sections of the hemisphere in *Sphenodon*, except near the rostral and caudal poles, and takes the form of a densely staining clump of cells situated at the lateral edge of the general cortex. In some measure, at least, this thickening is comparable with the feature described for *Cistudo* by Johnston, although the well-developed peripheral layer of cells described by him cannot be found in *Sphenodon.*

The lateral boundary of the general cortex in the caudal two-thirds of the hemisphere meets the pyriform cortex (figs. 6–15), while in the rostral third the general cortex turns round the dorso-lateral angle of the ventricle to become continuous with the hypopallium (figs. 1, 2, 3). Where it meets the pyriform cortex the distinction between the two, though never striking, can almost invariably be made by one means or another. Firstly may be mentioned the more densely packed clump of cells which formed the lateral boundary of the general cortex. At this point also the scattering of cells from the cortex towards the pia ceases abruptly. In the pyriform cortex itself two features which will be mentioned again below also tend to distinguish these cortical sheets; there is a tendency for the pyriform cortex to overlap the general cortex and a fairly constant flattening of the former against the ependyma. These features have been shown in many of the figures, e.g. figs. 7 and 15, where the flattening has been indicated (**X**).

In approximately the rostral third of the hemisphere the general cortex does not meet the pyriform cortex laterally, but passes deeply to it, close to the ependyma. It does not at once become continuous with the hypopallium, but very gradually descends as sections are traced rostrally, till ultimately it becomes continuous with the hypopallium round the dorso-lateral angle of the ventricle (fig. 3).

Examination of horizontal sections shows an interesting feature in the more rostral part of the brain wall and corresponding to the foremost portion of the general cortex. This consists in a slight, yet quite definite thickening of the brain wall wherein lies that portion of the general cortex which connects with the hypopallium. This feature is reminiscent of what occurs more strikingly in the brain of *Chelone mydas* in a similar position. Elliot Smith (1919) describes and figures the condition in that turtle, and discusses its causation on the grounds of neurobiotaxis. Certainly the appearance in *Sphenodon*, though less apparent than in *Chelone mydas*, lends support to Elliot Smith's view.

Pyriform cortex

The pyriform cortex lies along the dorso-lateral aspect of the hemisphere throughout its whole length. It extends further rostrally than the general and hippocampal cortices, and runs forwards into the peduncle. It is a better-defined sheet of cells than the general cortex, but does not present anything like the clear-cut outline of the hippocampus.

The relationship of the pyriform cortex to the general cortex on the one hand, and to the hypopallium on the other, varies as we examine sections of the brain rostrally and caudally. In the caudal two-thirds of the hemisphere the pyriform cortex is interposed between the general cortex medially and the hypopallium ventrally (figs. 5–15), whereas in the rostral third it ceases to be interposed between these two sheets and adopts a more superficial position in the brain wall. Simultaneously with this alteration in position of the pyriform cortex, the general cortex descends deep to it, and turning round the dorso-lateral angle of the ventricle becomes continuous with the hypopallium (figs. 2, 3). Rostrally, therefore, the sheet is quite cut off from the ependyma by the convergence of the general and hypopallial cortices deep to it. More caudally, where it is interposed between the general cortex and the hypopallium, it approaches the ependyma and just ventral to the general cortex lies closely in contact with it; nearer the angulus ventralis, however, it rises clear of the ependyma before bending medially to fuse with the hypopallium (fig. 8).

The transition from general cortex to pyriform cortex is marked by several features, which make the line of junction quite distinct. There is, as a rule, a tendency for the pyriform cortex to overlap the lateral border of the general cortex, and there may even be a narrow cell-free zone between them. Added to this there are definitely fewer cells scattered towards the pia over the pyriform cortex than over the general cortex, a feature which is better marked in the caudal half of the hemisphere.

The cell grouping in the pyriform cortex is also worthy of note; what would appear to be a quite constant feature is a flattening of its superficial surface just ventral to the lateral border of the general cortex, and coinciding with that part of the pyriform cortex which lies most closely upon the ependyma. This feature (marked **X** in figs. 7 and 15), moreover, is accentuated by the relative paucity of scattered cells lying superficial to it. Further ventrally, nearer the angulus dorso-lateralis, there are some cells scattered in the white matter overlying the pyriform cortex. This flattening of the pyriform cortex has been closely examined in all series, and although some do not show it in any marked degree, yet the majority confirm its presence. It may be distinguished as far rostrally as the point where the pyriform cortex commences to part company with the general cortex, and from there back to the caudal pole of the hemisphere. Its constancy is so marked that I regard it as an important feature in distinguishing this cortical sheet in *Sphenodon.*

Running ventrally from the edge of the pyriform cortex along practically its whole length there may be distinguished a layer of cells lying parallel with the pia. From their arrangement, obviously interposed in the course of the lateral olfactory tract, these cells will constitute the nucleus of that tract. Cairney (1926) has described and figured such a nucleus.

The presence of surface fissures indicating the limits of the pyriform cortex has been sought for in all series. No evidence of a rhinal fissure can be found, though the endorhinal fissure, bounding the cortical sheet ventrally, is constantly present. At this site the branches of the lateral striate artery enter the hemisphere (figs. 6, 8, 10).

THE SEPTUM

The ventro-medial segment of the forebrain of *Sphenodon* presents several clearly defined nuclear masses which are, however, rather difficult to compare with the masses occupying this region in other forms. Both Hines (1923) and Cairney (1926 *b*) have given some account of the cell masses in *Sphenodon* and their descriptions have certainly proved invaluable in this study; yet in view of the material now at my disposal I consider that a more detailed and somewhat different account of this region may be given.

The term septum is here applied to that portion of the ventro-medial segment of the brain wall which lies related to the ventral extremity of the hippocampal cortex throughout the extent of the hemisphere, excluding, however, that portion of the olfacto-striatum (nucleus accumbens) which lies medial to the angulus ventralis. This arrangement has been adopted purposely by Cairney (1926 *b*), for the nucleus accumbens is evidently of the same nature as that portion of the olfacto-striatum lying lateral to the angulus ventralis, and its separation from the septum would, therefore, seem reasonable.

Thus defined, the septum will be described in two parts, rostral and caudal, owing to the fact that division into separate nuclear masses varies in these two regions.

Detailed accounts of this region in the turtle and the alligator have been given by Johnston (1915) and Crosby (1917), but the correlation of my findings with the descriptions and figures published by them is by no means easy. *Sphenodon* presents a septum in which certain clearly definable masses are present, and my aim here is to describe them accurately rather than to attempt to unravel their homologies.

In the most rostral part of the hemisphere the septum is represented by a small mass of scattered cells lying between, and quite distinct from, the olfacto-striatum ventrally and the hippocampal cortex dorsally (fig. 1). These cells are of small size and stretch from pia to ependyma. Their distinction from the olfacto-striatum is effected by a relatively cell-free zone between the two masses, but perhaps more obviously by the very different texture of the olfacto-striatum. The latter cell mass is fairly densely packed and its cells, which stain deeply, are aggregated into small clumps, whereas in the septum the cells are discrete, small, and do not take the stain so deeply. This appearance is seen in figs. 1–5 (*n. sep. med.*). The gradually increasing proportions of the mass may be noted as traced caudally.

This first and rostral component of *Sphenodon's* septum, which I have labelled the *nucleus septi medialis*, has to this stage been unaccompanied by any other septal nucleus; but now as we proceed further caudally it comes to be separated from contiguity with the hippocampus by the advent of a second component, which appears quite suddenly (fig. 6), forming a projection into the ventricle. The cells occupying this thickening of the brain wall (the *nucleus septi lateralis*) are at first relatively few, but their large size is distinctive. At their first appearance they lie lateral to the vertical portion of the hippocampus, but when traced caudally the ventral edge of the latter recedes dorsally and, as it were, makes room for this new septal component.

The cells of the lateral septal nucleus, always distinctively large, become more and more numerous and adopt a whorled arrangement about a relatively acellular zone. This appearance is due to the fibres of the alveus system forming a bundle, which runs caudally to reach the anterior pallial commissure (figs. 7–9). The large-celled component is confined chiefly to the area lateral to the fibre bundle, and the medial small-celled septal nucleus, which lies in the main ventral to the large-celled mass, tends also to spread up the pial surface medial to the latter nucleus and the fibre bundle.

In naming the intra-ventricular sulci I have adopted the usage of Cairney (1926 *b*). The sulcus septo-striaticus is evident in all the more rostral sections, though it fades and is finally indistinguishable as the foramen of Monro is approached. It lies, I find, not strictly between the septum and the olfacto-striatum, but rather opposite the small-celled portion of the septum, a fact which might indeed justify a more accurate renaming of this sulcus in *Sphenodon* (figs. 4–7).

The sulcus fimbrio-dentatus appears suddenly like the bulge of the brain wall below it, due to the large-celled component of the septum (fig. 6). This bulge, though not projecting far into the ventricle, has a considerable dorso-ventral extent which, indeed, does not greatly vary throughout its length.

The above then represents the rostral part of the septum, clearly distinguishable by cell size and cell arrangement into its component parts and from adjacent cell masses. Caudal to this level there tends to be some merging of adjacent masses and a consequent lack of definition in their boundaries. Yet the large- and small-celled parts are distinguishable well caudally, almost to the foramen of Monro.

References in the literature to the nuclei of this region are numerous, Crosby (1917), Hines (1923), Johnston (1913 and 1915), Herrick, and Cairney (1926) have all of more recent years dealt with the subject. Hines, who treated of *Sphenodon*, did not distinguish with any degree of certainty the presence of lateral and medial septal nuclei in the adult; their presence in foetal *Sphenodon*, however, she stresses. From the foetal material at my disposal which, however, I admit is not so early as that used by her, I fail to see any evidence of better development of these nuclei in the foetus than in the adult. Cairney was unable to find evidence either from cell characters or from cell-free zones of the presence of medial and lateral septal nuclei in the adult. In describing a small-celled medial (and ventral) nucleus and a large-celled lateral (and dorsal) nucleus I, therefore, find myself in disagreement with these two writers regarding the condition in the adult brain. The appearances I have described and figured are constantly evident in all the cell preparations studied.

Concerning the condition of this region in other forms it would appear that my lateral or large-celled nucleus corresponds in some measure, at least, to the nucleus parolfactorius lateralis in *Alligator mississippiensis* (Crosby, 1917) and to the similarly named nucleus in *Cistudo carolina* (Johnston, 1915). The rostral part of my small-celled nucleus bears a very definite resemblance to a portion of the primordium hippocampi of *Alligator* and *Cistudo*; but, apart from such resemblances, the grouping of cells in these forms is very evidently different, and a correlation of the various masses would involve further evidence than is afforded by a study of cell preparations alone. In *Chrysemys marginata* Herrick (1910) figures a lateral septal nucleus which would appear to correspond with mine.

As the foramen of Monro is approached, the clear distinctions which were evident more rostrally cannot be found; the sulcus septo-striaticus is lost, no clear distinction exists between olfacto-striatum and septum, and within the septum itself one can no longer distinguish with such ease the large-celled from the small-celled nucleus. Further specialisations also appear.

The nucleus of the diagonal band (figs. 9, 10, 11) appears just rostral to the anterior and the anterior pallial commissures and lies ventro-medially in the septum. The cells of this nucleus, which are interposed in the course of the diagonal band, are more densely packed than the cells elsewhere in the septum. Medially it lies close to the pia, whilst laterally it is related to the medial forebrain bundle. Placed as it is, in close relation to the commissures, this nucleus is moulded by them so as to present a caudal concavity which lodges them. At its caudal extremity the nucleus of the diagonal band is related to the nucleus preopticus (fig. 11), whilst ventrally some of its cells sweep laterally and ventrally round the basal aspect of the hemisphere ventral to the medial forebrain bundle. This latter feature is not so well marked in *Sphenodon* as Johnston (1915) figures it for *Cistudo*. He also considers the cells of this nucleus to be amongst the smallest in the forebrain of that turtle, but this is not so in *Sphenodon*.

There remain now the supra- and post-foraminal regions of the septum. The cells of the pre-foraminal part of the septum continue back over the foramen but, as the nucleus of the posterior pallial commissure appears and increases in size, they soon come to form an insignificant portion of the pars fimbrialis septi. This latter nucleus consists of densely packed small cells massed round the ventro-lateral aspect of the fibre bundle running towards the posterior pallial commissure (figs. 11, 12). The caudal limit of the nucleus coincides with the sudden thinning of the hemisphere wall shown in fig. 13.

Accompanying the commissures across the mid-line are cells, which may be considered as uniting the septa of the two sides. Such cells are, however, not numerous.

THE STRIO-AMYGDALOID COMPLEX

The strio-amygdaloid complex comprises, in general, the ventro-lateral segment of the hemisphere and, in a section such as that depicted in fig. 6, forms a very considerable portion of the whole brain. Dorsally it projects into the ventricle to form what Elliot Smith (1919) has called the hypopallial eminence, and Johnston (1915) the dorsal ventricular ridge. Ventrally this segment comes to the surface of the hemisphere, and stretches from the endorhinal fissure laterally to the region of the septum on the medial aspect.

The hypopallial eminence is an elongated, somewhat fusiform swelling, of greatest proportions about its middle and tapering towards its extremities. It is bounded dorso-laterally and ventro-medially by ventricular sulci to which Cairney (1926 *b*) gave the names angulus dorso-lateralis and infra-hypopallial sulcus (fig. 8). Of these, the latter does not extend the whole length of the hypopallial eminence, but falls short both rostrally and caudally (figs. 5, 12). Certain variable ventricular sulci may disturb the contour of the hypopallial eminence, and one such sulcus is seen on the dorsal aspect of the eminence in figs. 4 and 5. There is, however, on the medial aspect a constant depression shown, for example, in fig. 6; this sulcus has been noted and figured by Elliot Smith (1919). Cairney (1926 *b*) considered that this depression might lodge the projecting portion of the septum on the opposite wall of the ventricle.

The whole strio-amygdaloid complex in *Sphenodon* is not so clearly divisible into separate cell masses as in either the turtle (Johnston, 1915) or the alligator (Crosby, 1917). Certain nuclear masses are, however, definable, and to these a brief reference will be made before giving the detailed description.

Dorsally and medially, i.e. on the ventricular aspect of the hypopallial eminence, the complex is roofed by a cortex-like layer of cells, named by Elliot Smith the hypopallium. This is clearly seen, for example, in fig. 6, where it is separated from the underlying cell mass by a cell-free zone. The main mass of the complex, i.e. the palaeostriatum, presents a fairly homogeneous texture in sections such as those depicted in figs. 6 and 7. Adopting the usage of Herrick (1926), that portion lying ventrally about the angulus ventralis will be described as olfacto-striatum, and the portion passing up towards the hypopallial eminence as the somatic striatum. Cairney (1926 *b*) was unable from the cell preparations at his disposal to draw any hard and fast line between these two areas, but he considered from his study of fibre preparations that they could fairly be described separately in *Sphenodon*. In the material at my disposal, certain additional features are evident, and from cell preparations alone it is possible to separate the two nuclei.

Under the heading, palaeostriatal cortex, will be mentioned certain nuclear masses which form a ventro-lateral cortical cap to the palaeostriatum. The two chief masses so related are the tuberculum olfactorium and the nucleus of the lateral olfactory tract (fig. 5). In the caudal part of the hemisphere the nucleus of the diagonal band and the amygdaloid nuclei also bear a similar relationship, as shown in figs. 10 and 15.

The two amygdaloid nuclei lie in the caudal pole of the hemisphere. The anterior one is of considerable size, and is placed immediately lateral to the forebrain bundles (fig. 12). The medial nucleus, much less well defined, lies lateral to the temporal horn of the ventricle, and dorso-medial to the anterior nucleus (fig. 12).

The branches of the lateral striate artery bear a quite striking relationship to the cell masses in this region, a feature which has been pointed out by Elliot Smith (1919). Throughout the major portion of the hemisphere, these vessels enter the brain at the endorhinal fissure, which is generally quite recognisable, and run dorsally and medially, sharply marking off the somatic striatum from the acellular zone immediately underlying the hypopallium (fig. 8). Towards the poles of the hemisphere this arrangement is not seen, for rostrally the branches are not in evidence at all, while caudally they run, not dorsal to the somatic striatum, but quite definitely through its midst (fig. 10). In these two regions also the somatic striatum has lost its clearly defined dorsal border, and become more diffuse; it would certainly appear, therefore, that these arteries have some influence on cell grouping in the intervening portion of the hemisphere. The various components of the strio-amygdaloid complex may now be discussed in a little more detail.

Hypopallium

This cortex-like sheet is, at the present day, being considered in two parts; an anterior part whose dominant feature is its relationship with the general cortex, and a posterior part more intimately concerned with the pyriform cortex and the amygdala. The fissure which divides these parts in some forms (fissura neo-archistriatica of Kappers, 1921) is not evident in *Sphenodon*, but the connection of the posterior part with the pyriform cortex and of the anterior part with the general cortex, which has been previously noted in *Sphenodon*, is very evident in all my series, and has been referred to above in the descriptions of the individual cortical areas. Those who have concerned themselves primarily with fibre connections, e.g. Dart (1920) and Cairney (1926 *b*), agree to such a division, and Herrick (1926) presents the same view. Dart's nomenclature will, therefore, be adopted for these two divisions of the hypopallium, viz. hypopallium anterius and hypopallium posterius.

Apart from the relationship of the hypopallium to the cortical fields, there is no precise line of demarcation between hypopallium anterius and hypopallium posterius but, in the more rostral and caudal parts of the hemisphere, quite clear differences in cell arrangement can be distinguished (compare figs. 3 and 12).

The whole hypopallium may be considered as forming in transverse section a somewhat L-shaped sheet of cells, with one limb lying horizontally and meeting a cortical field laterally, and the other placed more or less vertically (fig. 5). The horizontal limb is a better-defined layer than the vertical, but together they form throughout the major portion of the hemisphere a distinctly more compact column of cells than does either the general or the pyriform cortex. This generalisation does not hold, however, at the rostral and caudal limits of the sheet.

The cells comprising the hypopallium are, if anything, slightly smaller than those of the cortical fields.

The hypopallium anterius shows its typical appearance in fig. 3 where laterally, round the angulus dorso-lateralis, it becomes continuous with the general cortex. The horizontal part is separated from the ependyma by a slight interval, and scattering of cells from it is negligible; the vertical part, on the contrary, generally lies closely apposed to the ependyma, and scattering of cells is quite obvious as well as some fragmentation of the whole column. The ventral extremity of the vertical column is rather diffuse and ill defined.

This appearance persists throughout the anterior part of the hemisphere till the region of the peduncular base is reached. Here the hypopallium rapidly diminishes (figs. 1 and 2), and the vertical column becomes more fragmented and further removed from the ependyma until the whole hypopallium anterius is represented by an irregular mass of cells arranged in several clumps.

The hypopallium posterius in its rostral part presents features identical with those described for the adjacent region of the hypopallium anterius, except, of course, that laterally it meets the pyriform cortex round the angulus dorso-lateralis. When traced caudally, fragmentation of the sheet of cells appears and gradually increases. This change is first evident in the vertical portion, but ultimately the whole mass consists of more or less isolated clumps of cells (figs. 10–12). With the appearance of the infra-hypopallial sulcus the vertical portion is given a somewhat C-shaped outline in transverse section (figs. 6–9) and its ventral extremity constantly ends at the deepest part of the sulcus. The hypopallium posterius is further removed from the ependyma than the hypopallium anterius, and the interval gradually increases as sections are traced caudally. In the most caudal, as in the most rostral sections the whole hypopallial sheet, both horizontal and vertical portions, is massed into one irregular clump (fig. 13).

The palaeostriatum

The palaeostriatum forms a large and distinctive mass of cells almost completely occupying the ventro-lateral portion of the hemisphere (fig. 6). Medially it extends round the angulus ventralis to abut on the septum;

dorsally it is in general separated from the hypopallium by a cell-free zone and by branches of the lateral striate artery; ventrally and laterally it reaches the pia. It retains connection with the pyriform cortex by means of the nucleus of the lateral olfactory tract. These features are shown in figs. 5 and 6.

In other forms cell size and grouping have been of much assistance in determining the subdivision of this area into separate nuclear masses; but in *Sphenodon* no such clear subdivision exists as is figured, for example, in the brains of the alligator (Crosby, 1917) and the turtle (Johnston, 1915). Indeed Dart (1920) considers that the alligator and the turtle exhibit unusual features of the striatal complex; I at least can agree that these forms are vastly different from *Sphenodon* in the arrangement of the cell masses, different probably in the degree of differentiation.

The following constituent parts of the palaeostriatum will now be described in more detail: palaeostriatal cortex, olfacto-striatum, somatic striatum, and the amygdaloid nuclei.

1. *The palaeostriatal cortex.* Dart (1920) has insisted on the presence in vertebrates of a cortical covering to the palaeostriatum, a covering which in reptiles, however, may be inconspicuous. In *Sphenodon* this palaeostriatal cortex is sufficiently obvious to warrant description apart from the rest of the palaeostriatum. Only in certain places do the various nuclear masses, of which it is composed, give an impression of a continuous cortical sheet.

The tuberculum olfactorium is shown in fig. 4 as a distinct layer of cells overlying the olfacto-striatum. The cells tend to be aggregated into clumps, and their staining with toluidin blue is slightly deeper than that of other parts of the palaeostriatum. Laterally the tuberculum extends out, never far removed from the pia, to meet the nucleus of the lateral olfactory tract, these two forming a quite definite cortical sheet (fig. 5). Immediately deep to this layer there is a relatively cell-free zone which further accentuates the isolation of the cortex. The cells of the nucleus of the lateral olfactory tract from their disposition are obviously lying in the midst of a fibre tract running parallel with the pia. They do not present the distinctively clumped appearance of the tuberculum, nor are they so large. Just ventral to the level of the lateral striate artery the nucleus of the lateral olfactory tract presents an enlargement (fig. 5) which is reminiscent of a similar enlargement figured by Crosby (1917) for the alligator. Dorsally the nucleus of the lateral olfactory tract is continuous with the pyriform cortex.

Further caudally the continuity of the tuberculum olfactorium and the nucleus of the lateral olfactory tract is not evident, although both are individually still quite recognisable for some distance (fig. 9). Gradually, however, both become less well organised, the tuberculum being indistinguishable from the olfacto-striatum, and the nucleus of the lateral olfactory tract failing to extend as a distinguishable entity further ventrally than the endorhinal fissure. Caudal to the level of the foramen of Monro the latter nucleus cannot be distinguished with any degree of certainty.

At a still more caudal level the nucleus of the diagonal band has a superficial relationship to the olfacto-striatum (fig. 10), and further towards the caudal pole of the hemisphere the two amygdaloid nuclei (*vide infra*) are, to some extent, disposed superficially to the somatic striatum (fig. 12).

2. *The olfacto-striatum* is most distinctive in its rostral part, fig. 5 showing a typical appearance. It is arranged about the angulus ventralis, and is capped ventrally by the tuberculum olfactorium. Its cells are massed most densely towards the ependyma; occasionally they show a radial arrangement outwards from the region of the angulus ventralis (figs. 7, 8). The portion lying medial to the angulus ventralis (the nucleus accumbens) is particularly well defined; it bulges into the ventricle between the sulcus septo-striaticus and the angulus ventralis, while dorsally it meets the small-celled portion of the septum.

The border-line between the nucleus accumbens and the septum is worthy of note. A definite cell-free zone is quite frequently present, separating these two areas (figs. 3, 4, 5), and the dorsal convex border of the olfacto-striatum may show a row of densely packed cells, which very clearly denotes the line of demarcation. In addition to these features the general arrangement of the cells in the two areas is quite different, those of the medial septal nucleus being small and discrete while the olfacto-striatum presents larger cells arranged in coarse clumps. This arrangement of the cells of the olfacto-striatum in coarse clumps is, perhaps, its most striking feature.

The segment of the brain wall between the sulcus septo-striaticus and the angulus ventralis is not completely occupied by this portion of the olfacto-striatum (the nucleus accumbens). As mentioned in connection with the septum the sulcus septo-striaticus does not lie exactly between the areas indicated, but rather indents the medial aspect of the small-celled (medial) septal component. Further, this portion of the olfacto-striatum is, to some extent, kept from contact with the pia, on the one hand by a prolongation downwards of the septal cells, and on the other hand by a tendency for the tuberculum olfactorium to spread upwards (fig. 8).

That portion of the olfacto-striatum lying lateral to the angulus ventralis is very similar in the rostral part of the hemisphere to the more medial portion. It is approximately of the same size, but does not present the same clear outline. The cells are a little less densely packed and are aggregated into smaller clumps (fig. 5). Its lateral border is ill-defined and reaches out in a scattered manner as far as the ventral limit of the hypopallium anterius. The nucleus of the lateral olfactory tract lies on its ventro-lateral aspect (fig. 4). In this latter figure it may also be seen to be separated from the somatic striatum by a relatively cell-free zone.

When the olfacto-striatum is examined in sections rostral to that shown in fig. 5, its medial portion is seen to persist in its typical form just medial to the angulus ventralis, whereas the lateral portion becomes less extensive. The whole mass indeed becomes more circumscribed as well as smaller. As the angulus ventralis flattens out and disappears the olfacto-striatum also diminishes and is finally lost. It is impossible to distinguish the olfacto-striatum from the tuberculum olfactorium in the most rostral sections.

If now the olfacto-striatum is traced caudally from the level represented by fig. 4 it is seen at first to be represented by a well-defined mass both medial and lateral to the angulus ventralis. Between it and the tuberculum olfactorium there is often recognisable a more or less cell-free zone; laterally it abuts on the somatic striatum, but here there is an area where the cells are sparse, and thus a lateral boundary is denoted (fig. 5). Gradually the two masses fuse, with no suggestion of any intervening cell-free zone (fig. 6); nevertheless a distinction between them is possible, for the olfacto-striatum retains its coarsely clumped arrangement, whilst the somatic striatum, although presenting aggregations of cells, does not in general show such coarse clumps, but rather small aggregations often arranged in a linear manner. This arrangement suggests their interposition in the course of the lateral forebrain bundle as it sweeps dorsally, and is in keeping with Cairney's (1926 *b*) findings in connection with the disposition of that bundle. At a level such as that shown in fig. 6 the cell size of the two components of the palaeostriatum affords no evidence of their different nature.

Caudally from this they may again be distinguished, for the forebrain bundles, medial and lateral, are commencing to disperse the cells and divide the whole palaeostriatum into lateral and medial components (figs. 8, 9). To some extent in these two figures the olfacto-striatum may be said to possess again the features which were typical of it at a more rostral level. The lateral part tends to run along the ependyma, but cannot be said to reach the infra-hypopallial sulcus; rather the somatic striatum and the olfacto-striatum are connected here by a band of cells, but the exact boundary is quite indistinct. Nearer the pia, however, the intervention of the lateral forebrain bundle makes the boundary line more obvious.

Towards the foramen of Monro the olfacto-striatum becomes less densely packed, the clumping of cells is by no means so evident and a tuberculum olfactorium is less readily detected. The nucleus of the diagonal band (figs. 9, 10) runs round close to the pia, medial and then ventro-medial to the olfacto-striatum. In fig. 10, in the midst of the olfacto-striatum, the medial forebrain bundle is clearly identifiable, with a few cells in its midst.

3. *Somatic striatum.* This nuclear mass does not extend so far rostrally as the olfacto-striatum, so that, in figs. 2 and 3, where the latter is readily recognisable the somatic striatum is absent as a cell mass. At this level, and rostral thereto for a short distance, the interior of the hypopallial eminence is occupied by a few scattered cells from the hypopallial cortex. In fig. 4 the rostral extremity of the somatic striatum is shown rising up into the hypopallial eminence from below. It is covered ventro-laterally by the nucleus of the lateral olfactory tract. The cells here are irregularly arranged and present a few clumps; their size is not distinctive. The presence of a relatively cell-free

zone, however, between it and the olfacto-striatum enables it to be readily separated from the latter mass. The next two figures (4 and 5) show an extension dorsally which is limited above and laterally by the branches of the lateral striate artery, but which medially and below is not very clearly defined from the hypopallium and the olfacto-striatum.

With the appearance of the lateral forebrain bundle as a definite structure (fig. 8) the somatic striatum becomes chiefly confined to the dorsal part of the hypopallial eminence. The cells, which are frequently arranged in linear groups, extend over the infra-hypopallial sulcus into the overhanging portion of the hypopallial eminence. In the region of the endorhinal fissure the somatic striatum constantly extends towards the pia (figs. 7, 8, 9), and here comes into relation with the nucleus of the lateral olfactory tract.

The area occupied by the lateral forebrain bundle is relatively acellular; what cells there are, are distinguished by their large size and light staining with toluidin blue (figs. 8, 9, 10). This feature of the somatic striatum I take to have some relationship to the lateral large-celled (lenticular) nucleus in a similar position in *Cistudo* (Johnston, 1915). It is to be noted, however, that the large-celled area of *Sphenodon* is much less extensive than the similarly placed area described by Johnston. These large cells are no longer evident at the level of the foramen of Monro. The somatic striatum here is represented by relatively few cells occupying the core of the hypopallial eminence (fig. 11).

4. *Amygdaloid nuclei.* Two amygdaloid nuclei are distinguished in *Sphenodon* and, following the nomenclature chosen by Cairney, they are designated nucleus anterior amygdalae which is also lateral and nucleus medialis amygdalae.

The *anterior amygdaloid nucleus* is a conspicuous mass composed of densely packed small cells. In front it commences at a level just rostral to the foramen of Monro and immediately lateral to the lateral forebrain bundle on which the nucleus is moulded. Fig. 11 shows the mass a short distance caudal to its commencement. The nucleus possesses considerable antero-posterior extent, reaching back to the caudal pole of the hemisphere. There is nothing in cell preparations to suggest any continuity of this nucleus with the cell masses forming either olfacto-striatum or somatic striatum; it arises as a new structure, independent of these elements. Its lateral extremity, pointed and straggling, would appear to have some continuity with the nucleus of the lateral olfactory tract which, however, at this caudal level is not at all well defined.

Cairney (1926 *b*) has made the statement that this nucleus in *Sphenodon* may be divisible into medial and lateral components. I cannot find any evidence from cell preparations in support of such a division. The core of the nucleus is densely packed with cells and stands out very clearly in many sections (fig. 12); but this appears to be no more than a central denser aggregation.

In the caudal pole of the hemisphere the nucleus gradually diminishes; it here becomes related medially and dorsally to the medial amygdaloid nucleus (fig. 13).

There are two extensions medially from the anterior amygdaloid nucleus, one dorsal and one ventral to the forebrain bundles. Of these two extensions the dorsal is the more caudal and also the better marked.

The ventral extension is carried medialwards beneath both forebrain bundles as an interstitial nucleus of the diagonal band of Broca. It establishes a slender connection with the better-marked, more medially placed nucleus of the diagonal band (fig. 11).

The dorsal extension (fig. 12) sweeps medially over both forebrain bundles to establish continuity with the nucleus preopticus and the nucleus periventricularis hypothalami. It may, therefore, be looked upon as the interstitial nucleus of the tractus amygdalo-preopticus and of the tractus amygdalo-hypothalamicus anterior, both of which it accompanies.

The *nucleus medialis amygdalae* is an ill-defined mass, but is characterised by being composed of cells which, while staining less densely than those of the anterior amygdaloid nucleus, are definitely larger; this is in keeping with Johnston's findings for *Cistudo.*

It comes into existence with the temporal horn of the ventricle to which it lies lateral; traced caudally its bulk increases, and its ventral extremity approximates to the medial aspect of the anterior amygdaloid nucleus which is now becoming less conspicuous (fig. 13). At its best this nucleus is not nearly so well defined as either the hypopallium dorsal to it or the anterior amygdaloid nucleus placed ventro-laterally. Its distinction from the hypopallium posterius is made by the characteristic densely staining clumps of smaller cells composing the latter.

Dart (1920) describes in *Sphenodon* two nuclei of virtually the same position as these. The nucleus anterior amygdalae of this description would correspond with Dart's nucleus tractus taenia, and the nucleus medialis amygdalae with his nucleus amygdalae proprius.

CENTRES OF THE TELENCEPHALON MEDIUM

This region contains two nuclear masses which are proper to it, viz. the nuclear preopticus and the nucleus supraopticus. There are, however, as will be seen in the diagrams mentioned below, other masses abutting on it; these latter are described with the regions to which they belong.

The nucleus preopticus

The nucleus preopticus consists of densely-packed small cells arranged about the recessus preopticus of the third ventricle (figs. 11, 12). Its rostral extremity lies on a plane just anterior to the foramen of Monro and slightly precedes the appearance of the recess itself. Caudally the mass merges with the nucleus periventricularis hypothalami.

The cells are most densely packed ventrally (fig. 11) where the mass is closely adjacent to the optic chiasma. A distinct appearance of lamination is also evident in the ventral half of the nucleus. Huber and Crosby (1926) considered the lamination of this nucleus in the alligator to be less marked than that in the nucleus periventricularis hypothalami. I find that in *Sphenodon* the lamination is equally well marked in both nuclei (compare figs. 11 and 12).

The relationship of the nucleus to the ependyma varies; rostrally the two are closely related but, as sections are traced caudally towards the third ventricle, a gradually increasing interval exists between them. At the level of the third ventricle the interval has become quite considerable (fig. 13).

The nuclei of the diagonal bands of the two sides are immediate dorso-lateral relations in the rostral part of the nucleus, where indeed they appear to compress it. Further caudally, beyond the limits of the nucleus of the diagonal band, the nucleus preopticus becomes more diffuse at its periphery and extends further laterally to become directly related to the medial forebrain bundle (fig. 12).

A connection with the nucleus anterior amygdalae is established by means of the interstitial nucleus accompanying the tractus amygdalo-preopticus over the dorsal aspect of the forebrain bundles (fig. 12).

The nucleus supraopticus

At the level of the foramen of Monro, and lying ventro-medial to the forebrain bundles, between them and the chiasma, is found this somewhat flattened mass of cells (figs. 12, 13). They are characterised by their large size and deep staining with toluidin blue.

Fig. 12 shows the rostral extremity of the mass which does not at this level extend laterally; further caudally a few cells stretch ventral to the forebrain bundles almost as far as the lateral limit of the lateral forebrain bundle. At its medial extremity it meets the nucleus preopticus. There is a marked difference in size between the cells of these two nuclei.

Johnston (1915) has figured a similarly named nucleus in the turtle.

CENTRES OF THE DIENCEPHALON

THE EPITHALAMUS

The *epithalamus* or *habenula* of *Sphenodon* forms a prominent projection on the dorsal aspect of the diencephalon. It contains two distinct nuclear masses, whose essential relationship to each other is rostral and caudal. In accordance with the nomenclature used in other forms, Cairney (1926 *b*) has named these masses the medial and lateral habenular nuclei, and he claimed as justification for so naming them the fact that the caudal nucleus overlapped the rostral to some extent on its lateral aspect.

I cannot verify all Cairney's findings and, therefore, cannot agree to his nomenclature. That there are two distinct nuclear masses is beyond dispute, rostral and caudal; moreover, the caudal nucleus is somewhat dorsal, for it overlaps the caudal extremity of the rostral nucleus. I fail to find any evidence of the caudal nucleus lying lateral to the rostral. These masses have, therefore, been named the rostral and caudal habenular nuclei, and correspond to Cairney's medial and lateral nuclei. Dendy's (1910) habenular nucleus is undoubtedly, as Cairney notes, only the caudal (Cairney's lateral) nucleus of *Sphenodon*. There is no evidence of the greater size of the nucleus of one side as Dendy suggested.

The *rostral habenular nucleus* throughout the major portion of its extent lies just medial to the stria medullaris (fig. 14). Its ventral boundary is frequently marked by the presence of a row of densely packed cells, beneath which there is generally a quite distinguishable cell-free zone separating the habenular from the subjacent thalamic nuclear masses. This cell-free zone also extends between the ependyma and the rostral habenular nucleus—a feature in striking contrast to the intimate relationship of the caudal habenular nucleus and the ependyma (fig. 16).

Rostrally this habenular nucleus is poorly defined, scarcely making any projection on the dorsal aspect of the diencephalon. Its caudal extremity becomes related on its dorsal aspect to the caudal habenular nucleus (fig. 16). The latter nucleus at first lies rather dorso-medial than directly dorsal to the rostral nucleus. There is some fusion of the two masses where they are contiguous. The cells of the rostral nucleus are medium-sized and loosely packed. Subdivision of the mass into various components along the lines suggested by Huber and Crosby (1926) cannot be made in *Sphenodon*.

The *caudal habenular nucleus* is composed of slightly smaller cells which stain deeply with toluidin blue. It is characterised by its close association with the ependyma, from which, indeed, it often cannot be distinguished. Like the more rostrally placed nucleus it is somewhat elongated, and instead of lying medial to the stria medullaris it is invaded by it and so broken up into numerous islands, giving the whole mass a reticulated appearance (fig. 17).

Its rostral extremity appears as a densely staining mass of cells immediately subjacent to the ependyma and dorsal to the caudal extremity of the rostral nucleus. It rapidly grows as traced caudally and produces a well-marked prominence on the dorsal aspect of the diencephalon (figs. 16, 17). To this prominence the wall of the dorsal sac is attached.

At the level of the habenular commissure (fig. 18) the two nuclei of opposite sides are fused into a crescentic mass across the mid-line. They can be traced for only a short distance caudal to the habenular commissure, and retain the characteristic reticulated appearance and close association with the ependyma to their caudal extremity.

THE THALAMUS

The detailed work of Huber and Crosby (1926) on the thalamus of the alligator has greatly facilitated the study of the cell masses in *Sphenodon*, many of the thalamic nuclei of the latter being exactly comparable with those described for the alligator.

While the major part of the thalamus of *Sphenodon* is clearly divisible into nuclei, the remainder presents a somewhat ill-defined appearance. Cairney (1926 *b*) described only those masses which were readily demonstrable in his preparations, and to the clear accounts of such nuclei as he described I have been able to add but little. A description of several other nuclei, not included in his paper, is given here. The features of the third ventricle have been sufficiently reviewed by Cairney to make any further description unnecessary.

Nucleus ovalis

This is a small clearly circumscribed mass of cells lying dorsal to the basal forebrain bundle in the caudal part of the infra-foraminal region (fig. 13). It is deeply placed, being nowhere in contact with either pia or ependyma. It is closely comparable with the similarly named mass in the alligator (Huber and Crosby, 1926).

The stria medullaris lies lateral to it, and somewhat dorsal, as it sweeps upwards. Ventrally the basal forebrain bundle is in general related, but in the rostral part of the nucleus ovalis the tractus amygdalo-hypothalamicus and its interstitial nucleus intervene between it and the basal forebrain bundle. The recessus prenuclearis bounds the mass caudally. On its medial aspect some of the most rostral cells of the nucleus dorsomedialis anterior (*v.i.*) may be detected.

The mass is, as it were, clothed by a cortex of its own cells, giving the nucleus a quite characteristic appearance in sections through all planes. The core, within this cortical covering, is composed of relatively few loosely packed cells. This appearance might be due in part at least to shrinkage, but is nevertheless sufficiently marked in all series to be quite discernible and I, therefore, consider it a feature of this cell mass.

The cells comprising the nucleus ovalis are of medium size, and take only a light stain with toluidin blue.

There may be seen in fig. 13, lying a short distance lateral and ventral to the nucleus ovalis, a few large cells. They are not apparently part of the nucleus ovalis, nor can I find any reference to a similarly placed mass in other forms. It can be traced through only a few sections, and has no obvious continuity with any other cell mass.

Nucleus dorsomedialis anterior, nucleus dorsolateralis anterior, and nucleus rotundus

These three nuclei are very closely associated and almost completely occupy the dorsal portion of the diencephalon (figs. 14, 15, 22). The nucleus rotundus lies rather caudal to the other two and is interposed between them. They lie dorsal to the plane of the recessus prenuclearis. The three masses are so closely interrelated that they may best be described together.

The whole mass may be described as being related on its dorsal aspect to the habenula, a cell-free zone intervening (fig. 16). Medially it is separated from the ependyma by the periventricular fibre system (fig. 14), but as we shall see subsequently, the nucleus dorsomedialis anterior approximates closely in one place to the ependyma. Laterally lies the stria medullaris and the dorsal part of the lateral geniculate body (fig. 14). The recessus prenuclearis is related ventrally (figs. 14, 16).

Rostral to the level of the nucleus rotundus the dorso-medial and dorsolateral nuclei lie closely side by side, meeting along an oblique line (figs. 14, 16, 21, 22). The cells of the former are small, fairly densely packed and stain deeply with toluidin blue, while those of the dorso-lateral nucleus are definitely larger, loosely packed and take a more hazy stain. Both masses diminish in size when traced rostrally, but identification is possible almost to the level of the foramen of Monro where some cells of the dorso-medial nucleus, which proceeds further rostrally than its companion nucleus, become related to the medial aspect of the nucleus ovalis (fig. 13). The extension of the dorsomedial nucleus rostrally beyond the dorso-lateral nucleus is shown clearly in horizontal sections (figs. 21, 22).

The interposition of the nucleus rotundus between the other masses profoundly modifies them. The nucleus rotundus is, as it were, pushed in between them from the caudal aspect, but it is the dorso-medial nucleus which is most distorted. The latter mass is largely excavated to accommodate the nucleus rotundus, and is also displaced medially against the ependyma so that no interval is discernible between them (figs. 15, 22). In this manner the nucleus dorsomedialis is divided into a peripheral thicker part and a central thin area. Horizontal sections, therefore, show more massive rostral and caudal portions united by a narrow isthmus (fig. 22); in transverse sections the isthmus unites dorsal and ventral portions of the nucleus (fig. 15). In the latter figure the dorso-medial nucleus is seen to extend across the whole ventral aspect of the nucleus rotundus, and then even somewhat dorsally, to meet the dorso-lateral nucleus. Thus the nucleus rotundus is surrounded on three aspects by the nucleus dorsomedialis anterior and retains contact with the dorso-lateral nucleus over a relatively small area.

The dorso-lateral nucleus is of considerably less rostro-caudal extent than the other two masses under discussion, being related to little more than the rostral half of the nucleus rotundus. In horizontal sections it presents a well-defined caudal extremity and an oblique surface towards the nucleus rotundus (fig. 22).

The caudal extremities of the nucleus rotundus and the nucleus dorsomedialis anterior are ill-defined but are, in general, related to the nucleus lentiformis thalami (fig. 22). Ventrally and caudally the dorsal peduncle of the basal forebrain bundle sweeps up towards the nucleus rotundus and the nucleus dorsolateralis anterior, which in this region are therefore somewhat irregular and relatively acellular (figs. 17, 22).

The main features of the nucleus rotundus have already been covered in the description of the dorso-medial and dorso-lateral nuclei. Its cells are intermediate in size between those of the two masses between which it is interposed, and are not packed so densely as those in the dorso-medial nucleus. In horizontal sections it presents an elongated outline, a very well-defined rostral extremity, but a rather irregular caudal one due to the entrance of fibre bundles from the dorsal peduncle (fig. 22). Cairney has clearly figured the arrangement of these fibres relative to this mass.

Some cells of the nucleus rotundus extend caudally ventral to the recessus geniculi. In this region (figs. 19, 20) the nucleus rotundus is a rather indefinite mass, and has lost the clear outline which characterised it more rostrally. It is interposed between the nucleus periventricularis hypothalami medially and the nucleus lentiformis thalami laterally.

Corpus geniculatum laterale

This elongated mass has had its position in the thalamus clearly defined by Cairney (1926 *b*), who has also stated its fibre connections. On examination of many series the most striking attribute of the whole mass is the very marked difference in its definition in fibre and in cell preparations. In Weigert sections, such as Cairney figures in his paper, the lateral geniculate body is indeed well-defined and readily divisible into its two components, dorsal and ventral. A study of cell preparations, however, shows a much less convincing picture, although certainly the same two elements may be detected.

As seen in fig. 14 the mass lies lateral to the nucleus dorsolateralis anterior and to the area triangularis, and has the optic tract lying superficially.

The dorsal component, which is connected with only the rostral part of the ventral component, is directly caudal to the nucleus ovalis and is loosely packed with cells (figs. 14, 15). Medially the cells are condensed into a compact layer, where staining with toluidin blue is deeper. This aspect abuts directly upon the nucleus dorsolateralis anterior (fig. 22). Huber and Crosby (1926) have noted this deeply staining layer in the alligator. In *Sphenodon* it is very closely associated with the laminations of the area triangularis (*v.i.*) and will again be mentioned in that connection. The area triangularis forms a conspicuous medial relation of the lateral geniculate body, particularly of its dorsal component, and separation of the two masses is not distinct (figs. 14, 15, 16). The cells of the lateral geniculate body are slightly larger than those of the area triangularis.

The ventral portion of the lateral geniculate body is considerably more elongated than the dorsal but much less distinct in cell preparations; there is a notable paucity of cells (figs. 14, 15, 16). It also lacks the condensed medial layer and has not the same continuity with the area triangularis. Cairney found in some sections evidence of a medial condensation of cells in the ventral part of the lateral geniculate body. I find such a condensation to be confined to the dorsal component.

Area ventralis anterior and area triangularis

These names are taken from Huber and Crosby's paper (1926) on the alligator to describe what would appear to be a homologous cell mass in *Sphenodon.*

The area ventralis anterior may readily be picked up just ventral to the recessus prenuclearis, where it forms a well-defined wedge-shaped mass with the apex related medially to the nucleus periventricularis hypothalami and its scattered base laterally to the lateral geniculate body (fig. 14). This portion of the area ventralis anterior is so distinctive that Huber and Crosby have specially named it the area triangularis. Here there is a very definite lamination of the cells round the lateral aspect of the recessus prenuclearis; some of this mass is in apparent continuity with the medial compact portion of the lateral geniculate body. The relationship of the area triangularis to the lateral geniculate body is just as intimate in *Sphenodon* as Huber and Crosby have figured for the alligator.

The mass extends for some distance rostral to the level of the recessus prenuclearis, lying ventral to the nucleus dorsolateralis anterior, and still further rostrally it becomes related to the nucleus ovalis. This rostral portion is a poorly organised mass of cells, but is recognisable in all series.

Caudal to the recessus preopticus the area ventralis remains for a space as a definite laminated mass, but ultimately becomes indistinguishable from the nucleus entopeduncularis.

The mass is related ventrally to the basal forebrain bundle, and in its caudal part it adopts a curved outline in conformity with it (fig. 16).

Nucleus entopeduncularis

Huber and Crosby (1926) have described an ento-peduncular nucleus occurring in the midst of the lateral forebrain bundle in the thalamus. The mass here described lies amongst the fibre bundles of the dorsal peduncle of the basal forebrain bundle. It is evident in figs. 14, 15, 16 and 17. It consists of scattered groups of cells, mostly of medium size, but with an admixture of larger cells. In cell preparations this discrete arrangement of cells in an otherwise cell-free zone serves to distinguish the dorsal from the ventral peduncle, for the latter is practically acellular.

Nucleus lentiformis thalami

This nucleus, lying caudally in the thalamus, is related chiefly to the recessus geniculi of the third ventricle but extends for some distance rostral to this level (figs. 19, 20). It slopes ventrally from before back so that in a horizontal section such as fig. 22 only the caudal part of the nucleus is shown. It lies dorso-lateral to the nucleus rotundus, forming a sloping roof-like expansion over the caudal portion of this mass (figs. 19, 20) separating it from the more dorsally placed habenula and from the posterior commissure. The tractus habenulo-peduncularis runs between the nucleus rotundus and the nucleus lentiformis and is evident in cell preparations as a clear zone. The nucleus is best defined at the level of the recessus geniculi (fig. 20), where it extends round the lateral aspect of the recessus to lie for a short distance ventral to its blind extremity where it becomes related to the nucleus rotundus. In this region the cells are more densely packed and present some lamination.

Rostrally the mass is merely a scattered row of cells extending laterally and ventrally from the region of the organon subcommissurale. The cells in this rostral part are most densely packed laterally, and form medially a loose straggling column which is closely related above to the organon.

The cells of the nucleus lentiformis are not of uniform size. There is a well-defined zone of distinctly larger cells lying in that portion of the nucleus just dorsal to the extremity of the recessus geniculi. This mass of larger cells is not marked off in any way from the general contour of the nucleus lentiformis, but is nevertheless a distinct feature in all series examined.

It is difficult to find any resemblance between this mass and the nucleus posterocentralis of Huber and Crosby (1926), which they suggest might be homologous with the nucleus lentiformis of Kappers. The latter writer (1921) figures a nucleus lentiformis thalami in sagittal section, which corresponds to the mass described here both in position and in its relations to other masses.

THE HYPOTHALAMUS

The hypothalamus of *Sphenodon* is not differentiated into separate nuclei to such an extent as Huber and Crosby (1926) have described for the alligator. Apart from the well-marked nucleus periventricularis hypothalami it presents no clearly defined nuclear masses.

The *nucleus periventricularis hypothalami* surrounds the ventral part of the third ventricle. Rostrally it is continuous with the nucleus preopticus, and caudally comes into relationship with the cells of the tectum opticum. The nuclei of the two sides form a somewhat U-shaped mass (fig. 14) which is, as a rule, most densely packed with cells ventrally. Some degree of lamination of its cells may generally be seen.

There is a definite interval separating this nucleus from the ependyma, and this interval is occupied by the peri-ventricular fibre system. The interval is widest dorsally, and a few large cells are constantly found here at the level of the recessus prenuclearis (figs. 14, 16).

The dorsal extremity of the nucleus varies in different regions. Rostrally it receives the tractus amygdalo-hypothalamicus anterior and its interstitial nucleus which have crossed dorsal to the forebrain bundles. Some part of this interstitial nucleus may be seen in fig. 13. At the level of the recessus prenuclearis the dorsal extremity of the peri-ventricular nucleus sweeps laterally, ventral to the recess and gains contact with the area triangularis (figs. 14, 16), but is apparently not continuous with it, for the cells of the latter tend to end abruptly at its medial extremity, a feature clearly indicated in fig. 16.

Caudal to the level of the recessus prenuclearis the dorsal border of the peri-ventricular nucleus extends further dorsally, and becomes related to the caudal and ventral aspects of the nucleus rotundus and the nucleus dorsomedialis anterior (figs. 15, 19, 20).

In fig. 15, and in sections adjacent to it, the dorsal extremity of the periventricular nucleus may be seen to end in a somewhat enlarged mass of cells which lies ventro-medial to the nucleus rotundus, but separated from it by an extension of the nucleus dorsomedialis anterior. The cells forming this mass are larger than those of the main portion of the peri-ventricular nucleus, further ventrally with which it is connected by some much smaller cells. That this mass forms a portion of the peri-ventricular nucleus I am not at all certain. It bears some resemblance to the area ventromedialis of the alligator (Huber and Crosby, 1926), and may quite possibly be the corresponding mass. Their area ventromedialis is also connected to the nucleus periventricularis hypothalami by a microcellular nucleus.

The lateral border of the nucleus periventricularis is indefinite; cells scatter laterally into the adjacent white matter, becoming more and more sparse towards the pia. Dorsally it is related to the area triangularis, the nucleus entopeduncularis (fig. 14) and to the basal forebrain bundle. The latter bundle, to some extent, determines the contour of the lateral aspect of the peri-ventricular nucleus (figs. 19, 20).

Amongst the cells extending laterally from this nucleus towards the pia there are no identifiable nuclear masses such as Huber and Crosby (1926) have described in the alligator.

SUMMARY

1. The cerebral cortex is composed of three clearly definable sheets, a medial hippocampal cortex, a lateral pyriform cortex, and between these the general cortex. Attention is drawn to the densely staining clump of cells which as a rule forms the lateral boundary of the general cortex. The pyriform cortex presents laterally a flattened area of marked constancy but of obscure causation. The relationship of pyriform cortex laterally to the hypopallium varies; caudally the two sheets meet at the angulus dorso-lateralis while rostrally the pyriform cortex lies superficially in the brain wall, and is separated from the ependyma by the meeting of the general cortex and the hypopallium. The brain wall shows some increase in thickness where the general cortex and the hypopallium meet.

2. The septum shows, in its pre-foraminal part, two distinct nuclear masses which have been termed nucleus septi medialis (which is also ventral) and nucleus septi lateralis (also dorsal). The lateral nucleus does not extend so far rostrally as the medial and is composed of distinctively large cells. The

sulcus septo-striaticus is claimed to lie not opposite the interval between the septum dorsally and the olfacto-striatum ventrally, but rather opposite the medial small-celled septal nucleus. Caudally in the septum other specialised masses are described, viz. the nucleus of the diagonal band and the nucleus of the posterior pallial commissure.

3. The ventro-lateral segment of the hemisphere in *Sphenodon* is not at all similar in the appearance of its cell masses to such forms as the alligator and the turtle. The hypopallium is divisible into anterior and posterior parts, the former meeting the general cortex laterally and the latter the pyriform cortex. There is no sharp line of demarcation between these two components of the hypopallium within the cell mass itself, but towards the poles of the hemisphere they present quite different appearances due to dissimilar cell grouping.

The somatic striatum and olfacto-striatum are related to the lateral and medial forebrain bundles respectively. Their distinction in cell preparations depends almost entirely on differences in cell grouping, variations in cell size being of little assistance.

A palaeostriatal cortex has been described consisting of those nuclear masses which are arranged about the ventro-lateral aspect of the palaeostriatum as a cortical covering; the tuberculum olfactorium and the nucleus of the lateral olfactory tract are the chief masses so related, though towards the caudal pole of the hemisphere the nucleus of the diagonal band and the amygdaloid nuclei have a somewhat similar relationship to the palaeostriatum.

4. Two habenular nuclei are described and named rostral and caudal. These appear without any doubt to correspond to the medial and lateral nuclei of other forms, but I fail to detect any evidence of a medio-lateral relationship between them.

5. The individual descriptions of the cell masses in the thalamus and hypothalamus are not lengthy and will not, therefore, be discussed to any extent here. The majority of them are well-defined, circumscribed masses, readily lending themselves to reproduction in the figures. Some others, less definite in form and in significance, have been tentatively discussed. In connection with these latter masses the work of Huber and Crosby (1926) on the alligator has been found most useful.

REFERENCES

CAIRNEY, JOHN (1926 *a*). "The pallial commissures in *Sphenodon punctatum*." *Anat. Rec.* vol. XXXII, p. 203.

—— (1926 *b*). "A general survey of the forebrain of *Sphenodon punctatum*." *J. Comp. Neur.* vol. XLII, p. 255.

CROSBY, ELIZABETH C. (1917). "The forebrain of *Alligator mississippiensis*." *J. Comp. Neur.* vol. XXVII, p. 325.

DART, RAYMOND A. (1920). "A contribution to the morphology of the corpus striatum." *J. Anat.* vol. LV, p. 1.

Dendy, A. (1899). "On the development of the parietal eye and adjacent organs in *Sphenodon* (*Hatteria*)." *Quart. J. Micros. Sci.* N.S. vol. xlii, p. 111.

—— (1910). "On the structure, development and morphological interpretation of the pineal organs and adjacent parts of the brain in the tuatara (*Sphenodon punctatus*)." *Phil. Trans. Roy. Soc. Lond.* Ser. B, vol. cci, p. 227.

Gisi, Julia (1907). "Das Gehirn von *Hatteria punctata*." *Zool. Jahrb.* Bd. xxv.

Herrick, C. Judson (1910). "The morphology of the forebrain in Amphibia and Reptilia." *J. Comp. Neur.* vol. xx, p. 413.

—— (1917). "The internal structure of the mid-brain and thalamus of *Necturus*." *J. Comp. Neur.* vol. xxviii, p. 215.

—— (1926). *Brains of Rats and Men.* Univ. of Chicago Press.

Hines, Marion (1923). "The development of the telencephalon in *Sphenodon punctatum*." *J. Comp. Neur.* vol. xxxv, p. 483.

Holmgren, Nils (1925). "Points of view concerning forebrain morphology in higher vertebrates." *Acta Zool.* Bd. vi, S. 413.

Huber, G. Carl and Crosby, Elizabeth C. (1926). "On thalamic and tectal nuclei and fibre paths in the brain of the American alligator." *J. Comp. Neur.* vol. xl, p. 97.

Johnston, J. B. (1913). "The morphology of the septum, hippocampus and pallial commissures in reptiles and mammals." *J. Comp. Neur.* vol. xxiii, p. 371.

—— (1915). "The cell masses in the forebrain of the turtle, *Cistudo carolina*." *J. Comp. Neur.* vol. xxv, p. 393.

Kappers, C. U. Ariens (1921). *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen*, ii, Abt. Haarlem.

Smith, G. Elliot (1902). *Descriptive and illustrated catalogue of the physiological series of comparative anatomy contained in the Museum of the Royal College of Surgeons of England*, vol. ii, second edition, p. 123.

—— (1903). "On the morphology of the cerebral commissures in the Vertebrata, with special reference to an aberrant commissure found in the forebrain of certain reptiles." *Trans. Linn. Soc. Lond.* Second Series, Zool. vol. viii, p. 455.

—— (1910). "The Arris and Gale lectures on some problems relating to the evolution of the brain." *Lancet*, Jan. 1, 15, 22.

—— (1919). "A preliminary note on the morphology of the corpus striatum and the origin of the neopallium." *J. Anat.* vol. liii, p. 271.

Wyeth, F. J. (1924). "The development and neuromery of the forebrain in *Sphenodon punctatus*." *Proc. Zool. Soc. Lond.* p. 923.

EXPLANATION OF FIGURES

The figures accompanying this paper, with the exception of the last two, represent in the order of their numbers a series of transverse sections through the forebrain from before back. Figs. 1 to 13 and 16 to 18 are drawn from sections of the same brain (G.B. 82); likewise figs. 14, 15, 19 and 20 (G.B. 64). The last two figures, 21 and 22, show horizontal sections through the thalamus (G.B. 85).

Frequent reference to the figures has been made throughout the text where an indication of the level of the section is also frequently given. For this reason legends have not been attached.

All figures have been drawn to the same degree of magnification by projection of the actual sections. Cell size is not strictly to scale, but variation in the size of cells has been indicated.

ABBREVIATIONS USED IN FIGURES

a.triang.	Area triangularis.
ang.dl.	Angulus dorsolateralis.
ang.vent.	Angulus ventralis.
art.	Branch of the lateral striate artery.
b.f.b.	Basal forebrain bundle.

c.gen.l.d.	Corpus geniculatum laterale, pars dorsalis.
c.gen.l.v.	Corpus geniculatum laterale, pars ventralis.
ch.	Optic chiasma.
com.ant.	Commissura anterior.
com.hab.	Commissura habenularum.
com.pal.ant.	Commissura pallii anterior.
com.pal.post.	Commissura pallii posterior.
f.	Foramen of Monro.
fs.hip.	Fissura hippocampi.
gen.cx.	General cortex.
hip.	Hippocampus.
hyp.a.	Hypopallium anterius.
hyp.p.	Hypopallium posterius.
l.f.b.	Lateral forebrain bundle.
m.f.b.	Medial forebrain bundle.
n.ant.amyg.	Nucleus anterior amygdalae.
n.com.p.p.	Nucleus commissurae pallii posterioris.
n.d.b.	Nucleus of the diagonal band.
n.dl.a.	Nucleus dorsolateralis anterior.
n.dm.a.	Nucleus dorsomedialis anterior.
n.entop.	Nucleus entopeduncularis.
n.hab.c.	Caudal habenular nucleus.
n.hab.r.	Rostral habenular nucleus.
n.int.	Interstitial nucleus of tractus amygdalo-preopticus and of tractus amygdalo-hypothalamicus anterior.
n.lent.th.	Nucleus lentiformis thalami.
n.med.amyg.	Nucleus medialis amygdalae.
n.oval.	Nucleus ovalis.
n.periv.hyth.	Nucleus periventricularis hypothalami.
n.preop.	Nucleus preopticus.
n.rot.	Nucleus rotundus.
n.sep.lat.	Nucleus septi lateralis.
n.sep.med.	Nucleus septi medialis.
n.supraop.	Nucleus supraopticus.
n.tr.olf.lat.	Nucleus tractus olfactorii lateralis.
org.sc.	Organon subcommissurale.
ol.str.	Olfacto-striatum.
pyr.cx.	Pyriform cortex.
rec.gen.	Recessus geniculi.
rec.preop.	Recessus preopticus.
s.endor.	Fissura endorhinalis.
s.f.d.	Sulcus fimbrio-dentatus.
s.inf.hyp.	Sulcus infrahypopallialis.
som.str.	Somatic striatum.
s.sep.str.	Sulcus septo-striaticus.
temp.horn.	Temporal horn of the lateral ventricle.
tub.olf.	Tuberculum olfactorium.
w.d.s.	Wall of dorsal sac.
x.	Flattening of pyriform cortex referred to in text.

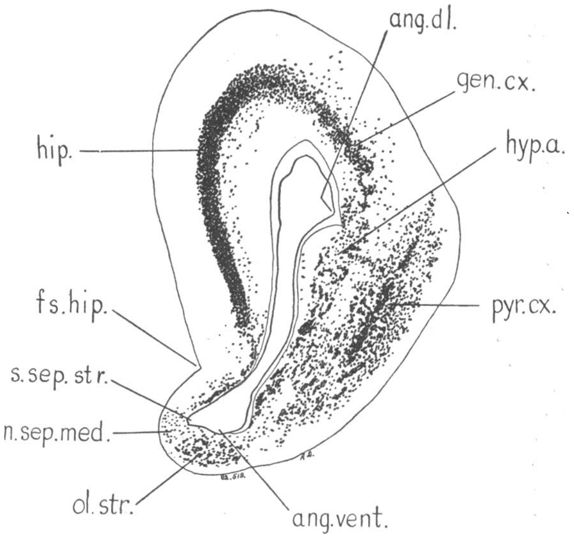
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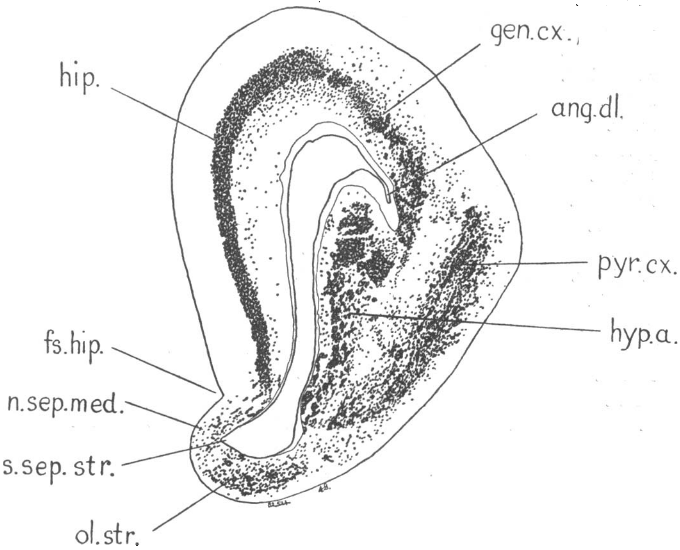
Fig. 1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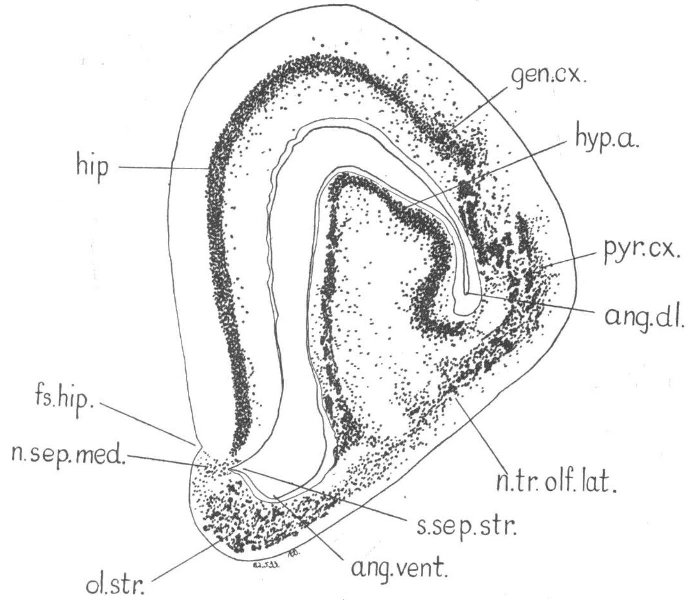
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Fig. 3

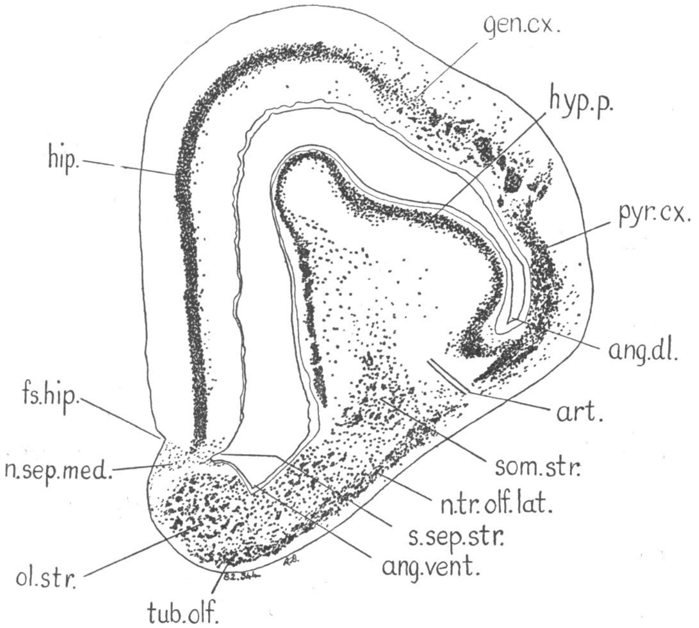
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Fig. 4

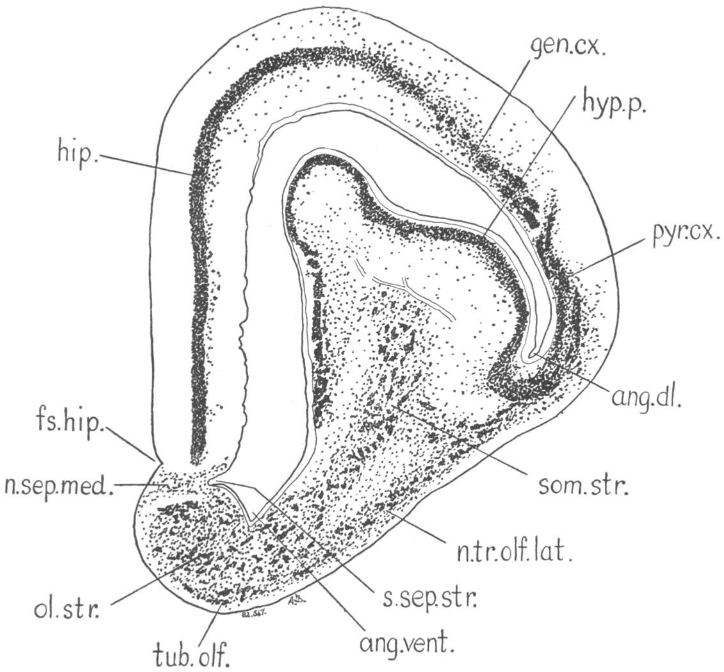
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Fig. 5

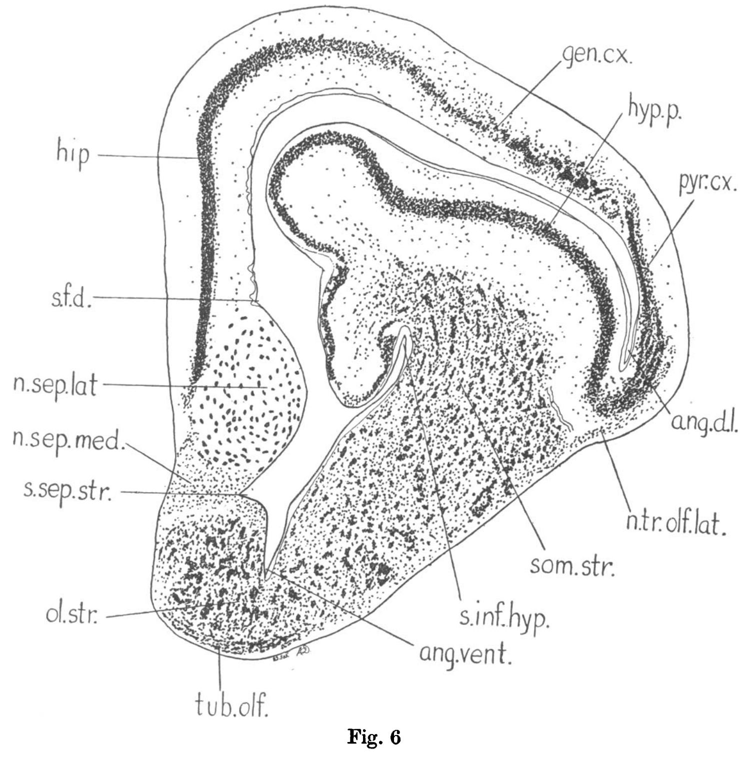
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Fig. 6

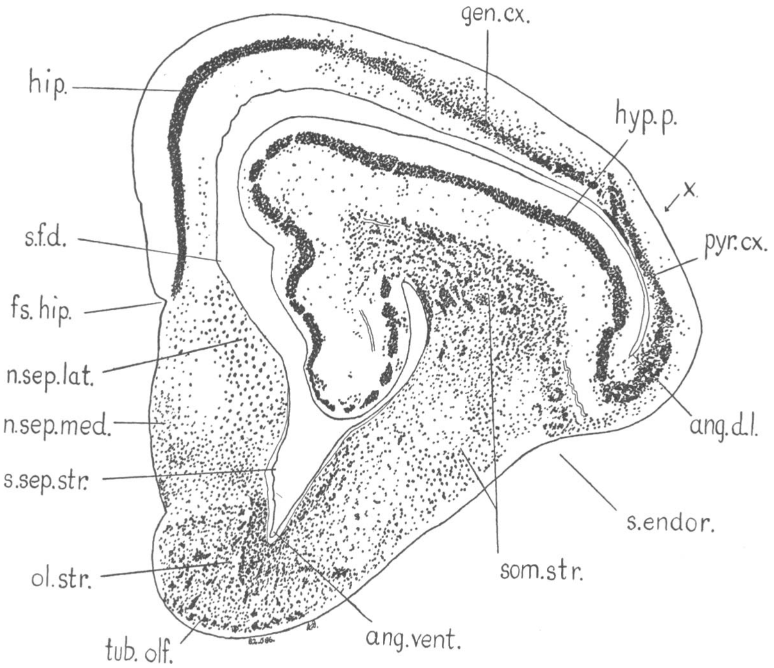
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Fig. 7

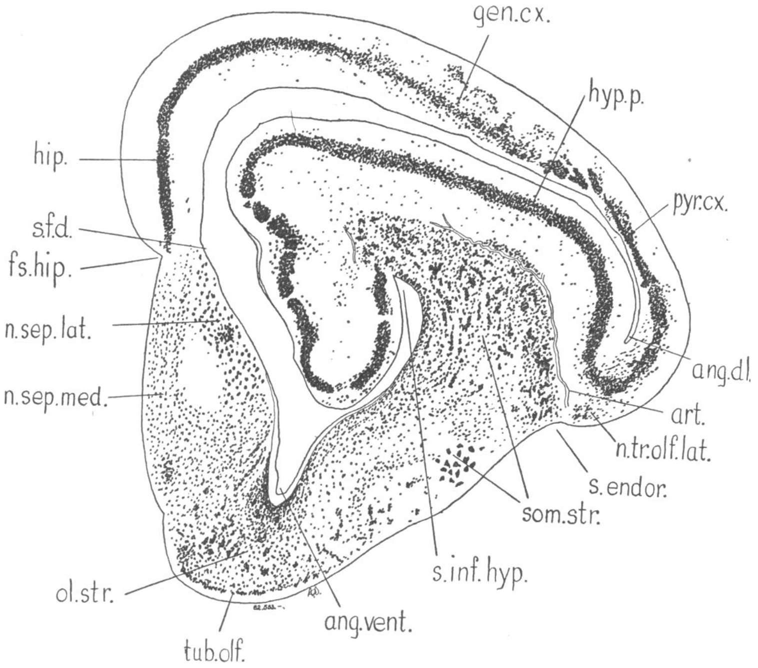
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Fig. 8

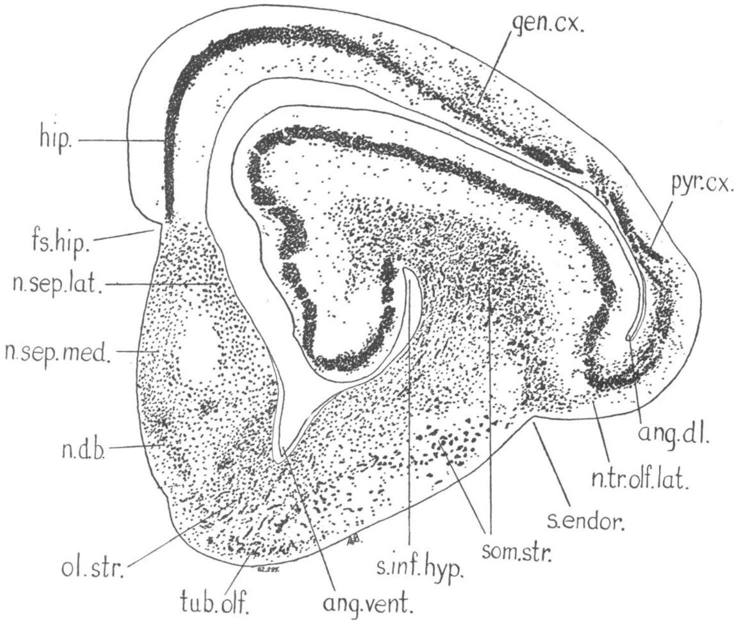
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Fig. 9

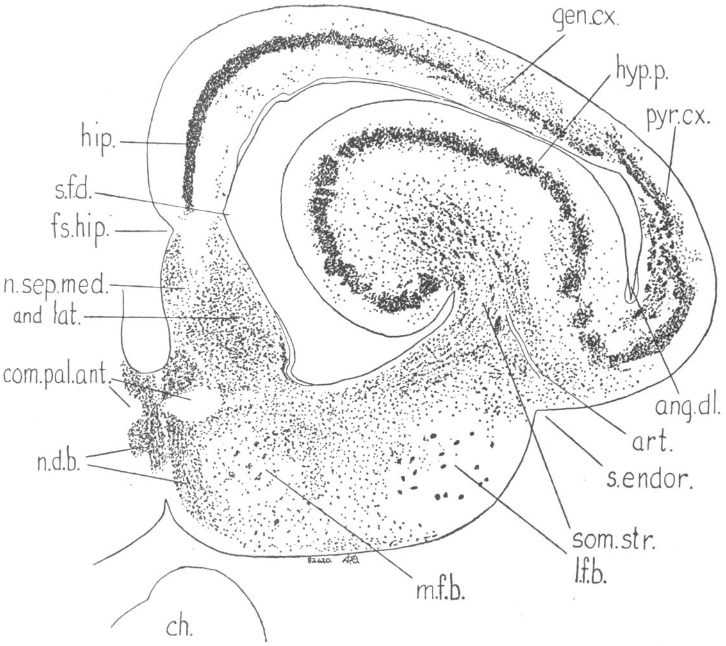
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Fig. 10

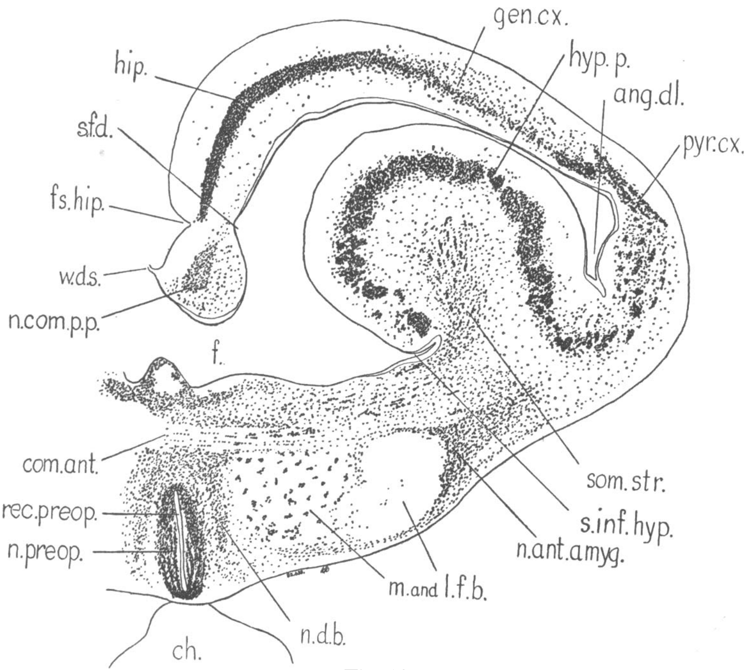
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Fig. 11

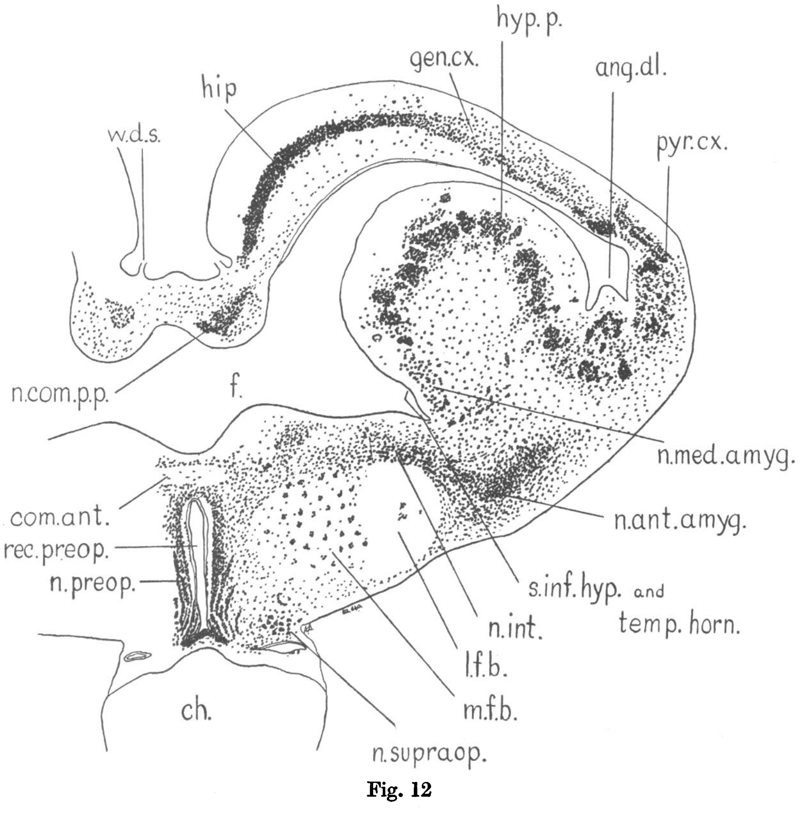
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Fig. 12

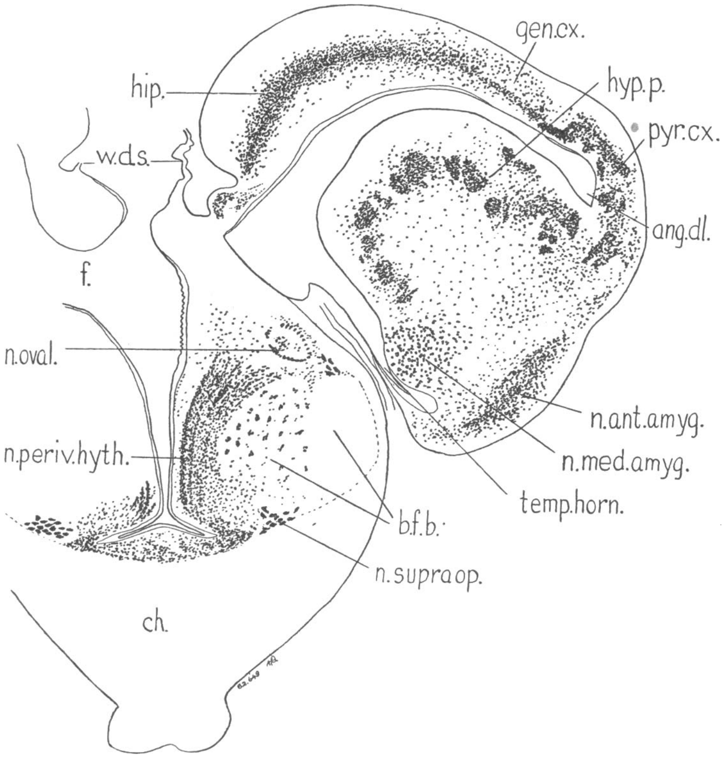
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Fig. 13

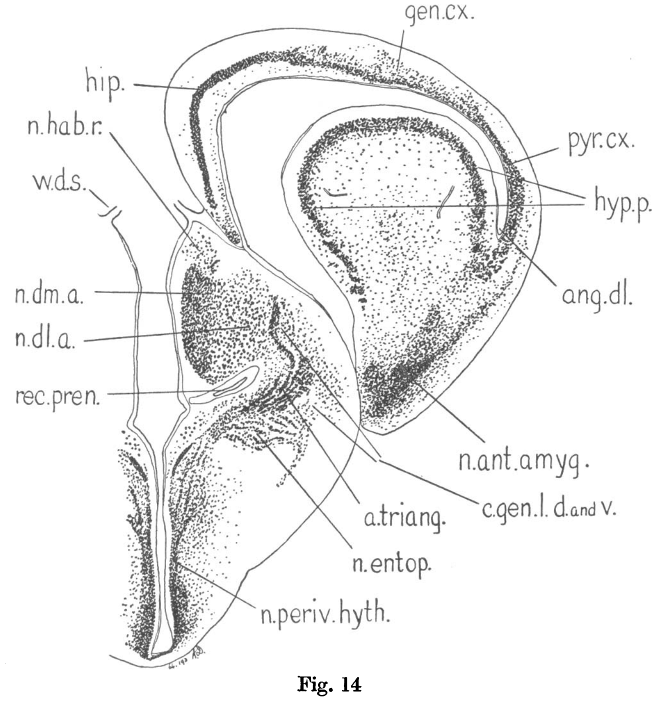
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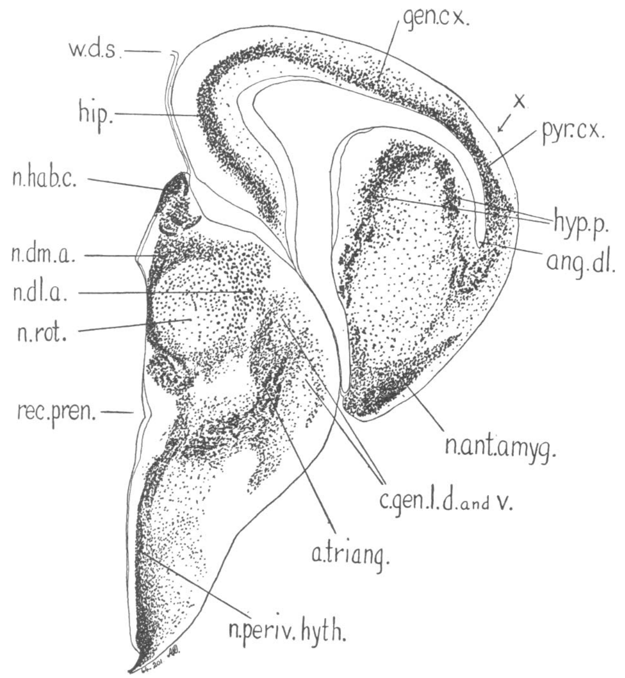
Fig. 14



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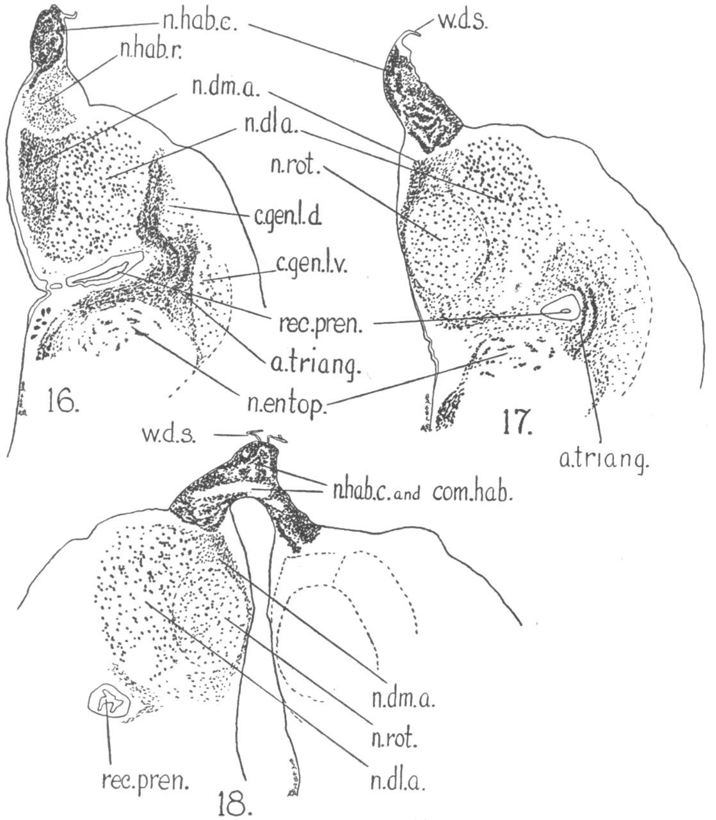
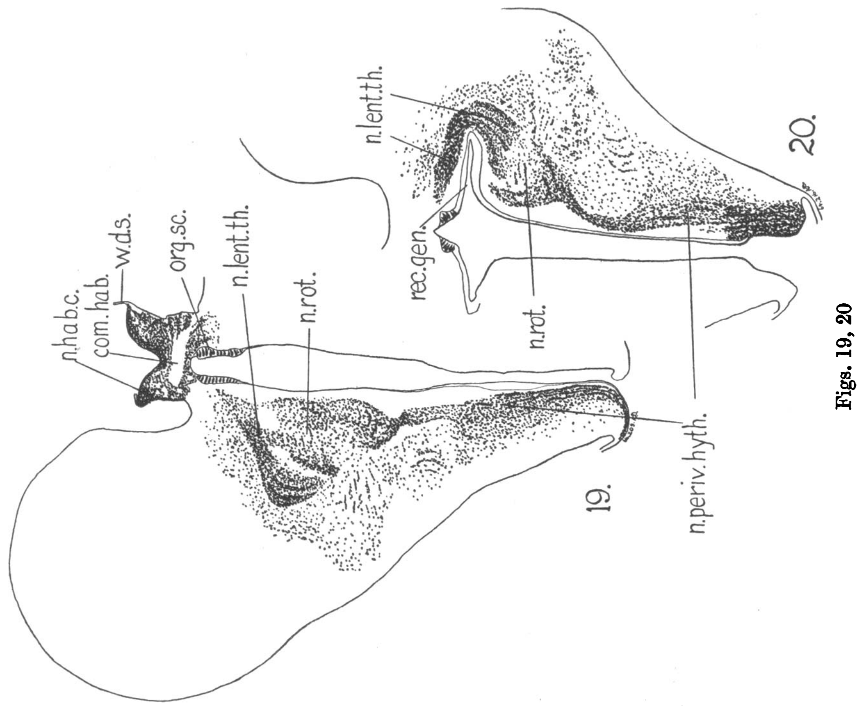
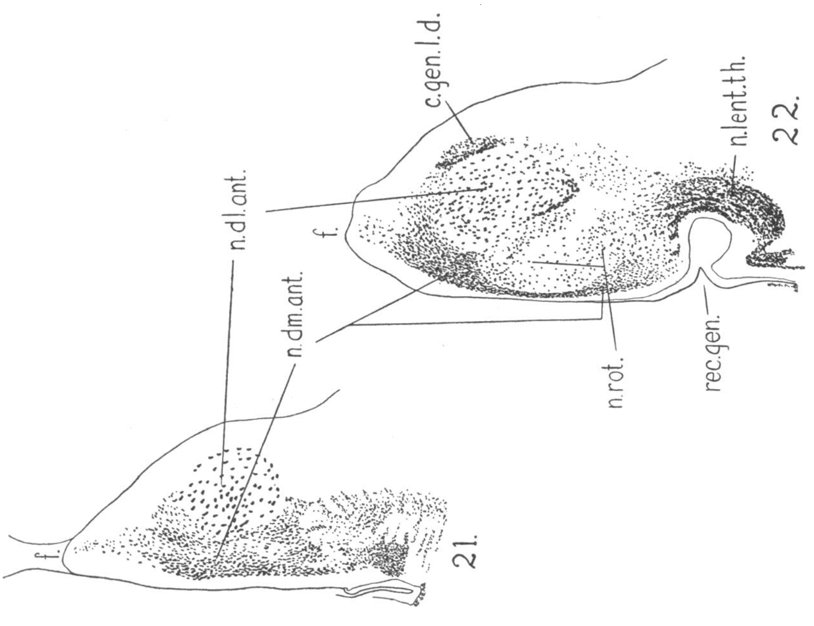


Figs. 16, 17, 18



Figs. 19, 20



Figs. 21, 22