THE NORMAL HISTOLOGY OF THE THALAMUS IN THE PHALANGER, *TRICHOSURUS VULPECULA*

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In recent years the thalamus in several orders of placental mammals has been studied, using both normal histological material and experimental methods. Knowledge of the main cytoarchitectural features and connexions of the different thalamic nuclei has been established on a firm basis, a consistent nomenclature has been developed, and a fundamental pattern has been described from which the condition in more advanced mammals, such as the higher primates, can be derived.

Of the marsupial mammals, only the relatively primitive polyprotodont, *Didelphys virginiana*, has been described in detail (Tsai, 1925; Chu, 1932*a*, *b*; Bodian, 1935, 1937, 1939, 1940). It seemed therefore desirable that an investigation of a more advanced diprotodont marsupial should be undertaken, the more so since an examination of the motor cortex and its connexions in such an animal (Goldby, 1939) had already shown important differences from the condition in the opossum. Work done on other mammals has emphasized the necessity for experimental methods if any precise information about thalamic connexions is to be obtained; such methods can be applied only on the basis of a knowledge of the normal histology of the thalamus, and it is the purpose of this paper to supply such a basis.

MATERIAL AND METHODS

The animals used were all adult specimens of the phalanger, *Trichosurus vulpecula*, and the description which follows is based principally on two complete series of sections: a transverse series cut at 40 μ and a sagittal series cut at 30 μ, both in celloidin. In both series alternate sections were stained by toluidine blue and by Weil's modification of the Weigert method. Several additional transverse series were used, cut from brains in which cortical lesions had been made about 3 months before the animal's death. The lesions were all unilateral, so that one side only was affected by them. For the most part they were cut at 40 μ in celloidin, and alternate sections mounted and stained by toluidine blue. Usually every eighth section was stained by Weil's method.

Two series were available, both transverse, cut in paraffin at 12 μ; alternate slides were stained with toluidine blue and Davenport's reduced silver method. Two other paraffin series stained with cresyl violet (transverse and sagittal) were prepared but were found to give no information which could not be obtained more readily from the thicker celloidin sections.

It is obvious that this material, though adequate for a description of the principal cell masses and fibre tracts of the thalamus, cannot give detailed information about its cytology or the connexions of its fibres. No fibre can be traced to its precise origin or termination, and in many cases it is impossible to distinguish between fibres of passage and fibres which begin or end in the region under examination. For these reasons more attention has been given to a description of the cell masses and the arrangement of fibres so far as these help to differentiate the cell masses, than to actual fibre connexions. In most cases, probably, the apparent ending of a fibre tract in a cell mass, or its intimate relationship to one, should be interpreted as an actual connexion; the evidence is of contiguity only however, and often, notably in the optic system, conclusions based on it have been found to be unreliable when tested by experimental methods. Some evidence of this kind can be found in the material used here, for most of the connexions that have been described, from similar evidence, in other primitive mammals. Because of its inconclusive nature it has not been thought necessary to report it all in detail.

In general the present material is similar to that used by most workers in this field. The results obtained should therefore be comparable with those of others; it is inevitable, however, that the personal factor should influence the decision when it is a question of what degree of differentiation is necessary before a particular mass of cells or fibres should be called a nucleus or tract and given a specific name. This is especially so with such nuclei as those of the midline, or the subdivisions of the principal nuclei. Apparently minor differences of technique, e.g. the use of thick or thin, celloidin or paraffin sections, may alter appearances considerably, and sometimes slight differences in the plane of section may have a similar effect. These difficulties must be carefully considered in making comparisons based on the examination of material of the kind used for this paper.

The classification of nuclei and the terminology which has been adopted is based mainly on the work of Clark (1932, and in other communications); some modifications have been introduced, partly for convenience of description in this particular animal, and partly to bring the work into line with that of Bodian on the opossum. In so far as the results justify phylogenetic or functional conclusions, they will be dealt with briefly in the discussion; such problems will need the more precise information which can be gained from experimental methods for their full elucidation.

GROSS ANATOMY OF THE THALAMUS

(Text-figs. 1, 2)

The thalamus of the phalanger consists of an obliquely placed ovoid mass of grey matter above and medial to the cerebral peduncle and the internal capsule, and anterior to the superior corpora quadrigemina (Text-figs. 1, 2). In general appearance it is very like that of most primitive mammals.

Its lateral surface, except where it is obscured by the internal capsule, is formed mainly by the lateral geniculate body, which overlaps posteriorly the prominent medial geniculate body. The latter has the usual relationship to the inferior brachium and to other midbrain structures. Optic tract fibres sweep over the lateral geniculate body and the posterior half of the dorsal surface of the thalamus, apparently going to the superior corpus quadrigeminum; at least the anterior part of the medial geniculate body is similarly covered. Many of these fibres are probably not of retinal origin, as Bodian (1937) has shown in the opossum. The posterior accessory optic tract (tractus peduncularis transversus) is not visible on the surface of the peduncle as in many mammals.

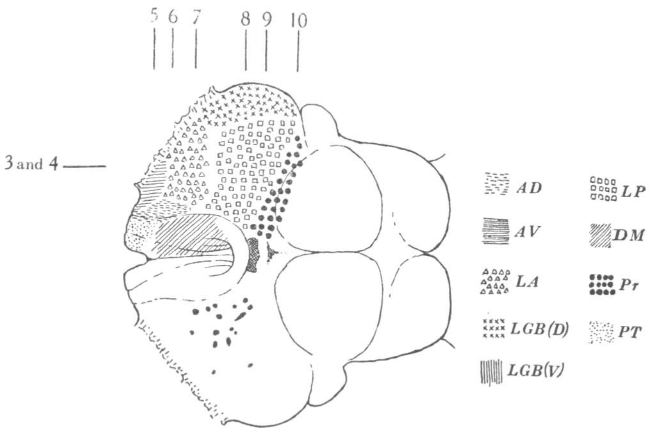


Fig. 1.

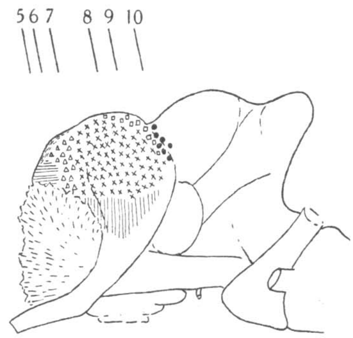


Fig. 2.

Text-fig. 1. A drawing of the dorsal aspect of the thalamus and midbrain of *Trichosurus vulpecula*, × 2·5. The lines marked 3–10 indicate the levels of the sections illustrated in the corresponding figures. In the left thalamus a number of vascular foramina are shown; in the right the position of some of the thalamic nuclei has been marked.

Text-fig. 2. A drawing of the lateral aspect of the thalamus and midbrain of *Trichosurus vulpecula*, × 2·5. The lines marked 5–10 have the same meaning as in the previous figure, and the same conventional markings have been used for the nuclei.

The dorsal aspect differs considerably from that of the opossum as illustrated by Tsai (1925). It is much broader posteriorly, an effect of the greater development of the posterior part of the lateral nuclear complex. There is a depression on this surface, not very well defined, lateral to the posterior part of the stria medullaris, which is penetrated by many fairly large blood vessels (Text-fig. 1, left side). It marks approximately the region of transition from the main anterior to the main posterior parts of the lateral complex. The pineal body is small; it lies as usual between the habenular and posterior commissures, but is scarcely raised above the surface. The rest of the epithalamus calls for no special comment.

Practically the whole of the medial surface is occupied by a large massa intermedia; the anterolateral and ventral surfaces are bounded by an external medullary lamina which has the usual relationships to the internal capsule and the subthalamus.

In Text-figs. 1 and 2 the position of some of the thalamic nuclei is shown, projected on the dorsal and lateral surfaces. The anteroventral nucleus appears smaller than it really is, since the slope of the anterior part of the thalamus causes considerable foreshortening, and in the lateral view it is partly concealed by the internal capsule.

In gross features the main difference from the opossum consists in the greater breadth of the posterior part of the thalamus, and in the slightly greater size of the lateral geniculate body. In the midbrain the superior corpus quadrigeminum is definitely larger than the inferior, while the opposite seems to be true in the opossum (Tsai, 1925). All these features suggest a greater development of structures related to the optic tract, or of the visual system in general. Although as a whole the shape is rather different, there are many resemblances to the thalamus of *Tupaia* (Clark, 1929*a*) where, however, the size of the optic tract and superior corpus quadrigeminum is relatively still greater. No pulvinar, visible on external examination, is present in the phalanger as there is in *Microcebus* (Clark, 1931).

It may be said that in external appearance the thalamus of the phalanger differs from that of the opossum in much the same way (but to a smaller degree) that the thalamus of more advanced placental mammals differs from the more primitive. This difference is largely due to growth of the posterior parts of the thalamus which are related to the visual system.

INTERNAL STRUCTURE OF THE THALAMUS

The thalamus as a whole is enclosed ventrally and laterally by an external medullary lamina, and is divided by an internal medullary lamina into a smaller dorsomedial and a larger ventrolateral part. In this description the anterior group of nuclei will be included in the ventrolateral subdivision. They are separated from the parataenial and paraventricular nuclei (dorsomedially situated) by an anterior extension of the internal medullary lamina in which is found the commissure and commissural nucleus of the anterodorsal nucleus. In higher mammals (e.g. Carnivora, Rioch, 1929; the macaque, Aronson & Papez, 1934) the internal medullary lamina and its nuclei appear to extend forwards below the whole anterior group of nuclei, separating them from the anterior part of the ventral nucleus. The close relationship between the nucleus commissuralis interanterodorsalis and the nucleus centralis lateralis was stressed by Clark (1930) for *Tarsius* and by Bodian (1939) for the opossum. The nucleus centralis lateralis is a nucleus of the internal medullary lamina, and its displacement ventral to the whole anterior group of nuclei and away from the nucleus of the anterodorsal commissure in higher mammals would appear to be secondary, perhaps a result of the relative decrease in size of the anterior nuclei and the growth forward beneath them of the ventral nucleus.

The two sides are separated in the median plane of the massa intermedia by a number of midline and commissural nuclei. These nuclei contain a network of fine medullated and non-medullated fibres connected with the internal and external medullary laminae and with the periventricular system. Some are commissural, but no predominance of transversely directed fibres was found in any part of the median plane. Commissural connexions between the two sides appear to be far less well developed in the phalanger than in the opossum (Bodian, 1940); it may be that failure in staining or silver impregnation is the reason for this finding, but such a failure was not obvious in any other parts of the sections.

Since the medullary laminae and their nuclei (including those of the midline) form a scaffolding in which the principal thalamic nuclei are set, it will be convenient for descriptive purposes to deal with them first. The nuclei are for the most part poorly defined from each other and from the principal nuclei, so that some of the differences between this and other descriptions will be of doubtful significance.

Nucleus centralis (Pl. 1, figs. 5–7)

This nucleus consists of a fairly compact mass of cells running anteroposteriorly in the massa intermedia at the level of the internal medullary lamina. It begins anteriorly (Pl. 1, fig. 5) between the parataenial and paraventricular nuclei above, and the nucleus reuniens below, and gradually disappears posteriorly about the level of the habenular commissure. It is made up of small cells, rounded or spindle-shaped, set in a dense feltwork of fine myelinated fibres mainly derived from the internal medullary lamina. This feltwork appears to receive contributions from the periventricular system both anteriorly and posteriorly.

In transverse section the nucleus is characteristically diamond-shaped (Pl. 1, fig. 7). The lateral angles extend between the dorsomedial and ventral nuclei into continuity with the paracentral nuclei, but anteriorly between the parataenial and paraventricular nuclei above and the anteromedial and anteroventral nuclei below. This anterior part of the lateral extension from the central nucleus forms the anterodorsal commissural nucleus. The dorsal angle is related to a median seam of cells which lies between the paraventricular and parataenial nuclei anteriorly and between the dorsomedial nuclei posteriorly. In this seam a number of commissural nuclei are developed. The ventral angle is related to the nucleus reuniens but is separated from it posteriorly by a fusion between the two ventral nuclei. A small collection of cells probably corresponding to Bodian's nucleus commissuralis interventralis anterior can be distinguished, but is poorly defined and variable; it hardly merits a separate name.

The rhomboid nucleus described by Bodian and other authors has been included in the central nucleus as described here, and is represented by the anterior and dorsal part of that nucleus. There seemed no adequate justification in this material for describing it separately. Commissural fibres, though present, are not conspicuous; otherwise the nucleus centralis of the phalanger does not appear to differ significantly from the same nucleus in other mammals.

The median raphe (Pl. 1, figs. 5–8)

Anteriorly, between the anterior paraventricular nuclei, there is a well-defined median seam of cells. Dorsally, near the ependyma, the cells are small, deeply stained and polygonal; ventrally they are slightly larger, paler, and spindle-shaped. These more ventral cells lie between the ventral parts of the parataenial nuclei; few if any commissural fibres could be seen among them. They are closely related to the anterior periventricular fibres.

A little posteriorly, just before the dorsomedial nuclei appear, this seam of cells becomes more extensive and less clearly defined. It blends below with the nucleus centralis and laterally with the anterior paraventricular nuclei and with some irregular clumps of small cells (Pl. 1, fig. 5) among the inferior and intermediate thalamic radiations which appear to be going mainly to the dorsomedial nucleus. These radiations are particularly abundant here and probably correspond with Rioch's anterior thalamic radiation (1931). The clumps of cells among them cannot be clearly defined from the commissural part of the anterodorsal nucleus.

Soon after the dorsomedial nuclei have appeared in a caudal direction the median seam of cells becomes inconspicuous, except for a small clump which may represent a commissural nucleus. For the most part it blends with the paraventricular nuclei to form a triangular mass of cells, dorsally situated beneath the ependyma and between the habenular nuclei (Pl. 1, fig. 8). This triangular mass is the beginning of the posterior paraventricular nucleus of most authors.

Paraventricular nuclei (Pl. 1, figs. 5–8; Pl. 2, fig. 9)

These nuclei are usually described in two parts, anterior and posterior, continuous with one another along the dorsal surface of the massa intermedia. The anterior paraventricular nuclei are well developed in the phalanger; they appear in the most anterior part of the massa intermedia as comma-shaped masses of small cells on either side of the median seam bounded laterally by the parataenial nuclei. In most descriptions the cells of the median seam have been included in the paraventricular nuclei; at least in the anterior part of the thalamus they are distinct in the phalanger. Passing backwards this distinction is practically lost at about the level of the middle of the dorsomedial nuclei. The nuclei of the two sides blend to form the triangular mass of cells already mentioned, although the cells actually in the median plane remain different from the rest, being slightly smaller and more deeply stained.

This triangular mass of cells is probably the beginning of the nucleus paraventricularis posterior described in the opossum (Bodian, 1939) and other mammals. It extends posteriorly above, below, and among the fibres of the posterior commissure (Pl. 2, fig. 9). It spreads ventrally to occupy the whole posterior border of the massa intermedia (where it blends with the medial part of the parafascicular nucleus) and laterally between the fasciculus retroflexus and the posterior commissure to reach the pretectal nucleus. It blends posteriorly with the central grey matter of the midbrain. It is continuous, below the parafascicular nucleus, with the nucleus subparafascicularis (Pl. 2, fig. 9).

Both anterior and posterior paraventricular nuclei are related intimately with the anterior and posterior parts of the periventricular fibre system. This is particularly so with the posterior nucleus, which might be described as an interstitial nucleus of that system. By this means the nuclei are probably linked with the hypothalamus and perhaps with the midbrain through the dorsal longitudinal bundle of Schütz. In addition the posterior paraventricular nucleus appears to have strong connexions with the posterior commissure. Bodian (1940) has described connexions between both nuclei and practically all the adjacent thalamic nuclei and the tectum; it is probable that similar connexions are present in the phalanger.

Nucleus paracentralis and Nucleus centralis lateralis (Pl. 1, figs. 6, 7)

The paracentral nucleus consists of cells that extend laterally from the nucleus centralis into the internal medullary lamina; they are of medium size and larger than those of the nucleus centralis. It is nowhere clearly defined from the dorsomedial nucleus above or the ventral nucleus below, and is especially diffuse posteriorly. It is coextensive with the ventral surface of the dorsomedial nucleus, giving place anteriorly to the irregular clumps of cells found between the dorsomedial and the parataenial nucleus, and to the commissural part of the anterodorsal nucleus; here it is indistinguishable from the nucleus centralis lateralis. Posteriorly it becomes more and more difficult to distinguish from the dorsomedial nucleus, and is finally replaced by the parafascicular nucleus.

In the part of the internal medullary lamina which turns dorsally towards the surface of the thalamus is found a similar group of cells (Pl. 1, fig. 6) which lacks clear definition and merges with the lateral part of the dorsomedial nucleus. This is the lateral central nucleus, and as with the paracentral it is mainly the presence of the fibres of the internal medullary lamina which serves to distinguish it from neighbouring nuclei. It disappears posteriorly in front of the upper end of the fasciculus retroflexus; anteriorly it seems to become the commissural part of the anterodorsal nucleus.

Both these nuclei are presumably connected with the fibres of the internal medullary lamina. Through it they may be brought into relationship with adjacent nuclei, the nuclei of the midline, the periventricular system and the thalamus of the opposite side. Both are penetrated by thalamic radiations, but these are probably fibres of passage on their way to or from the dorsomedial nuclei.

Nucleus reuniens (Pl. 1, figs. 5–7)

The nucleus reuniens of this description includes the nucleus subparataenialis and the nucleus reuniens anterior and posterior described by Bodian (1939) in the opossum. It corresponds therefore with the nucleus reuniens of Rioch (1929) in Carnivora and of Gurdjian (1927) in the rat. The three nuclei described by Bodian were recognizable as topographical regions, which did not seem to be differentiated clearly enough to justify description as separate nuclei.

The nucleus reuniens begins in the most anterior part of the thalamus as a mass of cells ventral to the parataenial nucleus from which it is not clearly defined; it is soon separated by the appearance of the commissural part of the anterodorsal nucleus. In this part of the thalamus it is separated from its fellow by a thin but nearly cell-free median raphe; laterally it is related to the anteromedial nucleus. Its cells are of medium size, but larger dorsolaterally than ventromedially. The dorsolateral part corresponds to Bodian's nucleus subparataenialis. Posteriorly it comes to lie between the ventral nuclei; here it is smaller, and fuses across the midline with its fellow (this fusion is already beginning in Pl. 1, fig. 5). The larger cells which it contained anteriorly gradually disappear; it loses definition and ends in a tail of small cells which runs back in the ventral border of the massa intermedia to the posterior paraventricular nucleus (Pl. 1, fig. 7).

The chief connexions of the nucleus reuniens appear to be with the anterior periventricular system among the fibres of which its cells are disposed. These fibres sweep from the dorsomedial part of the thalamus, through the nucleus parataenialis and the anterior paraventricular nucleus in the anterior border of the massa intermedia, into the nucleus reuniens. They continue ventrally to the hypothalamus, but a few of the most medial fibres pass backwards into the posterior periventricular system. The common relationship of these nuclei to the periventricular system suggests some community of function, perhaps as interstitial nuclei in the pathway between the dorsomedial nucleus and the hypothalamus. Some fibres from the inferior thalamic radiations run into the dorsolateral part of the nucleus anteriorly; these do not appear to be so abundant as the similar connexions described by Bodian (1940) in the opossum for the nucleus subparataenialis. Commissural fibres associated with the nucleus reuniens are scanty in the phalanger, but there are probably connexions with the nucleus centralis and the adjacent anteromedial and ventral nuclei.

Posteriorly the nucleus reuniens joins the paraventricular nucleus where it extends laterally ventral to the nucleus parafascicularis as far as the medial geniculate body (Pl. 2, figs. 9, 10). This lateral extension is the nucleus subparafascicularis (Bodian, 1939), and it is accompanied by a bundle of fine fibres which connect medially with the posterior paraventricular nucleus and the nucleus reuniens. This is the tractus tecto-reuniens described by Bodian (1940); in the phalanger it is not well developed and most of its fibres appear to end laterally in the posterior part of the ventral nucleus. A few can be traced to the medial geniculate body, but no other connexions could be determined from the material available. There is no well-developed interventral commissure in the phalanger, and none of the fibres of the tractus tecto-reuniens could be followed across the midline.

It seems probable that the nucleus reuniens of the phalanger is relatively a little smaller and less clearly differentiated than in the opossum, but better developed than in most mammals. From Clark's description it is not a very conspicuous feature of the thalamus either in *Tupaia* (1929*a*) or *Tarsius* (1930), but without first-hand knowledge of the material it is doubtful if these comparisons have much value. It is noteworthy that the nucleus reuniens of the macaque, as described by Aronson & Papez (1934), is very like that of the phalanger, while Walker (1938), in another account of the macaque thalamus, considered it too ill-defined to justify description as a separate nucleus.

Nucleus parafascicularis (Pl. 2, fig. 9)

This is a well-developed nucleus and is more clearly defined than any mentioned so far. It lies in the posterior part of the internal medullary lamina where it clothes the posterolateral surface of the dorsomedial nucleus. The fasciculus retroflexus divides it into two parts, medial and lateral, which are joined by a thin layer of cells on the anterior surface of the fasciculus. Posteriorly they remain distinct. Both parts lie posterior to the dorsomedial nucleus, from which they are quite clearly defined.

The cells of the nucleus as a whole are conspicuous from their deep staining; they are mostly of medium size, but those of the medial part are smaller and more closely packed than those of the lateral.

The medial part is related medially and posteriorly to the posterior paraventricular nucleus which separates it from the fibres of the posterior commissure; its boundaries are not sharp. The lateral, and much the larger part, lies posterior to the dorsomedial, paracentral and lateral central nuclei. In this region the only feature which distinguishes the paracentral and lateral central nuclei from the dorsomedial nucleus is the presence between their cells of the fibres of the internal medullary lamina. Posterodorsal to the lateral part is the pretectal nucleus; lateral to it the hinder end of nucleus lateralis B, and the ventral nucleus. Both parts lie above the subparafascicular nucleus. The lateral part extends posteriorly considerably further than the medial, but disappears from transverse sections as the fasciculus retroflexus enters the tegmentum.

The connexions of the parafascicular nucleus are mostly of a diffuse nature and difficult to define accurately in the material available. It contains a very dense feltwork of fibres of the internal medullary lamina through which it is probably connected with most or all of the adjacent nuclei. Its medial part is particularly closely associated with the posterior periventricular system, and a few of the thalamic radiations enter it ventrally and laterally. Connexions with the tectum are probably present.

No representative of the centre median nucleus of primates is present in the phalanger except the lateral part of the nucleus parafascicularis from which it is probably differentiated in higher mammals. In other respects the parafascicular nucleus of the phalanger does not show any significant peculiarities.

Nucleus subparafascicularis (Pl. 2, figs. 9, 10)

This nucleus is clearly present in the phalanger in the same form as in the opossum (Bodian, 1939). It appears anteriorly as a lateral extension of the posterior paraventricular nucleus ventral to the nucleus parafascicularis. Its cells are larger than the paraventricular cells, and fusiform in shape; they do not stain deeply. It can be followed laterally to the ventral surface of the medial geniculate body, and is accompanied by a tract of fibres, the tractus tecto-reuniens (see p. 205), most of which are non-myelinated so that it forms a conspicuous pale area in sections stained by Weigert's method. Possible homologies for this nucleus and tract have been discussed by Bodian (1939, 1940); they call for no further comment here.

THE DORSOMEDIAL SUBDIVISION OF THE THALAMUS

Nucleus parataenialis (Pl. 1, fig. 5)

This nucleus is found in the most anterior part of the thalamus ventromedial to the stria medullaris. It follows the stria medullaris posteriorly until it is replaced by the dorsomedial nucleus. It consists of medium to large cells which do not stain very deeply with toluidine blue.

The parataenial nucleus reaches ventrally in the anterior pole of the thalamus, medial to the stria medullaris, down to the anterior end of the nucleus reuniens, from which it can be distinguished only with difficulty. The apparent continuity is soon broken by the anterodorsal commissure and its nucleus. The parataenial nucleus now lies between the paraventricular nucleus medially and the stria medullaris and the anterodorsal nucleus laterally; ventrally it is separated from the nucleus reuniens and the anteromedial and anteroventral nuclei by the anterodorsal commissure. As was pointed out before, the latter seems to represent the most anterior part of the internal medullary lamina. The parataenial nucleus becomes rapidly smaller as it is traced posteriorly and ends in the dorsolateral part of the nucleus dorsomedialis.

The most obvious connexion of the parataenial nucleus in this material is with the anterior periventricular fibres (see description of nucleus reuniens).

It has few commissural fibres, but is connected with its fellow by a strand of cells above the anterior part of the nucleus centralis. Some of the inferior and perhaps of the superior thalamic radiations reach it as Bodian described in the opossum; the origin or destination of these fibres must await experimental investigation. Connexions with all adjacent nuclei are probably present.

The nucleus parataenialis of the phalanger corresponds very closely with that of the opossum (Bodian, 1939) and of other mammals. Such differences as have been observed are matters of detail and of doubtful significance.

Nucleus dorsomedialis (Pl. 1, figs. 6–8)

This nucleus is well developed and occupies most of the region dorsomedial to the internal medullary lamina, which, with the intralaminar nuclei, separates it from the ventrolateral complex. Anteriorly it is replaced by the nucleus parataenialis, and posterolaterally by the fasciculus retroflexus and the parafascicular nucleus. Dorsally it is covered by the stria medullaris and by the medial and lateral habenular nuclei, and medially the paraventricular nucleus and the seam of cells in the median plane are found. The latter is conspicuous anteriorly (Pl. 1, fig. 7), but posteriorly the two dorsomedial nuclei fuse almost indistinguishably above the nucleus centralis (Pl. 1, fig. 8).

Except posterolaterally, where Meynert's bundle and its surrounding nucleus make a precise boundary, the dorsomedial nucleus is nowhere clearly defined from adjacent nuclei. Anteriorly it blends with a tail of cells from the parataenial nucleus, but is separated from the main part of that nucleus by the irregular clumps of small cells already mentioned (see description of median raphe and Pl. 1, fig. 5). Both laterally and ventrally there is a gradual transition to the lateral central and paracentral nuclei respectively, and the same applies to the midline nuclei on the medial side. There are in fact three subdivisions of the dorsomedial nucleus, defined mainly by their relationship to the intralaminar and midline nuclei (Pl. 1, fig. 7): the principal part, dorsomedially situated and composed of medium to large cells, evenly spaced; a dorsolateral part of smaller more closely packed cells, blending with the nucleus centralis lateralis; and a ventral part of larger cells which stains more deeply, and which blends with the paracentral nucleus. The dorsolateral small-celled part is conspicuous in the slides stained by the Weigert method for the few fibres it contains. The other two parts contain a well-developed network of fine myelinated fibres.

The dorsomedial nucleus receives many of the inferior and intermediate thalamic radiations throughout its length; these, after piercing the internal medullary lamina, appear to end chiefly in the dorsomedial and ventral parts of the nucleus. It is closely related to the anterior and posterior periventricular fibres and is probably connected through the internal medullary lamina with adjacent nuclei and with the opposite side. Few if any direct commissural fibres between the two nuclei could be seen.

In general the dorsomedial nucleus shows no striking differences from the same nucleus as described in other mammals. Its subdivisions do not appear to correspond with those described by Chu (1932*a*) for the opossum, but Bodian (1939), in the same animal, does not appear to recognize any subdivisions. In its relationship to the parataenial nucleus it differs slightly from the opossum; in the latter the parataenial nucleus extends posteriorly on its medial side (Bodian, 1939) as also occurs in Carnivora (Rioch, 1929) and in the rat (Gurdjian, 1927). In this particular respect the phalanger resembles *Tupaia* (Clark, 1929*a*), but as boundaries are difficult to define in this region, no great importance can be attributed to the observation. It is perhaps more significant that the posterior boundary between the dorsomedial nucleus and the parafascicular nucleus is more precise in the phalanger than appears to be the case in the opossum (Bodian, 1939).

The most definite difference from the opossum lies in the appearance of a dorsolateral small-celled part. Topographically this part corresponds with a similar region in *Tupaia* and *Tarsius* (Clark, 1929*a*, 1930) and with the better developed dorsolateral part of the nucleus in higher primates (Clark, 1930). In the macaque, Walker (1938) describes this region as containing fewer fibres than the rest of the dorsomedial nucleus, as is the case in the phalanger. It may represent the main part of the nucleus mediodorsalis of Rioch (1929) in Carnivora, and if so is a constant element in the thalamus of all but the most primitive mammals. It is present in the armadillo (Papez, 1932, pars dorsalis of the medial nucleus), which in respect of the dorsomedial nucleus as a whole seems very similar to the phalanger. It may be added that no representative of the nuclei of the tractus habenulo-peduncularis, as described by Rioch and others in Carnivora, was found in the phalanger.

THE VENTROLATERAL SUBDIVISION OF THE THALAMUS

As was said earlier the anterior nuclei belong, at least topographically, to this part of the thalamus. They are well developed in the phalanger, and have the usual subdivisions clearly defined from each other.

Nucleus anterodorsalis (Pl. 1, figs. 5, 6)

Though the smallest of the anterior nuclei, the anterodorsal nucleus is conspicuous on account of its characteristic large, deeply staining and closely packed cells. It appears in the most anterior part of the thalamus partly among and partly lateral to the fibres of the stria medullaris. It is dorsomedial to the anteroventral nucleus and lateral to the parataenial nucleus. It runs posteriorly for a considerable distance (Text-fig. 1), always maintaining a close relationship to the stria medullaris, and ends about a third of the way towards the posterior end of the thalamus and on its dorsal surface. In its posterior part the nucleus lateralis A is ventral to it (Pl. 1, fig. 6), and it marks approximately the dorsolateral extremity of the internal medullary lamina.

A very well-marked commissural nucleus is associated with the anterior part of the anterodorsal nucleus. It consists of small fusiform cells, closely packed, lying between the parataenial nucleus (dorsomedially) and the anteroventral and anteromedial nuclei (ventrolaterally), and it joins the anterior part of the nucleus centralis (the nucleus is seen in Pl. 1, fig. 5, although continuity with the nucleus centralis is not visible in this section). It lies in what appears to be an anterior continuation of the internal medullary lamina, but instead of the network of fibres which is characteristic of the greater part of the lamina, it contains in this region fibres which run predominantly towards the median plane forming the commissure of the anterodorsal nuclei. Posteriorly this commissural nucleus passes without any defined boundary into the paracentral and lateral central nuclei.

The anteroventral and anteromedial nuclei (Pl. 1, figs. 5, 6; Text-figs. 3, 4)

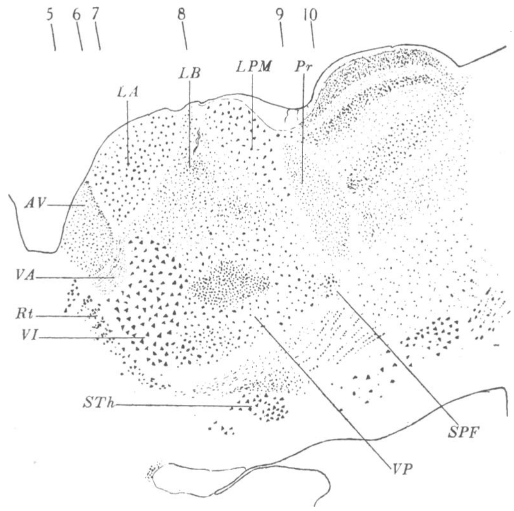
These nuclei form most of the ventrolateral subdivision of the thalamus in its anterior quarter; posteriorly they give place to the lateral and ventral nuclei.

The anteroventral nucleus is slightly the larger; it consists of cells which are smaller than those of the anteromedial nucleus, and stain less deeply. Its boundaries are very definite except where it borders on the anteromedial nucleus; it is separated from the latter posteriorly by the termination of the mammillo-thalamic tract, but elsewhere can be distinguished only by the difference in size of cell. It is related dorsomedially to the anterodorsal nucleus, until it is separated by the nucleus lateralis A (Pl. 1, fig. 6). Nucleus lateralis A also forms most of its posterior boundary (Text-fig. 3), and the anterior part of the ventral nucleus is posteromedial to it. Ventrolaterally it is related to the internal capsule and the nucleus reticularis.

The anteromedial nucleus lies between the anteroventral nucleus and the nucleus reuniens, resting on the external medullary lamina. It extends rather further posteriorly than the anteroventral nucleus, but is finally replaced by the most medial part of the ventral complex. This posterior part of the anteromedial nucleus is distinguished by the close and regular arrangement of its cells, which lie near to the midline between the nucleus centralis and the nucleus reuniens. In the transverse series these closely packed cells have the appearance of a separate nucleus, but in the sagittal series they appear as the most posterior part of the anteromedial nucleus.

The most characteristic connexion of the anterior nuclear group is the mammillo-thalamic tract, which enters from behind between the anteroventral and anteromedial nuclei. Fibres of this tract end in both nuclei, probably more in the anteroventral than in the anteromedial. None could be traced to the anterodorsal nucleus. Traced in the other direction the tract runs along the lateral border of the anteromedial nucleus until that nucleus disappears; it continues posteriorly in a depression in the most medial part of the ventral complex, finally turning down to the mamillary body. It does not pierce a part of the ventral nucleus as it does in some animals (e.g. in Carnivora, Rioch, 1929).

All three anterior nuclei receive fibres from the intermediate and superior thalamic radiations. These appear to be rather more abundant in the antero-ventral nucleus than in the others. The anterodorsal nucleus has fairly strong commissural connexions, and is probably linked to the nuclei of the midline; its very close association with the stria medullaris (some of the cells form an

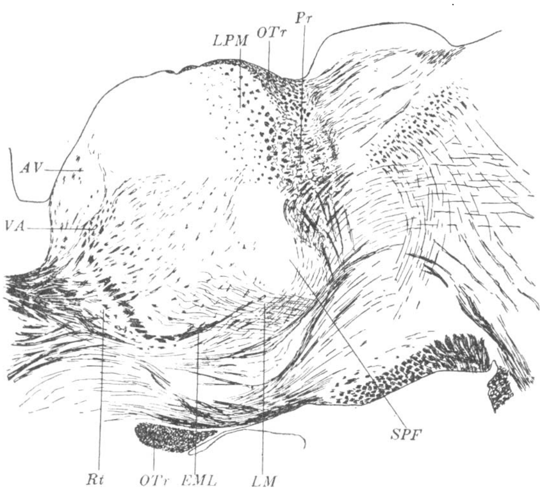


Text-fig. 3. A parasagittal section of the thalamus and midbrain of *Trichosurus vulpecula*, showing the disposition of the cell groups; ×6. Semidiagrammatic. The plane of this section is indicated in Text-fig. 1. The lines marked 5–10 have the same meaning as in the previous figures.

interstitial nucleus among its fibres) suggest a functional relationship with this system, although no conclusive evidence for this was found. The three anterior nuclei are probably connected with each other and with adjacent thalamic nuclei.

In general the anterior nuclei of the phalanger are very like those of the opossum (Bodian, 1939, 1940). As a minor difference it may be noted that the commissure of the anterodorsal nucleus is more closely related to the anterior than to the posterior part of that nucleus; also that the anteroventral and anteromedial nuclei can be differentiated on the basis of cell type in the phalanger but not in the opossum.

A similar difference in cell type between the anteroventral and antero-medial nuclei was noted by Clark (1929*b*) in *Erinaceus*, which, together with the poor development of the anterodorsal nucleus, he regarded as a primitive feature. There is, however, a considerable degree of variation in this anterior group of nuclei among mammals generally considered primitive; in the armadillo (Papez, 1932), though in most respects the thalamus is of a very generalized type, there is no distinction between the anteroventral and anteromedial nuclei, and the anterodorsal nucleus is well developed; marked variation was noted by Clark (1929*b*) among the Insectivora. For these reasons the slight differences observed between the phalanger and other primitive mammals seem of doubtful significance; one can say, however, that as a whole the anterior nuclei show none of that relative diminution in size and degree of differentiation characteristic of Carnivora and of the higher primates.



Text-fig. 4. A parasagittal section immediately adjacent to the one shown in Text-fig. 3, stained by Weil's method to show the disposition of myelinated fibres.

Nucleus lateralis (Text-figs. 3, 4; Pl. 1, figs. 6–8; Pl. 2, fig. 9)

The nucleus lateralis forms the whole dorsal surface of the thalamus between the stria medullaris medially and the lateral geniculate body laterally, except for a small area occupied by the anteroventral and anterodorsal nuclei (Text-fig. 1). Posterior to the habenular commissure its medial boundary is the pretectal nucleus which separates it from the superior corpus quadrigeminum. Laterally it is bounded by the external medullary lamina which intervenes between it and the reticular nucleus (anteriorly) and the lateral geniculate body (posteriorly). Ventrally it rests on the ventral nucleus from which it is never very clearly defined.

It presents three subdivisions, which, because they appear to correspond with the subdivisions described by Clark (1929*a*) in *Tupaia* and by Clark and others in several different mammals, have been named similarly: nucleus lateralis A and B, and nucleus lateralis posterior. It may be said at once that the subdivisions A and B have been taken to correspond with Bodian's pars intermedia in the opossum. His pars anterior seems to be present in the phalanger, where it is represented by a small collection of cells on the dorso-lateral surface of the thalamus anterior to the lateral geniculate body. These cells can be seen (though not very clearly) in Pl. 1, fig. 7. This collection of cells is very variable; sometimes it raises a small elevation on the surface, but in some specimens it is almost completely absent. The cells are slightly smaller than those of the nucleus lateralis A. There is no network of fibres among them as there is in the adjacent lateral geniculate body. They are covered superficially by fibres of the stratum zonale which constitute here the most superior of the thalamic radiations going to the hinder part of the anterodorsal nucleus. They are more or less completely separated from nucleus lateralis A by part of the external medullary lamina. The possible relationships of this group of cells will be discussed when the subdivisions of the lateral nucleus have been described.

The nucleus lateralis A first appears in a transverse series between the anterodorsal and anteroventral nuclei (Pl. 1, fig. 6). It soon replaces the latter and comes to occupy the whole region lateral to the internal medullary lamina, capped dorsomedially by the nucleus anterodorsalis (the section illustrated in Pl. 1, fig. 7, is just posterior to the anterodorsal nucleus). Its cells are of medium size, fairly widely and evenly spaced. The boundary between it and the ventral nucleus is not very definite; in the latter the cells stain rather more deeply and are embedded in a denser network of myelinated fibres. The nucleus lateralis B comes to intervene between the nucleus lateralis A and the ventral nuclei, and can be distinguished by its smaller, more numerous and more irregularly disposed cells (Text-fig. 3).

The nucleus lateralis A extends posteriorly only a little beyond the anterior margin of the lateral geniculate body. Its posterior border is difficult to define but is clearer in a sagittal than in a transverse series (Text-fig. 3). On the deep surface of nucleus lateralis A, between it and the ventral nuclei, the smaller cells of nucleus lateralis B have already appeared. They now extend to the dorsal surface of the thalamus where they form the posterior boundary of nucleus lateralis A, a region characterized by the entry of several large blood vessels.

Nucleus lateralis B is very soon displaced from the surface by the appearance of the nucleus lateralis posterior at a level a little in front of the habenular commissure. It extends posteriorly for a considerable distance, covered dorsally by the nucleus lateralis posterior, separated laterally by the external medullary lamina from the lateral geniculate body (Pl. 1, fig. 8), and medially by the internal medullary lamina from the posterior part of the dorsomedial nucleus. Ventrally it rests on the ventral nucleus from which it cannot always be distinguished. When the dorsomedial nucleus disappears from the series it comes into contact with the parafascicular nucleus (Pl. 2, fig. 9), but by this level its boundaries are so indefinite that it cannot be separated from the ventral nucleus with any confidence. Combined in this way with the ventral nucleus it can be followed posteriorly, lateral to the parafascicular and pretectal nuclei, and completely separated from the lateral geniculate body by the enlarged nucleus lateralis posterior. It is finally replaced by the nucleus suprageniculatus and the medial geniculate body.

The nucleus lateralis posterior (together with the lateral geniculate body) occupies about the posterior half of the dorsal surface of the thalamus (Text-figs. 1, 3, 4; Pl. 1, fig. 8; Pl. 2, figs. 9, 10). It extends forwards as a group of rather small cells further on the medial side than on the lateral, but the anterior boundary is not very precise. The extent of the dorsal surface is best marked by the fact that it is covered by fibres which appear to be passing from the optic tract to the tectum (Text-fig. 4). Bodian has shown that in the opossum by no means all these fibres are of retinal origin (1937). Below the surface it is penetrated by many similar fibres and also by fibres connecting the tectum with the lateral geniculate body or the cerebral cortex; these connexions cannot be determined with certainty in normal material.

The nucleus lateralis posterior shows two subdivisions, medial and lateral. The lateral subdivision, in preparations stained only for cells, cannot be distinguished from the medial part of the lateral geniculate body. It consists of medium-sized to small cells of the same type, but in sections stained by the Weigert method the dense network of fibres in the lateral geniculate body distinguishes it very clearly from the nucleus lateralis posterior. The medial subdivision consists of larger cells adjacent to the pretectal nucleus over most of its extent, but anteriorly related to the internal medullary lamina. The two subdivisions vary a little in their distinctness in different animals, but were recognized in all specimens examined; neither can be distinguished easily from the underlying nucleus lateralis B, except in Weigert preparations.

From the study of normal material no evidence was found that the fibre connexions of the nuclei of the lateral complex differ in any important respect from those described in other mammals. They clearly receive many fibres from the superior and intermediate thalamic radiations and are generally distinguishable from the ventral nuclei and the lateral geniculate body by the absence of any dense network of myelinated fibres between their cells. The relationship of the nucleus lateralis posterior to fibres of the optic system is very striking; its significance has been discussed by Bodian (1940) for the opossum, and his remarks probably apply to the phalanger.

If the small and variable group of cells which appears to correspond with Bodian's pars anterior is for the moment neglected, it is clear that the lateral nuclei of the phalanger correspond in all their main features with the description given for generalized placental mammals by Clark (1932), and in particular with the lateral nuclei of *Tupaia* (Clark, 1929*a*). They are as a whole perhaps more clearly differentiated than in *Tupaia*, and the subdivision of the nucleus lateralis posterior suggests comparison with the zones in that nucleus in *Tarsius* (Clark, 1930), although obviously there is no detailed correspondence.

In some placental mammals, e.g. the armadillo (Papez, 1932), the lateral complex is much less well developed than in the phalanger, but the same main parts are recognizable. The rat also does not seem to have advanced so far as the phalanger (Gurdjian, 1927); it may be noted that Gurdjian's nucleus ventralis pars dorsomedialis probably corresponds with the nucleus lateralis B of this description.

Following this same argument it would appear that Bodian's pars intermedia in the opossum corresponds with the nuclei laterales A and B of the phalanger, and that all parts of the lateral complex in the phalanger (with the exception of a possible representative of Bodian's pars anterior) are larger and more highly differentiated than in the opossum. This applies particularly to the nucleus lateralis posterior.

The significance of the cells which appear to correspond with Bodian's pars anterior in the opossum is doubtful. They were thought at first to belong to the lateral geniculate body; but they are in most cases separated from it by a short interval, they lack the characteristic network of fibres, and they fail to degenerate after cortical lesions which lead to almost complete degeneration of the lateral geniculate body. They may be a dorsal outlying group of cells belonging to the nucleus reticularis. They are smaller and less deeply stained than the cells typical of the nucleus reticularis, but have a very similar relationship to the thalamic radiations; they resemble, but at its dorsolateral extremity, the "nucleus reticularis medialis" of Bodian (1939). If these cells do indeed represent Bodian's pars anterior, and if the pars anterior corresponds, as he suggests (1939), with the nucleus lateralis A described in placental mammals, then the comparisons instituted above for the phalanger will need radical modification. Bodian's pars intermedia (my nucleus lateralis A and B) will presumably correspond with the nucleus lateralis B alone of *Tupaia* and other placental mammals, a very striking development for that nucleus in such primitive animals. Further evidence will be required to decide with confidence between these possibilities.

The ventral nuclei (Text-figs. 3, 4; Pl. 1, figs. 6–8; Pl. 2, fig. 9)

This complex extends throughout the whole ventral part of the thalamus from the posterior aspect of the anteroventral and anteromedial nuclei in front to the medial geniculate body and the nucleus suprageniculatus behind. Its separation from the lateral complex, never very clear, is practically non-existent in the posterior third of the thalamus.

Anteriorly the ventral complex is clearly separated from the anteroventral and anteromedial nuclei, but moulds itself into a depression between them (Pl. 1, fig. 6). This anterior boundary is accentuated by the presence of many fibres of the thalamic radiations. Dorsomedially the ventral complex is related to the internal medullary lamina and the paracentral nucleus, to the nucleus parafascicularis, and at its posterior end to the pretectal nucleus. The nucleus reuniens lies medial to the ventral complex in front, but in the posterior half of the massa intermedia the ventral nuclei are continuous across the midline below the central nucleus. Behind this fusion the posterior paraventricular nucleus forms a medial and the nucleus subparafascicularis a ventral relation. Ventrolaterally it is related to the external medullary lamina, the nucleus reticularis and the zona incerta.

The following subdivisions can be distinguished:

(i) *Anterior* (Text-figs. 3, 4; Pl. 1, fig. 6). A well-defined band of small cells immediately behind the anteroventral and anteromedial nuclei, scattered among the very numerous fibres of the thalamic radiations in this region. It has rather the appearance of an intralaminar than of a principal thalamic nucleus, but unlike the intralaminar nuclei it degenerates completely after hemi-decortication.

(ii) *Intermediate* (Text-figs. 3, 4; Pl. 1, fig. 7). This part of the ventral complex lies ventromedial to the nucleus lateralis A and lateral to the hinder part of the nucleus reuniens. It is partially separated from nucleus lateralis A by nucleus lateralis B, and is interposed between the anterior and posterior parts of the ventral complex, not very clearly defined from the latter. It is characterized by the large size and deep staining of its cells, and also by the numerous bundles of thalamic radiation which it contains (Text-fig. 4). In some sections the most medial cells of this nucleus are slightly smaller and more closely packed than in other regions, but, in normal material at least, the difference is not sufficiently marked to justify the description of a separate medial part. The difference is not evident in Pl. 1, fig. 7.

(iii) *Posterior* (Text-figs. 3, 4; Pl. 1, fig. 8; Pl. 2, fig. 9). This is the largest subdivision of the ventral complex, and is continuous (as described above) with its fellow across the midline. In general its cells are smaller than those of the intermediate part. Its principal relationships can be seen in Text-fig. 3, and Pl. 1, fig. 8. Dorsolaterally, it blends with nucleus lateralis B, and posteriorly the two nuclei cannot be separated with any confidence, although the ventral nucleus generally contains more myelinated fibres.

The posterior part of the ventral nucleus can be further divided into dorsomedial and ventrolateral regions. The former, next to the internal medullary lamina, may represent a nucleus submedius. The latter is chiefly characterized by the numerous large bundles of fibres which it contains. From a level a little in front of the habenular commissure back to the nucleus parafascicularis the two regions are separated by a well-defined condensation of cells, smaller and rather more deeply stained than in other parts of the ventral nucleus (Text-fig. 3 and Pl. 1, fig. 8). This condensation forms a core in the posterior part of the ventral nucleus, and is the most definite of all the differentiations in this part of the thalamus. It contains a particularly dense network of fibres which appears to come, partly at least, from the lemniscus systems.

Behind the nucleus parafascicularis the posterior part of the ventral nucleus extends as a very ill-defined mass of cells, more or less completely blended with nucleus lateralis B, back to the suprageniculate nucleus and the medial geniculate body (Pl. 2, fig. 9). These lie on its dorsolateral and lateral aspects respectively; the nucleus subparafascicularis is ventral to it. It is partly separated from the medial geniculate body by a layer of fibres, mainly constituted by the auditory radiations.

No important information concerning the connexions of the ventral nuclei could be obtained from this material. All parts have strong connexions with the intermediate and inferior thalamic radiations. The posterior part appears to receive the bulk of the fibres of the lemniscus systems, which enter it posteriorly, ventrally and laterally, but no analysis of these systems was possible. No lemniscus fibres were seen to enter the anterior part of the ventral nucleus. In spite of the broad fusion between the two ventral nuclei, commissural fibres are few in number.

There is obviously a fairly close correspondence between the ventral complex as a whole and the same region in the thalamus of other animals. There is no such close correspondence when the different subdivisions are considered. Before valid comparisons of a more or less detailed character can be made a more precise knowledge of the fibre connexions, and particularly of those from the lemniscus systems, is necessary. The following remarks must therefore be looked upon as provisional.

The pars anterior described by Bodian (1939) in the opossum seems to be the same as the anterior part in the phalanger. Its relationship to the anterior thalamic radiations is characteristic, and it is doubtful if a corresponding part has been described in the ventral nucleus of placental mammals. Bodian's pars medialis is represented in the phalanger by the medial region of the intermediate part, but is less clearly differentiated.

The intermediate and posterior parts in the phalanger correspond topographically with Bodian's pars principalis; this region of the thalamus appears therefore to show more intrinsic differentiation than in the opossum. The most striking feature of this differentiation is the appearance of a core of smaller, more closely packed, cells. This core resembles in some ways the pars arcuata of Carnivora (Rioch, 1929), but is less extensive; although in structure it is like the pars arcuata of primates (the posteromedial element in *Tarsius*, Clark, 1930) its situation is more anterior and it lacks the characteristic relation to the centre median nucleus. The latter is represented in the phalanger by the lateral part of the parafascicular nucleus. The difference between the pars arcuata of Carnivora and of primates was pointed out by Clark (1936). In general it seems that the ventral complex of the phalanger resembles that of the opossum more closely than that of other mammals, but that it has reached a higher level of differentiation which may in some respects parallel the differentiation of this complex in placental mammals.

Lateral geniculate body (Pl. 1, fig. 8; Pl. 2, fig. 9)

The lateral geniculate body is divided as usual into dorsal and ventral nuclei. It forms most of the lateral surface of the thalamus and is covered by optic tract fibres. On its medial side the dorsal nucleus is related anteriorly for a short distance to the nucleus lateralis A, and through the rest of its extent to nucleus lateralis posterior and nucleus lateralis B. The latter is related only to the most ventral part of its medial surface and is more or less completely separated from it by the external medullary lamina, containing in this region the optic radiations. The medial limit of the lateral geniculate body (dorsal nucleus) is clearly marked throughout by the abrupt cessation of the dense network of fibres which it contains.

The dorsal nucleus of the lateral geniculate body is characteristically laminated, the laminae being superficial and concave medially. The concavity is filled with medium-sized cells, evenly distributed for the most part, and like those of the lateral part of the nucleus lateralis posterior. Four laminae can be recognized and doubtful traces of a fifth. The outermost (first) lamina is thin. It consists of rather large deeply staining cells, sparsely scattered beneath the optic tract fibres. Except for the doubtful fifth lamina, this is the least clearly defined of the laminae. The second lamina contains mainly smaller cells and a denser network of fibres than either the first or the third; there are a few large cells like those of the first lamina. The third is the thickest and most definite; its cells resemble those of the second, but tend to be orientated at right angles to the surface. Fibres are less numerous in this lamina. The fourth lamina does not differ appreciably from the second, and the fifth is represented only by the outer cells of the non-laminated core, which tend to be arranged parallel to the other laminae in some sections (e.g. Pl. 2, fig. 9). The laminae can be recognized throughout the whole anteroposterior extent of the dorsal nucleus of the lateral geniculate body; the fourth and fifth laminae do not extend into its ventral quarter, where the first, second and third laminae are present, but fuse indistinguishably with each other. In general the lamination varies considerably in its distinctness in different sections and in different specimens.

The ventral nucleus is co-extensive with the dorsal nucleus of the lateral geniculate body. Anteriorly and posteriorly it consists of small spindle-shaped cells; in the intermediate region the cells are larger. It is always clearly separated from the dorsal nucleus by a thin layer of fibres, and, although well developed, is much smaller than the dorsal nucleus. In a transverse section through about the middle of the lateral geniculate body, the ventral nucleus has an area between one-quarter and one-third of that of the dorsal nucleus; anteriorly and posteriorly it is proportionately smaller.

The ventral nucleus of the lateral geniculate body[1] is related anteriorly to the nucleus reticularis; posteriorly it extends medially above the cerebral peduncle into the zona incerta, where it has no clear boundary; it also extends beneath the anterior part of the medial geniculate body for a short distance (Pl. 2, fig. 10). Its surface is covered by optic tract fibres. Immediately beneath the surface is a region comparatively free from fibres, but the deeper or more

[1] Recent studies have made it very doubtful whether any of the optic tract fibres have a terminal connexion with the ventral nucleus of the lateral geniculate body.

medial parts contain a dense network which spreads into the zona incerta, and are also pierced by many bundles running vertically from the optic tract to the dorsal nucleus.

So far as can be judged from normal material, the connexions of the lateral geniculate body do not differ significantly from those of most mammals; no useful purpose would be served by attempting a detailed description till they have been analysed experimentally. The most striking feature of the dorsal nucleus of the lateral geniculate body of the phalanger is its lamination. In this it differs from most generalized mammals, both placental and marsupial. The lamination resembles that described in *Tupaia* (Clark, 1929*a*), but appears to be a little more distinct. In their regular medial concavity the laminae suggest comparison with the inverted type of lateral geniculate body in the Lemuroidea, e.g. in *Microcebus* (Clark, 1931).

Medial geniculate body (Text-figs. 1, 2; Pl. 2, fig. 10)

The medial geniculate body of the phalanger corresponds in all its features so closely with the opossum (Bodian, 1939) that it hardly needs separate description. Its superficial position can be seen in Text-fig. 1. It lies posterolateral to the combined ventral nucleus and nucleus lateralis B, separated by a layer of fibres which probably consist partly of the auditory radiations, partly of corticotectal fibres. It is related dorsally to the nucleus lateralis posterior, and dorsomedially to the nucleus suprageniculatus which separates it from the pretectal nucleus.

It consists of a broad peripheral zone of medium-sized to small cells, well spaced, and best seen on the lateral and posterior surfaces. There is a central zone, not clearly defined from the peripheral, which extends anteromedially and consists of larger cells. These are more closely packed and vary somewhat in size, being smaller anteromedially than posterolaterally. The central zone contains many fibres; it receives the inferior brachium and gives rise to the auditory radiations.

As in the opossum, the ventral nucleus of the lateral geniculate body extends slightly beneath the medial geniculate body. Further caudally small fusiform cells are found in a similar position, which appear to be a lateral extension of the nucleus subparafascicularis as in the opossum (Bodian, 1939). Bodian has discussed the relationship of these cells to the ventral nucleus of the medial geniculate body described for other mammals; without a detailed comparative study it does not seem possible to come to a certain conclusion concerning their homologies in the phalanger.

Nucleus suprageniculatus (Pl. 2, fig. 10)

A small and rather poorly defined group of cells dorsomedial to the medial geniculate body, and posterior to the nucleus lateralis B. It is bounded dorsolaterally by the nucleus lateralis posterior, and dorsomedially by the pretectal nucleus from which it is separated by a layer of fibres. Its cells are of medium size; they stain deeply and are arranged in irregular clumps. Although not a well-defined structure in the phalanger, it is clear that the nucleus suprageniculatus corresponds closely with the nucleus described by the same name by most authors; e.g. Bodian, opossum (1939), Clark, *Tarsius* (1930, 1933*b*), and Rioch, Carnivora (1929).

Pretectal nucleus (Text-figs. 1–4; Pl. 2, figs. 9, 10)

The pretectal nucleus cannot be classified in either of the main subdivisions of the thalamus. It consists of a broad band of cells between thalamus and midbrain, and is well developed in the phalanger; the cells are small, closely packed, and stain weakly with toluidine blue. It is very distinct in sections stained by the Weigert method, being filled with a dense network of myelinated fibres.

Anteromedially it lies behind the dorsal end of the fasciculus retroflexus, above the parafascicular nucleus, and medial to the large-celled part of the nucleus lateralis posterior (Pl. 2, fig. 9). As it extends posterolaterally it comes to lie lateral to the posterior commissure and the posterior paraventricular nucleus; the superior corpus quadrigeminum appears on its dorsomedial side. Ventrolaterally it is separated from the medial geniculate body by the posterior end of nucleus lateralis B and the nucleus suprageniculatus (Pl. 2, fig. 10). This ventrolateral surface is marked by a lamina of fibres. Ventrally, when the parafascicular nucleus disappears, it overlies the beginning of the tegmentum, and this boundary is not clearly marked. It ends finally between the medial geniculate body and the lateral border of the superior corpus quadrigeminum. The most caudal part can be differentiated from the rest of the nucleus; its cells are slightly smaller and it contains fewer myelinated fibres. This is the pars caudalis of Bodian (1939), and, as he says, it seems more closely related to the tectum than to the thalamus.

Superficially the pretectal nucleus is traversed by dense bundles of fibres many of which come from the optic tract (Text-fig. 4); some of these have been superficial throughout their course, others have pierced the lateral geniculate body and the nucleus lateralis posterior. Among them a number of large multipolar cells can be seen in some sections. These cells are not conspicuous in every specimen, but some representative of them can always be found. They constitute the large-celled nucleus of the optic tract. The deeper parts of the pretectal nucleus are traversed by fibres which come from the external medullary lamina, through the nucleus lateralis posterior. They are probably corticotectal fibres and they enter the deeper part of the superior corpus quadrigeminum (Tsai's layer 5 in the opossum, 1925). The pretectal nucleus is probably connected with the posterior commissure, and with the medial lemniscus (unless these are fibres of passage).

The pretectal nucleus as described here corresponds very closely with that of Bodian in the opossum and with the previous descriptions of Tsai (1925) and

Chu (1932*a*), but in the phalanger a representative of the large-celled nucleus of the optic tract has been included in it. This nucleus appears to be a much less definite structure than it is in *Tupaia* (Clark, 1929*a*), but in other respects the correspondence with this animal is again close.

No nucleus posterior thalami is described here for the phalanger. This term has been used in different ways by different authors. With some (e.g. Tsai, 1925; Chu, 1932*a*) the nucleus posterior seems to represent the hinder part of nucleus lateralis B (Bodian's pars intermedia), and in Carnivora (Rioch, 1929) it is more closely related to the lateral than to any other group of nuclei. In the rat (Gurdjian, 1927) and the armadillo (Papez, 1932) it probably represents the deepest part of the pretectal nucleus described here, as it does in the macaque (Aronson & Papez, 1934). One may conclude provisionally that the nucleus posterior thalami is the deeper part of the pretectal nucleus of primitive mammals. Whether its degree of differentiation in more advanced mammals is enough to justify its description as a separate nucleus cannot be decided here.

DISCUSSION

The most obvious conclusion which can be drawn from this description of the thalamus in the phalanger is that it resembles closely the thalamus of primitive placental mammals.

The midline and intralaminar nuclei are built on essentially the same plan as in the placental mammals. Most of the differences which have been noted are in matters of detail where the personal factor before mentioned (p. 198) must have considerable importance. For example, the subdivision of the nucleus reuniens into a nucleus subparataenialis and a nucleus reuniens anterior and posterior, the presence or absence of a nucleus submedius, the separation of the rhomboid nucleus from the mass of cells that has been described here under the one name, nucleus centralis, are all differences of this type. In the absence of close collaboration between workers, with interchange of actual material, such comparative descriptions must be to some extent arbitrary. Except on a few points it is possible to conclude only that the nuclei of this group are well developed in the phalanger, as one would expect in a primitive mammal, but perhaps a little less highly differentiated than in the opossum. They unquestionably form a larger and more conspicuous feature in the thalamus than in the higher primates or in the Carnivora. Their general lack of clear differentiation from adjacent principal nuclei is in favour of Papez's suggestion (1932) that they are a residuum of the matrix from which the principal nuclei have been developed, a suggestion which is particularly applicable to the dorsomedial nucleus. Another point which may be stressed is the poor development of commissural fibres in the massa intermedia. Technical failure in staining or impregnation might account for this observation, but there seemed no reason why this should be likely. Apart from such a possibility, there is no doubt that commissural fibres are very much better developed in the opossum (Bodian, 1940) and probably in most primitive placental mammals. A lack of commissural fibres is more characteristic of higher mammals.

Concerning the dorsomedial subdivision of the thalamus, little comment is necessary beyond what has already been given in the descriptions of individual nuclei. It may be added that the comparatively large size of the parataenial nucleus is characteristic of primitive mammals; more important is the appearance of a small-celled differentiation in the dorsomedial nucleus comparable to the main part of the dorsomedial nucleus which in primates projects on to the prefrontal cortex.

The anterior nuclei present no striking peculiarities. In all their important features they resemble those of other mammals, and there is no outstanding development of one or other of the three nuclei. The relationship of the anterodorsal nucleus (and particularly its commissural part) to the internal medullary lamina and its nuclei suggests the possibility that it should be classed with the intralaminar nuclei. This is not by itself an adequate reason for modifying the usual classification, which is based on a common relationship to the mammillo-thalamic tract. It is true that in this material no fibres could be traced from the mammillo-thalamic tract to the anterodorsal nucleus, as Bodian found also in the opossum (1940); there is however evidence that such connexions exist in some placental mammals at least (Clark, 1932). Experimental methods have also demonstrated that, unlike the intralaminar nuclei, it has cortical connexions (e.g. in the cat, Clark, 1933*a*; Waller, 1938), although they may be less abundant than those of the other two anterior nuclei. Unless, therefore, further work can show some more fundamental difference between the anterodorsal nucleus on the one hand and the anteroventral and anteromedial nucleus on the other, the three must remain classified in one group. In the proportionate size of the anterior group of nuclei as a whole, and in its relationship, particularly to the ventral nuclei, the thalamus of the phalanger corresponds closely with that of primitive placental mammals.

So far the differences noted between the thalamus of the phalanger and of the opossum and other mammals have been for the most part matters of detail and of no clear significance; a few, e.g. the lack of commissural fibres, and the differentiation of the dorsomedial nucleus, have suggested a more advanced stage of development. This suggestion is confirmed by conditions found in the remaining parts of the thalamus.

The nucleus lateralis posterior, for example, is far better developed than in the opossum, the rat (Gurdjian, 1927) or the armadillo (Papez, 1932). It seems to be on the way towards the formation of a pulvinar visible to external examination, and is therefore a progressive feature. Its differentiation into medial and lateral parts is also suggestive of the more elaborate subdivisions of the pulvinar which make their appearance in higher mammals, but it would be unwise to put much reliance on this feature till it has been studied by experimental methods.

The appearance in the ventral complex of nuclei of a region which may be comparable with the pars arcuata in other mammals again suggests parallel development of a progressive kind, although in other respects there does not appear to be much resemblance between the subdivisions of the ventral complex and those in placental mammals. Obviously a more precise knowledge of fibre connexions is essential in this region.

The most definite evidence of all is to be found in the lateral geniculate body, where the laminated arrangement of the cells indicates a degree of differentiation in the visual system which is considerably higher than in any of the described primitive mammals except *Tupaia*. It seems in fact to have reached a slightly higher level than in *Tupaia*, approaching the lemuroid condition. This elaboration of the visual system is also reflected in the large relative size of the nucleus lateralis posterior and the superior corpus quadrigeminum. The pretectal region is, however, typically primitive, and it is doubtful if the appearance of a rudimentary large-celled nucleus of the optic tract has much significance.

Taking these facts together there seems to be considerable justification for saying that the thalamus of the phalanger shows marked progressive tendencies, clearly parallel to tendencies that have been more fully realized in placental mammals. The parallelism is perhaps closer to primitive members of the Order Primates than to any other group, as one might expect on functional grounds. Most of the primitive primates are nocturnal animals, with a well developed visual sense, and arboreal in habit; the phalanger is like them in all these respects.

There is in the thalamus of the phalanger a notable absence of any features which might be described as typically marsupial, and which would differentiate it from all placental mammals. There are two possible exceptions to this statement. The relationships of the nucleus lateralis pars anterior of Bodian have been discussed, and while admitting that the evidence at present available is inadequate for a firm conclusion, it seems possible that this nucleus may be a differentiation peculiar to marsupials. The same may apply to the nucleus ventralis, pars anterior, which, in its intimate relation to the anterior nuclei and to the thalamic radiations in this region, does not seem comparable to the anterior part of the ventral nucleus in placental mammals. Neither of these features can be considered very important without the confirmation of more detailed evidence. It should perhaps be added that an extensive study in a large number of marsupials might well reveal common features, not shared by placental mammals, which, seen only in one marsupial, could not be considered significant. It is likely, however, that such common features, were they observed, would be matters of detail, and would not invalidate the conclusions drawn from this and from Bodian's description: that the marsupial thalamus is essentially similar to the placental thalamus, both in fundamental structure and in the evolutionary tendencies shown by more advanced marsupials when compared with the more primitive.

SUMMARY

The thalamus of *Trichosurus vulpecula* has been described on the basis of serial sections of normal brains stained by toluidine blue, a modification of the Weigert method, and by Davenport's silver impregnation method.

In structure it is essentially similar to the thalamus of *Didelphys virginiana* (Bodian, 1939, 1940), and to that of primitive placental mammals; it shows however a number of progressive features in which it resembles rather closely the published account of *Tupaia* (Clark, 1929*a*).

These progressive features are shown most clearly in the following observations. The lateral geniculate body (dorsal nucleus) is laminated as in higher mammals. The nucleus lateralis posterior (the equivalent of the pulvinar) is large, and differentiated into medial and lateral parts. A possible representative for the "pars arcuata" has appeared in the ventral complex. There is a well-marked lateral differentiation in the dorsomedial nucleus which appears to correspond with the main part of that nucleus in the higher primates. Commissural fibres between the two sides are feebly developed. In nearly all other respects the structure is that typical of primitive mammals in general, and no undoubted marsupial specializations were observed.

The work is intended to serve as a basis for future experimental investigation.

ABBREVIATIONS USED IN FIGURES

AD Nucleus anterodorsalis.
AM Nucleus anteromedialis.
AV Nucleus anteroventralis.
C Nucleus centralis.
CL Nucleus centralis lateralis.
DM Nucleus dorsomedialis.
EML External medullary lamina.
HCo Habenular commissure.
LA Nucleus lateralis A.
LB Nucleus lateralis B.
LGBd Dorsal nucleus of lateral geniculate body.
LGBv Ventral nucleus of lateral geniculate body.
LM Lemniscus medialis.
LP Nucleus lateralis posterior.
LPL Nucleus lateralis posterior, lateral part.
LPM Nucleus lateralis posterior, medial part.
MGB Medial geniculate body.
OTr Optic tract.
PC Nucleus paracentralis.
PCo Posterior commissure.
PF Nucleus parafascicularis.
Pr Nucleus pretectalis.
PT Nucleus parataenialis.
PVA Nucleus paraventricularis anterior.
PVP Nucleus paraventricularis posterior.
R Nucleus reuniens.
Rt Nucleus reticularis.
SCQ Superior corpus quadrigeminum.
SG Nucleus suprageniculatus.
SPF Nucleus subparafascicularis.
STh Nucleus subthalamicus.
VA Nucleus ventralis, anterior part.
VI Nucleus ventralis, intermediate part.
VP Nucleus ventralis, posterior part.

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EXPLANATION OF PLATES 1 AND 2

The illustrations (figs. 5–10) in Pls. 1 and 2 are all untouched photographs of 40 μ transverse sections through the thalamus of *Trichosurus vulpecula*. They were all cut in celloidin and stained with toluidine blue. The magnification is $\times 12$. The approximate levels of the different sections are shown in Text-figs. 1 and 2.

Plate 1

Fig. 5. A section through the posterior part of the anterior group of nuclei.

Fig. 6. A section showing the most anterior parts of the lateral, ventral, and dorsomedial nuclei. It is 16 sections posterior to fig. 5.

Fig. 7. A typical section through about the middle of the dorsomedial nucleus. The intermediate part of the ventral complex is particularly well shown. It is 14 sections posterior to fig. 6.

Fig. 8. A section at the level of the habenular commissure. This section shows the condensation of cells (? pars arcuata) in the posterior part of the ventral complex.

Plate 2

Fig. 9. A section at the anterior end of the posterior commissure. It shows the structure of the lateral geniculate body particularly well.

Fig. 10. A section through the extreme hinder end of the thalamus, passing through the medial geniculate body; the nucleus subparafascicularis is scarcely visible on account of the pale staining characteristic of its cells.

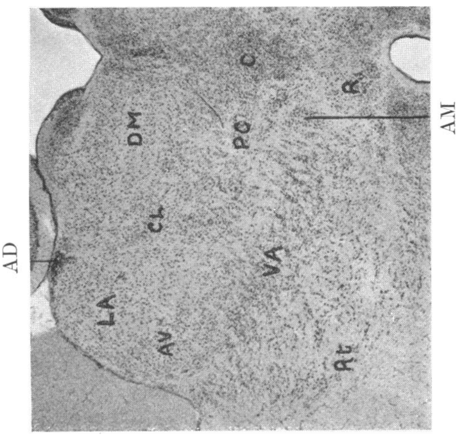

Fig. 6.

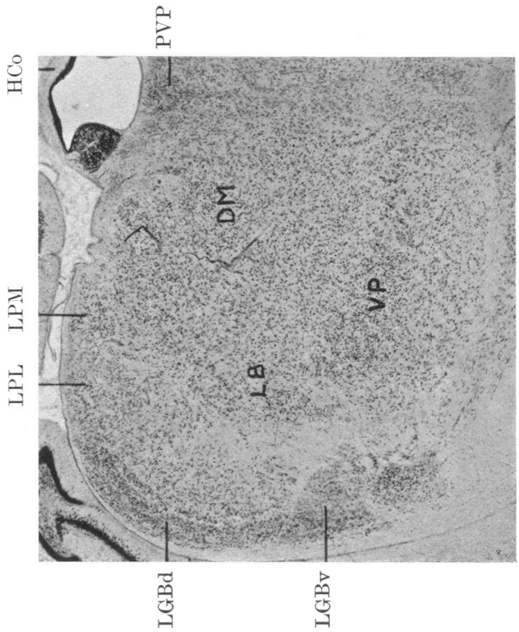

Fig. 8.

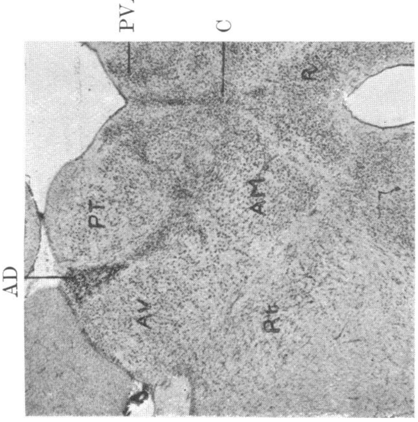

Fig. 5.

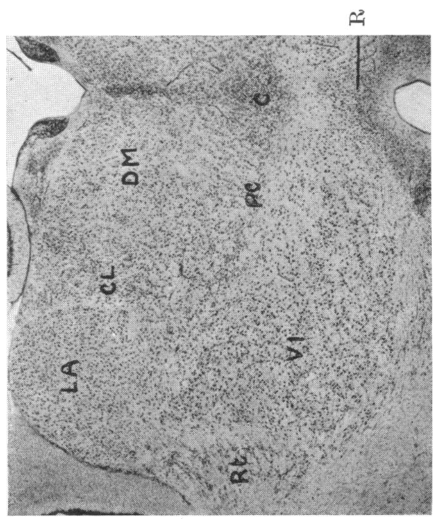

Fig 7.

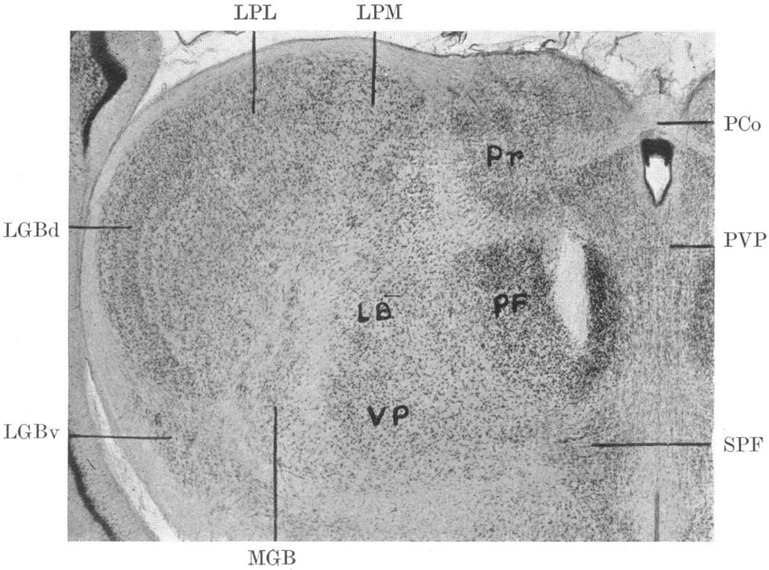
LPL
LPM
PCo
Pr
LGBd
PVP
LB
PF
VP
LGBv
SPF
MGB

Fig. 9.

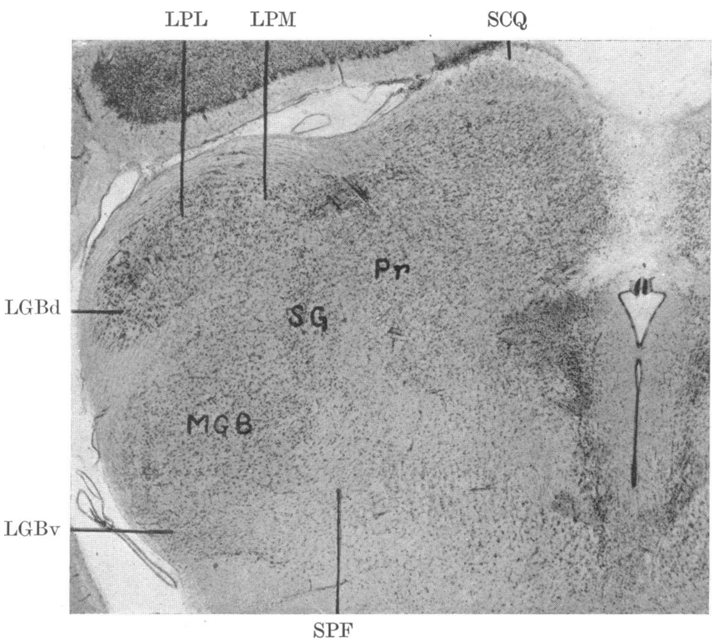
LPL
LPM
SCQ
Pr
LGBd
SG
MGB
LGBv
SPF

Fig. 10.