

STUDIES ON THE DIENCEPHALON OF THE VIRGINIA OPOSSUM

PART II. THE FIBER CONNECTIONS IN NORMAL AND EXPERIMENTAL MATERIAL¹

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THIRTEEN PLATES (TWENTY-SIX FIGURES)

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INTRODUCTION

The description of the nuclear pattern of the opossum diencephalon in the first report of this series represented not only a cytotopographic mapping of the gray centers but also an attempt to define the nuclear groups as far as possible on the basis of their fiber connections (Bodian, '39). These connections will now be considered, with special emphasis placed upon those fiber systems which hitherto have been least clear, and which the available material has been most capable of revealing.

No attempt will be made to discuss the literature in general, as such a review, to be adequate, would be beyond the scope of this paper. Of general works on the connections of the diencephalon, the works of Herrick ('33) and Huber and Crosby ('26 and '29) on submammalian forms, and, in mammals, the works of Koelliker (1896), Déjerine ('01), Edinger ('11), Ramón y Cajal ('04 and '11), Gurdjian ('27), Huber and Crosby ('29 a), Rioch ('29 and '31), Clark ('32), and Walker ('38) have been of special interest and value.

It is a pleasant duty to acknowledge again with appreciation the generous advice and assistance of Prof. Elizabeth C. Crosby during the course of this work. Our discussions and comparisons of the opossum with reptilian and avian forms have been both illuminating and stimulating to the writer.

MATERIAL AND METHODS

The normal material used in this study was listed in the first report. The Weigert series of the G. L. Streeter Collection were especially useful because of the beautiful differentiation of the myelin in mixed bundles, resulting from slow destaining in the course of years. The reduced silver preparations were valuable for study of unmyelinated fibers in the hypothalamus, although it was found that deeply stained Weigert sections reveal that a great number of fine fibers, usually considered to be unmyelinated, are really feebly myelinated fibers which often are destained in the course of preparation.

In addition to the normal series, a number of Marchi preparations were available and proved to be valuable. The Marchi material consisted of six brains, with localized lesions in various diencephalic centers, prepared in 1938 while the writer was working in the Department of Anatomy at The University of Chicago. The lesions were produced by passing a sharp von Graefe's knife through the parietal area of the cerebral cortex and into the underlying diencephalon, in various directions. Four of these specimens, prepared after 2 weeks by the Marchi method, were found to be especially useful because of the presence of restricted lesions in the diencephalon and of clearly stained degenerating fibers. No separate detailed description will be made of this material, but the most useful findings will be given in connection with the description of the normal material. The evidence from this material regarding the localized cortico-thalamic and thalamo-cortical projections will be considered further in the third report of this series, along with evidence obtained with the method of retrograde degeneration.

It is not assumed that any one method is capable of revealing more than a small part of the desired information concerning the structure and connections of the nervous system. Unfortunately, the least capricious of the histological methods, those of Nissl, Weigert, and Ramón y Cajal, and their various modifications, are least capable of revealing, in many cases, the ultimately necessary data as to the precise origin and termination of fiber systems. Consequently, some of the data recorded

in the following pages are to be regarded as being partly interpretative and tentative, until additional information can be obtained by experimental anatomical and physiological studies.

The figures of the sagittal sections are photomicrographs of Opossum C of the G. L. Streeter Collection. The other figures are photomicrographs of the horizontal and transverse Weigert-Pal series of the G. Carl Huber neurological collection of the Department of Anatomy of the University of Michigan.

INTERNAL CAPSULE AND THALAMIC RADIATIONS

The description of the internal capsule systems by Gurdjian ('27) in the rat appears to be the first thorough study of these important systems in lower mammals. In general, the correspondence between the rat and the opossum with respect to these connections is very close and so, for the most part, the terminology of Gurdjian will be followed in this account. The detailed study by Loo ('30 and '31) of the cortical projection systems, in dissections and in histological preparations of the opossum brain, has served to establish the rough topographic relations existing between the large bundles of these systems and has been of value in an experimental study of the thalamic projections to be published as the third report of this series. Since in our normal material it is not possible to determine the exact regional telencephalic connections of the components of the thalamic radiations, the more general terminology of Gurdjian will be used in describing the connections of the dorsal thalamic nuclei with the thalamic radiations.

The fibers of the internal capsule in the opossum, both cortical and striatal, after coursing through the striatum, collect in large bundles on the lateral surface of the rostral half of the diencephalon. Here they form the internal capsule characteristic of lower mammals. This is best seen in horizontal sections (figs. 14 to 18) and in transverse sections through the rostral half of the diencephalon. Considered as coming from the telencephalon, the bundles may be said to radiate medially, dorsally, rostrally, and caudoventrally into

the diencephalon. The posterior end of the broad connection between telencephalon and diencephalon is marked by the optic tract, which rounds off the lateral surface of the diencephalon for some distance caudal to this point (fig. 22). The more caudally directed bundles of the internal capsule accumulate as a dense mass dorsal and lateral to the medial forebrain bundle and continue caudalward as the cerebral peduncle. The more medial bundles of the cerebral peduncle constitute the homologue of the submammalian lateral forebrain bundle and separate the lateral or neopallial part of the cerebral peduncle from the medial forebrain bundle. The medial peduncular fibers are of striatal origin and are interspersed with small masses of gray connected rostrally with the globus pallidus. This gray, which perhaps may be considered as an interstitial nucleus for the strio-thalamic and strio-tegmental tracts, is a part of the nucleus entopeduncularis.

Gurdjian's ('27) separation of the thalamic radiations of the rat into superior, intermediate, and inferior parts, and his description of these, can be applied to the opossum, and will be used in the same sense in the following account. Apparently his inferior thalamic radiation corresponds to the inferior thalamic peduncle of earlier authors. Gurdjian was not sure as to the relative numbers of cortical or striatal fibers in the inferior thalamic radiation. Our normal and experimental material suggests that many of the fibers of the inferior thalamic radiation are of striatal or paleopallial origin, whereas the fibers of the superior and intermediate thalamic radiations are predominantly, if not wholly, neocortical in origin. In the case of the inferior thalamic radiation, as with the other thalamic radiations, there are both afferent and efferent fibers with respect to the thalamus (Déjerine, '01).

The superior thalamic radiation connects with the dorso-lateral regions of the thalamus and includes many of the fibers in the stratum zonale of the thalamus and in the optic tracts. Its fibers mingle medially with those of the intermediate thalamic radiation and connect with the anterior and lateral nuclear groups, with the geniculate nuclei, and with the tectum.

The intermediate thalamic radiation penetrates the dorsal thalamus from the external medullary lamina and sweeps dorsally and dorsocaudally in large bundles. These connect with the anterior, ventral, lateral, and medial nuclear groups, and with the tectum. The most rostral bundles correspond to the anterior thalamic radiation of Rioch ('31) and mingle with the inferior and superior thalamic radiations.

The inferior thalamic radiation is found only in the rostral part of the diencephalon and passes from the medioventral part of the internal capsule dorsalward to the medial regions of the rostral third of the dorsal thalamus (figs. 20 and 21). Gurdjian ('27) described connections with the nucleus reuniens, the parataenial nucleus, the anterior paraventricular nucleus, the medial portion of the nucleus medialis ventralis, and the nucleus medialis dorsalis. In our material connections with the nucleus subparataenialis, the nucleus parataenialis, the nucleus paracentralis, and the nucleus medialis dorsalis are most evident. The nucleus subparataenialis is most richly connected with fibers of the inferior thalamic radiation and it is plain that this nucleus corresponds to the medial part of the nucleus medialis ventralis of Gurdjian. Most of the fibers destined for the parataenial nucleus curve medially and pass through the nucleus subparataenialis first. Many of them end there, but others turn laterally and dorsally and pass to the parataenial nucleus and neighboring parts of the nucleus medialis dorsalis. Many fibers enter the internal medullary lamina and presumably connect with the paracentral nucleus, and perhaps also with the nucleus anterior dorsalis. The fibers of the inferior thalamic radiation which enter the caudal end of the nucleus subparataenialis curve sharply forward, as seen best in horizontal sections (fig. 15), and pass rostrally through this nucleus to reach the anteroventral tip of the parataenial nucleus. It was shown in the first report of this series that the nucleus subparataenialis and the nucleus parataenialis are continuous at this point. Their common connection with the inferior thalamic radiation, as well as the roundabout course of the latter through the nucleus subparataenialis before pass-

ing to the parataenial nucleus, suggests a close genetic and perhaps functional relationship between these two nuclei.

Following lesions of the inferior thalamic radiation, degenerating fibers can be traced in Marchi material to the above-mentioned nuclei, but not to the nucleus paraventricularis anterior, nor to the nucleus inter-medialis dorsalis.

DORSAL THALAMIC COMMISSURES AND INTERNAL MEDULLARY LAMINA

The majority of fibers which constitute the internal medullary lamina in the opossum appear to belong to the large dorsal thalamic commissures. These commissures form a more or less continuous and, in places, overlapping series from the rostro-dorsal part of the internal medullary lamina to the caudoven-tral end, and may be divided into six principal groups, from rostral to caudal end, as follows: commissura interparataenialis, commissura interanterodorsalis, commissura centralis, commissura inter-ventralis anterior, commissura interven-tralis, and commissura interparafascicularis.

The interventral commissures, strictly speaking, do not form a part of the internal medullary lamina but lie ventral and caudal to the most caudal of the laminary commissures, namely the central commissure.

There are several distinct nuclear groups in the dorsal thalamus which may be considered to represent, at least in part, interstitial or bed nuclei for some of the dorsal thalamic commissures and perhaps for other components of the internal medullary lamina. These are the nucleus commissuralis inter-anterodorsalis, the nucleus centralis, the nucleus paracentralis, and the nucleus parafascicularis.

In addition to commissural fibers, the internal medullary lamina contains a small number of longitudinal fibers, fibers of the inferior thalamic radiation, association fibers of the dorsal thalamus, and perhaps other components as well. At the caudal end, many of the longitudinal fibers appear to connect the parafascicular nucleus with the tectum and with the

pretectal area. This is especially evident in horizontal preparations (figs. 11 and 12, tr.tect.paraf.).

In the region of the central commissure numerous fibers from the nucleus subparataenialis pass dorsally and laterally into the internal medullary lamina, accompanied by fibers of the inferior thalamic radiation.

Commissura interparataenialis (fig. 14). The interparataenial commissure is a small but distinct system of fine myelinated fibers which connects the two parataenial nuclei across the midline. The fibers enter the parataenial nuclei at the ventral and medial angles, and mingle considerably with fibers of the commissura interanterodorsalis, which lies directly ventral to the interparataenial commissure. Some of the fibers connecting the caudal ends of the parataenial nuclei also appear to cross in the rostral part of the central commissure.

Commissura interanterodorsalis (fig. 14). This large commissure connects the anterior dorsal nuclei across the midline, where it is found at the rostral end of the central nucleus. Its fibers are continuous caudally with the rostral part of the central commissure and are associated with numerous cells along their course, the nucleus commissuralis interanterodorsalis.

Commissura centralis (figs. 14, and 20 to 22). The central commissure is quite large in the opossum and forms the largest part of the internal medullary lamina. Associated with it as bed nuclei are the large central and paracentral nuclei. It consists of fine myelinated fibers which cross the midline in the center of the dorsal thalamus and sweep laterally and dorsally. The commissure thus forms a spoon-shaped fiber lamina, containing within its dorsal concavity the medial and midline nuclear groups. The fibers of the central commissure are most numerous near the midline and become fewer in number as they extend laterally and dorsally close to the surface of the thalamus, lateral to the stria medullaris. It appears likely that the central commissure is only in part a true commissure, but also contains fibers which interconnect the medial, lateral, and ventral nuclear groups of both sides.

It has been remarked previously that the rostral end of the central commissure contains fibers from the anterior nuclear group. The caudal end, which is continuous below with the interventral commissures, contains fibers from the ventral nuclear group.

Commissura inter-ventralis anterior (fig. 22). The fibers of this commissure chiefly connect the two anterior parts of the ventral nuclei and form the rostral end of the large inter-ventral commissure. Fibers also mingle with the caudalmost ventral fibers of the central commissure. Associated with the commissura inter-ventralis anterior is a constant group of interstitial cells forming a bridge across the midline. Some of the fibers of this commissure connect with the medial parts of the ventral nuclei and also apparently with the nucleus reuniens anterior.

Commissura interventralis (figs. 14, 15, and 23). The principal ventral nuclei are broadly connected across the midline by a continuous mass of gray, and by a large commissure composed of fine myelinated fibers. These fibers appear to be only partly commissural, especially at the caudal end of the commissure where true commissural fibers mingle with many decussating fibers of the tractus tecto-reuniens and related fiber systems. These fibers can be seen clearly in horizontal sections (figs. 14 and 15), and will be discussed further in connection with the nucleus subparafascicularis.

Commissura interparafascicularis (fig. 23). This commissure consists of fibers which mingle with the dorsal part of the interventral commissure, as described also in the armadillo by Papez ('32). It contributes to the dense feltwork of fibers characteristic of the parafascicular nucleus.

SUPRAOPTIC DECUSSATIONS

Although attempts at detailed phylogenetic comparisons of the supraoptic decussations must necessarily be premature, in view of the great difficulty of establishing their connections beyond doubt, the recent detailed analysis by Herrick in *Amblystoma* ('39) has served to emphasize again the fundamental

similarity of these systems in all vertebrates. The present study, although in no sense complete, has added sufficient additional data to Tsai's earlier account ('25) to justify a reconsideration of these systems and to suggest that a clear definition of the components involved must ultimately be based upon phylogenetic studies. The subdivision of the parts of the supraoptic decussations in this account is based chiefly on the anatomical relations existing in and near the region of crossing, and on the apparent or suspected place of termination. The terminology follows in general that used by Huber and Crosby ('26) in their rather complete account of these systems in the alligator, since the components in the latter animal are not too unlike those of the opossum and of other mammals to preclude at least a tentative comparison. The following subdivisions, along with the designations generally applied in the literature on mammals, will be described: decussatio supraoptica dorsalis pars dorsalis (commissure of Ganser); decussatio supraoptica dorsalis pars ventralis (commissure of Meynert); decussatio supraoptica ventralis (commissure of Gudden).

Decussatio supraoptica dorsalis pars dorsalis

This system, frequently referred to as Ganser's commissure, is composed of extremely coarse myelinated fibers which cross at the caudal border of the chiasma below the third ventricle. In his classical description of this system in the mole, Ganser (1882) clearly noted some of its most characteristic features, which are also apparent in the opossum. Ganser recognized that all of the fibers of his "anterior subthalamic decussation" were not completely separated from the more ventrally placed commissure of Meynert, but that most of the fibers were characteristically the coarsest in the vicinity and about 3 μ in diameter. He divided the decussation into two parts, an anteroventral and a posterodorsal, with one part continuous with the other of the opposite side and with a sharp bend at the point of decussation in the midline. Ganser followed the fibers dorsally through the zona incerta and also into the interstices of

the internal capsule. He quoted Schnopfhagen (1877) as having traced comparable fibers in man caudally from the field H_2 of Forel into the fasciculus longitudinalis medialis, as have other workers (see Papez, '38). Ganser's description of this system as a decussation was confirmed by Darkschewitsch and Pribytkow (1891) in the mole. These workers, in a cat with a unilateral lesion of the ventral portion, noted the disappearance of the dorsal part of the decussation of the opposite side. They also followed the fibers of the ventral portion to the lenticular nucleus, and the fibers of the dorsal part to the region of the fornix column in the dorsal area of the hypothalamus.

In the opossum, from the point of crossing in the midline, the bulk of the coarse fibers of Ganser's commissure can be followed readily as they pass laterally and dorsalward around the lateral margin of the ventromedial hypothalamic nucleus (fig. 22). The fibers then accumulate at the lateral margin of the dorsomedial hypothalamic nucleus and there turn sharply caudalward (fig. 7). At this point they form a small bundle of fibers at the dorsomedial angle of the medial forebrain bundle and can be followed caudally in transverse sections for some distance as a rather compact group of fibers. These fibers probably correspond to the posterodorsal part of Ganser's commissure as described by that author. The remainder of their course is followed best in sagittal sections, in which they appear to join other fibers passing caudalward below the zona incerta. They have been followed as far caudally as the field of Forel in the present material but perhaps continue farther caudally to the ventral nucleus of the medial longitudinal fasciculus or even into the latter bundle, as described by several investigators. The fibers appear to decrease in number as they are followed caudalward in the dorsal part of the lateral hypothalamic area. This suggests a possible connection of some of these fibers in this region or in the field of Forel more caudally (see Magoun and Ranson, '40).

A smaller component of Ganser's commissure, forming the ventral or rostral division, is more difficult to follow, as its fibers which are somewhat scattered, appear to pursue an

erratic course. At their place of crossing they are mixed with the dorsalmost fibers of Meynert's supraoptic decussation and also mingle dorsally with the rest of Ganser's commissure. Instead of passing dorsalward with the latter, the fibers of the ventral division of Ganser's commissure pass laterally into the medial forebrain bundle. Some can be followed caudally, but only for a short distance, and, since their course is erratic, may conceivably turn back. Most of the fibers, however, can be followed rostrally near the ventromedial angle of the cerebral peduncle and appear to enter the globus pallidus.

Decussatio supraoptica dorsalis pars ventralis

The ventral part of the dorsal supraoptic decussation, as here designated, is considered to represent in general the so-called commissure of Meynert. It consists of the majority of fibers of the supraoptic decussations, and is furthermore made up of several distinct groups of fibers of varying caliber and of diverse terminations. This is the group of fiber systems which Weaver in a recent study in the cat ('37) described as the inferior hypothalamic decussation.

Lateral division. In the opossum with optic nerves completely degenerated it is obvious that the majority of fibers of the ventral part of the dorsal supraoptic decussation either penetrate the cerebral peduncle or course around its dorso-lateral margin and pass medially toward the zona incerta and nucleus subthalamicus. Whether or not all of these fibers have the same termination, they are here described as the lateral division of the ventral part of the dorsal supraoptic decussation. We can agree fully with Weaver that these fibers, in and near the midline, form a unitary system of fibers, of varying sizes, which cross in the posterior part of the optic chiasma and behind the chiasma. In the opossum the so-called transpeduncular fibers which penetrate the peduncle appear to be those which cross behind the chiasma. They remain medial to the optic tract, and enter the medial part of the cerebral peduncle, interweaving as small bundles between the medial bundles of the cerebral peduncle. Here many of the peduncle

fibers belong to the strio-tegmental system and are separated here and there by small areas of gray of the entopeduncular nucleus. The further course of the penetrating bundles of the lateral division of Meynert's decussation is not clear, but it is possible that the fibers pass to the entopeduncular nucleus or to the lenticular nucleus via the lateral forebrain bundle (compare Déjerine, '01, and Wallenberg, '26). The circumpeduncular fibers which pass around the dorsal margin of the peduncle are more readily traced and appear to pass to the zona incerta and the nucleus subthalamicus. In normal material these fibers are easily mistaken for optic fibers, as was done by Koelliker (1896) and by others. In sagittal sections many of them appear to join fibers from the zona incerta and pass caudally and dorsalward to the tectum (fig. 4). As they pass around the dorsolateral margin of the cerebral peduncle they are in relation to the ventral nucleus of the lateral geniculate body, but it is not apparent that any fibers terminate there.

Ramón y Cajal ('11, fig. 255) described collaterals of certain optic fibers, which he considered to be part of Gudden's commissure, arborizing within his "noyaux de la bandelette optique." This nucleus corresponds to the entopeduncular nucleus of the opossum and the collaterals could well be collaterals of the lateral division of Meynert's commissure, which is much more closely associated with the entopeduncular gray than with any other part of the supraoptic decussations.

Medial division. This system is composed of fine myelinated and unmyelinated fibers. At their place of crossing behind the caudal border of the chiasma these fibers intermingle with the fibers of the lateral division, many of which are of identical appearance. When the fibers of the two groups are followed caudally, however, they are seen to separate. Those of the lateral division pass through or around the cerebral peduncle in company with the optic tract, and those of the medial division remain medial to the peduncle and run dorsally and caudalward. The latter join the coarser fibers of the dorsal part of the dorsal supraoptic decussation in the upper portion of the medial forebrain bundle, after having passed around the

lateral border of the ventromedial hypothalamic nucleus as part of the capsule of that center. Here they mingle with fibers of similar size which descend from the lateral hypothalamic area to join the tractus hypophyseus.

The medial division cannot be followed as readily as the coarser fibers of the dorsal part of the dorsal supraoptic decussation but appears to accompany the latter caudalward. Both sets of fibers may correspond to the commissure of Ganser of Shaner's description. This the latter writer followed into the central tegmental bundle in pig embryos ('36).

Decussatio supraoptica ventralis (Gudden's commissure)

Fibers in the supraoptic decussations which connect with the medial geniculate bodies, as described by Gudden (1879), appear to be present in the opossum and are here designated as the ventral supraoptic decussation. They constitute, however, only a small fraction of the supraoptic decussations and, like a part of Meynert's commissure, are intimately intermingled with optic fibers in the optic chiasma. They remain in the optic tract as far back as the rostral pole of the medial geniculate body, where they separate from the optic fibers and enter the marginal portion of the nucleus (fig. 1). Some of the fibers also appear to pass caudalward in the brachium of the inferior colliculus, and these perhaps terminate in the nucleus parabigeminus.

The ventral supraoptic decussation in the opossum is crossed at the ventral angle of the medial geniculate body by the tractus geniculatus descendens, with which it may be confused in some sections. The courses of both systems are best traced in sagittal sections (fig. 1), in which the tractus geniculatus descendens is seen to be a part of the transverse peduncular tract and quite separate from the ventral supraoptic decussation.

Although there is considerable agreement among workers on submammalian forms as to the presence of a so-called commissure of Gudden, with connections with the tectum, nucleus

isthmi, and perhaps other centers, the case with respect to descriptions of this system in mammals is quite the reverse. The only point upon which any agreement exists is the use of the term Gudden's commissure for a dorsal thalamic component of the supraoptic systems, connecting with the medial geniculate body as described by Gudden and by many others (see Probst, '05). If such a system is shown not to exist in certain forms then obviously the term Gudden's commissure has no significance for that species. In the opossum there are indications of a small component from the medial geniculate body in the supraoptic systems. This component is assumed to be the commissure of Gudden in the above sense. Other workers have denied the existence of this bundle in other mammals, and it is interesting that Brugi ('37) has found no connection of the internal root of the optic tract with the medial geniculate body of primates. He described a connection of this root, which he believed represented the combined commissures of Meynert and of Gudden, with the griseum pregeniculatum of the monkey and of man. On the contrary, Probst ('05), in human cases with atrophy of the ocular bulb, and many other workers on other mammals, quoted by Probst, have described a connection with the medial geniculate body.

Wallenberg ('26) recently has studied the commissure of Gudden in Marchi preparations of the brain of the Iltis. In this carnivore he has traced fibers of this system to the corpus parabigeminum, and a few fibers to the medial geniculate body. Weaver ('37) similarly followed fibers of the supraoptic decussations in the cat to the medial geniculate body and to the pretectal region, but he does not give these fibers a separate designation.

The recent detailed study of the supraoptic decussations in *Amblystoma* larvae by Herrick ('39) perhaps represents a more complete analysis of these fascicles than has been possible in higher vertebrates. It cannot be expected that more than a partial and obviously tentative comparison between Amphibia and mammals can be made with respect to the supraoptic systems. Such a comparison, however, may be of some

value if only in emphasizing the constancy of pattern in these systems in vertebrates, as well as certain points of divergence.

According to Herrick's description of the postoptic decussations in *Amblystoma*, these systems consist of four principal components. These are, respectively, connections from the tectum, the dorsal thalamus, the ventral thalamus, and the hypothalamus which, after crossing in the postoptic decussations, descend in the complex group of tegmental fascicles. These components, which connect by collaterals with all the gray centers along their courses, and which are also accompanied by shorter fibers, are designated by Herrick as the tractus tecto-tegmentalis cruciatus, tractus thalamo-tegmentalis dorsalis cruciatus, tractus thalamo-tegmentalis ventralis cruciatus, and tractus hypothalamo-peduncularis. The last is the most caudal of these components and does not appear to have a homologue in the mammalian supraoptic decussations. The other systems, in the order named, appear respectively to correspond in general to the components described in the opossum as Meynert's commissure, Gudden's commissure and Ganser's decussation (*fibrae ansulatae*).

It is clear that the above-mentioned mammalian components are not simply crossed tecto-tegmental, dorsal thalamo-tegmental, and ventral thalamo-tegmental systems, and that the numerous side-connections of these systems in the *Amphibia* may be more or less exaggerated, at the expense of other connections of each system, in higher vertebrates. The decussation of Ganser in mammals is not excluded from consideration as a crossed ventral thalamo-tegmental system because of possible rostral connections with the striatum, since the boundary between ventral thalamus and striatum is not at all sharp. It is interesting that this system in *Amphibia* is composed of the coarsest fibers, as is characteristic of Ganser's decussation of the classical mammalian description.

Meynert's commissure is most probably connected with the tectum in mammals. Connections with the lower tegmentum have not been consistently described and are not apparent in our material, in which many fibers, both peripeduncular and

transpeduncular, appear to connect with the ventral thalamus in the regions near the strio-tegmental fascicles. It is entirely within the realm of possibility that some of these fibers descend to the tegmentum with the strio-tegmental fibers, but it has not been possible as yet to determine this in the available material.

Gudden's commissure appears to represent a connection of the dorsal thalamus, the medial geniculate nucleus in mammals, with the same or other centers of the opposite side. No fibers have been followed into the central tegmental fascicles, although connections with the tectum and lateral tegmental centers caudal to the medial geniculate nucleus have been described.

CONNECTIONS OF THE DORSAL THALAMUS

Anterior nuclear group

Nucleus anterior dorsalis (figs. 5 to 7, 12, 13, and 20). The principal connections of the anterodorsal nucleus are with the anterior part of the superior thalamic radiation and with the commissura interanterodorsalis. The numerous fibers which pass to the anterodorsal nucleus from the thalamic radiations encapsulate it and form a rather dense intercellular feltwork of fine myelinated fibers. These fibers enter the nucleus on its external surface from the stratum zonale thalami and, in even greater numbers, from the deeper portions of the anterior thalamic radiation.

Many fibers pass from the anterodorsal nucleus to the neighboring nucleus parataenialis and the nucleus medialis dorsalis. Most of them appear to be fibers of the thalamic radiations which traverse the anterodorsal nucleus in passing to the above-mentioned nuclei, but in reduced silver preparations the impression is obtained that a few of the fibers also originate in the anterodorsal nucleus. No fibers of the mammillo-thalamic tract could be traced to the anterodorsal nucleus in any of the preparations examined.

Nucleus anterior ventralis (figs. 5 to 8, 13, 14, and 20). The anteroventral nucleus is connected with the anterior parts of

the superior and intermediate thalamic radiations and with the bundle of Vicq d'Azyr. It forms the principal end-station for the latter tract. There are no direct commissural fibers between the anteroventral nuclei through the anteromedial nucleus, as Gurdjian ('27) described in the rat, but a few fibers from the anteroventral nucleus enter the commissura interanterodorsalis, and many commissural fibers are seen in horizontal sections to enter the anterior end of the central commissure (fig. 14).

Clark and Boggon ('33) have described osmium granules in the mammillo-thalamic tract of the rat in Marchi material after lesions of the anteroventral nucleus. These granules they attribute to degeneration of thalamo-mammillary fibers. In an opossum with a direct lesion of the mammillo-thalamic tract on one side, it has been possible to trace great numbers of osmium granules to the anteroventral and anteromedial nuclei in Marchi material, but no granules could be followed in the opposite direction to the mammillary bodies.

Nucleus anterior medialis (figs. 7 to 9, 15, and 20). This nucleus has connections similar to those of the anteroventral nucleus, namely fibers from the bundle of Vicq d'Azyr, from the anterior parts of the intermediate and inferior thalamic radiations, and commissural fibers from the commissura interanterodorsalis. As in the case of the anteroventral nucleus, numerous fibers seem to pass between this nucleus and the neighboring ventral nuclear group.

Medial nuclear group

Nucleus parataenialis (figs. 13, 14, and 20). The parataenial nucleus is rich in connections and contains a dense feltwork of myelinated fibers. Many fibers of the superior and inferior thalamic radiations penetrate it, as well as numerous commissural fibers (fig. 14, commissura interparataenialis). In places fibers of the commissura interanterodorsalis appear to pass to the opposite parataenial nucleus, via the closely associated interparataenial commissure, and it has already been noted that the parataenial nucleus seems to be connected with

the anterodorsal nucleus of the same side as well. There are indications that the parataenial nucleus is also connected with the neighboring nucleus subparataenialis, the nucleus medialis dorsalis, and the nucleus paraventricularis anterior, as well as with the most lateral fibers of the anterior periventricular system.

The connections with the thalamic radiations deserve special consideration. It has already been mentioned in the discussion of the inferior thalamic radiation that numerous bundles of the latter pass to the parataenial nucleus after having traversed the nucleus subparataenialis. This suggests a close association of the two nuclei, which is also apparent in the fusion of these nuclear masses at the rostral end of the diencephalon and in the presence of internuclear connections between them. Many fibers of the anterior part of the superior thalamic radiation, after coursing over and through the nucleus lateralis anterior, pass into the nucleus anterior dorsalis and continue medialward to the parataenial nucleus. Some of these fibers, like those of the inferior thalamic radiation, are of striatal origin, and thus it may be suggested that these two apparently separate striatal connections through the inferior and anterior superior thalamic radiations were originally a single system which became widely split by the development of the anterior nuclei.

Nucleus subparataenialis (figs. 10, 15, 20, and 21). The nucleus subparataenialis, as has been mentioned in previous discussions of the parataenial nucleus and of the inferior thalamic radiation, is richly connected with the latter system. The fibers of the inferior thalamic radiation enter the nucleus from the medial, ventral, and caudal surfaces and encapsulate it to some extent. Fairly large bundles pass rostrally through the nucleus, and others, after contributing fibers to it, pass dorsally to the parataenial nucleus and to the internal medullary lamina. Fibers from the nucleus subparataenialis itself pass dorsally and laterally into the internal medullary lamina, as well as laterally to connect with the nucleus anterior medialis. Other probable internuclear connections are with the

parataenial nucleus, and with the paracentral and anterodorsal nuclei by way of the internal medullary lamina.

Nucleus medialis dorsalis (figs. 7 to 9, 11 to 13, 21 and 22). The nucleus medialis dorsalis contains a dense intercellular plexus of myelinated fibers and obviously has widespread connections. All parts of this nucleus are permeated by fibers of the inferior and intermediate thalamic radiations. In addition, the nuclei of the two sides are brought into relation by commissural fibers which pass through the central commissure, and are also related with the neighboring nuclei of the medial and midline groups, as well as with the lateral habenular nucleus. Connections with the paracentral and central nuclei by way of the central commissure probably exist, and in horizontal sections there are suggestions of connections with the parafascicular nuclei.

The most medial part of the nucleus medialis dorsalis appears to be related with the anterior periventricular system.

Nucleus paracentralis (fig. 13). The paracentral nucleus, like the central nucleus, is an interstitial nucleus of the central commissure. By way of the latter it may affect connections with the opposite medial, lateral, and ventral nuclear groups. Anteriorly it appears to be related with the anterior paraventricular nucleus, and caudally, especially as seen in horizontal sections, longitudinal fibers pass between the paracentral and parafascicular nuclei. Whether any of these longitudinal fibers connect the paracentral nucleus with the midbrain is not clear. Many fibers which enter the internal medullary lamina from the nucleus subparataenialis and from the inferior thalamic radiation may possibly establish connections with the paracentral nucleus.

Nucleus parafascicularis (figs. 8 to 9, 11 to 13, and 23). The parafascicular nucleus is placed in the caudal portion of the internal medullary lamina and contains a fairly dense feltwork of fine and coarse fibers. It is connected with fibers of the thalamic radiations, with neighboring thalamic centers, and with the tectum. The tectal bundles are best seen in horizontal preparations (figs. 11 and 12, tractus tecto-parafascicularis).

Connections with the nucleus paracentralis, nucleus medialis dorsalis, and nucleus lateralis pars intermedia appear to be present, as well as those with the nucleus pretectalis and nucleus paraventricularis posterior. The latter fascicles may include ascending fibers of the posterior periventricular system, as suggested by Marchi preparations following lesions of that system as it passes through the posterior paraventricular nucleus.

Nucleus parafascicularis pars posterolateralis (figs. 7, 12, 13, and 24). The impression is obtained from the preparations examined that the nucleus parafascicularis pars posterolateralis is a differentiated caudal part of the parafascicular nucleus, with which it is connected and from which it is not easily separable. Connections with the nucleus paraventricularis posterior and with the pretectal nucleus appear to be present in our material, and connections with the surrounding ventral and lateral nuclear groups may also be present but are not easily demonstrated. The presence of a dense intercellular plexus within this nucleus, and its other relations as well, suggest a correspondence with the "noyaux semi-lunaires accessoires du noyaux sensitif" of Ramón y Cajal ('11), who described collaterals of the trigeminal lemniscus terminating within this nucleus. As in the case of the nucleus parafascicularis, there appear to be fiber connections with the tectum and with the posterior periventricular system.

Midline and commissural nuclei

Nucleus paraventricularis anterior (figs. 9 to 11, and 22). The anterior paraventricular nucleus seems to be connected with the neighboring habenular nuclei, and with the nucleus medialis dorsalis and the nucleus parataenialis. In addition, longitudinally coursing fibers within it connect caudally with the nucleus paraventricularis posterior, and some of these fibers may enter the posterior periventricular system in this region. Many of the fibers of the anterior periventricular system reach the anterior paraventricular nucleus.

Nucleus paraventricularis posterior (figs. 8 to 15, 24, and 25). This nucleus, of large size in the opossum, bears a striking resemblance in most of its relations to the nucleus lentiformis thalami of certain reptiles (Ariëns Kappers, '21; Beccari, '23; Cairney, '26). Because of its manifold connections it must be considered as a relatively undifferentiated mass of gray occupying a strategic position at the di-mesencephalic border. The available opossum material has been favorable for study of the diverse connections of this gray area. Perhaps the most striking connection of this nucleus is that with the posterior periventricular system, as described in the account of the latter, since the posterior paraventricular nucleus appears to be intercalated in the course of that important ascending and descending hypothalamic pathway. Both the infracommissural part and the supracommissural part (area pretectalis of Papez, '32) are clearly connected with the tectum and the pretectal nucleus, and probably with the posterior commissure, which penetrates this nuclear mass. It has been mentioned before that the cells of the nucleus paraventricularis posterior form strands through the posterior commissure which interrelate the supracommissural and infracommissural parts. Furthermore, the nucleus paraventricularis posterior is continuous caudally with the interstitial nucleus of the posterior commissure. The ventral part of this nucleus merges with the nucleus subparafascicularis, as was described previously, and is connected with many fibers of the tecto-reuniens bundle. Connections with the nucleus parafascicularis pars posterolateralis, the nucleus ventralis principalis, the lateral habenular nucleus, and the anterior paraventricular nucleus also appear to be present. We have not detected any optic connections to the supracommissural part as described by Papez ('32) for his corresponding area pretectalis. Direct lesions of the optic tract in the opossum result in no trace, in Marchi material, of osmium granules in this nucleus.

Nucleus rhomboidalis (figs. 14 and 21). The rhomboid nucleus, unlike the central nucleus, is not permeated by commissural fibers, but appears to be associated chiefly with the

anterior periventricular system, and with the neighboring nucleus medialis dorsalis and the nucleus paraventricularis anterior.

Nucleus centralis. The nucleus centralis occupies a strategic position in the dorsal thalamus, being, as it were, at the cross-roads of the important central commissure and the anterior periventricular system. It is an interstitial nucleus for the central commissure, and the preparations examined are suggestive of the fact that it is connected with the anterior periventricular system passing to the hypothalamus, especially since the periventricular fibers appear to be more numerous ventral to the central nucleus than dorsal to it. This is in accord with the suggestion of Rioch ('31) that the central nucleus brings the nuclei connected with the central commissure and internal medullary lamina into association with the hypothalamus via the periventricular system. Glorieux ('29) has noted in Marchi preparations of the dog that lesions of the nucleus centralis (his "noyau reunissant") produce fiber degeneration which can be traced to the hypothalamus, and to the medial, ventral, and lateral thalamic nuclear groups.

Nucleus reuniens anterior (figs. 15, 21 and 22). The nucleus reuniens anterior appears to be associated chiefly with the fibers of the anterior periventricular system, which gives most of its cells a vertical orientation. The commissural fibers are extremely few or absent, except dorsally where the ventral fibers of the central commissure pass. In reduced silver preparations a fairly dense intercellular feltwork of fine fibers is seen. Connections with the inferior thalamic radiation, as described by Gurdjian in the rat ('27), are not evident in our material, although the closely bordering nucleus subparataenialis is richly connected with such fibers.

Nucleus reuniens posterior (nucleus commissuralis interven-tralis). This nucleus consists of a strip of midline gray which fuses the principal ventral nuclei of both sides, and which is continuous rostrally with the nucleus reuniens anterior. It is in the course of the massive interven-tral commissure, as well as of the fibers of the periventricular system. The fibers of the

tecto-reuniens tract and the geniculo-reuniens tract also pass into this region, some crossing and some apparently terminating there. These tracts are described separately in greater detail elsewhere in this report (p. 236).

Nucleus inter-medialis dorsalis. The scattered gray between the nuclei mediales dorsales of the two sides, like the rhomboid nucleus, is not associated with commissural fibers but is in the course of fibers of the anterior periventricular system, with which it is probably connected.

Nucleus commissuralis interanterodorsalis. This nucleus, the bed nucleus of the commissura interanterodorsalis, is closely associated with the paracentral nucleus. Connections other than the commissural fibers are not evident in the preparations examined.

Nucleus commissuralis inter-ventralis anterior. This cell mass, which is apparently differentiated from the caudoventral part of the nucleus centralis, is associated with numerous commissural fibers interrelating the anterior parts of the ventral nuclei.

Lateral nuclear group

Nucleus lateralis pars anterior (fig. 12). The nucleus lateralis pars anterior is very small in the opossum and is connected with the anterior part of the superior thalamic radiation, and possibly with the anterior nuclear group. Experimental material suggests that at least some of the fibers of the anterior part of the superior thalamic radiation are of striatal rather than of neocortical origin.

Nucleus lateralis pars intermedia (figs. 4 to 6, 11 to 13, 22, and 23). The intermediate part of the lateral nucleus is connected chiefly with the cerebral cortex via the intermediate and superior thalamic radiations, fibers passing in both directions. The cortical projection of this nucleus will be considered in a separate study. Commissural fibers appear to connect the nuclei of both sides by way of the central commissure, and some fibers also pass between the lateral and ventral nuclear groups, as well as into the lamina medullaris interna.

Nucleus lateralis pars posterior (figs. 4 to 6, 11, and 23 to 25). The nucleus lateralis pars posterior is connected with the cerebral cortex by means of the superior thalamic radiation, with fibers passing in both directions. There are also connections with the nucleus lateralis pars intermedia, the dorsal lateral geniculate nucleus, and the medial geniculate nucleus. Connections with the tectum and with optic fibers have been described by several workers, usually in normal material. Most, if not all, of the fibers which seem to pass to the tectum and from the optic tract appear to be fibers of passage which do not establish connections with the nucleus lateralis pars posterior.

It has been shown in an earlier report (Bodian, '37) that many cortico-tectal and cortico-thalamic fibers enter the optic tract as the latter courses around the cerebral peduncle, and pass with the optic tract to the thalamus and to the tectum. Fibers are distributed, en route, to the dorsal lateral geniculate nucleus and to the nucleus lateralis pars posterior. Thus it appears to be unsafe to conclude, from normal material alone, that fibers which pass from the optic tract to the nucleus lateralis pars posterior are of retinal origin. Marchi preparations after optic nerve section show no fibers terminating in the nucleus lateralis pars posterior (Bodian, '37), although such preparations after large cortical lesions show numerous fibers entering this nucleus from the optic tract (stratum zonale thalami) and terminating there or continuing caudally to the tectum as the cortico-tectal fibers. These latter, which are fibers of passage in the nucleus lateralis pars posterior, can readily be mistaken for thalamo-tectal fibers in normal material.

Ventral nuclear group and medial lemniscus

Nucleus ventralis pars anterior (fig. 14). The small nucleus ventralis pars anterior is in the course of the main mass of the intermediate thalamic radiation, which penetrates the nucleus from below and gives many of its cells a vertical orientation. Some of the fibers terminate here. Due to the presence of the

great mass of fascicles of the thalamic radiations, it is difficult to be certain in normal material that fibers of the medial lemniscus reach this nucleus, although this appears likely. The nuclei of the two sides are widely connected across the midline by cells and by commissural fibers. The nucleus ventralis pars anterior forms a transitional cell mass between the nucleus anterior ventralis and the nucleus ventralis pars principalis, and it is probably connected with both of these nuclei. It degenerates completely after hemidecortication.

Nucleus ventralis pars medialis (figs. 8, 9, 15 and 22). The nucleus ventralis pars medialis is connected with the intermediate thalamic radiation, with the ventral division of the medial lemniscus, and with the opposite nucleus by commissural fibers. Connections with the neighboring nuclei of the ventral group, with the nucleus anterior medialis, and with the nucleus reuniens anterior also appear to be present.

Nucleus ventralis principalis and medial lemniscus. The principal ventral nucleus is connected with the intermediate thalamic radiation, which penetrates the nucleus at its anterior and ventral surfaces. The medial lemniscus penetrates the nucleus from the ventral, lateral, and posterior surfaces in two main groups. The ventromedial division of the medial lemniscus enters the caudal end of the external medullary lamina and passes forward along the latter, distributing fibers which pass dorsally into the ventral nucleus (figs. 6 to 8). The dorsolateral division of the medial lemniscus separates from the ventromedial division in the caudal part of Forel's field, and passes dorsally and rostrally into the pretectal nucleus (figs. 5 and 6). From here most of the fibers bend rostrally and penetrate the caudal and caudolateral surfaces of the principal part of the ventral nucleus. Because of the wealth of fibers within the pretectal nucleus it is difficult to determine whether fibers of the medial lemniscus actually terminate therein, but the available material suggests that many do, as Ramón y Cajal described ('11). Our material is not adequate to demonstrate other possible connections of the medial lemniscus except those associated with the mammillary peduncle.

The principal ventral nuclei are also widely connected across the midline by commissural fibers, and in this position receive the crossed fibers of the tecto-reuniens and geniculo-reuniens bundles. Connections with the neighboring medial geniculate nucleus, the dorsal lateral geniculate nucleus, and the lateral nuclear group are also present apparently.

The medial part of the principal ventral nucleus, continuous with the nucleus reuniens posterior, or nucleus of the inter-ventral commissure, apparently corresponds to the "noyau triangulaire" of Ramón y Cajal ('11, fig. 285) or his "n. médian" (p. 432). In addition to cortical connections in Golgi material he described collaterals of the commissural fibers and, presumably, lemniscus connections.

*Geniculate nuclei, and associated optic and auditory nuclei
of the di-mesencephalic junction. Tecto-
reuniens fiber systems*

Nucleus geniculatus lateralis dorsalis. The predominant connections of this nucleus are with the retina and with the cerebral cortex, as is well known. The retinal fibers penetrate the nucleus from the lateral and ventral surfaces and arborize within the nucleus or continue caudalward to the tectum. The cortical fibers accumulate in a dense mass at the ventromedial border of the nucleus and join the occipital radiation (Loo, '31). The geniculo-cortical fibers terminate solely in the striate area (Bodian, '37), from which fibers also pass in turn to the dorsal lateral geniculate nucleus. Connections of the dorsal lateral geniculate nucleus with the neighboring lateral and ventral nuclear groups, the pretectal nucleus, the ventral lateral geniculate nucleus, and the tectum have been described by various observers. In view of the exceedingly rich plexus of fibers in the dorsal lateral geniculate nucleus formed by retinal, geniculo-cortical, and cortico-geniculate fibers, as well as fibers of passage of cortico-tectal, cortico-thalamic, and retino-tectal systems, the proof of connections other than the well established retinal and cortical ones must rest with experimental studies.

Nucleus pretectalis (figs. 4 to 7, 11, 12, and 23 to 26). This nucleus was described in the opossum by Tsai ('25) who mentioned connections with the tectum, the lateral geniculate body, the optic tract, the medial lemniscus, and tegmental centers, especially the substantia nigra. It is the nucleus posterior of Ramón y Cajal ('11), who described the connections with the medial lemniscus. It is perfectly clear in the material examined that fibers of the medial lemniscus enter the pretectal nucleus, but many of these fibers are seen to turn rostrally in the nucleus and to pass forward into the nucleus ventralis pars principalis, so that the question must be raised as to what proportion of medial lemniscus fibers actually terminate within the pretectal nucleus. The connections of the pretectal nucleus with the tectum and with the tegmentum are most evident, and in addition to the pretecto-nigral fibers described by Tsai, a connection with the nucleus opticus tegmenti seems apparent in our material (fig. 5). Numerous fibers seem to enter the posterior commissure and also to make connections with the nucleus paraventricularis posterior and the nucleus parafascicularis pars posterolateralis.

Nucleus pretectalis pars caudalis (figs. 25 and 26). It was pointed out in an earlier report (Bodian, '37) that in Marchi material no myelinated fibers can be traced to the pretectal nucleus from the degenerating optic tract. A re-examination of this material has served to confirm this and has further revealed that very fine Marchi granules extend into the pars caudalis of the pretectal nucleus from the degenerating optic tract. In the earlier study the pars caudalis of the pretectal nucleus was considered to be a part of the deep gray of the tectum, with which it is closely related. The first report of this series contains a description of the topographic relations of the pars caudalis of the pretectal nucleus, which appears to be a constant differentiation of the rostral part of the deep tectal gray in the opossum. Its connections, other than those with the optic tectum and the rest of the pretectal nucleus, are with the optic tract and perhaps with the brachium of the inferior colliculus. Unlike the principal part of the pretectal

nucleus, it appears to receive very few, if any, fibers of the medial lemniscus.

Marchi material, following lesions of the pretectal nuclei, suggests that these centers are connected principally with the deeper layers of the optic tectum and to a lesser extent with the more superficial layers.

Nucleus geniculatus medialis (figs. 1, 3, 12 to 15, 25 and 26). The medial geniculate nucleus consists of two principal parts, marginal and central, not sharply separated from each other. In fiber preparations a dense feltwork of fine myelinated fibers is present between the two parts, and permeates the central mass to a greater extent than the marginal portion. The rich feltwork of fibers is formed chiefly by terminals of the large brachium of the inferior colliculus, which penetrates the caudal pole of the nucleus, and also by fibers of the auditory radiation, which penetrates the anterior and anteroventral surfaces of the medial geniculate body (fig. 3). The impression is obtained from normal material that both marginal and central cell masses are connected with the inferior quadrigeminal brachium and the lateral lemniscus, but that the central cell mass has a much richer cortical connection than does the marginal part. The latter, however, appears to be most concerned with the rich connection with the principal parts of the ventral nuclei of both sides by way of the tractus geniculo-reuniens and the tractus geniculo-ventralis, and is furthermore most intimately associated with the nucleus subparafascicularis. These systems will be described in detail in the account of the latter nucleus.

The relations of the commissure of Gudden to the medial geniculate body have already been described. Glorieux ('29) has demonstrated in Marchi material of the dog brain, prepared after lesions of the medial geniculate body, crossed and uncrossed connections with the ventral nucleus and these are apparent in the opossum material also.

Nucleus suprageniculatus (figs. 3, 25, and 26). The nucleus suprageniculatus is connected with the thalamic radiations and apparently also with the terminals of the brachium of the

inferior colliculus. This nucleus is apparently intimately associated with the medial geniculate body and with the nucleus lateralis pars posterior, but its special significance is not at all clear. It is possible that it should be considered, in the opossum at least, as a part of the medial geniculate body, since it is not easily differentiated from the latter. Some of the fibers of the posterior commissure appear to extend into the nucleus suprageniculatus.

Nucleus subparafascicularis (*nucleus of the tractus tecto-reuniens*), *tractus tecto-reuniens*, *tractus geniculo-reuniens*, and *tractus geniculo-ventralis*. In horizontal Weigert sections of the opossum brain one sees a prominent bundle of fine fibers passing forward from the caudal border of the medial geniculate body to the region of the commissura interventralis, in which place the fibers decussate (figs. 14 and 15). In the entire course of this large bundle is a well developed interstitial nucleus, the nucleus subparafascicularis, which merges caudally with the marginal part of the medial geniculate body and medially and rostrally with the nucleus paraventricularis posterior. This interstitial nucleus undoubtedly contributes fibers to the above described pathway, which in most of its relations appears to correspond to the tractus tecto-reuniens of reptiles (nomenclature of Huber and Crosby, '26), as remarked by Papez ('36) in a recent consideration of the evolution of the medial geniculate body. Papez shows figures of the brain of the bat and of the cat, in which this tract is present, and apparently the tract is present in most, if not all mammals. In the opossum it is possible to discern that the bundle is of a complex nature, although the fibers of apparently diverse origins intermingle beyond hope of separation in normal material. Rostromedially, connections are affected with the following centers: the ipsilateral principal part of the ventral nucleus, the nucleus paraventricularis posterior, and the ventral nucleus of the medial longitudinal fasciculus; the contralateral principal part and possibly medial part of the ventral nucleus by way of the commissura interventralis; and the nucleus reuniens posterior (nucleus commissuralis interven-

tralis). The caudal connections are clearly with the medial geniculate body, especially the marginal part, and probably also with the inferior colliculus and the nucleus parabigeminus via the inferior quadrigeminal brachium. The topographic relations of the nucleus subparafascicularis to this fiber system, and to some of the terminal nuclei, have been mentioned in the account of this nucleus in the first report of this series.

Although it is clear that the above system of fibers has complex relations and consists of intra-thalamic, tecto-thalamic, and perhaps thalamo-tectal connections, the term tractus tecto-reuniens will be used to designate the bundle where the various components are intermingled, in accord with the usage of Huber and Crosby ('26) in reptiles, and of Papez ('36) in mammals. Loo ('37) has apparently used the term "tractus geniculato-reuniens" to identify part of this fiber system.

Nucleus parabigeminus (nucleus of the inferior quadrigeminal brachium). This nucleus is in the course of the inferior quadrigeminal brachium, with which it is undoubtedly connected. It appears to contribute fibers also to the tractus tecto-reuniens and possibly connects with the commissure of Gudden. In the opossum it seems to be closely associated with the marginal part of the medial geniculate body and with the nucleus subparafascicularis.

The optic tracts and nucleus opticus tegmenti

The optic tracts of the opossum have been previously described by Tsai ('25) in normal series, and by the present writer in experimental material (Bodian, '37). We have re-studied carefully all available preparations pertinent to these tracts and now wish to summarize briefly the conclusions reached from the previous studies and from the newer data.

1. The optic tracts of the opossum contain crossed and uncrossed retino-geniculate and retino-tectal fibers. The details of the projection of these fibers will be found in a previous report (Bodian, '37).

2. An accessory optic tract is present (the so-called posterior accessory optic tract) which contains retinal fibers passing to the nucleus opticus tegmenti. This gray also receives fibers from the ventral nucleus of the lateral geniculate body and from the zona incerta, and appears to be connected in addition with the tectum, the pretectal nucleus, the substantia nigra, the lateral parts of the interpeduncular nucleus, and perhaps other tegmental centers. The fibers from the nucleus opticus tegmenti to the interpeduncular nucleus do not appear to be retinal fibers. Many of them cross the oculomotor roots at their exit from the brain, but do not ascend to the oculomotor nucleus, as Frey ('35) described in the guinea pig, squirrel, and opossum. The occurrence of apparently numerous connections of the nucleus opticus tegmenti in the opossum is in accord with the observations of Shanklin ('33) in Chameleon. Unfortunately, the connections in the opossum, with the exception of the retinal connections, are not entirely clear in the available material.

3. Unmyelinated collaterals of optic fibers possibly enter the ventral nucleus of the lateral geniculate body and perhaps the pretectal nucleus as well. Feebly myelinated fibers appear to terminate in the pars caudalis of the pretectal nucleus.

4. The optic tracts contain several components not of retinal origin. Below the dorsal level of the cerebral peduncle these consist of fibers of the commissures of Meynert and of Gudden. Above the dorsal angle of the cerebral peduncle (i.e., in the stratum zonale thalami) the optic tracts contain a few fibers of Gudden's commissure, external cortico-tectal fibers, and cortico-thalamic fibers to the dorsal lateral geniculate nucleus and to the nucleus lateralis pars posterior. The latter fibers enter the optic tracts from the dorsolateral part of the cerebral peduncle. Such fibers were described in the mole by Ganser (1882). In addition, geniculo-tectal fibers, predominantly from the ventral nucleus of the lateral geniculate body, are seen to pass into the optic tract in silver preparations of specimens with bilaterally degenerated optic nerves.

CONNECTIONS OF THE VENTRAL THALAMUS

Zona incerta. There now appears to be general agreement that the zona incerta represents an important substation in the course of descending cortical, striatal, and perhaps hypothalamic fibers and is itself functionally related with lower centers in the tegmentum and with the tectum. The various connections which occur in the opossum are grouped below as follows:

1. Cortical connections. Many collaterals of fibers of the cerebral peduncle pass to the zona incerta. Many of these may be of cortical origin (Ramón y Cajal, '11).

2. Striatal connections. The zona incerta appears to receive a great number of fibers from the striatum by way of the ansa lenticularis, the lenticular fasciculus, and the subthalamic fasciculus mentioned below. Many of the fibers of the ansa lenticularis are clearly derived from the globus pallidus.

3. Commissural connections. Many fibers of Meynert's commissure appear to connect with the rostral parts of the zona incerta. At the caudal end of this nucleus numerous fascicles connect the zonae incertae by way of the supramammillary decussation (figs. 25 and 26).

4. Hypothalamic connections. The fiber relations of the zona incerta with the hypothalamus are extremely prominent and widespread in the opossum. It is generally assumed that the direction of conduction in this system is toward the zona incerta, but our material is also suggestive of contrarywise conduction. This system is labeled in the figures as tractus hypothalamico-incertalis. It connects chiefly with the dorsal hypothalamic nucleus, the dorsomedial nucleus, and the posterior hypothalamic nucleus, and, to a lesser extent, with the dorsal part of the anterior hypothalamic nucleus, the filiform nucleus, and possibly with the ventromedial nucleus (figs. 22 and 23).

5. Tectal connections. Incerto-tectal fibers, as described by Gurdjian ('27) in the rat, appear to be present in the opossum as well. These seem to be accompanied in their course to the

tectum by some fibers of Meynert's commissure (fig. 2, dec.sup. opt.d.v.).

6. Tegmental connections. Connections of the zona incerta with tegmental centers are evident in the material examined. Most of these descending fibers form a diffuse but distinct bundle, the tractus incerto-tegmentalis, which descends in company with, and mingled with, the internal fibers of the tractus geniculatus descendens (figs. 2 and 4). In sagittal sections these fibers are seen to pass caudally in the zona incerta to its caudal end, where they turn sharply ventralward and descend to the nucleus opticus tegmenti and the substantia nigra. The most medial fibers are directed more caudally and were labeled by Tsai ('25 a, fig. 4) as "tractus strio-nigralis." It has not been possible to determine in the available material whether the predominantly incertal fibers are accompanied in their course to the substantia nigra by fibers of striatal origin, but this seems probable.

7. Internuclear connections. Connections of the zona incerta with other centers of the ventral thalamus probably exist but cannot be clearly established in the available material.

It has also been impossible to find any suggestions in our material of terminating medial lemniscus fibers in the zona incerta, as described by Ramón y Cajal ('11), and others.

Nucleus geniculatus lateralis ventralis. A thorough re-examination of all the normal and experimental material at hand allows us to add a few details to a previous study (Bodian, '37) and to summarize all the evidence of the connections of this center as follows:

1. Retinal connections. A few fibers enter the ventral part of the lateral geniculate nucleus from the optic tract. In reduced silver material some of these appear to be collaterals, and probably unmyelinated. It has been shown in an earlier study (Bodian, '37) that after optic nerve section Marchi granules of the terminal variety are not seen in this nucleus, although abundantly present in the dorsal nucleus. This also suggests that the retinal connections of this nucleus are by way of fine unmyelinated collaterals from the coarse myelinated

fibers of the optic tract. In deeply stained Weigert material one gets the impression that some of these fine fibers are feebly myelinated.

2. Tectal connections. In reduced silver preparations after bilateral optic nerve degeneration numerous normal fibers enter the degenerated optic tract from the ventral nucleus of the lateral geniculate body. These turn dorsally in the optic tract and presumably connect with the tectum, although it is impossible to follow them the entire distance. The direction of conduction is of course not certain, and it is conceivable that some of these fibers are connections of the zona incerta with the tectum.

3. Descending connections. These connections will be considered in the discussion of the tractus geniculatus descendens. There is a free passage of fibers between the ventral nucleus of the lateral geniculate body and the zona incerta.

4. Commissural connections. It has been mentioned in connection with Meynert's commissure that the latter system passes in close relation to the ventral lateral geniculate nucleus. It has not been possible to determine with certainty that synaptic relations are established, although it seems fairly clear that Meynert's commissure connects with the zona incerta, a closely related center.

Tsang ('37) in a recent interesting study of the optic tracts in the rat found that the cells of the ventral lateral geniculate nucleus never show atrophic changes in blinded rats, "irrespective of the time of operation and period of degeneration." He suggests, as have other workers, a less intimate relation of the optic tract to this nucleus than to the dorsal lateral geniculate nucleus or to the tectum, a view which is in agreement with all of our observations in the opossum.

Tractus geniculatus descendens and tractus peduncularis transversus. Since the description of the tractus geniculatus descendens by Beccari ('23) in the lizard, apparently homologous bundles have been recognized in other reptiles by Huber and Crosby ('26) and Cairney ('26). Rioch ('31) has further suggested that the connections of the ventral part of the lateral

geniculate body with the zona incerta as described by Gurdjian ('27) in the rat, by Clark ('30) in *Tarsius*, and by Rioch ('31) in carnivores probably represents the mammalian homologue of the reptilian tractus geniculatus descendens. A comparable bundle in the opossum has not been described before, but in the present study sagittal sections have revealed a large myelinated bundle which bears an astonishing resemblance in most of its relations to the tractus geniculatus descendens of reptiles, especially in *Sphenodon* (compare figs. 2 and 4 with Cairney, fig. 38, and Huber and Crosby, '26). The caudal connections of this tract in reptiles has not been elucidated, although it has been followed as far as the caudal end of the diencephalon by Huber and Crosby ('26) and as far as the "ventral part of the mesencephalon" by Cairney ('26).

It has been possible in the opossum to follow this bundle from the ventral nucleus of the lateral geniculate body and from the zona incerta into the nucleus opticus tegmenti via the so-called tractus peduncularis transversus, and also to more caudal centers of the tegmentum, including the substantia nigra.

The tractus geniculatus descendens is best followed in sagittal Weigert sections in the opossum. It arises as a large but diffuse bundle from the ventral nucleus of the lateral geniculate body and passes obliquely caudalward and ventrally, below the dorsal nucleus of the lateral geniculate body (fig. 1). There are two topographically separate parts to this system, a superficial bundle and a more diffuse internal group of fibers.

The superficial bundle passes caudally within the ventral nucleus of the lateral geniculate body until it reaches a position directly below the medial geniculate body. Here it turns sharply ventralward (fig. 1), and, emerging on the surface of the brain at the dorsolateral angle of the cerebral peduncle, swings ventrally and caudally around the latter as the major part of the so-called tractus peduncularis transversus (figs. 1, 2 and 26). The latter bundle joins the posterior accessory optic tract near the ventrolateral angle of the cerebral peduncle, a position occupied by the accessory optic tract throughout its

course, and the two systems then pass as a single bundle to the nucleus opticus tementi. This explains, therefore, why the main part of the transverse peduncular tract remains intact after complete degeneration of both optic nerves in the opossum, and thus cannot be considered as entirely composed of retinal fibers. The present findings also clarify the course of the transverse peduncular tract from the ventrolateral angle of the medial geniculate body, where it crosses the fibers of Gudden's commissure (fig. 1), to the nucleus opticus tementi, and suggests that the bundle which Frey ('37) described as originating in the nucleus opticus tementi and passing to the medial geniculate body, was probably the superficial part of the tractus geniculatus descendens. The latter bundle is also probably comparable with the fibers in the guinea pig which Castaldi ('23) regarded as passing from the tectum, over the surface of the medial geniculate body, to the nucleus opticus tementi. The fibers of the capsule of the medial geniculate body do not appear, however, to enter the transverse peduncular tract in the opossum.

The internal part of the tractus geniculatus descendens is continuous with the superficial part at the region of origin. More caudally it passes through, and medial to, the cerebral peduncle, mingled with incerto-tegmental fibers (figs. 2 and 4). The fibers appear to proceed to the nucleus opticus tementi, the substantia nigra, and probably other tegmental centers as yet to be determined. The course of the internal part is more comparable with that described in the peduncle-lacking reptiles, and the two parts of the tractus geniculatus descendens in mammals, superficial and internal, may then perhaps be considered as produced by the development, in the course of phylogeny, of a large cerebral peduncle in the caudoventral part of the single primitive reptilian tractus geniculatus descendens.

It may be concluded, in summary, that in the opossum the so-called transverse peduncular tract consists of two principal components, namely the superficial part of the tractus geniculatus descendens, and the posterior accessory optic tract. For

a summary of the earlier literature on the tractus peduncularis transversus, reference may be made to the work of Ariëns Kappers, Huber and Crosby ('36). In higher mammals there are apparently other systems, unrelated to that found in lower mammals, which pass as superficial bundles over the surface of the cerebral peduncle.

Nucleus reticularis. The connections of the reticular nucleus are obscure. The cells are embedded in the thalamic radiations and may conceivably be connected with them. In our reduced silver preparations cells of this nucleus are often seen in groups or strands oriented along fiber bundles of the dorsal amygdalo-hypothalamic tract, and other strio-hypothalamic bundles which penetrate the internal capsule. Ramón y Cajal ('11) stated that this nucleus receives fibers from the striatum.

The pars medialis of the nucleus reticularis apparently is a significant differentiation of the reticular nucleus in the opossum, and its connections are more readily studied. Many fibers of the dorsal amygdalo-hypothalamic tract pass through this nucleus on their way to the hypothalamus and many seem to terminate within it. The medial reticular nucleus also appears to receive fibers of the strio-hypothalamic and incerto-hypothalamic systems as they pass through the ventral part of the nucleus. As has been mentioned in the previous report on the cell groups of the diencephalon, the medial reticular nucleus is in close contact with the lateral surface of the dorsal hypothalamic nucleus, with which it appears to be intimately associated in its connections. The relations just described are most clearly seen in reduced silver preparations, in which both cells and fibers are impregnated.

In sagittal Weigert sections a small group of fibers has been seen to pass between the reticular nucleus and the nucleus subthalamicus. It is not possible to say that these fibers are connected with the reticular nucleus rather than being derived from the internal capsule.

Nucleus entopeduncularis. This nucleus is an interstitial nucleus in the course of descending striatal fibers and, as has been mentioned in the previous report, is more or less continu-

ous rostrally with the globus pallidus. It is in the course of the ansa lenticularis and the strio-peduncular systems of fibers, and probably is connected with these fibers. The intrapeduncular portion of this nucleus is associated not only with the descending strio-peduncular fibers but also with the perforating or transpeduncular fibers of Meynert's commissure. It probably corresponds also to the nucleus of Meynert's commissure described in pig embryos by Shaner ('36) and to the nucleus decussationis supraopticae dorsalis of reptiles, which is recognized as a differentiated entopeduncular group (Huber and Crosby, '26).

Nucleus subthalamicus (figs. 5, 17, 24, and 25). The nucleus subthalamicus appears to receive fibers from both the ansa lenticularis and the fasciculus subthalamicus (the medial division of the ansa lenticularis of von Monakow). In addition to its striatal connections, the subthalamic nucleus receives colateral and terminal fibers of cortical origin from the cerebral peduncle. Connections with the zona incerta and with Meynert's commissure have been mentioned elsewhere. Descending connections, although undoubtedly present, have not been evident in our material. Many fibers from the nucleus subthalamicus are seen to enter the supramammillary decussation (fig. 25).

Field of Forel. The nucleus of the field of Forel, as noted in the previous report of this series, is a diffuse area of gray continuous with the zona incerta at the dorsocaudal pole of the lateral hypothalamic area. It is a region of passage of numerous fiber systems, including the fasciculus lenticularis, and may be considered as a rostral continuation of the mid-brain tegmentum (Forel, 1877). In the human brain, Dejerine ('01) considered this field to be the anterior part of the capsule of the nucleus ruber. The cells in this area are probably connected with the lenticular bundle, as well as with the fibers of the ansa lenticularis, and are also associated with the zona incerta, the posterior hypothalamic nucleus, the neighboring ventral nucleus of the medial longitudinal fasciculus, and the tegmentum. Ramón y Cajal ('11 and '28) clearly described

and figured in the mouse a large bundle of collaterals of peduncle fibers passing to the field of Forel and perhaps to the nucleus ruber, which he compared with the radiations of Forel or H_2 bundle, and which he identified in the rabbit, rat, and cat later. We have seen this bundle, much as figured by Cajal in the mouse, in rat material, but have not found a correspondingly developed bundle in the opossum, unless the strio-tegmental bundle shown in figure 26 be so considered. The latter, in any case, in sagittal sections gives no evidence of being composed of collaterals, as is the case in the mouse and rat, and does not appear to be at all comparable with the H_2 bundle of Forel's description.

THE DESCENDING LENTICULAR SYSTEMS

Although the descending lenticular connections to the ventral thalamus and to the tegmentum are of considerable size and importance in the opossum, some of the fiber bundles are so intermingled with those of other systems, in and out of the cerebral peduncle, that they cannot be identified as separate fasciculi as readily as in some other forms. Three of these groups will be mentioned separately here because of their probable correspondence to similar but more discrete bundles in higher mammals. Of these only the *ansa lenticularis* is sufficiently compact, discrete, and characteristic in its relations, to be clearly homologous with the corresponding system in higher mammals including man (Dejerine, '01).

Ansa lenticularis (figs. 20 and 21). Loo ('31) has described this probably complex fasciculus in the opossum as the *ansa peduncularis*, with strio-tegmental, strio-subthalamic, and strio-hypothalamic components. In its passage into the dien-cephalon from the region of the globus pallidus, from which the majority of its fibers appear to originate, the *ansa* has a characteristic appearance and position. The fibers first pass medially as a strong fascicle ventral to the internal capsule, and then turn caudalward as a group of smaller bundles on the ventromedial aspect of the cerebral peduncle, between the rest of the peduncle and the medial forebrain bundle (tr.strio-

teg., figs. 22 and 23). In this position the fascicles are mingled with fibers of other systems and are in relation to small masses of gray of the entopeduncular nucleus (intrapeduncular nucleus of Livini, '07, and Loo, '31). As the strio-tegmental bundles descend they are crossed by the fasciculus lenticularis more caudally. The fibers of the ansa lenticularis may be divided into three main groups as was done by Loo. The strio-subthalamic component connects with the nucleus subthalamicus, the zona incerta, the entopeduncular nucleus, and the nucleus of Forel's field. It has not been possible to demonstrate satisfactorily a strio-hypothalamic component, but a connection with cells of the lateral hypothalamic area seems probable. The main mass of fibers derived from the ansa lenticularis descends as the tractus strio-tegmentalis to the level of the supramammillary decussation, where it turns dorsally between the nucleus subthalamicus and the rest of the cerebral peduncle (figs. 25 and 26) and passes to the tegmentum of the midbrain. Fibers could not be followed beyond the nucleus lateralis profundus mesencephali. Connections with the nucleus ruber and the substantia nigra could not be clearly determined, although they are probably present.

Fasciculus lenticularis and fasciculus subthalamicus (fig. 24). Ventral to the external medullary lamina one sees a diffuse bundle of fibers passing medially from the dorsal part of the cerebral peduncle. This bundle passes horizontally and somewhat ventrally into the most ventral part of the zona incerta and thus lies on the dorsal surface of the peduncle and of the nucleus subthalamicus (fig. 24). Rostrally its fibers mingle with those of the circumpeduncular part of Meynert's commissure, and medially and ventrally many fibers meet those of the ansa lenticularis and of the transpeduncular part of Meynert's commissure in the region of the nucleus subthalamicus. We have taken this rather diffuse group of fibers to be comparable with the lenticular fasciculus of other authors (see Ariëns Kappers, Huber and Crosby, '36). Many of its fibers pass to the nucleus subthalamicus, and these fibers may be comparable with the fasciculus subthalamicus of other

authors. Other fibers connect with the zona incerta and the gray of Forel's field. Some of the caudalmost fibers appear to enter the supramammillary decussation (commissure of Forel) but these are so intermingled with fibers of the zona incerta and of the nucleus subthalamicus in this region that it is not possible to determine this point with certainty in normal adult opossum material. Dejerine ('01) found no degeneration of fibers of this commissure after lesions of the striatum in man.

CONNECTIONS OF THE HYPOTHALAMUS

Fasciculus supraopticus and the so-called hypothalamic optic root of Frey. Both Tsai ('25) and Loo ('31) have described and clearly illustrated a bundle of fibers which passes in a cephalocaudal direction in contact with the dorsal surface of the optic chiasma. This bundle, the fasciculus supraopticus of Röthig ('09), and the fasciculus of the tuber cinereum of Ramón y Cajal, Tsai observed in Weigert material to connect the nucleus of the diagonal band of Broca with the tuber cinereum. Loo ('31), who termed this bundle the fasciculus suprachiasmaticus, thought that it contained fibers from the nucleus preopticus medianus, the nucleus preopticus periventricularis, and the nucleus epichiasmaticus (nucleus ovoid-eus), which pass chiefly to the infundibular stalk and hypophysis. Loo noted that part of the fibers cross in the anterior suprachiasmatic commissure. It has been possible to confirm some of Loo's findings and to note that many fibers of this bundle seem to terminate in the nucleus supraopticus diffusus and the ventromedial hypothalamic nucleus, whereas no fibers in our material have been followed into the hypophyseal stalk. Apparently only good Golgi material will be adequate to settle this point.

One of the reasons for considering this bundle again has been to suggest that probably the fibers which Frey ('37) has described as connecting the retina with the hypothalamus represent this fasciculus supraopticus of Röthig, as Frey's own figures show. Frey does not make mention of the work of Röthig, Loo, or Tsai, and apparently has not examined sagittal

sections, which are the only sections that demonstrate clearly the nature of the supraoptic fasciculus. In horizontal sections it is impossible to separate the fibers of the supraoptic fasciculus from the fibers of the optic chiasma, since the supraoptic fasciculus arches over the chiasma in contact with the optic fibers in the midline, where the chiasma forms a median ridge (compare figs. 10 and 20). It is this dorsal median ridge of the chiasma which Frey has identified in horizontal sections as a dorsally placed hypothalamic optic root. His uncrossed hypothalamic fibers, degenerated in Marchi preparations after removal of an eye, are evidently fibers which are about to cross, and which are clearly crossing in his figures 35, 37, and 39. He has not followed degenerated fibers out of the chiasma. This he maintains is due to the fact that the hypothalamic optic fibers become unmyelinated at the caudal border of the chiasma. A more obvious explanation is that the true optic fibers do not enter the hypothalamus, and that the unmyelinated fibers which enter the hypothalamus belong to the non-optic fasciculus supraopticus. In the opossum this bundle consists of both unmyelinated and feebly myelinated fibers. Ramón y Cajal considered most of the fibers to be unmyelinated in the mouse, and was convinced that none of these fibers were of optic origin.

It is thus possible to conclude that, if hypothalamic optic fibers do exist, they have not been demonstrated by Frey who has erroneously interpreted the relations of two other systems, namely the preoptico-hypothalamic fibers of the fasciculus supraopticus and optic chiasma fibers not destined for the hypothalamus. The theoretical conclusions of Frey regarding the phylogeny of the so-called hypothalamic optic root and the presumed function of this non-existent system in mammals in the sympathetic innervation of the pupil, and in the regulation of adaptive phenomena in the retina, are therefore largely unwarranted.

Periventricular region (grisea centralis)

Nucleus hypothalamicus periventricularis. The narrow zone of undifferentiated periventricular gray in the hypothalamus

appears to be connected with short fibers of the anterior periventricular system, some of which are unmyelinated, and with the neighboring gray of the medial group of hypothalamic nuclei.

Nucleus ovoideus. Gurdjian ('27) described connections of this nucleus with the stria terminalis and pointed out an intimate relation to the supraoptic complex of fibers. No connections with these systems have been found in our opossum material, although some fibers which enter the nucleus from a dorsal and lateral direction might conceivably be derived from the stria terminalis. Loo ('31) described connections with his anterior suprachiasmatic commissure and with the fasciculus supraopticus, which seems apparent in our material. It has also been possible to find connections with a few fibers from the anterior periventricular system and from the medial forebrain bundle.

Nucleus premamillaris dorsalis. The dorsal premammillary nucleus represents a condensation of the periventricular gray medial to the caudal part of the ventromedial hypothalamic nucleus, with which it is connected. There are also numerous short fibers, both unmyelinated and feebly myelinated, connecting with the ventral premammillary nucleus.

Nucleus premamillaris ventralis. The ventral premammillary nucleus receives fibers of the ventral olfacto-hypothalamic tract by way of the medial forebrain bundle, is connected with the dorsal premammillary nucleus by short periventricular fibers, and is also connected with the ventromedial hypothalamic nucleus and the mammillary nuclei.

Medial region

Nucleus hypothalamicus anterior. Except for the dorsal part, which is closely associated with the dorsal hypothalamic nucleus and merges with it caudal to the filiform nucleus, the anterior hypothalamic nucleus is inseparable from the medial preoptic nucleus except by definition, and has connections similar to those of the latter. Olfactory connections by way of the medial forebrain bundle are prominent. These are the tractus

olfacto-hypothalamicus of Tsai ('25) and the tractus olfacto-hypothalamicus ventralis of Loo ('31). The anterior hypothalamic nucleus is also connected with the most caudal fibers of the preoptic component of the stria terminalis (component 2 of Johnston, '23), with the medial cortico-hypothalamic tract, with the nucleus ovoideus, and with the nucleus hypothalamicus ventromedialis. The dorsal part of the anterior hypothalamic nucleus contributes fibers to the posterior periventricular system, and is related by fiber bundles with the dorsal amygdalo-hypothalamic tract and with the zona incerta.

Nucleus tangentialis. It has been difficult in the available normal material to determine clearly the connections of this undoubtedly important center. Terminals of the medial fore-brain bundle were described by Loo ('31, tr.olf.sop.) and appear to be present in our material. The relation of this nucleus to the tractus hypophyseus is described in the account of the latter. It remains only to emphasize that the cells of the medial or tuberal portion of this nucleus are embedded in the tractus hypophyseus as it passes along the floor of the infundibulum, and thus may be considered as an interstitial nucleus of the latter. Connections with the neighboring optic tract or Meynert's commissure have not been detected. Also no evidence has been found for connections with the stria medullaris as described by Koelliker (1896), Loo ('31, p. 41), and others.

Cells of the diffuse portion of the tangential nucleus, scattered along blood vessels in the lateral hypothalamic area, and forming a bridge between the supraoptic and tuberal parts of the tangential nucleus and the lateral filiform nucleus, are also seen along the course of fibers of the tractus hypophyseus and are often oriented parallel with the latter.

Nucleus filiformis. The lateral and, particularly, the paraventricular portions of this nucleus appear to be widely connected. The paraventricular part is related with the dorsal thalamus by way of the anterior periventricular system of fibers and receives terminals from the medial cortico-hypothalamic tract. Both parts are connected with the dorsal amygdalo-hypothalamic tract, and especially with the zona in-

certa. The direction of conduction in the fibers from the zona incerta is not clear, and it is possible that some of them are of striatal origin. The preparations examined suggest that the fibers are passing from the zona incerta to the filiform nucleus. Both the paraventricular and lateral parts of the filiform nucleus are connected with the neighboring dorsal hypothalamic nucleus and medial reticular nucleus, and contribute numerous fibers to the tractus hypophyseus as will be described in the account of the latter.

Tractus hypophyseus. This bundle is of large size in the opossum, and is composed of great numbers of unmyelinated and feebly myelinated fibers. It has been followed best in well-impregnated reduced silver material. Although the exact origin of this tract has not been observed in the available material, the course and distribution of the fibers where first seen suggest that they may arise from the large cells of the nuclei magnocellulares hypothalami, which consist of the various parts of the tangential and filiform nuclei. The scattered large cells of the diffuse part of the tangential nucleus are very numerous in the opossum, and some form bridges of cells between the lateral filiform and the tangential nuclei, frequently being found clustered along blood vessels. In one reduced silver series, prepared by a method previously described (Bodian, '36 and '37), all of the large cells of the tangential and filiform nuclei have been selectively and heavily impregnated with silver, as was mentioned in the first report of this series. None of the cells of the lateral hypothalamic area, large or small, caudal to the tangential nucleus, or rostral to the filiform nucleus, have been so heavily impregnated, so that from this preparation one gets the impression that the large cells of the filiform and tangential nuclei form a uniform group of cells of similar form and staining properties. There is evidence also that these cells, which have been shown by Scharrer ('33) to contain peculiar cytoplasmic inclusions, give rise to at least part, if not all, of the hypophyseal tract (see references cited, Bodian, '39, and Magoun and Ranson, '39). Many of

these cells are found in the course of the tract and are oriented along the fibers, especially in the lateral hypothalamic area.

From the paraventricular and lateral parts of the filiform nucleus, fibers appear to pass laterally and ventrally into the lateral hypothalamic area, where they join other fibers of this area which perhaps arise from the large cells of the nucleus tangentialis pars diffusa in this region. In the lateral hypothalamic area these fibers form a large but diffuse bundle which passes caudally and ventrally around the lateral border of the ventromedial hypothalamic nucleus, constituting part of the capsule of the latter. Here the most rostral fibers mingle with those of the dorsal supraoptic decussation. As the fibers of the hypophyseal bundle course ventrally and caudally around the ventromedial hypothalamic nucleus, they bend medialward until they reach the lateral margin of the infundibular stalk, where they form a compact bundle along the ventral margin of the hypothalamus. This bundle passes caudally around the base of the stalk and enters the latter to continue down into the pars nervosa of the hypophysis. As the tract which descends from dorsal parts of the hypothalamus reaches the ventral margin of the hypothalamus it is joined by fibers which pass medially and caudally, from the region of the supraoptic and tuberal parts of the tangential nucleus, along the ventral margin of the hypothalamus.

As the large hypophyseal tract passes into the central medullary portion of the spherical pars nervosa of the hypophysis, its fibers spread out, ramify, and form a dense feltwork of fine fibers which terminate between the cells of the pars nervosa. No fibers of the hypophyseal tract could be followed beyond the pars nervosa into the substance of either the pars intermedia or the pars distalis of the hypophysis.

Nucleus supraopticus diffusus. Gurdjian ('27) described this scattered gray as the bed nucleus of Ganser's commissure, and noted a contribution to the latter bundle from some of the cells. Our material is adequate only to show that these scattered cells, which perhaps do not deserve a separate appella-

tion, are intercalated between the fibers of both Ganser's and Meynert's commissure.

Nucleus hypothalamicus ventromedialis. This large and well differentiated hypothalamic center is permeated by a wealth of fine unmyelinated fibers, as is apparent in our protargol preparations, and as remarked by Ramón y Cajal many years ago. In Weigert preparations this principal nucleus of the tuber cinereum has a characteristic and pale appearance due to the presence of only a few feebly myelinated fibers within it. The fibers of the incoming and outgoing systems, as well as fibers of unrelated systems, tend to accumulate at the borders of the nucleus, thus encapsulating it to some extent. Descending fibers of the medial forebrain bundle, forming the tractus olfacto-hypothalamicus ventralis, enter the rostral, lateral, and ventral surfaces of the ventromedial nucleus and arborize within the latter. The chief descending discharge from the ventromedial hypothalamic nucleus passes by way of the posterior periventricular system, there being numerous unmyelinated as well as feebly myelinated fibers entering the latter important hypothalamic projection tract. Numerous descending fibers also appear to enter the medial forebrain bundle in company with fibers from the dorsomedial hypothalamic nucleus which form part of the hypothalamico-tegmental tract.

The ventromedial nucleus is also connected with neighboring centers, especially the ventral premammillary nucleus, and receives fibers from the fasciculus supraopticus, described above.

Nucleus hypothalamicus dorsomedialis. The dorsomedial hypothalamic nucleus receives fewer descending fibers from the medial forebrain bundle than does the ventromedial nucleus but, unlike the latter, it is connected widely with the zona incerta by means of a prominent bundle, the tractus hypothalamico-incertalis (figs. 22 and 23), which has its chief hypothalamic connections within the nucleus dorsomedialis. Descending bundles from the dorsomedial nucleus by way of the posterior periventricular system and with the coarse fibers of the hypothalamico-tegmental tract are also apparent, as

well as connections with neighboring hypothalamic nuclei, especially the ventromedial nucleus. It has been noted in the previous report in this series that cells of various types are present in this nucleus. Some of the largest cells perhaps contribute to the fairly coarse fibers of the hypothalamico-incertal and the hypothalamico-tegmental systems.

Possible connections of the dorsomedial hypothalamic nucleus with the medial cortico-hypothalamic and dorsal amygdalo-hypothalamic tracts have been mentioned in the consideration of these fiber systems.

Nucleus hypothalamicus posterior. The posterior hypothalamic nucleus is continuous rostrally with the dorsomedial hypothalamic nucleus and has somewhat similar connections. It receives fibers descending in the medial forebrain bundle and possibly also fascicles from the dorsal amygdalo-hypothalamic tract. Descending fibers enter the posterior periventricular system in large numbers and other fibers, fewer in number, enter the hypothalamico-tegmental tract. Laterally, it is intimately related to the gray of Forel's field and to the zona incerta and numerous fibers pass between these centers. There are indications that the lenticular fasciculus terminates in part in the posterior hypothalamic nucleus. The posterior hypothalamic nucleus is related ventrally to the mammillary complex, and caudally to that part of the central gray of the mesencephalon which we have designated as the ventral nucleus of the fasciculus longitudinalis medialis, and which perhaps correspond to the nucleus "4" of that bundle, as described by Keene and Hewer ('33).

The important connection with the posterior periventricular system and its caudal continuation, the fasciculus longitudinalis dorsalis of Schütz, was clearly described by Ramón y Cajal ('11—noyau postérieur du tuber) and, since then, by many others.

Nucleus hypothalamicus dorsalis. This nucleus was not described in the rat by Gurdjian ('27) but a comparable gray center is apparently present in some carnivores (Rioch, '29). In the opossum it is very large and apparently of some impor-

tance, judging by the richness of the related fiber feltwork. Rioch described the most striking connection of this nucleus as a bundle of finely myelinated fibers entering its dorsolateral surface from the medial end of the external medullary lamina, and connecting it with the ventral margin of the nucleus ventralis pars medialis. This apparently is the connection which we have succeeded in tracing, not to the ventral nucleus, but to the dorsal amygdalo-hypothalamic tract, for which the dorsal hypothalamic nucleus is the principal terminus. The fibers of this tract, which is described elsewhere in this account, enter the lateral surface of the dorsal hypothalamic nucleus and tend to encapsulate it partially before penetrating it and arborizing within it. With these fibers are apparently some derived from the medial reticular nucleus and from the zona incerta. The dorsal hypothalamic nucleus contributes numerous fibers to the posterior periventricular system, and is also associated with the neighboring filiform and dorsomedial nuclei, and with the nucleus reuniens.

Nucleus supramammillaris. The supramammillary nucleus forms a transition zone between the hypothalamus and the midbrain tegmentum and is a well differentiated group of cells of medium size. It is in a region of passage of fiber bundles of many systems, so that consequently its own connections, at least in our material, are not easily determined. It is associated topographically with the crossing fibers of the dorsal mammillary decussation below, and with the crossing fornix fibers in the supramammillary decussation above. It is penetrated by the mammillo-tegmental and mammillo-thalamic tracts. Connections with the posterior hypothalamic nucleus and with the mammillary nuclei are present, and its principal descending connection appears to be by way of the hypothalamo-tegmental tract. No fibers could be traced from this nucleus into the posterior periventricular system.

Connections of the mammillary bodies. In addition to the connections mentioned in the accounts of the fornix, the mammillary peduncle, and the mammillo-thalamic and mammillo-tegmental tracts, the mammillary bodies receive numerous

fibers which enter the capsule from the medial forebrain bundle and penetrate the lateral and medial nuclei. These fibers form the olfacto-mammillary tract and intermingle in the capsule of the mammillary bodies with fornix fibers. Short connections between the mammillary bodies and the supramammillary nucleus, the ventromedial hypothalamic nucleus, and the ventral premammillary nucleus have also been observed. Commissural connections within the mammillary complex are very numerous, and in addition to the crossing fibers within the median nucleus, two distinct bundles of fibers decussate in the anteroventral and posterodorsal regions of the mammillary complex. These are associated with interstitial gray.

The connections of the mammillary bodies have interested neurologists from the earliest times because of the conspicuous fiber bundles associated with these structures. Among modern neurohistological studies it is necessary to mention the fundamental observations of Ramón y Cajal ('04 and '11), Koelliker (1896), Dejerine ('01), Edinger and Wallenberg ('01), Castaldi ('23), Tello ('36), and other studies, which will receive attention in connection with the description of special connections.

Fornix. The fornix of the opossum has been considered in great detail by Loo ('31) who, however, mentioned but did not discuss its mammillary termination. Only the caudal connections of the fornix require consideration here therefore. As the columns of the fornix descend into the hypothalamus, they turn sharply caudalward above the caudal level of the optic chiasma and pass along the dorsolateral margins of the ventromedial hypothalamic nucleus to the dorsolateral margins of the mammillary bodies (fig. 6). At this point the fibers enter the capsule of the mammillary body, and then separate into three main groups. One group distributes to the lateral and medial nuclei on the same side, a second group crosses in the dorsal commissure of the mammillary bodies to the opposite side, and the third group passes dorsally and caudalward (fig. 26-F). The last bundle enters the supramammillary decussation (commissure of Forel), then crosses and turns caudally. In sagittal

sections, fibers from this region, of similar appearance but not clearly continuous with the fornix fibers, are readily followed to the dorsal margin of the interpeduncular nucleus. Here they turn dorsally in company with fibers from the latter nucleus and pass to the caudal part of the dorsal tegmental nucleus. It is interesting to note that after this relation had been observed, there came to our attention the important work of Tello ('36), who traced the decussating fornix fibers, in similar fashion, to the dorsal tegmental nucleus in the embryos of guinea pigs and cats. He found, as had Edinger and Wallenberg ('01), that considerable variability in the number of crossing fornix fibers existed in various mammals.

The mammillary peduncle. The large mammillary peduncle in the opossum has been described by Tsai ('25 a), who followed this bundle from the lateral part of the mammillary body to a level just caudal to the oculomotor roots, where the fibers appeared to intermingle with the fibers of the medial lemniscus. Tsai also suggested that some of the fibers might continue caudally and dorsally to terminate in the tegmental area. In the Weigert material examined in this study many fibers have been seen to turn sharply dorsalward just behind the point of exit of the oculomotor roots and to pass to the dorsal tegmental nucleus, in company with pedunculo-tegmental fibers. Others are lost in the medial lemniscus as Tsai mentioned. The most lateral fibers mingle with the fibers of the hypothalamo-tegmental and olfacto-tegmental tracts of the medial forebrain bundle and pass dorsal to the medial lemniscus. Some of these can be followed to the ventral tegmental nucleus and some to the rostral part of the dorsal tegmental nucleus, but the majority of fibers are lost in the tegmentum at the caudal end of the midbrain.

According to the present observations in normal material the mammillary peduncle connects with all parts of the ipsilateral mammillary body. The direction of conduction in the mammillary peduncle, whether ascending or descending, or both, has long been disputed, since the early demonstration by Ramón y Cajal ('04) in Golgi material of terminal fibers arbor-

izing in the lateral and medial nuclei of the mammillary body and, indeed, crossing to the opposite mammillary body in the mammillary commissures. For discussion of the various earlier viewpoints regarding this pathway the reader is referred to the works of Ramón y Cajal ('11) and Castaldi ('23). Recently, Papez ('23) has found that lesions in the mammillary peduncle in the rat produce only ascending degeneration in Marchi material, after 2 weeks, with terminals chiefly in the lateral mammillary nucleus but some also more rostrally in the tuber cinereum.

In a Marchi preparation of the opossum brain, 2 weeks after a unilateral lesion of the mammillary peduncle and medial lemniscus had been made, it has been possible to confirm the findings of Papez in the rat. Only ascending degeneration was detected and rostral to the lesion the entire mammillary peduncle appeared degenerated. Numerous Marchi granules could be followed into the lateral and medial mammillary nuclei on the side of the lesion, and also, for several sections rostral to the mammillary body, into the gray surrounding the fornix bundle. These observations agree with the decisive findings of Ramón y Cajal in Golgi material many years ago, and with the recent findings by Tello ('36) in mouse embryos.

Mammillo-thalamic and mammillo-tegmental tracts. The mammillo-tegmental tracts and mammillo-thalamic tracts are of great size in the opossum. They have been described briefly by Tsai ('25 a) in this beast. The mammillo-tegmental tracts arise in the median and medial nuclei of the mammillary body, pass directly dorsally and then turn sharply caudalward, as is best seen in sagittal sections (fig. 8). The dorsalmost bundles, which appear to arise in the most rostral part of the mammillary body, are joined where they turn caudally by bundles of the hypothalamo-tegmental and olfacto-tegmental tracts and proceed caudally into the midbrain tegmentum, beyond which they could not be followed. The ventral and caudal bundles of the mammillo-tegmental tract pass to the central tegmental nucleus, where many appear to terminate. Other fibers continue caudalward to an unknown termination.

Ramón y Cajal ('11) described in the mouse fibers of the mammillo-thalamic tract arising as collaterals from the mammillo-tegmental tract, as did Koelliker (1896), Gurdjian ('27) in the rat, and Tello ('34) in mouse embryos. Gurdjian followed fibers from the mammillary body directly into the mammillo-thalamic tract. This does not occur in the opossum. In the latter animal the mammillo-thalamic tract, when followed ventrally and caudally from its termination in the anteroventral and anteromedial nuclei, appears in Weigert material to pass ventrocaudally to a position dorsal and caudal to the mammillary body without apparent connections with the mammillo-tegmental bundles (fig. 9). It appears in this material that if these fibers are collaterals of the mammillo-tegmental fibers, then most of them must arise from the most ventral of the latter fibers. Most of the fibers cannot be traced beyond the supramammillary nucleus, although it is conceivable that from here fibers may pass ventrally, and rostrally into the capsule of the mammillary bodies.

As has been mentioned in connection with the anteroventral thalamic nucleus, an opossum brain, prepared by the Marchi method after a direct lesion of one bundle of Vicq d'Azyr, gave no evidence of fibers passing ventrally in this bundle, as was described by Clark and Boggon ('33) in the rat after lesions of the anteroventral nucleus. The presence of thalamo-mammillary fibers in the opossum appears further improbable because, as was mentioned, no fibers of the bundle of Vicq d'Azyr can be seen to pass directly into the mammillary body in this beast. The fibers are either all collaterals of the mammillo-tegmental bundles or must arise caudal to the mammillary bodies. Unfortunately, Golgi material necessary to settle this point is not available at present.

It is interesting that Fortuyn ('12) in an early developmental study of the thalamus in the rabbit, pointed out that the fibers of the bundle of Vicq d'Azyr grow only toward the anterior nuclei and not in the reverse direction. Because of the late appearance of the mammillo-thalamic tract in ontog-

eny, as compared with the mammillo-tegmental tract, Fortuyn concluded, with van Valkenburg ('12), on the basis of this inconclusive evidence, that these two bundles are independent in their origin, contrary to the direct observations of Ramón y Cajal and Koelliker in Golgi material (see also Tello, '36). Ibañez ('35) has recently reported on the basis of Marchi studies that the common bundle of origin of the mammillo-thalamic and mammillo-tegmental tracts arises in the medial nucleus, as observed by most workers, but that a small mammillo-tegmental component also arises in the lateral nucleus and is independent of the bundle of Vicq d'Azyr. It is quite possible that a certain amount of variability may be present in some of these phylogenetically young bundles in different species or even in different individuals of the same species, as was shown to occur in the final course and endings of the fornix bundle in the rabbit, by Edinger and Wallenberg ('01).

Tello ('34) has recently observed a partial crossing of the mammillo-tegmental bundles in the developing mouse embryo, the decussation occurring in the supramammillary commissure. He has also noted that many fibers of the mammillo-thalamic and mammillo-tegmental bundles arise as branches from a single fiber with origin in the mammillary body but that many mammillo-thalamic and mammillo-tegmental fibers also may have a direct origin from this center. This does not appear to be the case in the opossum, so far as the mammillo-thalamic tract is concerned.

Lateral region

Nucleus hypothalamicus lateralis. This diffuse nucleus is in part an interstitial nucleus of the medial forebrain bundle and probably has many diverse connections, especially with the medial group of hypothalamic nuclei and with the sub-thalamic nuclei. The designation of this large diffuse cell group as a distinct nucleus is arbitrary, since it contains cells of several types and is a region of passage of a great many different fiber systems.

Tractus cortico-hypothalamicus medialis

This bundle was described in the rat by Gurdjian ('27) and in the opossum by Loo ('31). It is possible to add some additional details to our knowledge of this system in the opossum. The medial cortico-hypothalamic tract in the opossum descends with the rest of the postcommissural fornix in company with the medial cortico-habenular tract. It separates from the latter, which is very large in the opossum, behind the inter-ventricular foramen (fig. 9). In transverse sections in this region it appears as a strong bundle of fibers, finer than those of the rest of the fornix, forming a triangular cap over the latter and placed in the ventral angle between the nucleus reuniens anterior and the vertically ascending bundle of the stria medullaris (fig. 20, and Loo, fig. 56). This bundle can also be followed readily in horizontal sections, in which it is seen to pass caudally below the lateral margin of the anterior part of the nucleus reuniens and to enter the periventricular system caudal to the latter. As it passes caudally it contributes fibers to the periventricular region of the preoptic and anterior hypothalamic areas. At the caudal end of the bundle a few fibers swing lateral to the fornix column and descend into the lateral hypothalamic area. In this region fibers are apparently connected with the medial, and parts of the lateral, filiform nucleus. In sagittal sections the tract is readily traced after it parts company with the medial cortico-habenular bundle (fig. 8). It can be followed to the dorsocaudal pole of the medial preoptic nucleus behind the fornix column, to the filiform nucleus, and in large part, apparently, to the dorsal hypothalamic nucleus and the dorsomedial hypothalamic nucleus.

According to Gurdjian ('27), this tract is accompanied toward its terminations by a medial amygdalo-hypothalamic tract, and supplies the periventricular gray of the preoptic and hypothalamic regions as well as the dorsomedial and ventromedial hypothalamic nuclei. It has been possible to confirm this in the opossum material studied. In the opossum, how-

ever, the medial amygdalo-hypothalamic tract is largely replaced by the dorsal amygdalo-hypothalamic tract, which is apparently more highly developed than that in the rat, and has a wider distribution. A separate account is given of the dorsal amygdalo-hypothalamic tract below.

Tractus amygdalo-hypothalamicus dorsalis

This prominent tract in the opossum diencephalon is present as a rather dispersed fiber lamina separating the dorsal from the ventral thalamus in the anterior half of the diencephalon. The constituent fibers pass transversely through the reticular nucleus and, coursing medialward and ventralward dorsal to the internal capsule, fray out in the dorsal hypothalamic region before terminating. This system, although apparent in the figures of Tsai and Chu, has not been labeled or described by them. Loo ('31, II, pp. 46 and 69) considered at least some of the fibers to be reticulo-periventricular fibers to the filiform nucleus (see also Roussy and Mosinger, '35). This was the first impression of the present writer, and it is of course possible that fibers from the reticular nucleus may join this system. Yet careful tracing of this system in Weigert and silver material cut in several planes has shown clearly that the great majority, if not all, of these fibers arise from the stria medullaris component of the stria terminalis (component 5 of Johnston, '23), and undoubtedly correspond to part 5x of that component as described by van der Sprenkel. The latter, in his extremely detailed and careful analysis of the stria terminalis in the opossum ('26), considered this bundle to be a system which probably arises in the reticular nucleus (Gitternucleus) and terminates in the lateral and medial parts of the tuberculum olfactorium. We have been able to trace the diencephalic connection of this system to the hypothalamus, rather than to the reticular nucleus, and the telencephalic connection to the medial amygdaloid nucleus.

In transverse Weigert sections a very considerable proportion of these fibers are seen to terminate in the dorsal hypothalamic nucleus (fig. 21). A large number pass dorsal to the

latter nucleus, enter the periventricular system, and turn rostrally and caudally within this system. In horizontal sections (fig. 16) these fibers can be traced caudally to the dorsomedial hypothalamic nucleus and as far caudally as the posterior hypothalamic nucleus. The fibers which turn rostrally appear to be destined for the rostral end of the dorsal hypothalamic nucleus. Many of the fibers of this system pass ventral to the dorsal hypothalamic nucleus and terminate in the filiform nucleus (see also Loo, '31, fig. 62, tr.ret.pv.), in the dorsomedial hypothalamic nucleus, and, especially, in the dorsal part of the anterior hypothalamic nucleus, the cells of which resemble those of the dorsal hypothalamic nucleus. In the region of their diencephalic terminations, the fibers of this system intermingle with those of the tractus cortico-hypothalamicus medialis, as was mentioned. The caudalmost fibers also mingle with fibers of the hypothalamico-incertal tract.

As the fascicles of this system enter the diencephalon, it is difficult to observe in any plane of section their origin from component 5 of the stria terminalis, since this component, unlike the rest of the stria terminalis, is composed of fibers resembling those of the heavily myelinated stria medullaris and interweaves with the fibers of the latter at its lateral and caudal margin. Only transverse or horizontal sections are adequate to show the continuity of these fibers as they pass through the stria medullaris. In horizontal sections they form a thin sheet of fibers which pass medially, ventrally, and caudally from the stria medullaris, enter the periventricular system near the midline, and pass rostrally and caudally in the latter to the dorsal hypothalamic nucleus and to the gray ventral to the latter (fig. 16).

From this account it is obvious that this system is greater in size and wider in distribution than the perhaps corresponding medial amygdalo-hypothalamic tract of the rat. Gurdjian ('27) has described the latter tract as a rather small bundle joining the medial cortico-hypothalamic tract at the level of the middle third of the anterior commissure. In the opossum, fibers pass medially from the stria terminalis (component 5)

not only at the level of the vertically coursing stria medullaris just behind the anterior commissure, but also for a considerable distance caudally, and here pass medially through the reticular nucleus to the large dorsal hypothalamic nucleus. It is interesting that Ramón y Cajal ('11—p. 479) followed fibers of the stria terminalis to his "noyau superieur" and "n. posterieur" of the hypothalamus, which correspond respectively to the dorsomedial and posterior hypothalamic nuclei of this account. He did not find, however, the terminal arborizations of these fibers and his very brief note does not mention or give any indication as to which component of the stria terminalis was involved.

Tractus hypothalamico-tegmentalis

A sizable bundle of coarse myelinated fibers is readily identified in the caudal half of the hypothalamus. The fibers appear to arise from the dorsomedial and posterior hypothalamic nuclei chiefly, pass laterally into the lateral hypothalamic area and then turn ventrally and join the olfacto-tegmental fascicles in the medial forebrain bundle (fig. 24). Some fibers seem to join this system from the ventromedial hypothalamic nucleus, the lateral hypothalamic area, and the supramammillary nucleus as well. In the region of the mammillary bodies the bundle, composed largely of coarse fibers, comes to lie dorsal and lateral to the mammillary peduncle (fig. 25). Here the fibers mingle with the mamillo-tegmental bundles and all pass caudally together into the midbrain tegmentum.

The periventricular systems of fibers

The periventricular fibers of the diencephalon in the opossum are conveniently divided into two principal groups, an anterior group and a posterior group, the latter extending caudally into the fasciculus of Schütz. This subdivision is not only topographically distinct but, because of the difference in the main regions which are brought into relation by these

separate systems, seems to have a functional significance as well. There are unquestionably several distinct components in each of these groups as will be pointed out below.

Marburg ('31) has made a careful study of the entire extent of the posterior periventricular system (fasciculus periependymalis) in a series of normal mammalian, including human, brains, and in his comprehensive account has reviewed most of the pertinent literature on this interesting and somewhat neglected system. He emphasizes the relation of this system to the following: the hypothalamus; the dorsal tegmental nucleus of Gudden and the neighboring mesencephalic gray associated with olfactory dependencies, including the interpeduncular nucleus; and several gray centers surrounding the hypoglossal nucleus, and presumably related to vestibular, gustatory, vagal, and trigeminal impulses. He is in agreement with Edinger and later workers as to the "sympathetic" affinities of this system, and further suggests a possible role in the mechanism of nausea and vomiting.

The anterior periventricular system. The anterior periventricular system, in general, consists of fibers which pass vertically along the walls of the third ventricle, or on either side of the midline, and serve to connect chiefly the dorsal thalamus, and perhaps the epithalamus, with the periventricular gray of the hypothalamus. The fibers apparently conduct in both directions, and undoubtedly belong to several different systems. In the dorsal thalamus the fibers appear to connect with the nucleus parataenialis, the nucleus medialis dorsalis, the anterior paraventricular nuclei, the rhomboid nucleus, and the nucleus inter-medialis dorsalis. There are indications that some fascicles are related with the habenular nuclei, in addition to the fairly large bundles of the medial olfacto-habenular tract.

In the hypothalamus the fibers of the anterior periventricular system apparently connect with the periventricular gray and the lateral hypothalamic area as far back as the mammillary nuclei and fibers can be traced as far ventrally as the ventral premammillary nucleus.

The fascicles of the anterior periventricular system are very numerous in the dorsal thalamus and consist chiefly of fine myelinated fibers. As they are traced ventrally into the hypothalamus they rapidly decrease in number below the level of the dorsal hypothalamic nucleus and the filiform nucleus, in which many fibers appear to terminate. In the ventral part of the hypothalamus the periventricular fibers are few in number, very feebly myelinated or unmyelinated, and in reduced silver preparations give the appearance of being composed of many short fibers. Some of them cross under the ventral angle of the third ventricle, above the supraoptic decussations.

As has been mentioned, most of the fibers of the anterior periventricular system course vertically along the midline. Within the anterior paraventricular nuclei, however, scattered fine myelinated fibers pass in a rostrocaudal direction. In addition, some of the most medial periventricular fibers of the dorsal thalamus pass caudalward near the midline and join the most dorsal fibers of the posterior periventricular system. These fibers appear to terminate chiefly if not entirely in the nucleus paraventricularis posterior.

Lesions in the periventricular system in the midbrain produce no degeneration, as seen in Marchi material, in the fibers of the anterior periventricular system, although fibers of the posterior periventricular system appear to be affected, as will be described.

The posterior periventricular system (fasciculus periependymalis). The posterior periventricular system is an extensive group of fine myelinated fibers, a large part of which arises in the hypothalamus and descends in the central gray of the brain-stem. Here it forms a large part of the fasciculus of Schütz. This system is the fasciculus periependymalis of Ramón y Cajal and of Marburg ('31), the fasciculus longitudinalis griseus of Koelliker (1896—fig. 637), and the hypothalamic division of the periventricular system of fibers of Gurdjian ('27), Krieg ('32), and others. The fibers appear to arise in great numbers from the dorsal, the dorsomedial, and the posterior hypothalamic nuclei. Some fibers also appear to

connect with the dorsocaudal part of the anterior hypothalamic nucleus and with the ventromedial hypothalamic nucleus. It was mentioned previously that the cells of the dorsocaudal part of the anterior hypothalamic nucleus resemble those of the neighboring dorsal hypothalamic nucleus. The fibers from these two regions converge to form a Y-shaped system with the stem of the "Y" directed caudally above the dorsomedial and the posterior hypothalamic nuclei, as seen in sagittal sections. Fibers from the latter nuclei join the Y-shaped system, and all sweep dorsally and caudalward in the central gray (fig. 10). Most of the fibers continue caudalward into the central gray of the midbrain without apparent synapse, but many terminate in the nucleus paraventricularis posterior. Some fibers pass laterally and dorsally through the latter nucleus, along with additional fibers from it, and continue into the tectum and pretectal region. Fibers from the nucleus paraventricularis posterior also appear to join the descending hypothalamic periventricular fibers (fig. 10).

Fibers from the nucleus paraventricularis posterior pass into the tegmentum of the midbrain, but it has not been possible to determine whether any of such fibers are derived directly from the periventricular system. Few myelinated fibers of the posterior periventricular system were traced to the ventromedial hypothalamic nucleus, although in reduced silver preparations numerous fibers are seen to enter this system. No fibers of this system have been traced as far forward as the nucleus tangentialis, as described by Krieg ('32) and by Clark ('38).

As the fibers of the posterior periventricular system pass caudally in the central gray they form a large part of the dorsal longitudinal bundle of Schütz. In the opossum many are seen to terminate in the rostral part of the dorsal tegmental nucleus caudal to the oculomotor nucleus. Many also, however, pass caudally without synapse and are joined by fibers arising in the dorsal tegmental nucleus and in neighboring gray. Fibers are distributed from the dorsal longitudinal bundle into the tegmentum all along its course, and finally the

bulk of these fibers turn abruptly ventrally into the region of the vagal nuclei.

Interesting evidence regarding the connections of the posterior periventricular system has been obtained from two favorable Marchi preparations of the opossum brain. In one, in which the dorsal hypothalamic nucleus and dorsomedial hypothalamic nucleus of one side were injured by a relatively small lesion, osmium granules could be traced caudalward in the posterior periventricular system of the same side as far as the posterior paraventricular nucleus. In the other case the lesion was restricted to the posterior periventricular system of one side, within the confines of the posterior paraventricular nucleus and the rostral end of the central gray of the midbrain. From this region, osmium granules could be followed within the periventricular system in both rostral and caudal directions. Rostrally, degenerated fibers were followed ventrally into the hypothalamus, with most fibers passing into the dorsal hypothalamic nucleus and some also into the dorsomedial hypothalamic nucleus. Granules were traced rostrally in the dorsal hypothalamic nucleus up to the caudal border of the filiform nucleus. From the lesion granules were also followed caudally in the central gray of the midbrain, in a position just dorsal to the oculomotor nucleus. No fibers could be traced clearly below the level of the dorsal tegmental nucleus. Degenerated fibers appeared to pass dorsally and laterally from the lesion in the posterior paraventricular nucleus into the parafascicular and pretectal nuclei, but it is of course impossible to determine in this case whether these fibers had their origin in the posterior paraventricular nucleus or were part of the posterior periventricular system.

Most workers have hitherto assumed that most, if not all, of the fibers of the periventricular system are descending fibers from the hypothalamus. The evidence described above indicates that large numbers of fibers of the posterior periventricular system are ascending, as suggested by Marburg ('31), and pass to the hypothalamus, especially the dorsal hypothalamic nucleus, from more caudal centers. Among these the tectum,

the central gray of the midbrain, and the posterior paraventricular nucleus appear to be the most likely sources, but more caudal centers are not excluded as possible sites of origin of ascending fibers. Some of the latter may conceivably be visceral lemniscus fibers.

No indication of crossing of these fibers occurs rostral to the dorsal tegmental nucleus, in which a few fibers appear to cross in the Marchi material. In the second case described above, a sharp boundary in the midline separates the degenerated fibers of one side from the normal fibers of the other side, at a level such as that represented in figure 24. This unilateral distribution also seems to be clear enough in normal sections through the diencephalon.

Ramón y Cajal ('11) separated his fasciculus periependymalis (voie longitudinale péri-épendymaire, p. 193) into dorsal and ventral components, the dorsal one of which he was able to follow into the dorsal thalamus. These fibers perhaps correspond to those we have described as passing into the posterior periventricular system from the anterior and posterior paraventricular nuclei of the dorsal thalamus. Ramón y Cajal also pointed out that long and short fibers, and collaterals, were present in the periventricular systems. He was unable to ascertain the rostral connections of the ventral part, which forms the principal component in the opossum.

CONNECTIONS OF THE EPITHALAMUS

The chief afferent connections of the habenular nuclei pass by way of the stria medullaris, which was considered in some detail in the opossum by Loo ('31). The strong habenulo-peduncular tract with lateral and medial parts, derived respectively from the lateral and medial habenular nuclei, forms a direct efferent connection from the habenular nuclei to the interpeduncular nucleus. The fibers of this tract, on reaching the latter nucleus, penetrate its rostral and lateral surfaces and apparently then lose their myelin sheaths. In reduced silver preparations prepared with the protargol method, the fibers of the habenulo-peduncular tract are seen to form bundles of fine unmyelinated fibers which pass medially and

caudally through the interpeduncular nucleus, cross to the opposite side, and then turn back. Presumably collaterals are given off en route, as first described by Ramón y Cajal. Sagittal sections are suggestive of the possibility that some fibers of the habenulo-peduncular tract pass dorsal to the interpeduncular nucleus and join fibers from the latter nucleus which proceed dorsally to the dorsal tegmental nucleus.

The lateral habenular nucleus is connected with the nucleus medialis dorsalis, with the tectum, and with the nucleus paraventricularis posterior.

It has not been possible in our material to confirm the existence of a tractus olfacto-habenularis supraopticus, arising from the tangential nucleus, as described by Loo ('31).

The tractus cortico-habenularis medialis has been described in the opossum by Johnston ('23), by Loo ('31), and by Chu ('32), and appears also in the figures of Johnston ('13) and Tsai ('25 a). It is apparently entirely comparable to the bundle to which the term was applied in *Amphibia* by Herrick ('10), and to similar bundles in reptiles and in mammals (see Gurdjian, '25). This tract is of great size in the opossum, and has been described in sufficient detail by Loo ('31), to whom the reader is referred for a description.

DISCUSSION AND SUMMARY

The opossum diencephalon, with respect to nuclear configuration as well as to fiber connections, gives every evidence of being quite generalized, although typically mammalian. This much has been made clear from the many earlier studies on the brain of this lowly marsupial. It is the purpose here to review those features of the structure of the opossum diencephalon which are either newly described, more or less specifically characteristic, or otherwise worthy of emphasis. Although there are many indications of primitive features in the diencephalon as a whole, it is in the dorsal thalamus that the contrast with more specialized mammalian brains is most plain.

1. The marked development of the dorsal thalamic commissures, with greatest condensations in the interparataenial, interanterodorsal, central, and interventral regions (fig. 14) is worthy of special note. The central commissure, with its interstitial gray, the central and paracentral nuclei, is very prominent and forms a sizable component of the internal medullary lamina. It contains decussating as well as true commissural fibers, which probably serve to interconnect the nucleus medialis dorsalis, the paracentral, and the lateral nuclei of both sides. The first two nuclei appear to be associated with the striatum by way of the inferior thalamic radiations, and the nucleus medialis dorsalis and the central nucleus are further associated with the hypothalamus by way of the anterior periventricular system. This suggests the large central nucleus and the surrounding gray as a pivotal area in the integration of pallial, striatal, dorsal thalamic, and hypothalamic mechanisms. A similar relation appears to obtain in the case of the combined interparataenial and interanterodorsal commissures, which associate the pallial dependencies, in this case the anterior nuclei, with the closely related parataenial and perhaps subparataenial nuclei. The latter two nuclei are in turn strongly connected with the striatum by way of the inferior thalamic radiations and with the hypothalamus by way of the anterior periventricular system. The anterior paraventricular nucleus, closely linked with the anterior periventricular system of fibers, and perhaps with the habenular complex as well, is possibly involved in the functions of the neighboring parataenial nucleus, and the nucleus reuniens anterior appears to bear a similar relation to the nucleus subparataenialis. The prominence of the midline gray centers and the associated dorsal thalamic commissures and anterior periventricular system appears to be a predominantly mammalian characteristic which, however, in the form in which it is developed in the opossum, is comparable generally only with that in other relatively lowly mammals. In higher mammals, namely those in which the neopallium and associated centers of the dorsal thalamus attain a high development, the com-

missural portion of the midline complex is reduced, to a greater or lesser degree, but the anterior periventricular system and associated gray of the dorsal thalamus remains and forms an important link between the dorsal thalamus and the hypothalamus.

The interventral commissure must be considered to be of an entirely different nature from the other dorsal thalamic commissures. In the opossum the commissural fibers are probably exceeded in numbers by decussating fibers of primitive systems connecting the ventral nuclei, or chief sensory nuclei of the dorsal thalamus, with more caudal centers, and especially with the auditory centers of the tectum and thalamus. These strongly developed systems in the opossum are clearly homologous with the corresponding tractus tecto-reuniens and related tecto-thalamic tracts of reptiles (Huber and Crosby, '26 and '33), in which the commissural and decussating features are apparently not present. In the reptiles the nucleus reuniens and nucleus rotundus represent the thalamic centers which are connected with the tectum by means of these tracts. In the opossum, the perhaps corresponding nucleus reuniens posterior and the ventral nuclear group are connected with the tectum by crossed and uncrossed fibers of the tractus tecto-reuniens and tractus tecto-ventralis. In addition, and superimposed upon the primitive reptilian pattern, the above-mentioned tracts are mingled with fibers from the medial geniculate nucleus which form a geniculo-reuniens and geniculo-ventral connection. In the course of these combined systems of fibers (fig. 14, tr.tect.reun.) a prominent interstitial nucleus is found in the opossum, the nucleus subparafascicularis, which forms a bridge of cells between the medial geniculate nucleus and nucleus parabigeminus caudally and laterally, and the nucleus reuniens posterior and the poorly differentiated gray of the posterior paraventricular nucleus medially and rostrally.

2. The nuclei of the dorsal thalamus are clearly differentiated into the main groups characteristic of all mammals, as is also true of most of the constituent nuclei of these groups, but no striking specializations are apparent. The elementary

pattern of the projection of the dorsal thalamic nuclei on the neopallium is clearly present, as will be described in detail in a later report, so that the general homology of the nuclei involved with those of higher mammals is made possible on this basis, as well as on other grounds. The nuclei connected directly with the neopallium may be mentioned briefly. They are the anterior nuclear group, the entire ventral group, the lateral group, with the possible exception of the small nucleus lateralis anterior, the nucleus medialis dorsalis, the dorsal nucleus of the lateral geniculate body, and the pars centralis of the medial geniculate nucleus. The ventral group of nuclei and the pretectal nucleus appear to be the chief thalamic end-stations for the medial lemniscus. The marginal portion of the medial geniculate nucleus has little direct connection with the neopallium, but appears to be more closely associated with the subparafascicular nucleus, the nucleus parabigeminus, and the nucleus ventralis than is the central part of the medial geniculate nucleus. The former three nuclei are all associated with the primitive tractus tecto-reuniens and with related fiber systems, as has been described. A "ventral part" of the medial geniculate body belonging to the ventral thalamus and associated with either the principal nuclei of the medial geniculate body, or with any other auditory centers, has not been demonstrated in the opossum, although described in other mammals by Clark and by others. This question has already been considered in the first paper of this series.

The large pretectal nucleus in the opossum appears to correspond to the combined pretectal and posterior nuclei of other lowly mammals as described by Gurdjian ('27), and by others. A caudal portion, very closely associated with the deep gray of the tectum, has been described in this report and appears to be more directly related to the optic tract than is the principal pretectal nucleus.

3. The findings with respect to the ventral thalamus are in close agreement with those of Gurdjian ('27) and Rioch ('29 a), in the rat and carnivores, respectively, and apparently the mammalian pattern of connections of the ventral thalamus,

as also in the case of the hypothalamus, is relatively stable. Worthy of emphasis is the strong connection of the hypothalamus with the zona incerta and the gray of the field of Forel. Evidence has been presented that the so-called tractus peduncularis transversus in the opossum consists of two components, namely the posterior accessory optic tract, and the pars superficialis of the tractus geniculatus descendens. The latter forms the principal component of the transverse peduncular tract as it courses around the peduncle and is clearly comparable with a similar bundle in reptiles as first described by Beccari ('23). The pars superficialis in the opossum terminates with the posterior accessory optic tract in the nucleus opticus tegmenti, and is part of a complex of descending fibers from the ventral nucleus of the lateral geniculate body and from the zona incerta to lower tegmental centers.

4. The hypothalamus of the opossum shows a higher degree of specialization than any other part of the diencephalon, with perhaps as clear a differentiation of nuclear groups as is found in mammals. The stability of the hypothalamus throughout the mammals has been noted many times in the past, and Clark ('36) has recently emphasized that all the essential features found in the hypothalamus of lower mammals are also present in the human hypothalamus. The opossum, as also many of the other lowly and macrosomatic mammals, shows a rather clearer differentiation of hypothalamic centers and their connections than is apparent in higher mammals, perhaps associated with the strong development of the basic olfactory connections, and has thus been found to be especially favorable for study of this region.

Among the striking features of this part of the diencephalon in the opossum, the following are of special interest: (1) The clearly unitary character of the so-called nuclei magnocellulares hypothalami, comprised of the several parts of the filiform and tangential nuclei, and apparently all associated with the tractus hypophyseus. The distribution of the cytologically similar cells in a continuous chain is clearly a primitive feature as was early pointed out by Röthig ('11) and is evident also,

although less clearly, in higher mammals according to several observers. The filiform group is, however, more closely associated with the dorsal hypothalamic region, and also with the dorsal thalamus and with the amygdala by way of the anterior periventricular system and the dorsal amygdalo-hypothalamic tract respectively. On the other hand, the tangential group is apparently more closely associated with the medial forebrain bundle, although its detailed connections are not nearly as clear as are those of the filiform nucleus.

(2) The prominence of the dorsal hypothalamic nucleus in the opossum is of some interest because of its position as the principal end-station of the extensive dorsal amygdalo-hypothalamic tract, its connections with the filiform nucleus and posterior periventricular system, and its possible connection also with the dorsal thalamus by way of the anterior periventricular system and the nucleus reuniens anterior. The dorsal amygdalo-hypothalamic tract has been discussed in detail in this account, and has been considered to have a different origin and significance than has been attributed to it by other authors, who also have designated it variously.

(3) The posterior periventricular system in the opossum is of great size, and connects chiefly the dorsal, posterior, and dorsomedial hypothalamic nuclei with lower centers. It passes caudally in the central gray, with many fibers terminating in the posterior paraventricular nucleus as a way-station. The latter large and poorly differentiated nucleus connects with the tectum and the pretectal nucleus, and also contributes fibers caudalward into the posterior periventricular system. The latter, caudal to this level, forms the largest part of the dorsal longitudinal bundle of Schütz. The latter system makes connections along its course with the dorsal tegmental nucleus, and contributes fibers to the tegmentum of the hindbrain in many places. At the caudal level of the medulla oblongata, the bulk of the remaining fibers turn ventrally into the region of the hypoglossal and vagal nuclei. Evidence from experimental material is presented for conduction in both directions in the posterior periventricular system.

(4) The medial group of hypothalamic nuclei, including the mammillary bodies, also have widespread descending connections with the tegmentum by way of the related hypothalamo-tegmental and mammillo-tegmental tracts and the associated olfacto-tegmental bundles. These tracts cannot be readily followed caudally in the tegmentum, and a diffuse spread in the tegmentum is further suggested by the physiological experiments of Magoun, Ranson and Hetherington ('38).

(5) The connections of the mammillary bodies, as observed in normal and experimental material, are also described in some detail.

(6) The supraoptic decussations have received special attention in this study, but the reader must be referred to the account of these systems for details as to the findings. The existence of the so-called hypothalamic optic root of Frey has received no credence from this study, but the possibility is suggested that Frey's identification of such a connection rests upon a misinterpretation of the relations of the non-optic fasciculus supraopticus of Röthig ('09).

In conclusion, it may be worth noting again the presence of abundant tecto-thalamic and thalamo-tectal connections, characteristic of primitive brains. Such connections are present in all four subdivisions of the diencephalon, but are especially prominent in two ancient systems, the tecto-reuniens bundle and the periventricular system.

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ABBREVIATIONS

<i>Δ.</i> , auditory radiation	<i>Com.int.-paraf.</i> , commissura interpara-
<i>Acq.</i> , aqueductus cerebri	fascicularis
<i>Ansa</i> , ansa lenticularis	<i>Com.int.-parat.</i> , commissura interpara-
<i>Br.col.inf.</i> , brachium colliculi inferioris	taenialis
<i>Caps.int.</i> , capsula interna	<i>Com.int.-vent.</i> , commissura interventralis
<i>Ch.opt.</i> , chiasma opticum	<i>Com.int.-vent.ant.</i> , commissura inter-ven-
<i>Col.forn.</i> , columna fornicis	tralis anterior
<i>Col.inf.</i> , colliculus inferior	<i>Com.mam.p.d.</i> , commissura mamillaris
<i>Col.sup.</i> , colliculus superior	posterodorsalis
<i>Com.ant.</i> , commissura anterior	<i>Com.post.</i> , commissura posterior
<i>Com.cent.</i> , commissura centralis	<i>C.pineale</i> , corpus pineale
<i>Com.hab.</i> , commissura habenularum	<i>Dec.br.conj.</i> , decussatio brachii conjunc-
<i>Com.int.-ant.dor.</i> , commissura interan-	tivi
terodorsalis	

- Dec.sup.mam.*, decussatio supramamillaris
Dec.sup.opt., decussatio supraoptica
Dec.sup.opt.d.d., decussatio supraoptica dorsalis pars dorsalis
Dec.sup.opt.d.v., decussatio supraoptica dorsalis pars ventralis
Dec.sup.opt.d.v.l., decussatio supraoptica dorsalis pars ventralis lateralis
Dec.sup.opt.v., decussatio supraoptica ventralis
F., fornix
FF, field of Forel
F.lent., fasciculus lenticularis
F.L.D.S., fasciculus longitudinalis dorsalis of Schütz
F.L.M., fasciculus longitudinalis medialis
F.subthal., fasciculus subthalamicus
F.sup.opt., fasciculus supraopticus
F.thal.tect.et pret., fibrae thalamo-tectalis et pretectalis
Gl.pal., globus pallidus
Gr.cent., grisea centralis
Inf.thal.rad., inferior thalamic radiation
Inter.thal.rad., intermediate thalamic radiation
L.m.e., lamina medullaris externa
Lem.lat., lemniscus lateralis
Lem.med., lemniscus medialis
Lem.med.d., lemniscus medialis pars dorsolateralis
Lem.med.v., lemniscus medialis pars ventromedialis
M.F.B., medial forebrain bundle
N.III, nucleus oculomotorius
N.IV, nervus trochlearis
N.ant.dor., nucleus anterior dorsalis
N.ant.med., nucleus anterior medialis
N.ant.vent., nucleus anterior ventralis
N.caud., nucleus caudatus
N.col.inf., nucleus colliculi inferioris
N.Dark., nucleus of Darkschewitsch
N.fil.lat., nucleus filiformis pars lateralis
N.fil.parav., nucleus filiformis pars paraventricularis
N.g.l.d., nucleus geniculatus lateralis dorsalis
N.g.l.v., nucleus geniculatus lateralis ventralis
N.g.m., nucleus geniculatus medialis
N.g.m.c., nucleus geniculatus medialis pars centralis
N.g.m.m., nucleus geniculatus medialis pars marginalis
N.hab.lat., nucleus habenularis lateralis
N.hab.med., nucleus habenularis medialis
N.hyp.ant., nucleus hypothalamicus anterior
N.hyp.dor., nucleus hypothalamicus dorsalis
N.hyp.dor.med., nucleus hypothalamicus dorsomedialis
N.hyp.post., nucleus hypothalamicus posterior
N.hyp.vent.med., nucleus hypothalamicus ventromedialis
N.inp., nucleus interpeduncularis
N.int-med.dor., nucleus inter-medialis dorsalis
N.lat.ant., nucleus lateralis pars anterior
N.lat.intermed., nucleus lateralis pars intermedia
N.lat.post., nucleus lateralis pars posterior
N.lat.prof., nucleus lateralis profundus mesencephali
N.mam.lat., nucleus mamillaris pars lateralis
N.mam.med., nucleus mamillaris pars medialis
N.med.dor., nucleus medialis dorsalis
N.opt.teg., nucleus opticus tegmenti
N.ovid., nucleus ovoideus
N.paracent., nucleus paracentralis
N.paraf., nucleus parafascicularis
N.paraf.p.l., nucleus parafascicularis pars posterolateralis
N.parataen., nucleus parataenialis
N.parav.ant., nucleus paraventricularis anterior
N.parav.post.inf., nucleus paraventricularis posterior pars infracommissuralis
N.parav.post.sup., nucleus paraventricularis posterior pars supracommissuralis

- N.premam.dor.*, nucleus premamillaris dorsalis
N.premam.vent., nucleus premamillaris ventralis
N.preop.med., nucleus preopticus medialis
N.pret., nucleus pretectalis
N.pret.caud., nucleus pretectalis pars caudalis
N.ret., nucleus reticularis
N.ret.med., nucleus reticularis pars medialis
N.reun.ant., nucleus reuniens anterior
N.rhomb., nucleus rhomboidalis
N.ruber, nucleus ruber
N.subparaf., nucleus subparafascicularis
N.subparat., nucleus subparataenialis
N.subthal., nucleus subthalamicus
N.supragen., nucleus suprageniculatus
N.supramam., nucleus supramamillaris
N.tang.sup., nucleus tangentialis pars supraoptica
N.teg.dor., nucleus dorsalis tegmenti
N.vent.ant., nucleus ventralis pars anterior
N.vent.F.L.M., nucleus ventralis fasciculi longitudinalis medialis
N.vent.med., nucleus ventralis pars medialis
N.vent.pr., nucleus ventralis pars principalis
Opt.rad., optic radiation
Ped.cer., pedunculus cerebri
Ped.c.mam., pedunculus corporis mamillaris
Periv.ant., anterior periventricular system
Periv.post., posterior periventricular system
R.III, radix nervi oculomotorii
Rec.mam., recessus mamillaris
Rec.infund., recessus infundibuli
S.nigra, substantia nigra
Str.med., stria medullaris
Str.term., stria terminalis
Str.opt., stratum opticum
Sup.thal.rad., superior thalamic radiation
Thal.rad., thalamic radiation
Tr.amyg.hyp.dor., tractus amygdalo-hypothalamicus dorsalis
Tr.cort.hab.med., tractus cortico-habenularis medialis
Tr.cort.hab.lat., tractus cortico-habenularis lateralis
Tr.cort.hyp.med., tractus cortico-hypothalamicus medialis
Tr.cort.tect., tractus cortico-tectalis
Tr.cort.teg., tractus cortico-tegmentalis
Tr.gen.desc.int., tractus geniculatus descendens pars interna
Tr.gen.desc.sup., tractus geniculatus descendens pars superficialis
Tr.gen.vent., tractus geniculo-ventralis
Tr.hab.ped., tractus habenulo-peduncularis
Tr.hab.ped.med., tractus habenulo-peduncularis medialis
Tr.hab.ped.lat., tractus habenulo-peduncularis lateralis
Tr.hyp.incert., tractus hypothalamico-incertalis
Tr.hyp.teg., tractus hypothalamico-tegmentalis
Tr.inc.tect., tractus incerto-tectalis
Tr.mam.thal., tractus mamillo-thalamicus
Tr.mam.teg., tractus mamillo-tegmentalis
Tr.olf.hab.med., tractus olfacto-habenularis medialis
Tr.olf.hyp.vent., tractus olfacto-hypothalamicus ventralis
Tr.olf.mam., tractus olfacto-mamillaris
Tr.olf.teg., tractus olfacto-tegmentalis
Tr.opt., tractus opticus
Tr.opt.acc.post., tractus opticus accessorius posterior
Tr.ped.tr., tractus peduncularis transversus
Tr.pret.teg., tractus pretecto-tegmentalis
Tr.pret.nigr., tractus pretecto-nigralis
Tr.str.teg., tractus strio-tegmentalis
Tr.tect.hab., tractus tecto-habenularis
Tr.tect.nigr., tractus tecto-nigralis
Tr.tect.paraf., tractus tecto-parafascicularis
Tr.tect.reun., tractus tecto-reuniens
Z.inc., zona incerta
III, ventriculus tertius

PLATES 1 TO 13

EXPLANATION OF FIGURES

The figures are all photomicrographs prepared from Weigert material described in the section on Material and Methods. Figures 1 to 10 are sagittal sections, figures 11 to 19 are horizontal sections, and figures 20 to 26 are transverse sections. All are magnified at $9\times$, except figures 1 and 2, which are magnified at $20\times$. Figures 2 and 4 are from the same section.

























