

STUDIES ON THE DIENCEPHALON OF THE VIRGINIA OPOSSUM

PART I. THE NUCLEAR PATTERN IN THE ADULT

DAVID BODIAN

National Research Council Fellow in Medicine, Laboratory of Comparative Neurology, Department of Anatomy, University of Michigan, Ann Arbor

ELEVEN PLATES (TWENTY-TWO FIGURES)

CONTENTS

Introduction	259
Terminology and literature	261
Material and methods	263
Description of nuclear masses	264
The dorsal thalamus	264
Anterior nuclear group	264
Medial nuclear group	266
Midline and commissural nuclei	271
Lateral and ventral nuclear groups	277
Geniculate nuclei and associated optic and auditory nuclei of the di-mesencephalic junction	282
The ventral thalamus or subthalamus	288
The hypothalamus and the preoptic area	291
Periventricular region (grisea centralis)	292
Medial region	294
Lateral region	304
The epithalamus	305
Discussion and summary	306

INTRODUCTION

The last decade has witnessed an unusual acceleration in the study of the problems of diencephalic structure and function in many laboratories. Much progress has already been made by means of systematic comparative and experimental

studies, and providing that too much is not expected in the way of exact structural correspondence, the comparative method will continue to be one of the principal tools of neurological investigators in achieving an understanding of the structure and functions of the mammalian and human thalamus. Of primary importance in all comparative studies of cerebral histology is the accurate and detailed description of nuclear configurations, with special emphasis, in the modern phase of localization studies, on the determination of accurate limits of nuclear groups. This assumes as a fundamental axiom what is now generally accepted, namely that morphological differentiation is invariably associated with more or less functional differentiation of nervous centers. Even where superficial examination reveals a cytoarchitecture in the nature of a 'nucleus diffusus,' as especially in certain parts of the hypothalamus, a closer analysis of cell localization and fiber connections, as suggested by, or in anticipation of functional analysis with electrical and other methods, cannot but be of ultimate importance in most cases.

With this in mind the present study was begun as a preliminary to an analysis of a primitive and generalized mammalian brain by the methods of experimental neurology and embryology. The opossum, among readily available mammals, occupies a particularly strategic position with respect to phylogenetic problems. Its relation to the reptiles on the one hand, and to the higher mammals on the other, and, in addition, as a 'living fossil' its relation to the diversely adapted marsupials as a relatively primitive and unspecialized prototype, give it this position. Furthermore, the ready availability of the amazingly immature pouch embryos suggests many unique possibilities for embryological studies of this animal. The fiber connections of the adult diencephalon will be considered in the second report of this series, and an experimental anatomical analysis of the thalamo-cortical connections in a third report. Material is now available also for the investigation of the histogenesis, including fibrogenesis of the brain of the pouch embryos.

It is interesting to mention here that these studies represent the continuation of a program of investigation of the opossum brain in progress at the Hull Laboratories of Anatomy at The University of Chicago during the past 15 years, under the supervision of Prof. C. Judson Herrick. The great debt of comparative neurology to him, as well as my own incalculable personal indebtedness, has become acutely evident to me during this phase of that program.

In the course of the opossum program, Loo ('30 and '31) has touched on the diencephalon in his detailed account of the forebrain, as have Tsai ('25) and the present writer in studies on the optic centers ('35 and '37). Chu ('32 and '32 a) has published an account of the cell groups and fiber connections of the diencephalon of the opossum, but it has been felt that his description and that of Warner on the hypothalamus ('29) are not sufficiently detailed, especially as far as the connections and the limits of nuclear masses are concerned, to be an adequate basis for experimental or embryological studies. The reader is referred to the papers of Loo ('30) and Tsai ('25) for illustrations of the gross form of the forebrain and diencephalon.

These studies also form a part of the comprehensive program of study of the vertebrate diencephalon which has been in progress in the Laboratory of Comparative Neurology at the University of Michigan during the past 13 years, under the direction of the late Prof. G. Carl Huber and of Prof. Elizabeth C. Crosby. For the privilege of taking part in this program and making use of the extensive comparative material of the laboratory, as well as for innumerable kindnesses and invaluable consultations and counsel, I take this opportunity of expressing deep gratitude to Professor Crosby.

TERMINOLOGY AND LITERATURE

The rapidly expanding literature on the diencephalon has sharply accentuated the problem of nomenclature. A complete and rational standardization of terminology is of course impossible until sufficient data have been accumulated to make

possible reasonably accurate homologies on morphological and functional grounds. This probably will never be completely realized because of the inherently plastic and dynamic nature of nuclear differentiation in various vertebrate groups. This does not preclude, nor diminish the importance of, a gradual standardization of terminology, however. It seems fairly clear that this now depends upon accurate topographical description of nuclear groups, coupled with and controlled by studies of the fiber connections of the nuclei with all available methods.

In the present study the attempt has been to make the description of nuclei sufficiently detailed, with the aid of numerous figures in all conventional planes, so that there would be no doubt as to the position and relations of all nuclei mentioned. In addition the fiber connections in normal material have been considered, and experimental studies by the methods of Wallerian and retrograde degeneration have been carried out in an attempt to compare the opossum nuclei, on the basis of fiber connections, with those of other less primitive mammals recently studied with these methods. The terminology used in this account follows, in general, that which has gradually come into common use following the pattern established for the dorsal thalamus by Nissl (1889 and '13) in the rabbit, and later extended by Fortuyn ('12), d'Hollander ('13), Gurdjian ('27), Clark ('29 and '32), Rioch ('29), Papez ('32), Crouch ('34 and '34 a), and many others, in various mammals. The present account follows the terminology of Gurdjian ('27) and Rioch ('29) more than that of any other worker on the diencephalon, with additions or changes only as appeared necessary. No general review of the literature will be attempted here as this has been done adequately in several places in recent years (Gurdjian, '27; Rioch, '29; Clark, '32; Ariëns Kappers, Huber and Crosby, '36; and Walker, '38). We have examined a great number of the older and more recent descriptions of the nuclear patterns in various mammals. These works have been reviewed elsewhere and most of them have been of little value for our

purpose because of the absence of adequate descriptions of the fiber connections. The literature which we have found to be of comparative value will be mentioned in connection with our own findings.

MATERIAL AND METHODS

In this study of the nuclear masses of the opossum diencephalon, every center was examined from the viewpoint of its connections as well as of its location, and in addition the experimental material on the thalamo-cortical connections was found extremely useful. For convenience of publication, the fiber connections and thalamo-cortical projection will be considered separately in the second and third communications of this series, although it must be expressly stated that the first three reports in this series of studies of the opossum diencephalon represent work done as a unit on Nissl, Weigert, and reduced silver material cut in the three conventional planes.

We have been unusually fortunate in having available abundant material prepared by the above-mentioned methods. This material includes not only the excellent preparations of the G. Carl Huber Neurological Collection of the Department of Anatomy of the University of Michigan, but also some of the material of the G. L. Streeter and R. E. Sheldon Collections, loaned to the Department of Anatomy at The University of Chicago, and made available for this study through the kindness of Dr. N. L. Hoerr. In addition to the normal material listed below, extensive use has been made of a large number of complete series of sections of brains with small and large cortical lesions (to be listed in the third report of this series) which have been cut in various planes, and stained with the methods of Nissl, of Weigert, and of the writer ('37 a). All of the normal series listed below are complete:

Three Weigert-Pal series, cut in transverse, horizontal, and sagittal planes, are from the University of Michigan collection. Three Weigert series, sectioned in the sagittal (Op.C.) and transverse (Op.D, Op.E) planes, belong to the Streeter

Collection. The Nissl (toluidine blue) series, also from the Huber Collection, include a transverse series (fixed in alcohol), horizontal and sagittal series (fixed in Huber's fluid; Huber, '27), and a transversely cut series (*Didelphis marsupialis aurita*, fixed in Huber's fluid). Three transverse reduced silver series were also available. Two of these series, from the Huber Collection, were prepared by the method of Ramón y Cajal; the other was stained by the method of Bodian ('37) and cut at 20 μ .

Figures 2 to 24 are drawings prepared by projecting the outlines of the cell groups with an Edinger apparatus at a magnification of 20, and filling in the nuclear detail under microscopic control. The drawings have been reduced to one-fourth for publication.

DESCRIPTION OF NUCLEAR MASSES

THE DORSAL THALAMUS

Anterior nuclear group

The anterior nuclear group in the opossum can be clearly subdivided into the three nuclei apparently characteristic for most mammals so far described. The unitary nature of this group is indicated by the close regional association of the constituent nuclei, with mingling of cells of all three at their borders, and by their connections. The anterior limit of all of these nuclei in the opossum is formed by the vertically streaming fibers of the stria medullaris (figs. 13, 14).

Nucleus anterior dorsalis (figs. 3, 4, 13, 19, 20). This nucleus may be described as a wedge-shaped group of homogeneous and deeply staining cells of medium size, densely packed. The base of the wedge is dorsolaterally placed and adjoins the surface of the inconspicuous anterior tubercle of the thalamus, just lateral to the stria medullaris. The nucleus anterior dorsalis first appears rostrally, along with the anterior ventral nucleus, in a transverse plane a few sections in front of the anterior tip of the habenular nuclei and passing through the caudal fibers of the vertical portion of the stria

medullaris. Rostrally this nucleus is bounded above and medially by the stria medullaris and the nucleus parataenialis, below and laterally by the nucleus anterior ventralis and nucleus anterior medialis (fig. 3). Caudally the nucleus is placed in a vertical position with the base of the wedge narrowed, the stria medullaris and the nucleus medialis dorsalis medially, and the nucleus lateralis pars intermedia laterally (fig. 4). The nucleus anterior dorsalis, which is the smallest of the anterior group, disappears caudally at the plane of the rostral tip of the dorsal nucleus of the lateral geniculate body, and here is replaced by the nucleus of the interanterodorsal commissure, which occupies the same relations in several sections caudal to the nucleus anterior dorsalis (fig. 5).

Nucleus anterior ventralis (figs. 3 to 5, 13, 14, 20, 21). The nucleus anterior ventralis, the largest of this group, appears rostrally in transverse series simultaneously with the nucleus anterior dorsalis. It extends somewhat farther posteriorly, however, where it passes over without clear demarcation into the similar cells of the nucleus ventralis pars anterior at the rostral extreme of the latter. The nucleus anterior ventralis is a roughly ovoid mass of cells, well delimited from neighboring groups and composed of fairly large, well staining, and closely grouped cells (fig. 13). In anterior sections it reaches laterally to the surface of the thalamus (fig. 3). Here it is bounded dorsally by the nucleus anterior dorsalis, ventromedially by the nucleus anterior medialis, and ventrally by the nucleus reticularis. Posteriorly, the intermediate part of the lateral nucleus covers its dorsal and lateral surfaces, the paracentral nucleus lies dorsomedially, the nucleus anterior medialis ventromedially, and the anterior part of the ventral nucleus forms the caudal boundary (fig. 5).

Nucleus anterior medialis (figs. 3 to 5, 14 to 16, 21). This nucleus is ovoid in shape and consists of cells similar in type to those of the nucleus anterior ventralis, but clearly separated from the latter by fiber bundles of the inferior thalamic radiations (fig. 21). The nucleus anterior medialis is bounded laterally by the nucleus anterior ventralis, dorsally in rostro-

caudal order by the nucleus anterior dorsalis and the nucleus paracentralis, medially by the nucleus subparataenialis, and ventrally by the nucleus reticularis and the nucleus hypothalamicus dorsalis (figs. 3, 14, 15). Posteriorly it is replaced by the nucleus ventralis pars medialis, from which it is separated for a few sections by the nucleus ventralis pars anterior (fig. 16).

Medial nuclear group

This group of nuclei in the opossum is well developed and apparently very similar to the homologous nuclei of other lowly mammals.

Nucleus parataenialis (figs. 2 to 4, 16, 20, 21). The parataenial nucleus is a group of medium and large multangular and spindle-shaped cells intercalated between the nucleus paraventricularis anterior and the nucleus medialis dorsalis. It extends from the rostral end of the thalamus to a transverse plane close to the caudal pole of the nucleus anterior dorsalis. Rostrally it is found below and lateral to the anterior paraventricular nucleus, with the stria medullaris in front, above, and laterally (fig. 2). Farther caudally, the habenular nuclei form its dorsal boundary, the nucleus medialis dorsalis borders it laterally, and the nucleus anterior dorsalis and its commissure form part of the ventral boundary, along with the rhomboid and paracentral nuclei (figs. 3 and 4). At its posterior end the parataenial nucleus merges imperceptibly with the nucleus medialis dorsalis before being replaced by the latter. The lateral border of the parataenial nucleus is not clearly separated from the nucleus medialis dorsalis, with which it appears to be intimately associated. Furthermore, the cells on the medial surface of the parataenial nucleus intermingle to a certain extent with those of the lateral part of the anterior paraventricular nucleus, with which it is also closely connected.

In the caudal half of the parataenial nucleus, the ventral part of the nucleus forms a more or less circumscribed group of cells more closely grouped than those of the rest of the

nucleus. This group, which appears in some sections to be intimately associated with the paracentral nucleus, bordering it ventrally, has been described in the rat by Gurdjian, who noted a characteristic plexus of nerve fibers within it in silver preparations. This plexus is present in the opossum also, but a similar less dense feltwork of mostly coarse fibers also occurs in the rest of the parataenial nucleus and in the nucleus medialis dorsalis.

Nucleus subparataenialis (figs. 3, 4, 16 to 18, 21). This nucleus has not been described in the opossum before, but is clearly present, although small, and is apparently similar to the 'noyau paramédial' described by d'Hollander ('13) in the rabbit. It appears to correspond to the medial part of the nucleus medialis ventralis of Gurdjian ('27), to the dorso-lateral large-celled part of the rostral portion of the nucleus reuniens of Rioch ('29), and to at least a part of the nucleus submedius of Papez ('32). At its anterior pole the nucleus subparataenialis is directly below the anterior end of the parataenial nucleus, and the similar cells of the two nuclei intermingle to some extent, as remarked by Papez ('32) in the armadillo. Both nuclei are bounded rostrally by the vertical portion of the stria medullaris. In tracing transverse sections caudally, or in longitudinal sections, the subparataenial nucleus is seen to become separated very soon from the parataenial nucleus by the interposed rhomboid nucleus. Still farther caudally the nucleus centralis comes to occupy a dorsal position with respect to the subparataenial nucleus. The latter is bounded laterally throughout most of its course by the nucleus anterior medialis, from which it is separated in cell preparations by a fairly broad clear zone. Medially, the subparataenial nucleus presses closely upon the nucleus reuniens anterior, and caudally it is replaced by the nucleus ventralis medialis. Its relation to the parataenial nucleus will be considered in the discussion of its fiber connections.

Nucleus medialis dorsalis (figs. 3 to 8, 14 to 17, 19). This is the largest nucleus of the medial group and extends almost as far rostrally as do the anterior nuclei, appearing first as

scattered cells among the fibers of the stria medullaris (fig. 15). The cells of this nucleus are large and multangular, and intermingle freely with the smaller cells of the nucleus intermedius dorsalis which separates the two nuclei mediales dorsales. Rostrally the nucleus medialis dorsalis is covered by the habenular nuclei and the stria medullaris dorsally, by the nucleus anterior dorsalis and its commissure laterally, and by the nucleus parataenialis medially (fig. 4). Farther caudally it replaces the parataenial nucleus as a lateral neighbor of the anterior paraventricular nucleus, and is bordered ventrolaterally by the nucleus paracentralis. The caudal third or more of the nucleus medialis dorsalis is bordered laterally by the nucleus parafascicularis, which finally replaces it entirely (figs. 9, 14, 15, 19). The cells of the latter two nuclei intermingle freely at their borders, which are consequently not at all sharp. The cells of the parafascicular nucleus are slightly smaller and more flattened than those of the nucleus medialis dorsalis.

Nucleus paracentralis (figs. 4 to 6, 13 to 15, 20). The paracentral nucleus in the opossum is large and may be considered to be a lateral extension of the central nucleus, with cells of identical appearance, medium in size, and somewhat flattened in the plane of the fibers of the central commissure. Along with the central nucleus it is an interstitial nucleus of the latter commissure, and in addition is the principal nucleus of the internal medullary lamina, of which the central commissure is a large component. The paracentral nucleus projects forward slightly beyond the anterior limit of the central nucleus to form the lateral boundary of the rostral end of the rhomboid nucleus. It extends back a short distance caudal to the middle of the central nucleus, where it merges with the parafascicular nucleus and is replaced by it (figs. 14, 15). At its anterior end, the paracentral nucleus is continuous laterally with the nucleus of the interanterodorsal commissure, which it replaces a few sections caudalward (figs. 5, 6). Here it is in the path of the interanterodorsal commissure, which forms part of the internal medullary lamina. Through-

out its course, the paracentral nucleus separates the lateral and ventral nuclei from the nucleus medialis dorsalis.

Nucleus parafascicularis (figs. 7 to 9, 13 to 15, 19). This nucleus can be considered as the caudal extension of the paracentral nucleus, but is a clearly differentiated entity and is also very intimately associated with the nucleus medialis dorsalis. The cells of the latter mingle with those of the parafascicular nucleus at its medial border to such a degree that a sharp boundary can nowhere be defined except where the bundles of the fasciculus retroflexus intervene. In general, the cells of the rostral part of the parafascicular nucleus are flattened in comparison with those of the nucleus medialis dorsalis. The most lateral cells are oriented in the plane of the fibers of the internal medullary lamina, like those of the paracentral nucleus, but the more medial cells may be oriented in strands running in divers directions. The reason for this is made apparent in fiber preparations, in which the parafascicular nucleus is seen to be traversed by fibers of several different systems.

Rostrally, where it is placed lateral to the large bundles of the fasciculus retroflexus, the intermediate part of the lateral nucleus and the principal ventral nucleus form its lateral and ventrolateral boundaries, the nucleus centralis is below, and the medial border is formed by the nucleus medialis dorsalis and by Meynert's bundle (fig. 7). At its caudal end, the parafascicular nucleus proper is continuous above and posteriorly with the pars posterolateralis, and the cells of these two parts mingle to a great extent (figs. 9, 14). The caudal pole of the parafascicular nucleus abuts medially against the infracommisural part of the nucleus paraventricularis posterior, and the fasciculus retroflexus, which separates these two nuclei in part (fig. 15).

Nucleus parafascicularis pars posterolateralis (figs. 8 to 10, 13, 14, 19). This nucleus appears to correspond to a similar cell mass described by Clark ('30 and '31) and by Rioch ('31), and which these authors have identified with the centre médian of primates. It is continuous rostrally with the rest of the

parafascicular nucleus, but its cells are more compactly grouped and stain more deeply than those of the latter. It appears rostrally at the level of the habenular commissure, simultaneously with the rostral end of the pretectal nucleus. It lies ventral to the latter, but does not extend so far caudally. It lies dorsal to the caudal end of the principal ventral nucleus, which is replaced still more caudally by the nucleus subparafascicularis. Its relation to other surrounding nuclei may be seen in the figures. Although the cells of this nucleus mingle to some extent with the bordering nuclei, it is possible in well-stained material to delimit it by the close grouping, deep staining, and uniform medium size of the cells.

This nucleus in sagittal sections (fig. 13) also appears to correspond to the caudal "noyaux semi-lunaires accessoires du noyau sensitif" of Ramón y Cajal ('11) as he represents it in figure 261, E. Cajal describes collaterals of his "voie sensitive centrale du trijumeau" to this nucleus (fig. 321).

Strands of small, flattened cells intercalated among the large bundles of the fasciculus retroflexus are sometimes seen in sagittal sections medial to the nucleus parafascicularis pars posterolateralis (fig. 15). In some sections these cells appear to be continuous with those of the lateral habenular nucleus which in places stream down between the bundles of the habenulo-peduncular tract. The most lateral of these cells merge with those of the nucleus parafascicularis pars posterolateralis. Small strands of cells of the nucleus paraventricularis posterior are also occasionally segregated by the habenulo-peduncular fascicles in an inconstant manner, and it thus appears likely that these small groups of cells in the opossum have no special significance apart from their location, and should not be considered as a distinct entity. However, it is also possible that some of these cells may correspond to the medial and lateral nuclei of the habenulo-peduncular tract described by Rioch ('29) in carnivores, in which the cell groups of this region appear to be more highly developed and apparently associated with the posterior paraventricular and parafascicular nuclei.

Midline and commissural nuclei

In this group are included those gray centers of the dorsal thalamus associated with the periventricular fiber system, and with the abundant commissural fibers connecting the medial, ventral, and lateral thalamic groups of both sides. Both the medial and the midline gray centers are well developed in the opossum and are closely comparable with the homologous gray of the rat, as described by Gurdjian ('27).

There is considerable gray associated with the thalamic commissures, with a few groups of cells sufficiently well defined to justify separation into distinct nuclei. Chu ('32) designated all of the gray between the medial groups as the nucleus commissuralis. Here, part of this gray will be termed the nucleus inter-medialis dorsalis to distinguish it from the nuclei associated with the commissures of the ventral and the anterior nuclear groups. These nuclei are very distinctive in all of our material, but apparently were not recognized by Chu.

Nucleus paraventricularis anterior (figs. 2 to 7, 17 to 20). The anterior paraventricular nucleus in the opossum is a continuous and homogeneous mass of gray extending almost the entire length of the thalamus, from the bed nucleus of the anterior commissure in front to the nucleus paraventricularis posterior behind. The cells throughout the column are of the same type, although in the anterior third of the nucleus they are more compactly grouped. The nucleus occupies the dorsomedial angle of the thalamus anteriorly and, for most of its course, borders closely the trough formed by the dorsal part of the third ventricle. The gray of the nuclei of both sides meets in the midline below the ventricle, but the latter separates the main mass of the two nuclei throughout their extent. The parataenial nucleus and, more caudally, the nucleus medialis dorsalis, form the lateral boundary of the anterior paraventricular nucleus, as noted in the description of the former. The nucleus inter-medialis dorsalis lies ventral to the anterior paraventricular nucleus throughout most

of its course, and is not easily separable from it. Except at the anterior pole of the thalamus, the habenular complex lies directly dorsal to the anterior paraventricular nucleus. The anterior compact part of this nucleus is divided roughly into medial and lateral portions by the vertically coursing fibers of the periventricular system, and especially by the fairly large bundles of the medial olfacto-habenular tract.

Nucleus paraventricularis posterior (figs. 8 to 11, 15 to 18, 19 to 21). This nucleus, which corresponds to the nucleus of the same name of the rat as described by Gurdjian ('27), is a large and homogeneous mass of cells in the opossum, with, however, numerous and diverse connections. It forms the caudalmost cell mass of the dorsal thalamus near the mid-plane and extends back into continuity with the central gray of the superior colliculus (fig. 16). In transverse sections it appears first rostrally below the caudal end of the habenular nuclei and medial to the pretectal nucleus (fig. 8). At this level it is above the nucleus inter-medialis dorsalis. At more caudal levels through the posterior commissure (fig. 10) it is seen to consist of a supracommissural portion below the anterior edge of the tectum and a larger infracommissural portion medial to the habenulo-peduncular tract. The cells of the two parts are identical and are connected by cell bridges in front of and through the posterior commissure (fig. 16). Ventrally its cells fuse with those of the ventral nucleus of the medial longitudinal fasciculus at the dorso-caudal border of the latter (fig. 17), and ventrolaterally the nucleus paraventricularis posterior is continuous with the medial extension of the nucleus subparafascicularis (figs. 10, 21). Rostrodorsally the cells of the nucleus paraventricularis posterior are also more or less continuous with and of similar appearance to those of the lateral habenular nucleus (fig. 16). Caudally it passes over without sharp boundary into the interstitial nucleus of the posterior commissure. The supracommissural portion of this nucleus corresponds to at least part of the nucleus of the posterior commissure of Rioch ('29) and to the pretectal area of Papez ('32). The infra-

commissural portion is the posterior periventricular nucleus of Papez ('32). The characteristic relationship of this nuclear mass to the posterior commissure, to the habenulo-peduncular tract, and to the diencephalic periventricular system of fibers suggest at least a partial homology with the nucleus lentiformis thalami of *Varanus*, *Lacerta*, and *Sphenodon* as described by Ariëns Kappers ('21), Beccari ('23), and Cairney ('26) respectively.

This nucleus apparently decreases in size in higher mammals, where its place is perhaps taken by more differentiated centers. It is of much greater size in the opossum than in the rat, as depicted by Gurdjian ('27).

Nucleus rhomboidalis (figs. 4 to 6, 15 to 18, 20). The rhomboid nucleus in the opossum is present in the rostral half of the thalamus as a midline gray mass, located between the anterior paraventricular nucleus above and the central nucleus below. It extends slightly farther rostrally than the central nucleus, however, as can best be seen in sagittal sections (fig. 17). Except at its rostral end, where it is bordered laterally by the paracentral nucleus, its lateralmost cells mingle to some extent with those of its neighbor, the nucleus medialis dorsalis, but it does not have the dense intercellular feltwork of fibers characteristic of the latter nucleus. More caudally, the nucleus medialis dorsalis also forms its dorso-lateral boundary. The rhomboid nucleus fuses above and caudally with the more scattered gray of the nucleus intermedialis dorsalis, which has similar cells.

In transverse sections, the rhomboid nucleus does not have the shape that its name suggests, but at most levels consists of two more or less compactly grouped cell masses connected across the midline by less densely arranged cells, where the numerous fibers of the periventricular system traverse it (fig. 6). The cells of the rhomboid nucleus are somewhat smaller than those of the nucleus medialis dorsalis and resemble those of the nucleus centralis, with which they intermingle to some extent. The cells of the rhomboid nucleus, however, are not oriented transversely, as are those of the

central nucleus, since very few commissural fibers traverse it except at its anterior pole. It thus appears to be associated chiefly with the periventricular system of fibers rather than with the commissural systems.

The caudal portion of the rhomboid nucleus has been designated by Chu ('32) as the nucleus medialis ventralis. We have found no reason for thus separating it from the rest of the rhomboid nucleus. The rhomboid nucleus as here described corresponds to the nucleus of the same name of Rioch ('29), Clark ('30), and Papez ('32).

Nucleus centralis (figs. 4 to 8, 16 to 18, 20, 21). The nucleus centralis is a midline center which extends almost the entire length of the thalamus. It lies dorsal to the nucleus reuniens and the nucleus commissuralis interventralis and is covered dorsally by the rhomboid nucleus rostrally, and the nucleus inter-medialis dorsalis caudally. Laterally its cells are continuous with, and of the same type as, those of the nucleus paracentralis. The two are separated in places by the vertically coursing fibers of the thalamic radiations. The central nucleus is apparently a bed nucleus for the large central commissure, and its cells are oriented horizontally between the fibers of the latter. In the middle portion of its rostro-caudal extent, the central nucleus is in relation ventrally to the nucleus commissuralis inter-ventralis anterior and the nucleus ventralis medialis (figs. 6, 7, 16). More caudally, the parafascicular nucleus replaces the paracentral nucleus as its lateral neighbor, and the nucleus medialis dorsalis and nucleus inter-medialis dorsalis cover it dorsally (figs. 7, 8).

At its caudal end, where it lies above the nucleus commissuralis interventralis, the central nucleus is traversed by fibers passing between the ventral nuclei of both sides. It is thus intimately associated, through its long rostrocaudal extent, with the nuclei of the anterior, medial, and ventral groups, as well as with other nuclei of the midline group of which it forms an important part. It may be thought of as being at the crossroads of the large and important periventricular and commissural systems of fibers of the dorsal thalamus.

Nucleus reuniens anterior (figs. 3 to 7, 17, 18, 21). The nucleus reuniens anterior consists of a midline group of cells of medium size forming the ventral part of the massa intermedia below the central nucleus. Rostrally it appears first in transverse sections at the level of the commissura interanterodorsalis, where it forms a small mass of vertically oriented cells between the two subparataenial nuclei. It extends caudally to the caudal border of the nucleus ventralis medialis where it fuses with the nucleus reuniens posterior (figs. 17, 18). At its rostral end, the ventral part of the nucleus reuniens anterior is divided into bilateral halves by the third ventricle, but farther caudally the ventral part spreads laterally beneath the subparataenial nuclei, which indent the lateral surfaces of the nucleus reuniens anterior. Although the cells of the nucleus subparataenialis are larger than those of the nucleus reuniens anterior, they intermingle to a great extent at the borders. In its caudal half, where the nucleus ventralis medialis replaces the nucleus subparataenialis as the lateral neighbor of the nucleus reuniens anterior, the latter is broader than at more rostral levels. Throughout most of its extent the nucleus reuniens anterior is traversed by vertical fibers of the periventricular system. It differs from the nucleus reuniens posterior, with which it is continuous caudally, in having very few commissural fibers, except dorsally where the ventralmost fibers of the central commissure and the fibers of the commissura inter-ventralis anterior cross.

Nucleus reuniens posterior (*nucleus commissuralis inter-ventralis*) (figs. 8, 9, 17, 18, 21). Between the two principal ventral nuclei, caudal to the nucleus reuniens anterior and below the nucleus centralis, one sees a distinctive cell mass which is fused laterally with the ventral nuclei, and rostrally with the nucleus reuniens anterior. Caudally, it reaches to the nucleus paraventricularis posterior and here to some extent is covered dorsally by the parafascicular nuclei. Below it are the dorsal hypothalamic nuclei.

This nucleus is in the course of the large interventral commissure, and forms a broad zone of fusion between the principal ventral nuclei of the two sides. Its cells are continuous with, and of the same type as, those of the nucleus reuniens anterior. The relation to the large interventral commissure, and other special connections, have led to this separate designation.

Nucleus inter-medialis dorsalis (figs. 6 to 9, 18). This rather ill-defined gray is present in the midline between the nuclei mediales dorsales and parafasciculares of both sides throughout most of their extent. The cells are small and oriented vertically, for the most part, between the fibers of the periventricular system. Anteriorly the cells are relatively few in number and scattered between the nuclei mediales dorsales, with the anterior paraventricular nuclei above and the rhomboid nucleus below. Posteriorly, between the parafascicular nuclei, these cells are more numerous and compact. They extend back as far as the caudal extreme of the parafascicular nuclei, where they are replaced by the nucleus periventricularis posterior. These cells were mentioned by Gurdjian ('27) in the rat, but not described separately. They were designated by Chu ('32) as the nucleus commissuralis although they are not apparently associated with commissural fibers but rather with fibers of the periventricular system.

Nucleus commissuralis interanterodorsalis (figs. 3 to 5, and 13). This cell group is very characteristic in the opossum, appearing medial to and at the caudal end of the nucleus anterior dorsalis, in the course of the commissural fibers of the latter nucleus. Anteriorly the cells are found closer to the midline, mingling with those of the paracentral nucleus. A few sections caudalward, the cells form a rather compact group at the caudal pole of the nucleus anterior dorsalis. A few sections posteriorly, they are replaced by the lateral wing of the paracentral nucleus. Lying in the rostral part of the internal medullary lamina, these cells are flattened, as a rule, and are somewhat smaller than those of the anterior dorsal

nucleus, which they resemble in their staining qualities. The caudal part of this nucleus is comparable in its relations to the nucleus centralis lateralis of other forms, as Clark ('30) has shown.

Nucleus commissuralis inter-ventralis anterior (figs. 6, 17, 21). At the rostral end of the nucleus ventralis medialis, in all specimens examined, one sees a condensation of cells between the nucleus centralis and the nucleus reuniens, separated only in part from the former by commissural fibers. These cells extend between the anterior parts of the two ventral nuclei, but also merge with the cells of the nucleus centralis, which they resemble closely. This nucleus has a very short rostrocaudal extent as does the nucleus ventralis anterior. It is possible that this nucleus is also in the path of fibers passing between the rostral poles of the medial parts of the ventral nuclei.

Lateral and ventral nuclear groups

Nucleus lateralis pars anterior (figs. 4, 19). This nucleus has not been described before in the opossum. It apparently corresponds to the nucleus lateralis A of *Tupaia* (Clark, '29) and to the larger nucleus lateralis pars anterior of carnivores (Rioch, '29) which, as in the opossum, extend forward into the anterior tubercle of the thalamus. The nucleus lateralis pars anterior is a clearly differentiated, although very small nucleus, in the opossum, composed of cells more compact and more deeply staining than those of the nucleus lateralis and of similar or of slightly smaller size. It appears on the lateral wall of the anterior tubercle of the thalamus, near the caudal end of the nucleus anterior dorsalis and a few sections rostral to the anterior end of the nucleus lateralis pars intermedia. Here it is in the path of the superior thalamic radiations and is bounded medially and ventrally by the nucleus anterior ventralis, and dorsomedially first by the nucleus anterior dorsalis and, more caudally, by the nucleus lateralis pars intermedia. It is replaced caudally by the anterior tip of the dorsal lateral geniculate nucleus, which forms a more

prominent eminence on the lateral surface of the thalamus and which is clearly separated from the nucleus lateralis pars anterior in Nissl and in silver preparations.

Nucleus lateralis pars intermedia (figs. 4 to 10, 13, 19, 20). The intermediate part of the lateral nucleus is one of the most extensive nuclear masses in the dorsal thalamus. It is first seen anteriorly at a level just behind the rostral end of the habenula. Here it is in relation to the surface of the thalamus dorsally, the nucleus anterior dorsalis medially, the nucleus lateralis pars anterior laterally, and the nucleus anterior ventralis ventrally (fig. 4). More caudally the dorsal lateral geniculate nucleus replaces the nucleus lateralis pars anterior as the lateral neighbor of the pars intermedia and maintains this relation to their caudal poles. Caudal to the anterior nuclear group, the pars intermedia is separated from the medial group of nuclei by the internal medullary lamina, reaches the dorsal surface of the thalamus, and is bounded laterally by the lateral geniculate nuclei, ventrolaterally by the reticular nucleus, and ventrally by the principal ventral nucleus (fig. 6). At the caudal half of the thalamus, the nucleus lateralis pars posterior forms the dorsal boundary of the pars intermedia, from which it is not clearly separated. Near the caudal end of pars intermedia, the nucleus parafascicularis and the nucleus parafascicularis pars posterolateralis form its medial boundary, the nucleus lateralis pars posterior lies dorsally, the lateral geniculate nuclei laterally, the zona incerta ventrally, and the principal ventral nucleus ventromedially (fig. 8). At the caudal tip of the intermediate portion of the lateral nucleus, the medial geniculate nucleus occupies a ventrolateral position relative to it, and the pretectal nucleus a dorsomedial position. The pars intermedia and the lateral geniculate nuclei disappear caudally at about the same level. At caudal planes of the thalamus, the boundaries of the nucleus lateralis pars intermedia are quite indistinct, and it can be but poorly separated from the pars posterior of the lateral nucleus, the principal ventral nucleus, the medial geniculate nucleus, and the supra-

geniculate nucleus. In Nissl preparations it is also not clearly delimited from the dorsal lateral geniculate nucleus, but, in silver preparations, the characteristic neuropil of the latter makes a clear-cut boundary evident.

Nucleus lateralis pars posterior (figs. 7 to 10, 13, 19). The nucleus lateralis pars posterior occupies the dorsolateral surface of the caudal portion of the thalamus, beneath the optic tract. At its anterior end it displaces the intermediate part of the lateral nucleus, with which it is continuous, from this position and lies above and medial to the dorsal border of the dorsal lateral geniculate nucleus (fig. 7). At the level of the habenular commissure, the pretectal nucleus and nucleus parafascicularis pars posterolateralis lie medially, the parafascicular nucleus ventromedially, the intermediate part of the lateral nucleus ventrally, and the dorsal part of the lateral geniculate nucleus ventrolaterally (fig. 8). This relation is maintained more or less until the caudal end of the nucleus is reached. Here the nucleus lateralis pars posterior is bounded laterally by the optic tract, ventrally by the nucleus geniculatus medialis, medially by the suprageniculate nucleus, and dorsomedially by the pretectal nucleus (fig. 10).

In most specimens the caudal part of the nucleus lateralis pars posterior forms a distinct protuberance on the surface of the thalamus, dorsal to the rostral end of the medial geniculate body (fig. 10). The cells of the pars posterior of the nucleus lateralis are slightly larger and stain more deeply than those of the pars intermedia and, at the caudal end, are more widely spaced due to the passage among them of the large bundles of optic tract fibers bound for the tectum. This caudal pole of the nucleus lateralis pars posterior is the dorsal nucleus of the medial geniculate body of Ramón y Cajal ('11), and of other authors. Clark ('33) has pointed out that this homology is erroneous, as also appears apparent from our material.

Nucleus ventralis pars anterior (figs. 6, 14, 21). The nucleus ventralis pars anterior is a small nucleus which separates the nucleus anterior ventralis from the nucleus ventralis

pars principalis and is not clearly separable from either. It is connected across the midline with the opposite nucleus ventralis pars anterior by numerous fibers and by a commissural cell mass, the nucleus commissuralis inter-ventralis anterior. The cells of the nucleus ventralis pars anterior are similar to those of the neighboring nuclei of the lateral and ventral groups but are more scattered due to the passage of the main bundles of the intermediate thalamic radiations among them. The cells of the nucleus are thus frequently seen to be oriented in short vertical strands. The nucleus ventralis pars anterior stands out as a distinct entity in longitudinal, and especially in horizontal, sections (figs. 16, 21). It has not been described before in the opossum, but apparently corresponds to the anterolateral part of the ventral nucleus described in *Tupaia* by Clark ('29).

Nucleus ventralis pars medialis (figs. 6, 7, 16). The nucleus ventralis pars medialis replaces the nucleus anterior medialis at the caudal end of the latter, and extends back to the level of the nucleus reuniens posterior, in which region it is replaced by the medial part of the nucleus ventralis pars principalis. Throughout its relatively short rostrocaudad extent, it lies between the principal ventral nucleus laterally and the nucleus reuniens anterior medially, and its cells merge with those of both of these nuclei. Above it at the rostral end is the nucleus commissuralis inter-ventralis anterior and, more caudally, the central nucleus lies dorsally. The nucleus ventralis medialis in most places is clearly separated from the nucleus reuniens and nucleus ventralis pars principalis by fiber bundles, and its cells, in general, are more compactly grouped and more deeply staining than those of the principal ventral nucleus. This nucleus appears to correspond to the lateral part of the nucleus medialis ventralis of Gurdjian ('27), but in the opossum is clearly associated with the ventral nuclear group as noted also by Chu ('32). It seems to correspond clearly to the anteromedial part of the ventral nucleus of *Tupaia* (Clark, '29).

Nucleus ventralis pars principalis (figs. 7 to 10, 13 to 16, 20, 21). The principal ventral nucleus is a large, more or less ovoid cell mass in the caudal half of the thalamus. It replaces the nucleus ventralis anterior rostrally, where it is separated ventrally and laterally from the reticular nucleus by the external medullary lamina. It is here bounded dorsally by the nucleus lateralis pars intermedia, dorsomedially by the paracentral nucleus, and ventromedially by the nucleus ventralis pars medialis (fig. 7). After the disappearance caudally of the latter nucleus, the nucleus reuniens posterior joins the nuclei of both sides. At a level through the habenular commissure the principal ventral nucleus forms a large ovoid mass bounded ventrally in lateromedial order by the zona incerta, field of Forel, and the nucleus hypothalamicus dorsalis (fig. 8). At this level the nucleus lateralis pars intermedia is lateral and dorsal, the parafascicular and central nuclei are dorsomedial, and the nucleus reuniens posterior separates the two principal ventral nuclei. At its caudal end, the principal ventral nucleus appears as a round mass in transverse sections, with the medial geniculate nucleus laterally, the zona incerta ventrally, the subparafascicular nucleus ventrally and medially, the nucleus parafascicularis pars posterolateralis dorsomedially, and the nucleus supra-geniculatus dorsolaterally (fig. 10). No pars dorsomedialis, such as Gurdjian ('27) described in the rat, is present in the opossum. The principal ventral nucleus appears to correspond to both the medial and lateral parts of the posterior ventral nucleus of Tupaia (Clark, '29).

The borders of the principal ventral nucleus are by no means clear-cut in all places and the cells appear at times to merge imperceptibly with those of the nucleus ventralis pars anterior, the nucleus lateralis pars intermedia, the nucleus ventralis pars medialis, and the nucleus reuniens posterior. The cells of the medial part of the principal ventral nucleus are spaced somewhat differently than are those of the rest of the cell mass, due to the presence of many commissural, as well as other, fibers.

*Geniculate nuclei and associated optic and auditory nuclei
of the di-mesencephalic junction*

Nucleus geniculatus lateralis dorsalis (figs. 5 to 10, 19 to 21). The lateral geniculate nuclei of the opossum, with some of their connections, were described by Tsai ('25) and Chu ('32). Experimental studies of the optic tracts and geniculo-cortical projection have been published by Bodian ('35 and '37). These nuclei, which occupy the lateral surface of the thalamus, underneath the optic tract, from the anterior thalamic tubercle to the medial geniculate body, require no further description. Their relations are indicated in the accompanying figures. Although Nissl preparations show a certain degree of continuity between the dorsal lateral geniculate nucleus and the surrounding nucleus lateralis, pars intermedia and pars posterior, fiber preparations sharply delimit these nuclei because of the presence of a wealth of nerve fibers within the dorsal lateral geniculate nucleus.

Nucleus pretectalis (figs. 8 to 11, 13, 14 and 19). The pretectal nucleus is a large and very characteristic nuclear mass in the opossum, in which it has been described by Tsai ('25) and Chu ('32). It extends from the level of the habenular commissure back to a position beneath the anterolateral part of the optic tectum. It is largest just behind the rostral tip and tapers off caudally. At its anterior end, as it replaces the medial part of the nucleus lateralis pars posterior, it is covered by the optic tract dorsally and is bordered laterally by the nucleus lateralis pars posterior, ventrolaterally by the nucleus lateralis pars intermedia, ventrally by the nucleus parafascicularis pars posterolateralis and medially by the nucleus paraventricularis posterior (fig. 8). Farther caudally it is bounded dorsally by the pars caudalis, from which it is not clearly separated. At this level the nucleus suprageniculatus lies ventrolaterally and the midbrain tegmentum ventrally and medially (fig. 11). The cells of the pretectal nucleus are closely packed, small and medium in size, and resemble those of the adjacent optic tectum. The nucleus pretectalis

appears to correspond to the nucleus posterior of Ramón y Cajal ('11), d'Hollander ('13), and others, and to the combined pretectal and posterior nuclei of Gurdjian ('27) and of Papez ('32). In view of the confusion of terminology which has resulted from attempts to homologize the nuclei of this region in higher mammals with those of lower forms, it is felt that a satisfactory interpretation depends upon comparison with more or less closely related forms on the basis of fiber connections as well as of topography. The interpretation of the opossum pretectal nucleus as the combined pretectal and posterior nuclei of the rat as represented by Gurdjian ('27) appears to satisfy these criteria of homology. The relations in sagittal sections clearly are comparable with the 'noyau posterieure' or 'prébigéminale' of Ramón y Cajal ('11, fig. 261, C), who described collaterals of medial lemniscus fibers passing to this nucleus.

Nucleus pretectalis pars caudalis (figs. 12 to 15). This nucleus was apparently not described by Tsai ('25) or Chu ('32). It is somewhat smaller than the pretectal nucleus, and is directly dorsal and caudal to the latter (figs. 13 to 15). Its cells are similar to those of the pretectal nucleus and also to those of the deep gray of the tectum, with which it is continuous caudally. In most sections its borders are well delimited from those of its neighbors, however, and it has specific connections. Behind the caudal end of the pretectal nucleus it lies above and medial to the medial geniculate body, replacing the pretectal nucleus in this position. It appears to be chiefly, if not entirely, a tectal center and is apparently related to the optic tract.

Nucleus geniculatus medialis (figs. 10 to 12, 20, 21). The medial geniculate body is the most caudal of the thalamic centers in the opossum, extending well back into the mid-brain region as the characteristic rounded protuberance on the lateral wall of the anterior mesencephalon. It appears first rostrally at the anterior level of the posterior commissure and is separated here from the lateral surface of the thalamus by the caudal end of the dorsal nucleus of the lateral

geniculate body (fig. 10). The nucleus lateralis pars posterior is above and the intermediate portion of the lateral nucleus in a dorsomedial position. The principal ventral nucleus is situated medially and the zona incerta below. Farther caudally (fig. 11), the suprageniculate and pretectal nuclei lie dorsomedially and the nucleus subparafascicularis is in a ventromedial position. Except at its rostral and caudal poles, the medial geniculate body is composed of a marginal semi-circular cell mass containing in its medial concavity a medial or central cell group, with neurons of slightly larger size. In fiber preparations the separation of the central from the outer part is seen to be produced by a dense feltwork of fine myelinated fibers between the two, permeating the central portion to a greater extent than the outer mass. This feltwork of fibers is produced chiefly by the terminations of the brachium of the inferior colliculus and by the fibers forming the auditory radiation. The neurons of the two parts of the medial geniculate nucleus intermingle to such an extent that only a rarefied zone separates the two. The cells of the central mass appear more densely packed and more deeply staining than those of the outer mass, whereas the cells of the latter have a more or less concentric arrangement around the central group. This arrangement of the parts of the medial geniculate nucleus appears to be due not only to the fiber architecture of the nucleus, but also to differences in the connections of the parts. The central part suffers the greater degeneration in ablation of the temporal cortex, whereas only a few cells of the outer part are thus affected. Fibers of the brachium of the inferior colliculus and lateral lemniscus connect with both parts. It is likely that the central portion corresponds to the pars magnocellularis of the carnivore medial geniculate nucleus as described by Rioch ('29), and the cup-shaped marginal portion to his pars principalis.

It has not been possible to identify in our material a ventral part of the medial geniculate body, corresponding with the ventral nucleus of the lateral geniculate body in its relation to the zona incerta (Clark, '30 and '33). At the rostral

end of the medial geniculate body the ventral nucleus of the lateral geniculate body extends below it for a short distance (fig. 10). Farther caudally the zona incerta lies ventral to the medial geniculate body (fig. 11) but clearly separated from the latter by a fiber lamina. Caudal to this (fig. 11, right, and fig. 12) the nucleus subparafascicularis is immediately ventral to the medial geniculate body, but neither it nor the medial geniculate body has been observed to bear any special relation to the zona incerta, except that of contiguity. It appears conceivable that the nucleus subparafascicularis as here described may correspond to the ventral nucleus of the medial geniculate body of Clark ('33) and of Papez ('36). Neither of these workers, however, mentions the mediorostral fusion of this nucleus with the nucleus paraventricularis posterior. This fusion, and the other relations and connections of this nucleus, as will be described in the next report of this series, have led us to identify this nucleus in the opossum with respect to its most obvious relation, namely its constant association with the tractus tecto-reuniens and related fiber systems (see account of nucleus subparafascicularis). Furthermore, it has not been possible to become convinced that Kuhlenbeck ('35) in his study of the ontogeny of this region in the rabbit has shown the separate existence of a ventral part of the medial geniculate body, associated with the zona incerta as described by Clark ('30). His figures give the impression that he is dealing with the ventral nucleus of the lateral geniculate body, which extends below the rostral pole of the medial geniculate body, and with the zona incerta itself. He does not mention a nuclear mass associated with the tractus tecto-reuniens.

The impression obtained from examination of the text-figure 2 of Clark ('33), showing a sagittal section of the brain of *Tarsius*, is that his geniculo-subthalamie tract represents part of our tractus geniculatus descendens, described in the second report of this series. As far as can be ascertained, the tractus geniculatus descendens in all of its relations has not been described in detail in mammalian brains up to the

present. In the opossum, as will be pointed out further in the second report of this series, this bundle, derived from the ventral nucleus of the lateral geniculate body and from the zona incerta, passes caudalward underneath the medial geniculate body on the pathway to various tegmental centers. It may be tentatively suggested that some of the scattered cells of the so-called ventral nucleus of the medial geniculate body of other authors may consist of interstitial cells in the course of this bundle, which as far as has been discovered, bears no relation to the medial geniculate body or to auditory pathways.

Nucleus suprageniculatus (figs. 10, 11). This nucleus, not previously described in the opossum, appears to correspond exactly to the nucleus suprageniculatus described in carnivores by Rioch ('29). As noted by the latter author, this nucleus fuses both with the lateral nucleus and with the medial geniculate nucleus, the cells of all being similar in appearance. The nucleus suprageniculatus is small but well defined and is present in all sections through the middle two-thirds of the medial geniculate nucleus. At its anterior end it is separated from the latter nucleus by the nucleus lateralis pars posterior, but throughout the rest of its extent it lies directly dorso-medial to the marginal part of the medial geniculate nucleus. Its cells are somewhat larger than those of the latter but merge imperceptibly with them in many places. At all levels in which it is present the suprageniculate nucleus lies between the pretectal nucleus and the medial geniculate nucleus.

Nucleus subparafascicularis (*nucleus of the tractus tecto-reuniens*) (figs. 10 to 12, 13 to 16, 20, 21). The nucleus subparafascicularis is a quite large nucleus in the opossum, extending from the medial and caudoventral border of the medial geniculate nucleus, forward and medially to the caudal border of the nucleus reuniens posterior, in which region it is continuous with cells of the nucleus paraventricularis posterior. These relations are best seen in horizontal sections (figs. 20, 21). In these sections it separates the principal ventral nucleus of the thalamus from the tegmental region

of the midbrain. This is also evident in medial sagittal sections (figs. 13 to 16) in which its relations to the nucleus parafascicularis pars posterolateralis above and the zona incerta below are also shown. In caudal levels of transverse series the nucleus of the tecto-reuniens bundle hugs the medial and ventral borders of the medial geniculate body (figs. 11, 12) and its cells extend laterally almost to the surface of the thalamus, in the angle between the medial geniculate body and the cerebral peduncle. Its cells mingle to some extent with those of the marginal part of the medial geniculate body (fig. 11), and more caudally with the cells of the anterior pole of the nucleus parabigeminus.

Only the anterior end of this nucleus, where it fuses with the anteroventral extremity of the nucleus paraventricularis posterior, was described by Chu ('32), who called it the nucleus subfascicularis. Papez ('32) also described a similar nucleus in the armadillo, which he thought corresponded to the nucleus subparafascicularis of Rioch ('29) in carnivores. In this we can concur, but consider this nucleus to be perhaps partly comparable to the nucleus Z described by Huber and Crosby ('26) in the alligator in relation to the tractus tecto-reuniens.

Papez ('36) has compared the so-called ventral nucleus of the medial geniculate body of mammals with the nucleus Z of Huber and Crosby, which further suggests the possibility that the so-called ventral nucleus of the medial geniculate body is really a lateral extension of the nucleus subparafascicularis. In our material it is the nucleus subparafascicularis, rather than the medial geniculate body, which is connected with the nucleus reuniens posterior and which forms a bridge between the nucleus reuniens posterior and the medial geniculate body. We are not prepared to discuss here the subtle questions of the genetic origins of the dorsal and ventral parts of the medial geniculate body, in the sense of Clark, Kuhlenbeck ('35), and Papez, but are not convinced that all the facts necessary for a solution of this problem are available as yet. The significance and connections of this

region will be discussed in greater detail in the second paper of this series.

Nucleus parabigeminus (*nucleus of the inferior quadrigeminal brachium*) (figs. 12, 21). This nucleus, the 'nucleus del corpo parabigemino' of Castaldi ('26), and the most rostral of the various nuclei of the lateral lemniscus of other authors, is present within the eminence on the lateral surface of the midbrain formed by the brachium of the inferior colliculus. It is composed of medium sized cells and some smaller cells which mingle rostrally with the most caudal cells of the nucleus subparafascicularis (fig. 21). The rostral pole of this nucleus overlaps slightly the medial border of the caudal pole of the medial geniculate nucleus (fig. 12). The caudal part of the nucleus consists of scattered cells in the course of the brachium, and can be followed as far caudally as the caudal border of the superior colliculus. This nucleus probably corresponds to a similar, but much larger nucleus in *Tarsius* which Clark ('33) has identified as the nucleus isthmi.

THE VENTRAL THALAMUS OR SUBTHALAMUS

For a review of the literature on this portion of the diencephalon, the reader is referred to the paper of Rioch ('29 a).

Nucleus entopeduncularis (figs. 2 to 4, and 22). Loo ('31) has described several cell groups in the opossum which he terms the entopeduncular nuclei. Of these the cells intercalated among the fibers of the ansa peduncularis, and more or less continuous with the cells of the globus pallidus form the nucleus entopeduncularis proper, following the nomenclature of Rioch ('29 a). The other groups consist of interstitial cells of the cerebral peduncle and are extremely few except at the medial and superior borders. These are the intrapeduncular and suprapeduncular groups of Loo ('31). The intrapeduncular group is found chiefly in the course of the medial, or strio-tegmental, bundles of the peduncle. The entopeduncular nucleus proper in the opossum consists of relatively few cells, slightly smaller than those of the globus

pallidus, which extend medially from the latter nucleus among the fibers of the ansa peduncularis. This nucleus can be recognized with certainty only in levels through the anterior half of the optic chiasm.

The relatively small size of the entopeduncular cell group in the opossum may perhaps be correlated with the relatively small size of the globus pallidus.

Nucleus reticularis (figs. 3 to 6, 13, 14, 20, 21). This nucleus, characteristic in all mammals, extends from the anterior pole to about the center of the thalamus, where it is replaced by the zona incerta, which overlaps it for some distance (fig. 13). The nucleus reticularis is an interstitial nucleus in the thalamic radiations and is bordered ventrolaterally by the internal capsule, except at its posterior end, where the zona incerta separates it from the cerebral peduncle. Dorsally, the reticular nucleus borders the anterior, lateral, and ventral nuclear groups in turn. These relations can be seen in the figures. Laterally, the reticular nucleus reaches almost to the surface of the thalamus, from which it is separated more caudally by the ventral part of the lateral geniculate body. Medially it is in close relation to the medial reticular nucleus which separates it from the nucleus hypothalamicus dorsalis (fig. 5). The latter in the opossum is more or less continuous laterally with the zona incerta. Caudally the cells of the nucleus reticularis gradually merge with those of the zona incerta.

Nucleus reticularis pars medialis (figs. 4, 5, 15). At the medial tip of the reticular nucleus, in sections rostral to the anterior end of the zona incerta, one sees in the opossum a sizable and compact group of cells, slightly smaller than those of the reticular nucleus, but otherwise similar in appearance. These cells merge with those of the reticular nucleus in places, but often are sharply separated by fibers of the inferior thalamic radiations. This group apparently has not been described separately before, but appears to be a constant medial differentiation of the reticular nucleus in all of our material. It is in close relation medially with the nucleus

hypothalamicus dorsalis, which anteriorly has a cup-shaped lateral margin in which the medial reticular nucleus is placed. Below the latter nucleus are the lateral filiform nucleus and the lateral hypothalamic nucleus.

Nucleus geniculatus lateralis ventralis (figs. 5 to 10, 20, 21). We wish to add to Tsai's description of this nucleus in the opossum ('25) only the observation that it is intimately associated with the zona incerta, with which its cells merge to a great extent. Caudally it extends below the anterior end of the medial geniculate body.

Zona incerta (figs. 6 to 11, 13, 14). The uncertain zone in the opossum is a fairly large and characteristic gray area, which appears in transverse sections as a transverse band of small, flattened cells above the dorsal and dorsomedial aspects of the cerebral peduncle. It extends from the infundibular region back to a transverse plane through the middle of the medial geniculate body. Anteriorly, it is placed between the reticular nucleus above and the lateral hypothalamic nucleus below, and its cells merge medially with those of the dorsal hypothalamic nucleus. Farther caudally, it becomes continuous laterally with the ventral nucleus of the lateral geniculate body, and medially with the field of Forel. Here it is dorsal to the subthalamic nucleus (figs. 8 and 9). Caudal to the reticular nucleus, it is bounded dorsally by the external medullary lamina, and more caudally by the medial geniculate body (figs. 10, 11). The grouping of the cells among the fibers of passage gives a picture suggestive of the division of the zona incerta into two parts as in the carnivores (Rioch, '29 a).

Field of Forel (figs. 8 to 10, 14, 15). The field 'H' of Forel is found in the opossum in the caudal third of the diencephalon. It consists of an area of small and medium cells, with occasional large cells, dorsal and caudal to the lateral hypothalamic nucleus, with which it is continuous. It is also continuous with the zona incerta laterally and with the posterior and dorsal hypothalamic nuclei medially. This area of diffuse gray is the field of passage of many fibers, especially the

lenticular bundles, which correspond to the bundles H_1 and H_2 of Forel (1877). The scattered gray of the field 'H' of Forel should probably not be considered as a nuclear and functional entity, but is an area of diffuse gray of uncertain relationships, associated rostrally with the hypothalamus and caudally with the midbrain tegmentum and the tegmental bundles, as noted in the early descriptions of Forel (1872 and 1877).

Nucleus subthalamicus (figs. 8 to 10, 13, 14, 22). The nucleus subthalamicus or corpus Luysii is a lenticulate group of fairly large cells which lies on the medial surface of the cerebral peduncle in the caudal third of the thalamus. It is bounded above by the zona incerta, dorsomedially by the field of Forel, and medially by the lateral hypothalamic nucleus, which separates it at its caudal end from the supramammillary nucleus. The latter and the subthalamus extend caudally to about the same level.

THE HYPOTHALAMUS AND THE PREOPTIC AREA

In addition to some of the most characteristic nuclei of the diencephalon, such as the tangential, filiform, and mammillary nuclei, the hypothalamus contains some of the most undifferentiated and ill-defined cell groups. Consequently, it is impossible in some cases to delimit accurately nuclear areas such as the periventricular, dorsomedial, and posterior hypothalamic nuclei in the opossum, in which these groups merge imperceptibly into one another. However, the essential features of nuclear topography are sufficiently clear to make possible a clear definition of boundaries in some cases and an adequate, though approximate, delimitation in other cases, for the purposes of homology and functional analysis.

No attempt to subdivide the nuclear groups of the hypothalamus can be entirely satisfactory, since the interrelationships of the constituent nuclei are quite intimate. Furthermore, the principal afferent and efferent connections of any selected group of nuclei are sure to overlap with those of a neighboring group, so that any subdivision, such as the rostro-

caudal subdivision proposed by Clark ('36 and '38) and others, must, in the nature of things, be arbitrary on both cytographic and functional grounds. A more general subdivision, the significance of which has been emphasized by Crosby and Woodburne ('39) in a recent comparative study, is the separation of the hypothalamic gray into three longitudinal regions, periventricular, medial, and lateral. This subdivision will be followed in the present account, and has the advantage of being based upon the established dynamics of ontogenetic and phylogenetic differentiation, as well as following the principal lines of fore and aft conduction. Superimposed upon this primitive mediolateral subdivision is, of course, the complicating differentiation in the dorsoventral and rostrocaudal planes, and here any attempt at further subdivision strikes the snag of interwoven connections, as will be apparent in the considerations of the second report of this series. In general, however, the nuclei of the three longitudinal subdivisions have been arranged in rostrocaudal order in this account, with a few exceptions in the case of the medial group in anticipation of relationships to be brought out in the discussion of the fiber connections.

Periventricular region (grisea centralis)

Nucleus preopticus periventricularis (figs. 2, 3, 18, 22). Loo ('31) has described the preoptic area in the opossum in considerable detail, so that no further discussion is needed here. It is enough to mention that the periventricular preoptic nucleus, as represented here, corresponds only to the pars medialis of Loo's preoptic periventricular nucleus and is continuous caudally with the nucleus hypothalamicus periventricularis.

Nucleus hypothalamicus periventricularis (figs. 4 to 7, 18). This is the gray which lines the third ventricle in the hypothalamic region. It is composed of small neurons and is nowhere more than several cells in width. It appears at the caudal border of the optic chiasm, where it is continuous anteriorly with the preoptic periventricular gray, and ex-

tends caudally to the level of the dorsal premammillary nucleus. One may speak of an anterior part extending back to the dorsomedial hypothalamic nucleus, in which region it is continuous caudally with the posterior part, but such a delimitation of these gray masses is arbitrary. Laterally, the anterior part of the periventricular nucleus is bounded by the anterior and ventromedial hypothalamic nuclei in turn. Below it is in relation to the nucleus supraopticus diffusus. The posterior part extends caudally to the level of the posterior end of the stalk of the hypophysis. Continuous with it, below the ventricle, in the midline, is a denser accumulation of cells of similar type, the ventral premammillary nucleus.

Nucleus ovoideus (figs. 2, 3, 16 to 18). This gray mass represents a condensation of the periventricular gray of the rostroventral part of the hypothalamic periventricular nucleus. It is clearly identical with the nucleus of the same name described in the rat by Gurdjian ('27) and was described by Loo ('31) in the opossum as the pars suprachiasmatica of the preoptic periventricular nucleus. It extends rostrally into the preoptic area and caudally into the anterior hypothalamic region, and it is continuous with the periventricular nuclei of both regions.

Nucleus premammillaris dorsalis (figs. 8, 9, 18). The premammillary nuclei in the opossum appear to be enlarged portions of the periventricular nucleus. In longitudinal sections it is especially evident that the dorsal premammillary nucleus is an enlarged caudal continuation of the nucleus hypothalamicus periventricularis (fig. 18). The cells of the two are identical and no separation can be made on cyto-architectural grounds. Caudal to a transverse level near the posterior end of the hypophyseal stalk, the dorsal part of the periventricular gray medial to the ventromedial hypothalamic nucleus gradually enlarges laterally and remains large up to the caudal end of the ventromedial nucleus, in which region it also disappears, being replaced by the posterior hypothalamic nucleus (figs. 8, 9). This mass of gray is continuous ventrally with the ventral premammillary nucleus, which is

characterized by a denser grouping of cells. It is bounded dorsally by the posterior hypothalamic nucleus. The enlarged portion of the dorsal periventricular hypothalamic gray anterior to the mammillary nuclei will be referred to as the dorsal premammillary nucleus in this account.

Nucleus premamillaris ventralis (figs. 6 to 10, 17, 18). The ventral premammillary nucleus may be considered as a caudal enlargement of the ventral part of the nucleus hypothalamicus periventricularis, beginning anteriorly somewhat rostral to the anterior pole of the dorsal premammillary nucleus (fig. 17). It also extends much farther caudally than the dorsal premammillary nucleus and can be traced caudally to the middle third of the mammillary nuclei. It is continuous dorsally with the dorsal premammillary nucleus at first, but more caudally the posterior hypothalamic nucleus and, still more caudally, the mammillary nuclei form its dorsal boundary. At the caudal end of the infundibular recess, it extends below the ventricle, fusing with its fellow of the opposite side, and finally becomes a midline cell mass below the anterior part of the mammillary bodies (fig. 10). Here it surrounds the recessus mamillaris.

Medial region

Nucleus preopticus medialis (figs. 2, 3, 16, 17, 22). This cell mass has been described in sufficient detail by Loo ('31). It corresponds to the anterior and principal preoptic nuclei of his description, and is continuous caudally with the anterior hypothalamic nucleus.

Nucleus hypothalamicus anterior (figs. 4, 5, 16 to 18, 22). This nucleus forms a transition zone between the medial preoptic area and the more caudal medial hypothalamic nuclei and is not clearly separable from either. It has a short rostrocaudal extent above the posterior half of the optic chiasm and the nucleus tangentialis pars tuberalis. Lateral to the anterior hypothalamic nucleus are the fornix and lateral hypothalamic nucleus. Below is the nucleus supraopticus diffusus, medially, the nucleus hypothalamicus periventricu-

laris, and above, the filiform nucleus and the nucleus hypothalamicus anterior pars dorsalis. The cells of the anterior hypothalamic nucleus are small and medium in size, stain moderately well, and resemble the cells of the preoptic area and of the ventromedial hypothalamic nucleus.

Nucleus hypothalamicus anterior pars dorsalis. This nuclear group is composed of cells more closely packed than those of the rest of the anterior hypothalamic nucleus, with which however it fuses ventrally. The pars dorsalis is found below and lateral to the filiform nucleus (fig. 5). Farther caudally it is bounded ventrally by the dorsomedial hypothalamic nucleus. Here it fuses dorsally with the nucleus hypothalamicus dorsalis (figs. 6, 16).

Nuclei magnocellulares hypothalami. The term nuclei magnocellulares hypothalami will be used in this account as a generic designation for the following nuclei, since they possess several important characteristics in common, including a probable association with the pars nervosa of the hypophysis:

Nucleus tangentialis pars supraoptica (nucleus supraopticus).

Nucleus tangentialis pars tuberalis.

Nucleus tangentialis pars diffusa.

Nucleus filiformis pars paraventricularis (nucleus paraventricularis).

Nucleus filiformis pars lateralis.

Röthig ('11) noted the close relationship of the cells of these groups in *Didelphis marsupialis*, and considered them all to be homologous with the preoptic magnocellular nucleus of fishes, Amphibia, and reptiles. Similar conclusions have been reached by Spiegel and Zweig ('17), Scharrer ('33), Meyer ('35), and others. Malone ('16), Gagel ('28), Nicolesco and Nicolesco ('29), Scharrer ('33), Scharrer and Gaupp ('33), Meyer ('35), Boon ('38), and others, have noted the similar cytological characteristics of these cells, and their rich vascular supply, as well as their intimate relationship to the capillaries and small blood vessels. Scharrer ('33)

has described cytoplasmic 'colloid' globules in the cells of these nuclei in various vertebrates and, on this basis, and because of the intimate association with blood vessels, has suggested that these cells are secretory in nature. Every one of the above-mentioned characteristics is clearly evident in the opossum, in which all of these nuclei form a continuous chain of large cells, as has been noted by many in other mammals including man (Gagel, '28; Meyer, '35; Clark, '36 and '38, and others).

Furthermore, in one of our reduced silver preparations, prepared by an accidental modification of the protargol method (Bodian, '37), all of the cells of the nuclei magnocellulares hypothalami are deeply and differentially stained, in striking contrast to all of the other cells of the hypothalamus, large and small, which are much less heavily impregnated with silver (fig. 1). It is interesting to note that Gagel ('28), working with the Bielschowsky method on human material, found that the neurofibrils in these cells showed very poorly, and that the silver was deposited instead in the form of fine granules.

Nucleus tangentialis (figs. 1 to 6, 13 to 18). The nucleus tangentialis of Ramón y Cajal ('11) has been described and figured in some detail in the opossum, as the nucleus supraopticus, by Loo ('31). We have followed Gurdjian ('27) and others in using Ramón y Cajal's term, because the designation of nucleus supraopticus, first used by von Lenhossék (1887) to describe an entirely different entity (see Malone, '16, p. 473), leads to possible confusion with neighboring unrelated nuclei, such as the nucleus supraopticus diffusus and the nucleus suprachiasmaticus. Meynert's earlier term, ganglion opticum basale, has been discarded generally, as being inappropriate for this non-optic center.

The prominent and characteristic tangential nucleus has achieved considerable importance in recent years with the description of its connections with the pars nervosa of the hypophysis (Kary, '24; Pines, '25; Stengel, '26; Greving, '28; Laruelle, '34; Roussy and Mosinger, '34 and '35; Fisher

et al., '35; Rasmussen, '37) and with the demonstration of its probable role in the hypothalamic water metabolism mechanism (see Fisher, Ingram and Ranson, '35 and '38). In the opossum, the principal part of the tangential nucleus is perched above the dorsolateral angle of the optic chiasm (fig. 3), astride the di-telencephalic fissure. It consists of a homogeneous group of cells, separated only in some sections into lateral and medial portions by the large vessels which enter at the afore-named fissure. This conspicuous group of large, deeply staining cells, which we shall call the *pars supraoptica*, connects with its fellow of the opposite side by strands of cells which extend medially and caudally along the dorsal surface of the chiasm and meet in the midline behind the chiasm in a group of cells stretched along the ventral surface of the tuber cinereum between the optic tracts, below the anterior part of the ventromedial hypothalamic nucleus (fig. 5). These cells forming the *pars tuberalis* are more numerous on either side of the midline than in the midplane, where a few scattered cells surround the anterior part of the base of the hypophyseal stalk. The lateral portions extend farther caudally, at the medial angles of the optic tracts, where they disappear before reaching the transverse plane passing through the center of the hypophyseal stalk (fig. 6).

From the supraoptic parts of the tangential nucleus, near the caudal border of the chiasm, numerous cells forming the *pars diffusa* of the tangential nucleus extend along prominent blood vessels dorsally toward the lateral part of the nucleus *filiformis*, with which they actually merge in some sections (figs. 1, 4). These cells perhaps correspond to the anterior part of the nucleus *tubero-mamillaris* of Malone ('16). In the opossum they are clearly continuous with the *pars supraoptica* of the tangential nucleus.

Nucleus *filiformis* (figs. 2 to 6, 16 to 18, 22). This nucleus has been described in the opossum by Röthig ('09), by Loo ('31), and by Chu ('32) as the nucleus *magnocellularis hypothalami*. Loo described it in some detail, reconstructed it, and divided it into medial and lateral portions. This nucleus

corresponds to the nucleus filiformis of Fortuyn ('12), Nissl ('13), Gurdjian ('27), and others, and to the nucleus filiformis principalis of Rioch ('29). It is the nucleus paraventricularis of Malone ('10 and '16), and the 'noyau sous-ventriculaire' of Ramón y Cajal ('11). In the opossum, as Loo pointed out, it appears to be as much a preoptic nucleus as a hypothalamic one. In the rat and dog (Gurdjian and Rioch) it is largely if not entirely placed within the anterior hypothalamic area. In the opossum, Loo and Chu recognized only large and deeply staining cells in this nucleus. In addition to these large cells, it is clear that a considerable number of small and medium sized, poorly staining cells of oval and spindle shapes are present as well, and continuous with identical cells of the preoptic and hypothalamic periventricular nuclei. These cells are found along with the large cells only in the paraventricular or medial part of this nucleus, however, and are comparable with similar cells described by Gurdjian in the rat and by Malone ('16) and by Greving ('28) in man. In the rat the small cells are medially placed, the medium sized cells more laterally, and the large, deeply staining cells dorsally within the nucleus. In the dog, according to Rioch, only small and medium sized cells occur, both with deeply staining granulations, in the nucleus filiformis anterior, which is placed between the preoptic and hypothalamic areas. His nucleus filiformis principalis, which is composed of larger, compactly grouped cells, corresponds in position with the caudal portion of the paraventricular part of the filiform nucleus of the opossum.

Apparently, then, a constant feature of this cell mass is its position in the dorsal periventricular region of the preoptic and anterior hypothalamic areas, where the typical large cells may be more or less intermingled with the small undifferentiated cells of the periventricular gray.

Nucleus filiformis pars paraventricularis. The paraventricular part of the filiform nucleus extends from a transverse plane through the middle of the optic chiasm, to its caudal limit near the anterior end of the hypophyseal stalk.

Rostrally it is continuous with the periventricular preoptic nucleus, the cells of which are identical with the small cells of the paraventricular part of the filiform nucleus. Throughout its course it has a roughly triangular shape, with a broad base clearly applied to the third ventricle and with an apex directed laterally. In the anterior part of its extent its lateral boundary is formed by the nucleus preopticus medialis (figs. 2, 3), but farther caudally it is placed in the angle between the nucleus hypothalamicus dorsalis and the dorsal part of the nucleus hypothalamicus anterior. Here it connects laterally with the lateral filiform nucleus by means of a few rows of cells (fig. 5). The nucleus hypothalamicus dorsalis forms most of its dorsal boundary (fig. 17).

Nucleus filiformis pars lateralis (figs. 4, 5, 14, 15). The nucleus filiformis pars lateralis is a small nucleus which is continuous with the nucleus filiformis pars paraventricularis medially and with the scattered perivascular cells of the diffuse part of the tangential nucleus ventrolaterally, as already described. It differs from the nucleus filiformis pars paraventricularis in that it contains only large cells. It appears anteriorly in the lateral hypothalamic area, below the nucleus reticularis pars medialis, and does not extend so far caudward as does the paraventricular part of the filiform nucleus.

Nucleus supraopticus diffusus (figs. 5, 17, 18). This nucleus was described by Loo ('31) in the opossum, as the nucleus suprachiasmaticus diffusus. The present term was used by Gurdjian ('27) and Rioch ('29), who considered this nucleus to be a bed nucleus for the supraoptic decussations. In the opossum it appears to consist of a small, diffuse group of cells, similar to those of the anterior hypothalamic nucleus, placed in the midline between the ventricle and the tuberal part of the tangential nucleus, behind the optic chiasm.

Nucleus hypothalamicus ventromedialis (figs. 6 to 8, 16 to 18). This nucleus is one of the most prominent and clearly delimited cell groups of the hypothalamus, and is the principal nucleus of the tuber cinereum. It is ovoid in shape and extends from the posterior border of the optic chiasm to the

anterior limit of the mammillary nuclei (fig. 16). It is placed just lateral to the periventricular hypothalamic nucleus, and caudally is lateral to the dorsal premammillary nucleus. Laterally its cells mingle to a certain extent with those of the lateral hypothalamic nucleus. Its dorsal boundary is formed rostrally by the nucleus hypothalamicus dorsomedialis and caudally by the posterior hypothalamic nucleus. Its cells are of medium size, deeply staining and closely grouped.

Nucleus hypothalamicus dorsomedialis (figs. 6, 16, 17, 22). This cell mass is much less clearly delimited than the ventromedial nucleus, and extends as far rostrally as the latter nucleus but only half as far caudally. It is situated just dorsal to the ventromedial nucleus and is replaced caudally by the posterior hypothalamic nucleus, with which it merges imperceptibly (fig. 16). Laterally its cells also mingle with those of the lateral hypothalamic nucleus. It is bordered above by the nucleus hypothalamicus dorsalis. Its cells at the rostral and dorsal angle are slightly larger than those of the ventromedial nucleus. Here the dorsomedial nucleus is below the caudally projecting dorsal part of the anterior hypothalamic nucleus. Farther caudally and ventrally the cells are smaller and are identical in appearance with those of the posterior hypothalamic nucleus.

Nucleus hypothalamicus posterior (figs. 7 to 9, 16 to 18, 22). The nucleus hypothalamicus posterior makes its appearance at the caudal end of the dorsomedial nucleus, where it occupies the same relative position with reference to the surrounding gray centers. At its dorsocaudal pole it becomes continuous with the ventral nucleus of the medial longitudinal fasciculus, being separated from the latter to some extent by the tractus mamillo-thalamicus (fig. 17). The cells at the dorsolateral angle of this nucleus mingle with those of the field of Forel, which borders it laterally, and form finger-like processes around the bundles of the fasciculus retroflexus.

Nucleus hypothalamicus dorsalis (figs. 3 to 8, 15 to 18). This nucleus is the gray mass which Chu ('32) described as the nucleus filiformis. It appears in general that the dorsal

hypothalamic area has been variously differentiated in the mammals described, and the exact homologies of some of the groups do not seem to be altogether clear. Gurdjian did not describe any separate nucleus that might correspond to the nucleus hypothalamicus dorsalis in the rat, but apparently the dorsal part of his nucleus dorsomedialis has similar relations ('27). Rioch's nucleus hypothalamicus parvocellularis corresponds in cell type and position with the rostral end of our nucleus hypothalamicus dorsalis, and in addition his dorsal hypothalamic area appears to be homologous with the rest of this nucleus ('29). In the opossum the cells of the anterior half of the nucleus hypothalamicus dorsalis are much more compactly grouped than those of the caudal part of the nucleus.

The nucleus hypothalamicus dorsalis extends almost the entire length of the thalamus, from a transverse level through the posterior third of the optic chiasm to one through the anterior limit of the posterior commissure, where it is replaced by the most ventral part of the nucleus paraventricularis posterior (fig. 17). Throughout its entire course it is situated below the nucleus reuniens near the midline and thus separates the dorsal thalamus from the hypothalamus. Anteriorly it is above the filiform nucleus, but, at the caudal end of the latter, it touches below the dorsal part of the anterior hypothalamic nucleus, which has similar cells (figs. 6, 16). In its caudal half, the nucleus hypothalamicus dorsalis is bounded ventrally by the nucleus hypothalamicus posterior. Laterally, it borders closely on the nucleus reticularis pars medialis in its anterior half, but in its caudal half is intimately associated with the zona incerta and, at its caudal end, with the cells of the field of Forel (figs. 6 to 8).

Corpus mamillare (figs. 10, 11, 16 to 18). The mammillary bodies of the opossum have been described by Tsai ('25) and by Chu ('32). The nuclear arrangement appears to be comparable to that described in the rat by Gurdjian ('27). The terminology of the various authors varies considerably, although most workers agree as to the presence of a rela-

tively large medial group and a smaller lateral part. This disparity in size, however, is not great in the opossum. The terminology to be used here follows in general that used by Gurdjian in the rat, and differs from that of Tsai and Chu.

The mammillary bodies of the opossum occupy the base of the diencephalon behind the infundibulum, and extend back beneath the tegmental region of the anterior mesencephalon. The cells of all the constituent nuclear parts are more or less similar in type, being small and medium in size. The cells of the pars lateralis and those of the pars medialis are more compactly grouped than elsewhere. The posterior fusion of the lateral parts of the medial mammillary nucleus, as Gurdjian ('27) described it in the rat (nucleus mamillaris medialis pars posterior), does not occur in the opossum.

Nucleus mamillaris pars mediana. This nucleus is the first to appear anteriorly and occupies a midline position throughout most of the extent of the mammillary bodies, but it is not present at the caudal end of the nuclear group. At its anterior end it is placed directly below the supramammillary nucleus, above the nucleus mamillaris pars commissuralis anteroventralis, and medial to the bundles of the mammillo-tegmental tract. Farther caudally, the nucleus mamillaris pars commissuralis posterodorsalis forms its dorsal boundary. The cells of this principal medial nucleus are small and medium in size, closely grouped except caudally, and in fiber preparations are seen to be surrounded by a dense felt-work of fibers.

Nucleus mamillaris pars medialis. This is a small group of cells which present as a distinct mass, separate from the median nucleus, only at the rostral end of the latter. It lies at the lateroventral angle of the median nucleus, between the latter and the lateral mammillary nucleus. The cells of this small nucleus are more compactly grouped and apparently more deeply stained than those of the other mammillary nuclei. At its caudal end it merges with a lateral extension of the median nucleus.

Nucleus mamillaris pars lateralis. The lateral mammillary nuclei form the principal bulk of the caudal half of the mammillary bodies. At the rostral end they are separated from the median nucleus by the mammillo-tegmental bundles, and form comma-shaped masses with concavities directed medially. Caudally they are covered by the mammillary capsule and form the lateral rounded prominences of the mammillary bodies. The cells of this group are compactly grouped, especially ventrally, but become more scattered caudally, where they comprise the entire masses of the caudal poles of the mammillary bodies.

Nucleus mamillaris pars commissuralis anteroventralis. This nucleus forms a transverse strip of cells between the ventral premammillary nucleus and the median mammillary nucleus and connects the two lateral mammillary nuclei (fig. 10). The cells are similar to those of the latter.

Nucleus mamillaris pars commissuralis posterodorsalis. This nucleus is prominent in the opossum, and first appears rostrally somewhat behind the anterior end of the median mammillary nucleus, where it occupies a position between the latter and the supramammillary nucleus. It forms a transverse band of cells, slightly larger than those in the median nucleus, and connects laterally with the nucleus mamillaris lateralis.

Nucleus supramamillaris (figs. 10, 11, 16 to 18, 22). This nucleus is quite prominent and discrete in the opossum and apparently is entirely comparable with that described in carnivores by Rioch ('29). It lies above the medial mammillary nuclei throughout most of its extent, with the posterior hypothalamic nucleus rostrally and dorsally placed. It lies below, and partly in the course of, the supramammillary decussation, and consists of medium-sized, well-staining cells, which resemble those of the posterior hypothalamic nucleus, and those of the midbrain tegmentum which mingle with those of the supramammillary nuclei to a certain extent. Anteriorly the nuclei of both sides are fused in the midline, with lateral wings separated from the central mass by the mam-

millo-thalamic bundles. Posteriorly, the nuclei separate, and gradually disappear near the caudal end of the mammillary nuclei.

At the caudal end of the supramammillary nucleus one sees a group of smaller cells just dorsal to the supramammillary nucleus. These cells are similar to, and continuous with, those of the surrounding midbrain tegmentum, but they form a condensation in the course of the supramammillary decussation. This group of cells appears to correspond to that labeled by Rioch ('29) as the nucleus interstitialis pars decussationis supramamillaris.

Lateral region

Nucleus preopticus lateralis (figs. 2, 3, 13 to 15, 22). This nucleus is continuous with, and indistinguishable from, the lateral hypothalamic nucleus, both being interstitial nuclei of the medial forebrain bundles. It corresponds to both the nucleus preopticus interstitialis and the nucleus preopticus magnocellularis of Loo ('31).

Nucleus hypothalamicus lateralis (figs. 3 to 9, 13 to 15, 22). This nucleus extends the length of the thalamus and is continuous in front with the lateral preoptic nucleus and behind with the interstitial tegmental nucleus of the midbrain (fig. 14). It is impossible to draw a line anywhere between these nuclei so that arbitrary limits are set for the lateral hypothalamic nucleus at the optic chiasm and at the level of the mammillary nuclei. The lateral hypothalamic nucleus is a diffuse, interstitial nucleus in the course of the medial forebrain bundle. It is bordered dorsolaterally by the internal capsule, medially by the medial group of hypothalamic nuclei as seen in the figures, and above by the reticular nucleus, the nucleus hypothalamicus dorsalis, the zona incerta, and the field of Forel, in rostro-caudal order. The cells are medium and large in size and stain well as a rule. Rostrally the ventral border is formed by the optic tract and the tangential nucleus, but caudally it extends to the ventrolateral surface of the hypothalamus. Caudally, its cells fuse medially with

those of the dorsomedial, ventromedial, and posterior hypothalamic nuclei, and in a position just lateral to the ventromedial nucleus form a denser group of large cells around the fornix bundle. This condensation of cells has been called the nucleus perifornicalis by Chu ('32), and is probably only in part the nucleus perifornicalis of Rioch ('29), who recognized that the accumulations of cells around the fornix bundles in the hypothalamus were always identical in type with those of the region through which the fornix passed. This has seemed quite clear in our preparations and consequently no separate nucleus perifornicalis will be described.

It is a matter of some interest, however, that in addition to the large cells around the premammillary portion of the fornix, large cells are scattered throughout the lateral hypothalamic area and mingle with similar cells between the bundles of the medial part of the cerebral peduncle (the suprapeduncular and intrapeduncular nuclei of Livini, '07, and of Loo, '31). These cells very likely correspond at least in part to the large cells of the nucleus tubero-mamillaris of Malone ('16), and Clark ('36) has recently emphasized the fact that such large cells are especially numerous in man.

The large cells of the lateral hypothalamic nucleus just discussed should not be confused with the large cells of the nucleus tangentialis pars diffusa, which are scattered in the anterior part of the lateral hypothalamic nucleus, and have special cytological characteristics linking them with the cells of the filiform nucleus and of the principal or supraoptic part of the tangential nucleus.

THE EPITHALAMUS

Nucleus habenularis medialis (figs. 4 to 8, 16 to 18). The medial habenular nucleus extends from a level just caudal to the anterior end of the thalamus to a level near the anterior end of the nucleus paraventricularis posterior. It is placed in characteristic fashion just below the taenia thalami, bordering on the ependyma of the third ventricle and medial to the stria medullaris and the lateral habenular nucleus (fig. 5).

It lies above the nucleus paraventricularis anterior, except caudally, where the nucleus paraventricularis posterior lies ventrally (fig. 8). At the caudal end of the thalamus, the habenular commissure and pineal body cover the medial habenular nucleus dorsally. The medial habenular nucleus shows the characteristically close grouping of deeply staining, medium sized cells. It has been divided into dorsal and ventral parts by Tsai ('25) and Chu ('32) in the opossum, and by others in various mammals. These parts in the opossum are separated by fibers of the stria medullaris, and are probably not significantly different in other respects.

Nucleus habenularis lateralis (figs. 4 to 7, 14 to 16). The lateral habenular nucleus extends almost as far rostrally as the medial habenular nucleus, but does not reach so far caudally. Throughout its entire extent it is lateral to the medial habenular nucleus and medial and ventral to the stria medullaris (fig. 6). The nucleus medialis dorsalis forms its ventral boundary. It is composed of cells more loosely arranged than those of the medial habenular nucleus, and of small and medium size. It may be roughly divided in the middle two-thirds of its course into a dorsal portion, containing more large cells, and a ventral portion composed of smaller and more scattered cells. These two portions blend into each other imperceptibly (fig. 15), and caudally merge with the cells of the nucleus paraventricularis posterior.

DISCUSSION AND SUMMARY

The description of the nuclear groups in the preceding pages has been conditioned by and dependent upon a concurrent study of the fiber connections in normal and experimental material. These connections will form the subject of the two subsequent reports in this series. Since an adequate understanding of the nuclear configuration of the diencephalon cannot be achieved without a coordinative consideration of the fiber connections of the nuclear masses, a detailed discussion of the separate cell groups will be reserved for the second of this series of reports.

It has frequently been remarked that the diencephalic pattern within the mammalian group is relatively uniform (d'Hollander, '13). To this statement the opossum diencephalon forms no exception. Considered as a whole, this undoubtedly generalized mammalian diencephalon is remarkable not only for its primitive features, of which there are abundant examples, but also for its possession of most of the typical features of higher mammalian brains.

Comparison with other mammalian brains, most of the available descriptions of which we have examined carefully, reveals no outstanding specializations in the opossum, although most of the nuclei are clearly differentiated. In general, the closest resemblances appear to occur between the opossum and the rat, as described by Gurdjian ('27), *Tupaia*, as described by Clark ('29), and the armadillo, as described by Papez ('32) and Howe ('33). The difficulties of homology of most groups are not inordinately great, except for the barriers interposed by differences of terminology, and by inadequate descriptions of the connections of nuclear masses and of their precise limits.

Special consideration has been given to some of the centers hitherto not described adequately in the opossum, and to those centers which have recently been the subject of morphological and physiological investigations in other mammals. Among these may be mentioned, in the dorsal thalamus, the nucleus subparataenialis, the nucleus paraventricularis posterior, the pretectal nucleus, and the medial geniculate nucleus and its associated center, the subparafascicular nucleus; in the ventral thalamus, the medial reticular nucleus; and in the hypothalamus, the magnocellular nuclei and the dorsal hypothalamic nucleus.

LITERATURE CITED

- ARIËNS KAPPERS, C. U. 1921 *Vergleichende Anatomie des Nervensystems*. E. F. Bohn, Haarlem.
- ARIËNS KAPPERS, C. U., G. C. HUBER AND E. C. CROSBY 1936 *The comparative anatomy of the nervous system of vertebrates, including man*. Vol. 2. The Macmillan Co., New York.

- BECCARI, N. 1923 Il centro tegmentale o interstiziale ed altre formazioni poco note nel mesencefalo e nel diencefalo di un rettile. *Arch. Ital. Anat. e Embr.*, T. 20, pp. 560-619.
- BODIAN, D. 1935 The projection of the lateral geniculate body on the cerebral cortex of the opossum. *J. Comp. Neur.*, vol. 62, pp. 469-494.
- 1937 An experimental study of the optic tracts and retinal projection of the Virginia opossum. *J. Comp. Neur.*, vol. 66, pp. 113-144.
- 1937 a The staining of paraffin sections of nervous tissues with activated protargol. The role of fixatives. *Anat. Rec.*, vol. 69, pp. 153-162.
- BOON, A. A. 1938 Comparative anatomy and physiopathology of the autonomic hypothalamic centres. *Academisch Proefschrift. E. F. Bohn, Haarlem.*
- CASTALDI, L. 1926 Studi sulla struttura e sullo sviluppo del mesencefalo. *Arch. Ital. Anat. e Embr.*, T. 23, pp. 481-609.
- CAIRNEY, J. 1926 A general survey of the forebrain of *Sphenodon punctatum*. *J. Comp. Neur.*, vol. 42, pp. 255-348.
- CHU, H. N. 1932 The cell masses of the diencephalon of the opossum. *Monographs Nat. Res. Inst. of Psychol., Peiping, China*, No. 2. 36 pp.
- 1932 a The fiber connections of the diencephalon of the opossum. *Ibid.*, No. 3. 34 pp.
- CLARK, W. E. LE GROS 1929 The thalamus of *Tupaia minor*. *J. Anat.*, vol. 63, pp. 177-206.
- 1930 The thalamus of *Tarsius*. *J. Anat.*, vol. 64, pp. 371-414.
- 1931 The brain of *Microcebus murinus*. *Proc. Zool. Soc., London*, Part 2, pp. 463-486.
- 1932 The structure and connections of the thalamus. *Brain*, vol. 55, pp. 406-470.
- 1933 The medial geniculate body and the nucleus isthmi. *J. Anat.*, vol. 67, pp. 536-548.
- 1936 The topography and homologies of the hypothalamic nuclei in man. *J. Anat.*, vol. 70, pp. 203-214.
- 1938 Morphological aspects of the hypothalamus. In 'The hypothalamus,' by W. E. L. Clark, J. Beattie, G. Riddoch and N. M. Dott. Oliver and Boyd, Edinburgh.
- CROSBY, E. C., AND R. T. WOODBURN 1939 The comparative anatomy of the submammalian hypothalamic area. *Proc. Ass. Res. Nerv. and Ment. Disease*. In press.
- CROUCH, R. L. 1934 The nuclear configuration of the hypothalamus and subthalamus of *Macacus rhesus*. *J. Comp. Neur.*, vol. 59, pp. 431-449.
- 1934 a The nuclear configuration of the thalamus of *Macacus rhesus*. *Ibid.*, pp. 451-485.
- FISHER, C., W. R. INGRAM, W. K. HARE AND S. W. RANSON 1935 The degeneration of the supraoptico-hypophyseal system in diabetes insipidus. *Anat. Rec.*, vol. 63, pp. 29-52.
- FISHER, C., W. R. INGRAM AND S. W. RANSON 1935 Relation of hypothalamico-hypophyseal system to diabetes insipidus. *Arch. Neur. and Psychiat.*, vol. 34, pp. 124-163.
- 1938 Diabetes insipidus and the neurohumoral control of water balance. *Edwards Bros., Ann Arbor, Mich.*

- FOREL, A. 1872 Beiträge zur Kenntnis des Thalamus opticus und der ihn umgebenden Gebilde bei den Säugetieren. (Sitzb. k. Akad. Wiss. in Wien, Bd. 66.) Ges. hirnanat. Abhandlungen, München, 1907, S. 17-43.
- 1877 Untersuchungen über die Haubenregion und ihre oberen Verknüpfungen im Gehirne des Menschen und einiger Säugetiere. (Arch. f. Psychiat., Bd. 7.) Ibid., S. 45-139.
- FORTUYN, B. D. 1912 Die Ontogenie der Kerne des Zwischenhirns beim Kaninchen. Arch. f. Anat. u. Physiol., Anat. Abt., S. 303-352.
- GAGEL, O. 1928 Zur Topik und feineren Histologie der vegetativen Kerne des Zwischenhirns. Zeitschr. f. Anat. u. Entwicklungsgeschichte (Abt. I, Zeitschr. f. d. ges. Anat.), Bd. 87, S. 558-584.
- GREVING, R. 1928 Die zentralen Antelle des vegetativen Nervensystems. V. Die vegetativen Zentren im Zwischenhirn. v. Möllendorff's Handbuch der mikr. Anat. des Menschen, Bd. 4, S. 974-1060. Springer, Berlin.
- GURDJIAN, E. S. 1927 The diencephalon of the albino rat. J. Comp. Neur., vol. 43, pp. 1-114.
- D'HOLLANDER, F. 1913 Recherches anatomiques sur les couches optiques. Le Névraxe, T. 14-15, pp. 469-519.
- HOWE, H. A. 1933 The basal diencephalon of the armadilla. J. Comp. Neur., vol. 58, pp. 311-375.
- HUBER, G. C. 1927 New method of fixation and staining of the central nervous system for purpose of study of cytoarchitecture. Contrib. to Med. Science, dedicated to Aldred Scott Warthin, pp. 1-12. Wahr, Ann Arbor, Mich.
- HUBER, G. C., AND E. C. CROSBY 1926 On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. J. Comp. Neur., vol. 40, pp. 97-227.
- KARY, C. 1924 Pathologisch-anatomische und experimentelle Untersuchungen zur Frage des Diabetes insipidus und der Beziehungen zwischen Tubercinereum und Hypophyse. Arch. f. path. Anat. u. Physiol., Bd. 252, S. 734-747.
- KUHLENBECK, H. 1935 Über die morphologische Stellung des Corpus geniculatum mediale. Anat. Anz., Bd. 81, S. 28-37.
- LARUELLE, M. L. 1934 Les centres végétatifs du diencéphale médian. Rev. Neurol., T. 1, pp. 809-842.
- LENHOSSÉK, M. V. 1887 Beobachtungen am Gehirn des Menschen. Anat. Anz., Bd. 2, S. 450-461.
- LIVINI, F. 1907 Das Vorderhirn und Zwischenhirn eines Marsupialiers: *Hypsiorymnus rufescens*. Anat. Anz., Bd. 31, S. 1-11.
- LOO, Y. T. 1930 The forebrain of the opossum, *Didelphis virginiana*. I. Gross anatomy. J. Comp. Neur., vol. 51, pp. 13-64.
- 1931 Idem. II. Histology. J. Comp. Neur., vol. 52, pp. 1-148.
- MALONE, E. F. 1910 Über die Kerne des menschlichen Diencephalon. Neur. Centralbl., Bd. 29, S. 290-300.
- 1916 The nuclei tuberis laterales and the so-called ganglion opticum basale. Johns Hopkins Hosp. Reports, vol. 17, pp. 441-510.

- MEYER, W. C. 1935 Phylogenetische Ableitung des Nucleus supraopticus vom Nucleus paraventricularis. *Dtsch. Zeitschr. Nervenheilk.*, Bd. 138, S. 65-74.
- NICOLESKO, I., AND M. NICOLESKO 1929 Quelques données sur les centres végétatifs de la région infundibulo-tubérienne et de la frontière diencéphalo-téleencéphalique. *Rev. Neurol.*, T. 2, pp. 289-317.
- NISSL, F. 1889 Die Kerne des Thalamus beim Kaninchen. *Neur. Centralbl.*, Bd. 8, S. 549.
- 1913 Die Grosshirnanteile des Kaninchens. *Arch. f. Psychiat.*, Bd. 52, S. 867-953.
- PAPEZ, J. W. 1932 The thalamic nuclei of the nine-banded armadillo (*Tatusia novemcincta*). *J. Comp. Neur.*, vol. 56, pp. 49-103.
- 1936 Evolution of the medial geniculate body. *J. Comp. Neur.*, vol. 64, pp. 41-61.
- PINES, I. L. 1925 Über die Innervation der Hypophysis cerebri. II. Über die Innervation des Mittel- und Hinterlappens der Hypophyse. *Zeitschr. f. d. ges. Neur. u. Psychiat.*, Bd. 100, S. 123-138.
- RAMÓN Y CAJAL, S. 1911 *Histologie du système nerveux de l'homme et des vertébrés*. A. Maloine, Paris.
- RASMUSSEN, A. T. 1937 Reaction of the supraoptic nucleus to hypophysectomy. *Proc. Soc. Exp. Biol. and Med.*, vol. 36, pp. 729-731.
- RIOCH, D. MCK. 1929 Studies on the diencephalon of Carnivora. I. The nuclear configuration of the thalamus, epithalamus, and hypothalamus of the dog and cat. *J. Comp. Neur.*, vol. 49, pp. 1-119.
- 1929 a Studies on the diencephalon of Carnivora. II. Certain nuclear configurations and fiber connections of the subthalamus and midbrain of the dog and cat. *J. Comp. Neur.*, vol. 49, pp. 121-153.
- 1931 A note on the centre médian nucleus of Luys. *J. Anat.*, vol. 65, pp. 324-327.
- RÖTHIG, P. 1909 Riechbahnen, Septum und Thalamus bei *Didelphys marsupialis*. *Abh. Senckenbergischen Naturfor. Ges.*, Bd. 31, S. 1-19.
- 1911 Beiträge zum Studium des Zentralnervensystems der Wirbeltiere. 3. Zur Phylogenese des Hypothalamus. *Folia Neurobiol.*, Bd. 5, S. 913-927.
- ROUSSY, G., AND M. MOSINGER 1934 Etude anatomique et physiologique de l'hypothalamus. *Rev. Neurol.*, T. 1, pp. 848-887.
- 1935 L'hypothalamus chez l'homme et chez le chien. *Rev. Neurol.*, T. 63, pp. 1-35.
- SCHARRER, E. 1933 Die Erklärung der scheinbar pathologischen Zellbilder im Nucleus supraopticus und Nucleus paraventricularis. *Zeitschr. f. d. ges. Neur. u. Psychiat.*, Bd. 145, S. 462-470.
- SCHARRER, E., AND R. GAUPP 1933 Neuere Befunde am Nucleus supraopticus und Nucleus paraventricularis des Menschen. *Zeitschr. f. d. ges. Neur. u. Psychiat.*, Bd. 148, S. 766-772.
- SPIEGEL, E. A., AND H. ZWEIG 1917 Zur Cytoarchitektonik des Tuber cinereum. *Arb. a. d. neur. Inst. a. d. Wiener Univ.*, Bd. 22, S. 278-295.

- STENGEL, E. 1926 Über den Ursprung der Nervenfasern der Neurohypophyse im Zwischenhirn. Arb. a. d. neur. Inst. a. d. Wiener Univ., Bd. 28, S. 25-37.
- TSAI, C. 1925 The optic tracts and centers of the opossum, *Didelphis virginiana*. J. Comp. Neur., vol. 39, pp. 173-216.
- WALKER, A. E. 1938 The primate thalamus. 321 pp. The University of Chicago Press, Chicago.
- WARNER, F. J. 1929 The hypothalamus of the opossum. J. Nerv. and Ment. Disease, vol. 70, pp. 485-494.

EXPLANATION OF PLATES

Figures 2 to 22 drawn at $\times 40$ and reduced to $\times 10$.

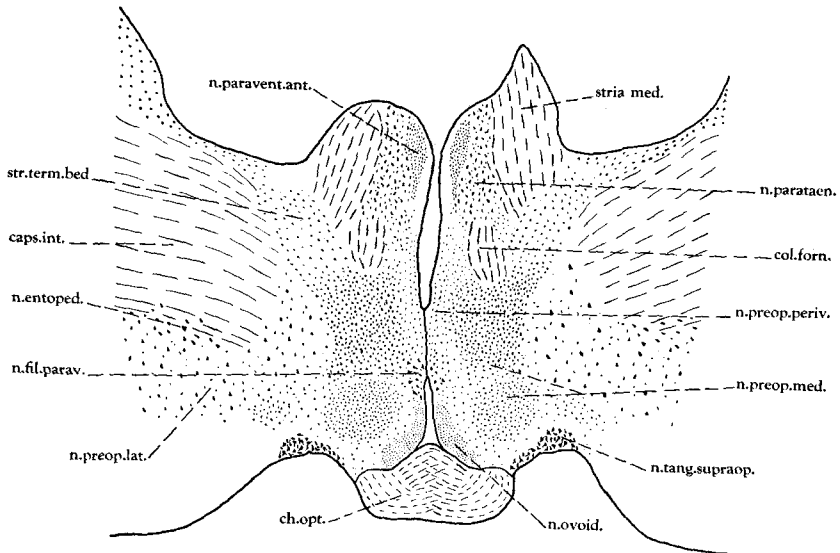
ABBREVIATIONS

- | | |
|--|--|
| <i>acq.</i> , aqueductus cerebri | <i>n.g.l.v.</i> , nucleus geniculatus lateralis ventralis |
| <i>c.pineale</i> , corpus pineale | <i>n.g.m.cent.</i> , nucleus geniculatus medialis pars centralis |
| <i>caps.int.</i> , capsula interna | <i>n.g.m.marg.</i> , nucleus geniculatus medialis pars marginalis |
| <i>ch.opt.</i> , chiasma opticum | <i>n.hyp.ant.</i> , nucleus hypothalamicus anterior |
| <i>col.forn.</i> , columna fornicis | <i>n.hyp.ant.dor.</i> , nucleus hypothalamicus anterior pars dorsalis |
| <i>col.sup.</i> , colliculus superior | <i>n.hyp.dor.</i> , nucleus hypothalamicus dorsalis |
| <i>com.ant.</i> , commissura anterior | <i>n.hyp.dor.med.</i> , nucleus hypothalamicus dorsomedialis |
| <i>com.ant.bed</i> , bed nucleus of <i>com.ant.</i> | <i>n.hyp.lat.</i> , nucleus hypothalamicus lateralis |
| <i>com.hab.</i> , commissura habenularum | <i>n.hyp.periv.</i> , nucleus hypothalamicus periventricularis |
| <i>com.post.</i> , commissura posterior | <i>n.hyp.post.</i> , nucleus hypothalamicus posterior |
| <i>FF</i> , Forel's field H | <i>n.hyp.vent.med.</i> , nucleus hypothalamicus ventromedialis |
| <i>gl.pal.</i> , globus pallidus | <i>n.inp.</i> , nucleus interpeduncularis |
| <i>gr.cent.</i> , stratum griseum centrale | <i>n.int.com.post.</i> , nucleus interstitialis commissurae posterioris |
| <i>hypoph.</i> , hypophysis cerebri | <i>n.int.F.L.M.</i> , nucleus interstitialis fasciculi longitudinalis medialis |
| <i>n.ant.dor.</i> , nucleus anterior dorsalis | <i>n.int.med.dor.</i> , nucleus inter-medialis dorsalis |
| <i>n.ant.med.</i> , nucleus anterior medialis | <i>n.lat.ant.</i> , nucleus lateralis pars anterior |
| <i>n.ant.vent.</i> , nucleus anterior ventralis | <i>n.lat.hab.</i> , nucleus habenularis lateralis |
| <i>n.c.int.-a.dor.</i> , nucleus commissuralis interanterodorsalis | |
| <i>n.c.int.-vent.ant.</i> , nucleus commissuralis inter-ventralis anterior | |
| <i>n.cent.</i> , nucleus centralis | |
| <i>n.cent.teg.</i> , nucleus centralis tegmenti | |
| <i>n.Dark.</i> , nucleus of Darkschewitsch | |
| <i>n.E.-W.</i> , nucleus of Edinger-Westphal | |
| <i>n.entoped.</i> , nucleus entopeduncularis | |
| <i>n.fil.lat.</i> , nucleus filiformis pars lateralis | |
| <i>n.fil.parav.</i> , nucleus filiformis pars paraventricularis | |
| <i>n.g.l.d.</i> , nucleus geniculatus lateralis dorsalis | |

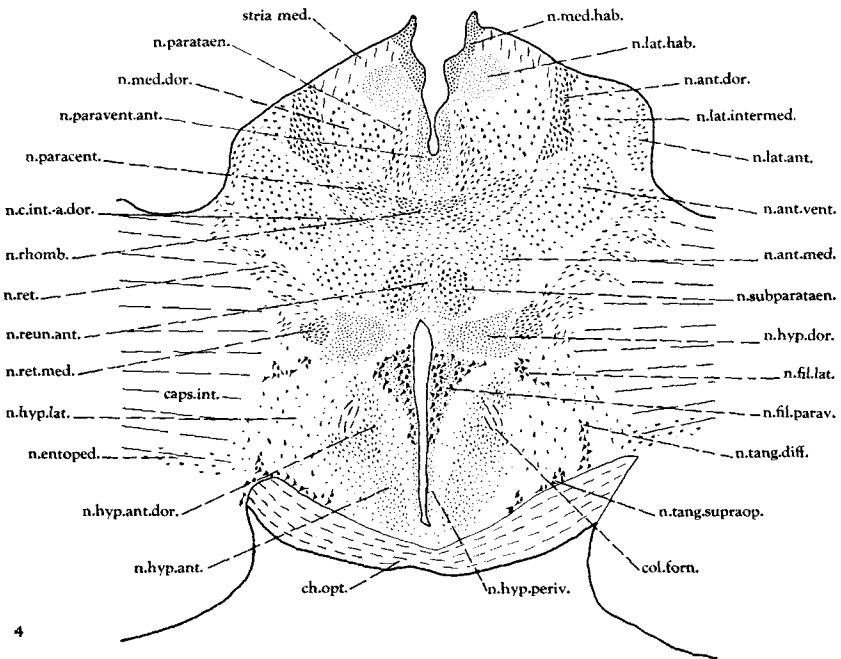
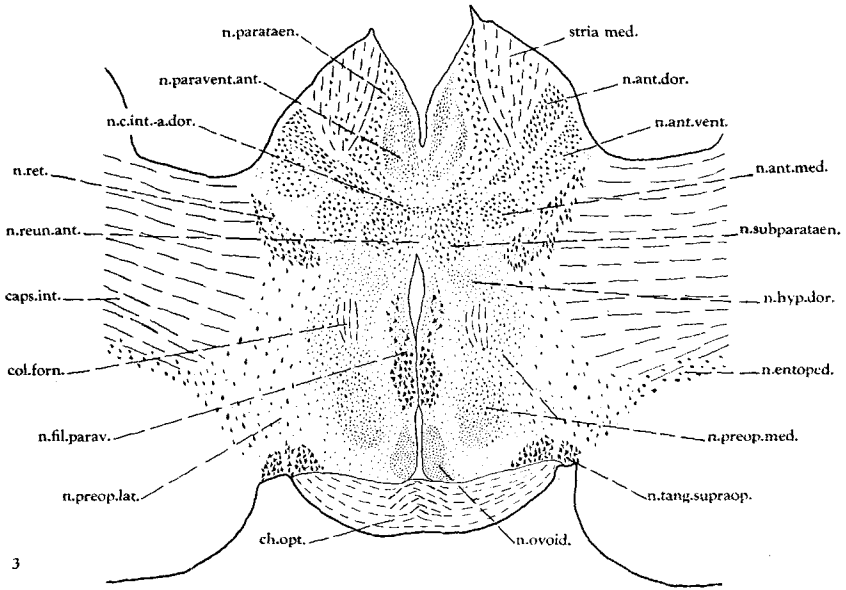
- n.lat.intermed.*, nucleus lateralis pars intermedia
n.lat.post., nucleus lateralis pars posterior
n.lat.prof., nucleus lateralis profundus tegmenti
n.mam.c.a.v., nucleus mamillaris pars commissuralis anteroventralis
n.mam.c.p.d., nucleus mamillaris pars commissuralis posterodorsalis
n.mam.lat., nucleus mamillaris pars lateralis
n.mam.m., nucleus mamillaris pars mediana
n.mam.med., nucleus mamillaris pars medialis
n.med.dor., nucleus medialis dorsalis
n.med.hab., nucleus habenularis medialis
n.mes.V., nucleus mesencephalicus V
n.opt.teg., nucleus opticus tegmenti
n.ovid., nucleus ovoideus
n.p.p.infracom., nucleus paraventricularis posterior pars infracommissuralis
n.p.p.supracom., nucleus paraventricularis posterior pars supracommissuralis
n.parabigem., nucleus parabigeminus
n.paracent., nucleus paracentralis
n.paraf., nucleus parafascicularis
n.paraf., pars p.l., nucleus parafascicularis pars posterolateralis
n.parataen., nucleus parataenialis
r.paravent.ant., nucleus paraventricularis anterior
n.premam.dor., nucleus premamillaris dorsalis
n.premam.vent., nucleus premamillaris ventralis
n.preop.lat., nucleus preopticus lateralis
n.preop.med., nucleus preopticus medialis
n.preop.periv., nucleus preopticus periventricularis
n.pret., nucleus pretectalis
n.pret., p.caud., nucleus pretectalis pars caudalis
n.ret., nucleus reticularis
n.ret.med., nucleus reticularis pars medialis
n.reun.ant., nucleus reuniens anterior
n.reun.post., nucleus reuniens posterior
n.rhomb., nucleus rhomboidalis
n.ruber, nucleus ruber
n.subparaf., nucleus subparafascicularis
n.subparataen., nucleus subparataenialis
n.subthal., nucleus subthalamicus
n.supragen., nucleus suprageniculatus
n.supramam., nucleus supramamillaris
n.supraop.diff., nucleus supraopticus diffusus
n.tang.diff., nucleus tangentialis pars diffusa
n.tang.supraop., nucleus tangentialis pars supraoptica
n.tang.tuber. (or tub.), nucleus tangentialis pars tuberalis
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
n.vent.teg., nucleus ventralis tegmenti
n.III, nucleus oculomotorius
ped.cer., pedunculus cerebri
r.III, radix nervi oculomotorii
rec.infund., recessus infundibuli
s.nigra, substantia nigra
stria med., stria medullaris
stria term., stria terminalis
stria term.bed., bed nucleus of *stria term.*
subcom., subcommissural organ
tr.hab.ped., tractus habenulo-peduncularis
tr.mam.teg., tractus mamillo-tegmentalis
tr.mam.thal., tractus mamillo-thalamicus
tr.opt., tractus opticus
z.inc., zona incerta

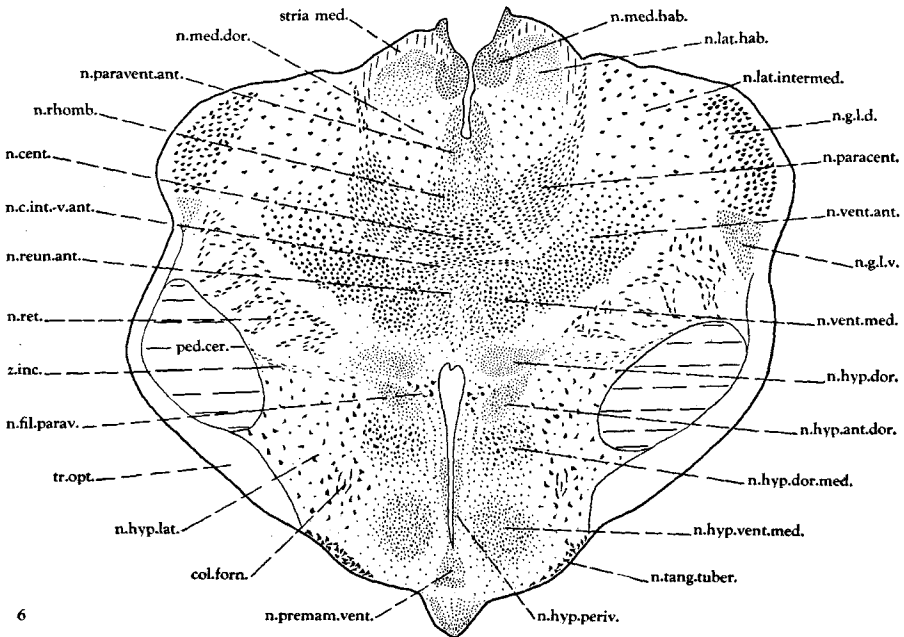
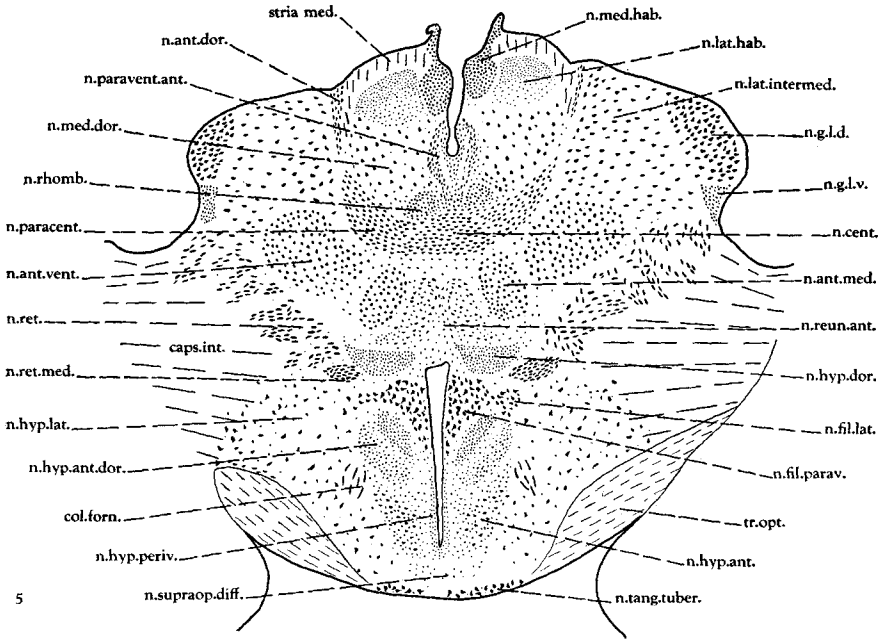


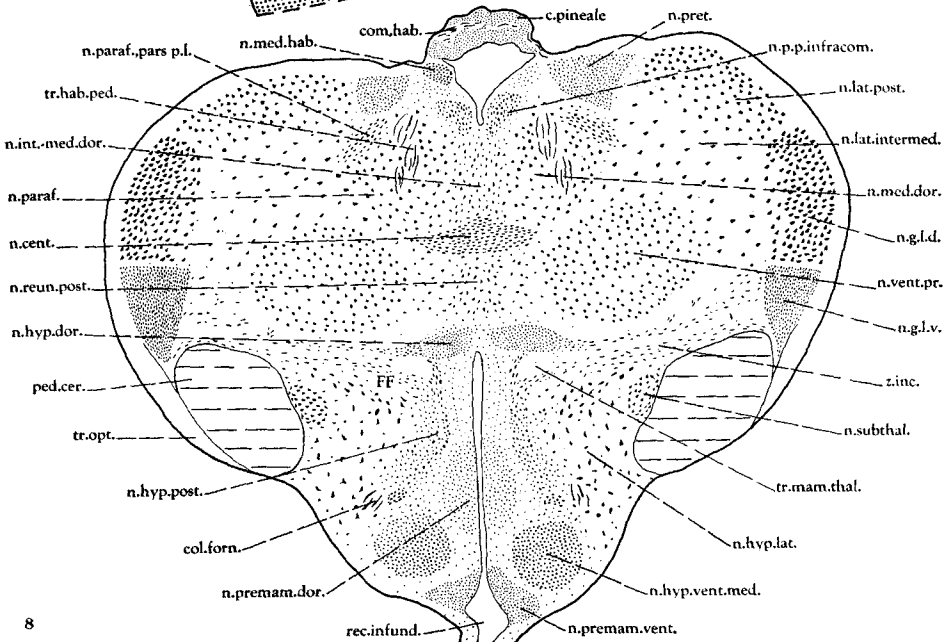
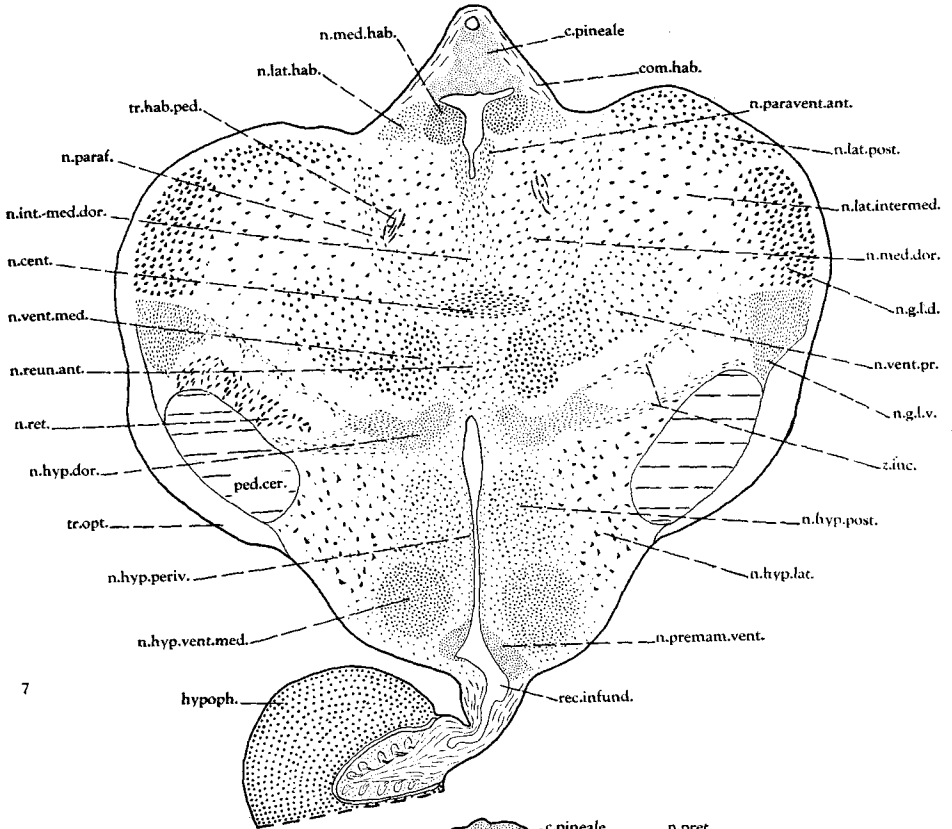
Fig. 1 Photomicrograph at $\times 20$, showing the nuclei magnocellulares hypothalami. The pars supraoptica of the tangential nucleus lies rostral to this level. Reduced silver preparation, protargol method. Series V34, 13-1-4.

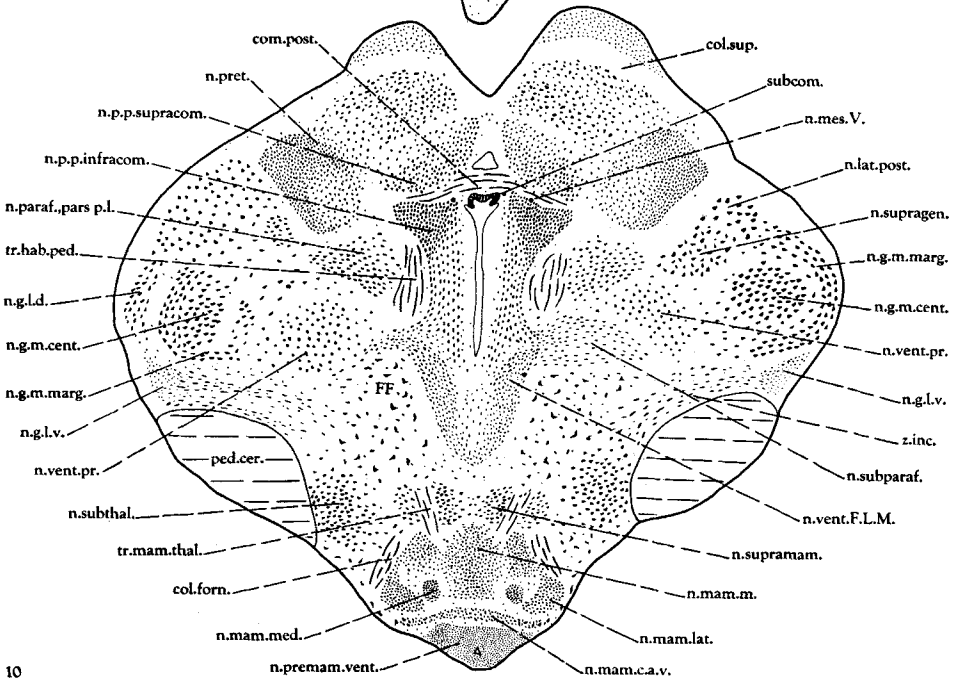
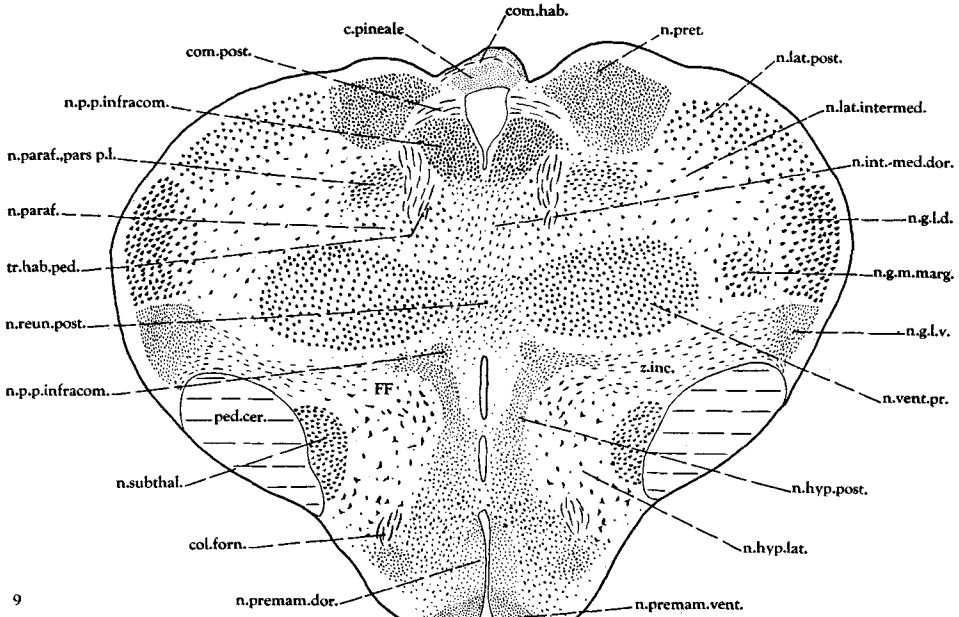


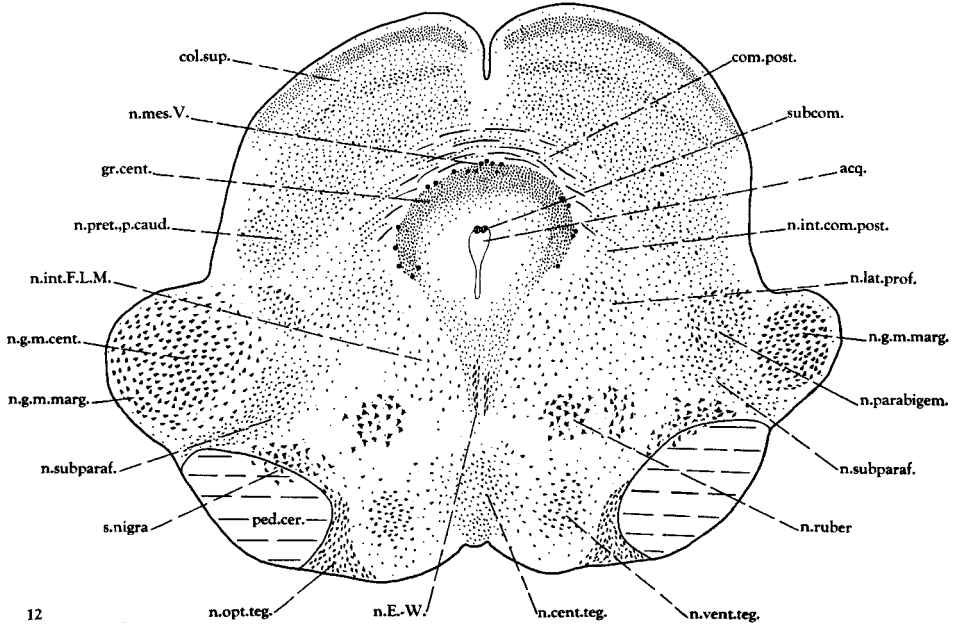
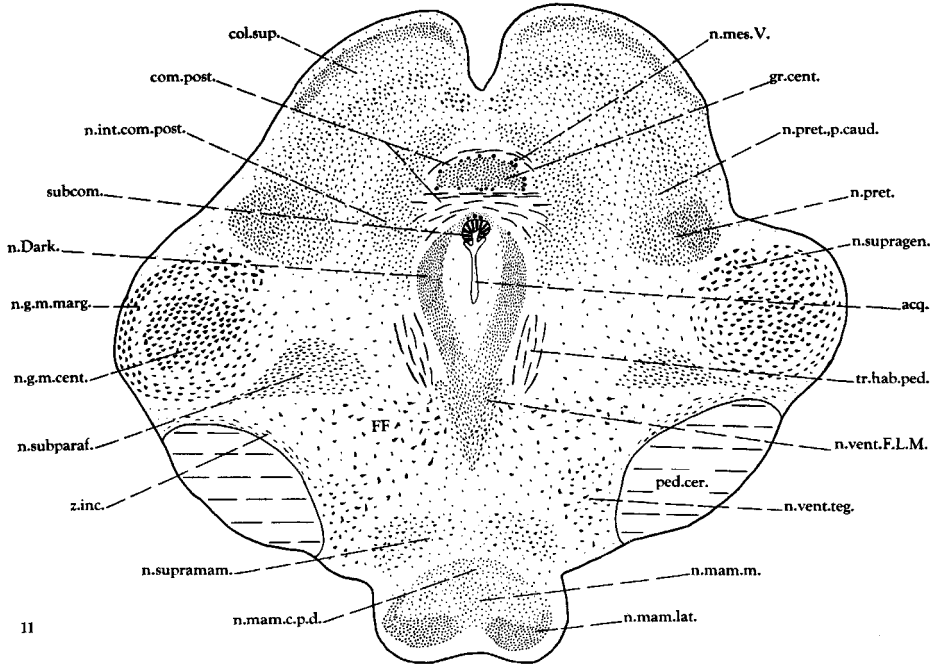
Figs. 2 to 12 A series of drawings of 50μ transverse paraffin sections, stained with toluidin blue. The levels shown are spaced at intervals of ten to fifteen sections and, relative to figure 2, subsequent figures represent sections 10, 20, 30, 40, 55, 65, 75, 90, 100, and 115, respectively.

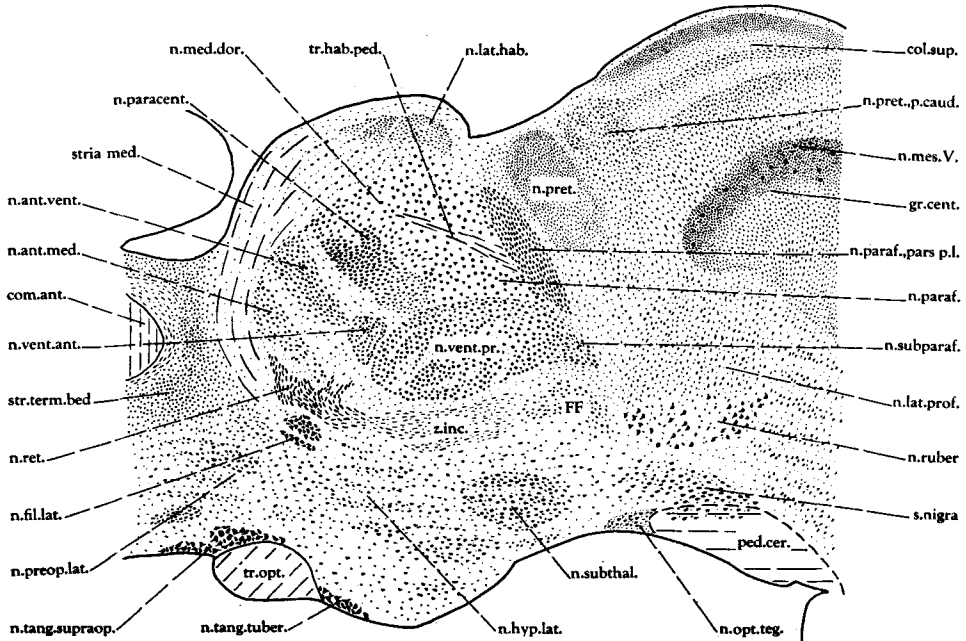
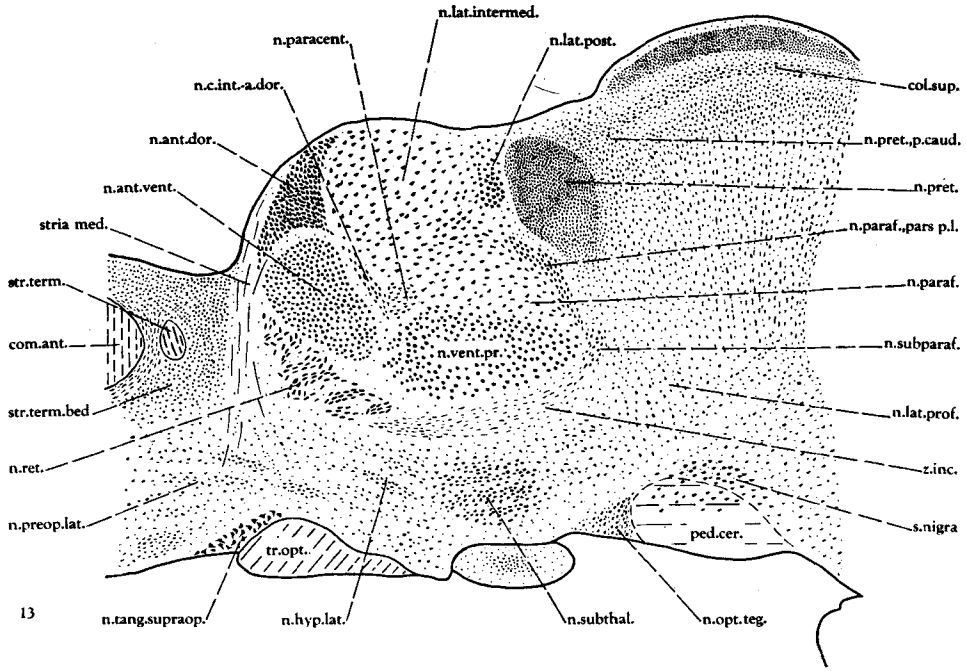






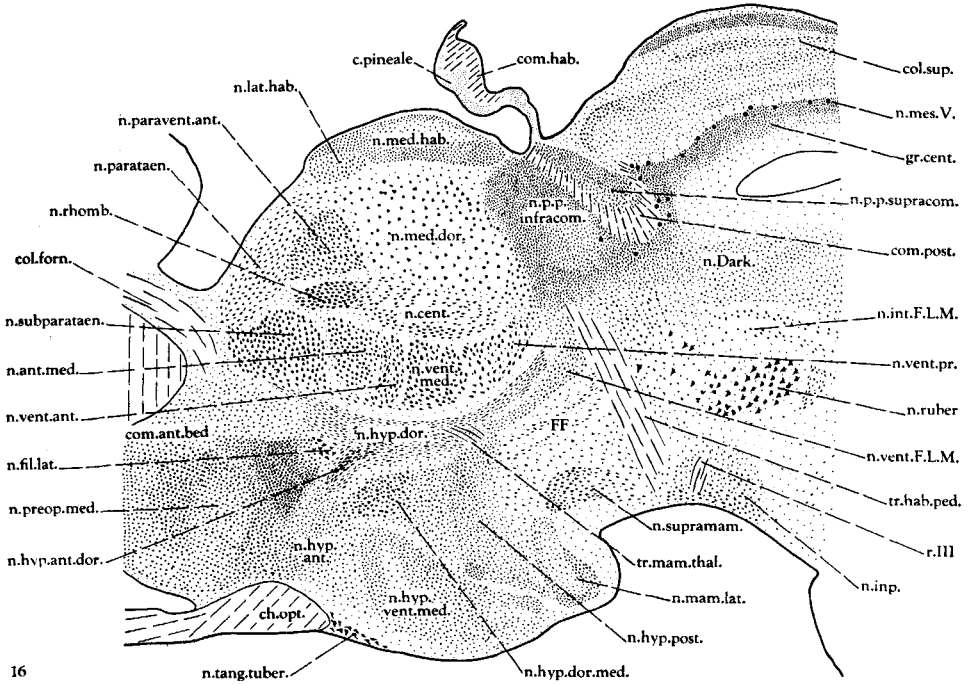
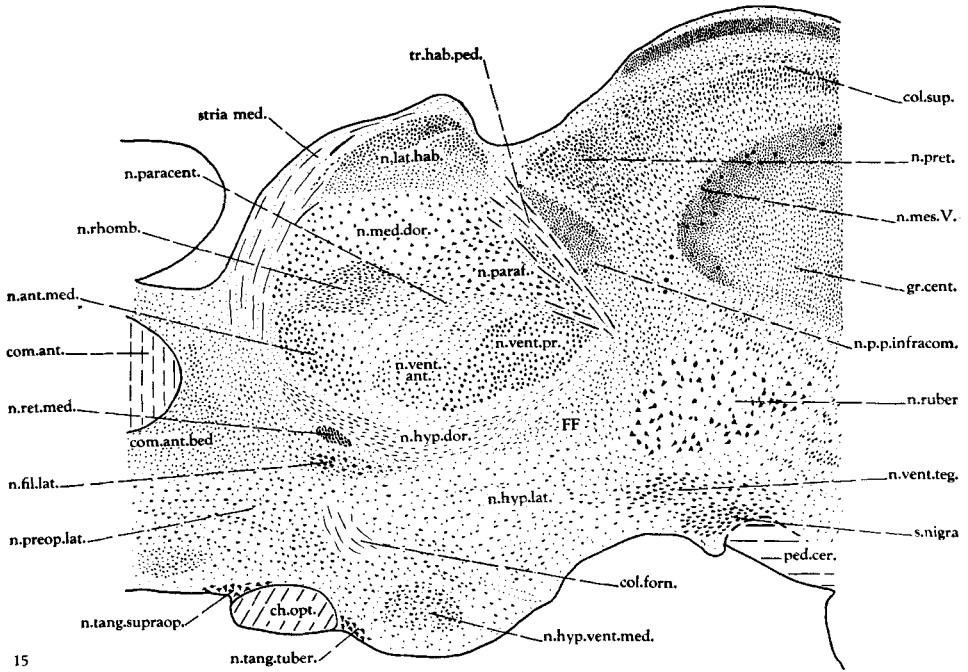


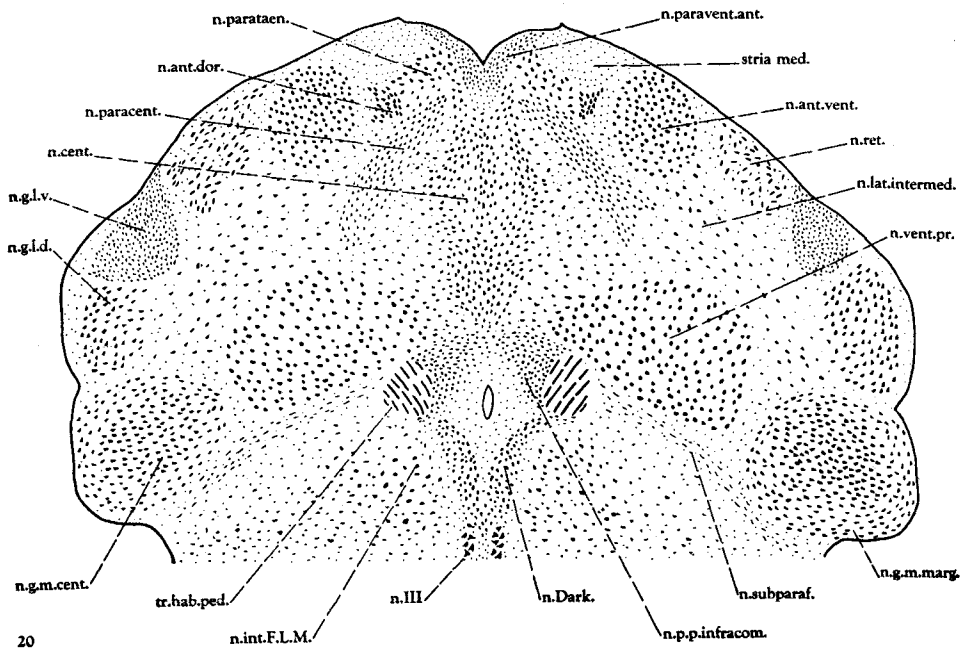
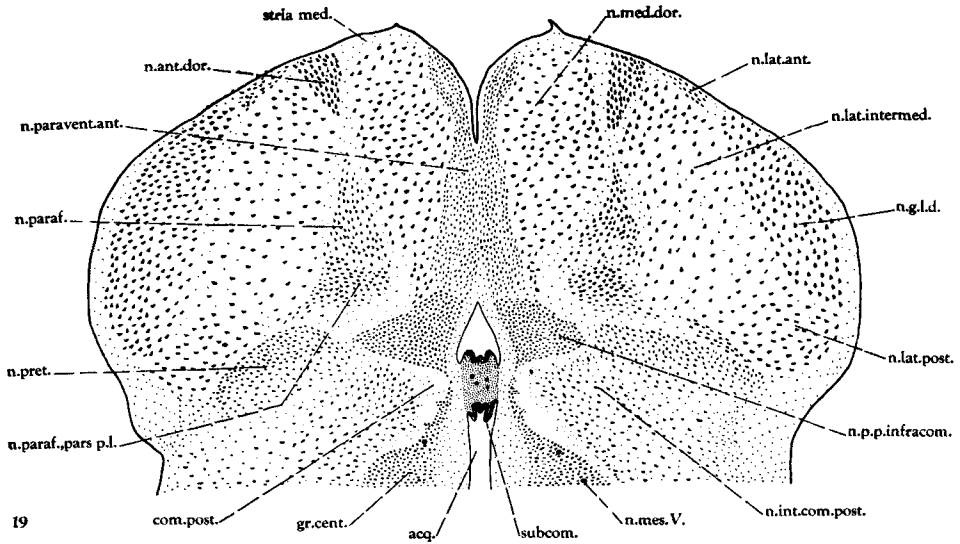




14

Figs. 13 to 18 A series of drawings of 30 μ sagittal paraffin sections, stained with toluidin blue. The levels shown are spaced at intervals of five to ten sections and, relative to figure 13, subsequent figures represent sections 10, 15, 25, 30 and 35, respectively.





Figs. 19 to 22 A series of drawings of $40\ \mu$ horizontal paraffin sections, stained with toluidin blue. Relative to figure 19, the subsequent figures represent sections 30, 45, and 100, respectively.

