# THE NUCLEAR PATTERN OF THE NON-TECTAL PORTIONS OF THE MIDBRAIN AND ISTHMUS IN THE OPOSSUM

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SIX PLATES (TWELVE FIGURES)

## INTRODUCTION

It is logical that the present series of descriptions of the nuclear pattern of the midbrain tegmentum in mammals should begin with the account of this region in marsupials, since the American opossum presents a simplified and generalized type of mammalian midbrain. The material employed in the present study consists of toluidin blue series, cut in various planes, of the brain of the American opossum, Didelphis virginiana. These preparations are a part of the Huber Neurological Collection of the Department of Anatomy of the University of Michigan.

The literature particularly pertinent to specific nuclear descriptions will be discussed in connection with such descriptions and the general literature dealing with other than marsupial forms is dealt with in other sections of this series of papers and complete reference made in the comprehensive bibliography. There are, however, certain papers of which some mention should be made. The series of papers by Castaldi ('23, '24, '26) gave the basis for the nomenclature and the general pattern of subdivision followed here. Tsai's ('25) account of portions of the marsupial midbrain, although concerned primarily with tectal and pretectal areas, gave some aid in orientation. Certain of the pretectal regions were considered in the light of earlier accounts of Chu ('32) and Bodian ('40). The text of Ariëns Kappers, Huber and Crosby ('36) was used for general orientation and comparative information.

## THE PERIVENTRICULAR GROUPS

### *General areas of periventricular gray*

The region around the ventricle is occupied chiefly by a relatively undifferentiated, primitive central gray, in the ventral portion of which, however, secondarily differentiated nuclear masses make their appearance at various midbrain levels. In general this periventricular gray may be divided into (1) a pars dorsalis (figs. 4 to 10), which constitutes the periventricular layer of the superior colliculus and is continuous with the chief nucleus of the inferior colliculus and so belongs to the tectum, (2) a pars lateralis (figs. 4 to 10) which intervenes between the pars dorsalis or tectal portion and the pars ventralis but lies dorsal to sulcus limitans, and (3) a pars ventralis (figs. 4 to 12) which is below sulcus limitans. Pars dorsalis and pars lateralis are thus to be regarded as lying on the sensory side of the arc and are probably of a correlative character. Pars ventralis, which is on the efferent side of the arc, has differentiated within it various efferent centers, some of which are prominent nuclear masses either giving origin to efferent nerve roots or to descending paths of the central nervous system.

Since pars dorsalis belongs to the tectal areas, it need not be described in detail in this paper. It will be sufficient to state that it extends throughout the length of the midbrain, from the level of the posterior commissure to the anterior medullary velum, and that it contains within its limits numerous cells belonging to the nucleus of the mesencephalic root of the trigeminal nerve.

Far rostrally the mesencephalic periventricular gray beneath pars dorsalis is represented only by scattered cells which remain sparse until the level of the nucleus of Darkschewitsch is reached. At such a level there is an undifferentiated region dorsal to the upper tip of this nucleus and above sulcus limitans which has the appearance of intercalate cells along the periventricular fibers and which is representative of pars lateralis of the periventricular gray. The nucleus of Darkschewitsch lies beneath sulcus limitans within the rostral portion of pars ventralis of the periventricular gray. As pars lateralis (figs. 4 to 10) is followed caudalward it becomes somewhat better differentiated and, in transverse levels through the main oculomotor complex, is fairly discrete in character. However, it is never sharply delimitable from the rest of the central gray but is recognizable through its more compact arrangement and through the deeper staining of its constituent neurons. It resembles more nearly pars dorsalis or the tectal region of the periventricular gray than pars ventralis but is separated from such tectal gray by its subtectal position. Pars lateralis remains fairly large throughout its extent behind the oculomotor

complex but, unlike pars ventralis, does not show secondary differentiation into nuclear groups. It decreases in planes through the anterior medullary velum, disappearing as the aqueduct widens out into the fourth ventricle. At its caudal end it is continuous with the chief nucleus of the inferior colliculus.

The most rostrally differentiated nuclear mass of pars ventralis of the central gray is the nucleus of Darkschewitsch (figs. 2 and 3). Behind the plane of this nucleus the ventral part of the central gray gradually becomes more compact and acquires a fairly definite character at levels through the Edinger-Westphal nucleus (fig. 5). Caudal to the oculomotor nuclei, pars ventralis shows various other secondary differentiations which have been designated by a variety of names. Among these may be mentioned the trochlear nucleus, the dorsal nucleus of the raphé, the laterodorsal tegmental nucleus, and the dorsal tegmental nucleus. The scattered cells in the periventricular region surrounding these more differentiated masses may still be designated as pars ventralis of the central gray. Obviously the amount of such cells will vary inversely from level to level, with the amount of differentiated gray at a given plane; such differences are best illustrated by an examination of the photomicrographs. Caudally the ventral part of the central gray passes over without demarcation into the undifferentiated periventricular gray of the pons area (fig. 12).

*Nuclear groups associated with posterior commissure*

There are three differentiated portions of the nucleus of the posterior commissure, pars intracommissuralis, pars magnocellularis and pars centralis subcommissuralis. Not all of these are differentiations of the central gray, as will be seen from the descriptions, but for convenience they are all considered here.

Pars intracommissuralis of the nucleus of the posterior commissure (fig. 2) is scanty, being composed of cells scattered along the course of the fibers, in or near their region of decussation. In the opossum it is found throughout the length of the commissure but most of the cells lie laterally, few if any of them being situated in the midline at the rostral end of the mesencephalon and only occasionally in the midline farther caudally. The lateral spread of the nucleus and its accompanying fibers is marked and the gray passes over without demarcation into pars magnocellularis of the nucleus of the posterior commissure. A nuclear group in the opossum to which the name of pars centralis subcommissuralis might be applied lies medial to the commissure, evidently differentiated from the subtectal periventricular gray. The last mentioned portion (figs. 2 and 3) not only lies wholly

medial to the commissure but shows no sharp rostral limits, passing over without demarcation into the lateral portion of the central gray. Caudally for a short distance pars centralis subcommissuralis is relatively distinct but then its cells become scattered and fade out into the central gray. It is well marked in planes through the nucleus of Darkschewitsch. It disappears in transverse sections through the rostral part of the magnocellular portion of the red nucleus.

*Nucleus of Darkschewitsch*

The nucleus of Darkschewitsch (figs. 2 and 3) is not very clearly differentiated in the opossum. It occupies the usual position in the periventricular gray, medial to the interstitial nucleus of the medial longitudinal fasciculus, in transverse levels in which pars centralis subcommissuralis of the nucleus of the posterior commissure is relatively clearly developed and well in front of the cephalic tip of the Edinger-Westphal nucleus. Thus this nucleus lies in planes which cut the anterior end of the superior colliculus dorsally and the caudal pole of the mammillary body ventrally. Rostrally and caudally it passes over into undifferentiated periventricular gray. It is short, ovoid in shape, and composed of intermingled medium-sized cells interspersed with fiber fascicles. Its neurons show more grouping and greater density of arrangement than do the surrounding cells of the periventricular gray and, even in cell preparations, its relation to posterior commissure fibers can be seen.

*Eye-muscle nuclei*

*Oculomotor complex.* The main oculomotor nuclear gray is not clearly separable into ventromedial and dorsolateral oculomotor nuclei (figs. 6 and 7), although for convenience in comparison with other forms such names may be used. The first gray of this nucleus appears rostrally in planes toward the caudal end of substantia nigra and at levels which show clearly the entire course of the emerging oculomotor roots. At such levels the cells lie medial to the medial longitudinal fasciculus and this portion may be termed a ventromedial oculomotor nucleus. Very shortly, however, through cell increase, the nucleus caps the medial longitudinal fasciculus dorsally, the whole mass of gray thus formed representing both the ventromedial and dorsolateral oculomotor nuclei. Still farther caudalward, in planes behind substantia nigra, the medial part of the gray disappears but the dorsal portion continues caudalward until it is replaced by the trochlear nucleus, the connection being reduced to a narrow strip of gray represented by only one or two neurons. The trochlear nucleus appears in planes cutting the cephalic tip of the inferior colliculus and behind the caudal pole of the red nucleus.

In many mammals the Edinger-Westphal complex consists of two portions, a rostral portion (figs. 3 to 5; termed also nucleus medianus anterior) and a caudal portion (fig. 6; often designated simply the Edinger-Westphal nucleus). In the opossum, both portions are represented but are directly continuous with each other, and the rostral is better developed than the caudal end of the nuclear complex. The rostral portion which is unpaired throughout, appears in levels which mark the frontal tip of the red nucleus, lying in the midline between the medial longitudinal fasciculi. At such levels, this rostral portion has largely replaced the rostral end of the linear nucleus, there being some overlapping of cell types. It continues caudalward into direct continuation dorsally with the caudal portion of the Edinger-Westphal complex in planes through the frontal tip of the main oculomotor nucleus.

The caudal Edinger-Westphal nucleus of the oculomotor nerve is relatively poorly developed in marsupials, consisting of a median mass of gray with short, paired, forward extensions. It appears caudally in planes in which the chief oculomotor nuclear gray caps the medial longitudinal fasciculus and it extends forward a few sections in front of the rostral tip of the remainder of the oculomotor complex. Its cells are smaller, somewhat more spindle-shaped and relatively less deeply stained than those of the chief oculomotor gray.

*Trochlear gray.* The trochlear nucleus is directly continuous rostrally with the dorsolateral portion of the chief oculomotor gray, its rostral pole lying in planes through the cephalic end of the inferior colliculus. The trochlear nucleus is relatively short, extending in the series for approximately .3 mm. Its cells are large, multipolar neurons, which form a cell group that fits into a cup-shaped depression in the medial longitudinal fasciculus. There is no accessory trochlear nucleus on either side in the marsupial material studied.

### *Dorsal nucleus of raphé*

This nuclear complex (figs. 8 to 10) appears caudal to the Edinger-Westphal nucleus, from which it is separated by undifferentiated central gray. Its cephalic pole thus lies in planes through the caudal end of the oculomotor complex, dorsal to the dorsolateral portion of the oculomotor gray. At such planes the dorsal nucleus of the raphé is pale and is represented by only a few cells. Traced caudalward in the series, the nuclei of the two sides enlarge and meet in the midline as a V-shaped mass. In planes through the trochlear nucleus, the dorsal nucleus of the raphé increases still further and is represented by a central mass (composed of two columns of gray interconnected by less closely arranged cells) and lateral extensions of medium-sized,

deeply stained, more scattered neurons intermingled with the less differentiated nucleus of the central gray. Behind the trochlear nucleus, the lateral extensions disappear and the remainder of the dorsal nucleus of the raphé, which has lost its columnar arrangement, gradually decreases, disappearing at levels through the rostral pole of nucleus medialis profundus. It is replaced by undifferentiated raphé gray.

*Laterodorsal tegmental nucleus*

This cell mass (figs. 11 and 12) is composed of medium-sized, deeply staining neurons which lie in the lateral part of the periventricular gray, lateral and dorsolateral to the dorsal tegmental nucleus. Rostrally it begins in front of the cephalic pole of the dorsal tegmental nucleus, in planes through the caudal end of the inferior colliculus and the frontal pole of nucleus medialis profundus. At such levels it extends from a dorsomedial position in the central gray ventral to the floor of the aqueduct, lateroventrally through this gray. A few neurons filter ventrolateralward through the fibers bounding the periventricular region into the adjacent tegmental area. With the appearance of the dorsal tegmental nucleus, the laterodorsal tegmental nucleus lies lateral to it but still invades the tegmental gray. Still farther caudalward the number of deeply staining neurons increases. Behind the caudal pole of the dorsal tegmental nucleus, at upper pontine levels, the laterodorsal tegmental nucleus shows a differentiation into two portions: a medial part directly continuous with the more rostral region of this cell complex and a lateral somewhat differentiated portion with neurons differently oriented and more angular which is probably comparable to the nucleus of locus coeruleus (fig. 12). The laterodorsal tegmental nucleus disappears in transverse planes through the motor nucleus of the trigeminal nerve.

*Dorsal tegmental nucleus*

The term dorsal tegmental nucleus (figs. 11 and 12), as here used, actually applies to an area rather than to a discrete, sharply circumscribed nuclear mass such as is visible in the region in some forms. This area appears in planes caudal to the rostral pole of the laterodorsal tegmental nucleus and medial to that nucleus. It is separated from the midline by gray of the raphé and is dorsal to the medial longitudinal fasciculus. It lies caudal to the trochlear nucleus in the region of the isthmus and the rostral end of the pons and caudally fades imperceptibly into the pontine central gray. In the opossum two parts, a central and a peripheral portion, may be recognized. The central portion is small, round in cross section and composed of deeply stained, closely arranged small to medium-sized neurons, easily

distinguished from the surrounding gray but passing over into it by insensible gradations. The peripheral part encircles the central portion and is intermediate in cell arrangement and cell staining between the central mass and the surrounding undifferentiated nucleus of the central gray. The whole area corresponds in position to the more sharply circumscribed dorsal tegmental nucleus of higher mammals.

*Nucleus of mesencephalic root of V*

The mesencephalic nucleus of the trigeminal nerve in the opossum appears rostrally at the frontal end of the optic tectum dorsal to the posterior commissure and extends caudalward to approximately the end of the isthmus region (figs. 2 to 9). Its most rostral representation is a median group of very large deeply staining neurons, not all of which appear to be unipolar, and intermingled smaller, less deeply staining, and in some instances multipolar neurons. Slightly farther caudalward with the increase in size of the optic tectum, the cells of this nucleus line up along the tectal periventricular gray ventrolaterally so that a median and a lateral group may be recognized. The median group soon disappears but the lateral group remains, variously developed from section to section, until the caudal end of the oculomotor complex is approached. This latter group, which is composed chiefly of exceedingly large unipolar elements, decreases markedly toward the caudal end of the superior colliculus and through inferior collicular levels. An isthmus group particularly related to the overlying crossing fibers of the trochlear nerve consists mainly of conspicuously large unipolar neurons although an occasional smaller cell is found. It decreases behind the decussation of the trochlear nerve and practically no trigeminal group, at the level of entrance of the trigeminal nerve, has been demonstrated in the available material. Moreover no cells of the mesencephalic nucleus of V have been found in the oculomotor, trochlear or trigeminal nuclei nor along the entering or intrabulbar course of the trigeminal root fibers.

## MIDTEGMENTAL NUCLEAR GROUPS

*Nuclear groups associated with medial longitudinal fasciculus*

Two nuclear groups, nucleus interstitialis and nucleus annularis, are usually associated with the medial longitudinal fasciculus in mammals.

The interstitial nucleus of the medial longitudinal fasciculus (figs. 3 to 5) appears lateral and lateroventral to the caudal part of the nucleus of Darkschewitsch, in the region overlying the fasciculus. It extends in part into this bundle. It can be followed caudalward,

behind the rostral tip of the Edinger-Westphal nucleus, to planes approximately through the cephalic pole of the dorsolateral oculomotor nucleus. It is never large and never sharply defined but is characterized by larger multipolar neurons overlying and intermingling with the medial longitudinal fasciculus and varying in number from section to section throughout the extent of the nucleus.

There is practically no representation of the annular nucleus in the opossum. Occasionally there is a small cluster of cells or a single neuron situated at the edge of the medial longitudinal fasciculus or among its fascicles, but nothing faintly resembling a ring can be seen in the preparations available.

### *Red nucleus*

The red nucleus (figs. 3 to 7) shows the magnocellular and parvocellular portions typical of this complex in mammals. There are three special relations which should be emphasized in marsupials as compared with other mammalian forms. They may be listed as follows:

The red nucleus is relatively far caudalward with reference to the other midbrain structures in marsupials. The parvocellular portion is comparatively small and does not extend nearly so far in front of the rostral tip of the magnocellular portion as in some other mammals, and it is poorly delimited from the surrounding gray. The magnocellular portion tends at some levels to be broken up into clusters of cells and to show a much greater development toward its caudal end than in its rostral portion.

Pars parvocellularis of the red nucleus (figs. 3 and 4) begins in planes behind the rostral tip of substantia nigra and through the caudal pole of the mammillary body. The front end of the nucleus of the basal optic root appears in approximately the same planes. This portion of the red nucleus is very indistinctly delimited from the small-celled tegmental gray and, within two sections of its rostral tip, shows traces of an intermingling of the large-celled portion of the red nucleus. The parvocellular portion has only a slight extent, its terminal portion occupying the dorsal part of the red nucleus and lying in the same plane as does the rostral tip of the pars reticulata of substantia nigra. The cells of this parvocellular portion show no differentiating characteristics from those of the surrounding gray, the recognition of the nucleus depending upon the presence of encapsulating fibers.

The magnocellular part of the red nucleus (figs. 3 to 7) appears as scattered cells almost immediately behind the rostral tip of the small-celled portion of the nucleus. These cells soon increase in number and the red nucleus in the opossum is definable largely on

the basis of its magnocellular component. In planes through the ventromedial oculomotor nucleus and approximately the caudal tip of pars lateralis of substantia nigra, the magnocellular portion thins out very distinctly so that it is represented only by clusters of cells. Within a few sections, however, it increases again in size and reaches its maximum development near its caudal pole. It continues slightly behind the caudal end of substantia nigra, then reduces very rapidly in size and disappears from the field.

*Deep mesencephalic gray (nucleus mesencephalicus profundus)*

The tegmental gray surrounding the red nucleus — nucleus mesencephalicus profundus — is relatively undifferentiated. It is composed of intermingled medium-sized and larger neurons, the latter approaching in size those of the red nucleus. These larger cells are not numerous and they do not show sufficient clustering to justify any separation into precise nuclear groups. They are somewhat more numerous in the region between the rostral end of the red nucleus and substantia nigra, suggesting nucleus mesencephalicus profundus pars ventralis seen in some other mammals (shown but not labeled in fig. 3). The number of larger cells increases again somewhat caudal to the plane of the red nucleus. In such levels of the tegmentum, occasional groups of neurons occur, although such clusters vary from level to level, in the field lateral to the red nucleus in the position in which pars lateralis of nucleus mesencephalicus profundus develops in some other forms. Similar small masses are found farther caudalward and are more numerous there. The general tegmental gray of the midbrain grades over without demarcation into the pontine tegmental area.

The so-called nucleus interstitialis tegmenti of Tsai ('25, fig. 13, p. 189) appears in the material studied to be a continuation of stratum griseum profundum into the underlying tegmentum (fig. 4), along the course of efferent and largely tecto-tegmental tracts. Its cells constitute an interstitial nucleus of these tracts. It bears about the same relation to the deep tectal layer that the nucleus of the posterior commissure bears to commissural fibers. The extension forming this interstitial nucleus begins in planes through the rostral pole of the tectum, lateral to the interstitial nucleus of the posterior commissure. The mass gradually increases caudalward, encroaching upon the interstitial nucleus and then the dorsal nucleus of the commissure, and ultimately replacing them. It reaches its greatest size caudal to the dorsal nucleus of the posterior commissure, at which level it is a conspicuous element in the field. Thereafter it gradually decreases and disappears in planes through the rostral pole of the dorsolateral

oculomotor nucleus by passing over without demarcation into undifferentiated tegmental gray.

*Ventral tegmental area and nucleus of mammillary peduncle*

The nucleus of the mammillary peduncle as designated by Papez ('32) belongs to the area termed earlier the ventral tegmental nucleus by Tsai ('25) and more recently described under the latter name by Bodian ('40). The general ventral tegmental area (figs. 2 to 6) begins rostrally in planes through the caudal pole of nucleus subthalamicus. Its caudal end is continuous lateralward with pars compacta of substantia nigra at levels through the oculomotor nucleus. It is associated with fibers of the mammillary peduncle which lie partly ventral and partly ventromedial to it and to some extent are intermingled with it. To the neurons immediately associated with the fascicles of the mammillary peduncle the name of nucleus of this peduncle is particularly applicable. The general term, ventral tegmental area, may be used to designate the whole region. This ventral tegmental area lies lateroventral to the medial forebrain bundle and dorsal and dorsomedial to the cerebral peduncle. Lateral to it are the striatal components of the lateral forebrain bundle, laterorostralward zona incerta and laterocaudalward the midbrain tegmental gray. Throughout the extent of the basal optic root and its nucleus, this ventral tegmental area, with the nucleus of the mammillary peduncle and the associated tract, lies internal to them. The constituent neurons of the nucleus of the mammillary peduncle (fig. 3) are quite angular, medium-sized, and deep-staining. They appear to be oriented along the course of fiber fascicles running dorsolateralward over substantia nigra.

*Nucleus medialis profundus*

*Nucleus ventralis tegmenti of von Gudden*

This nucleus (fig. 11) begins frontalward in planes through the inferior colliculus and the rostral pole of the laterodorsal tegmental nucleus. It is a sharply circumscribed mass, approximately circular in outline, lying immediately ventral to the medial longitudinal fasciculus. It is surrounded by a cell-free area encapsulated by a ring of neurons having the character of tegmental gray. Its constituent cells are medium-sized and deeply stained. Nucleus medialis profundus (of Castaldi, '23, figs. 37 to 39) disappears in planes through the pons in front of the cephalic tip of the motor nucleus of the trigeminal nerve. It has an approximate length of 1 mm. and, for all of its extent, is confined to the isthmus region.

*Certain pretectal and subtectal components of tegmentum*

*Pretectal nucleus.* Tsai ('25), Chu ('32) and Bodian ('40) have located and described a pretectal nucleus in the opossum, and Bodian has called its caudal extension nucleus pretectalis pars caudalis, this part not having been separated by the previous workers. Since Bodian's work was done in this laboratory and checked in part on the material available for study, any further description of the nuclear groups here is unnecessary. The positions of nucleus pretectalis and nucleus pretectalis pars caudalis are indicated on the photomicrographs (figs. 2 to 4).

*Nuclear gray associated with lateral lemniscus.* At the region of transition from the pons into the isthmus, in the dorsolateral part of the field along the course of the lateral lemniscus, there is an enlarged gray mass frequently not sharply separable from the caudal ventral nucleus, which constitutes a dorsal nucleus of this tract (figs. 10 to 12). This consists of a group of deeply staining cells, comparable to those of the caudal ventral nucleus, the caudal mass being bordered by scattered neurons. In slightly more cephalic planes the enlarged portion disappears but scattered neurons accompany the lateral lemniscus until its partial termination within the inferior colliculus. From the level of the inferior colliculus forward for a considerable distance as the lateral lemniscus runs toward the medial geniculate, there is a patch of less deeply staining, less well organized neurons which ultimately becomes reduced to little differentiated gray at cephalic tectal levels and fades out into the medial geniculate. This latter cell cluster constitutes a rostral ventral nucleus (figs. 5 to 7) of the lateral lemniscus. The more caudal collections of gray, extending from superior olivary to inferior collicular levels along the lemniscus, may be designated as the caudal ventral nucleus of the lateral lemniscus (figs. 10 to 12). This cell mass may be secondarily divided into a ventromedial and a lateral portion (fig. 12) comparable to these subdivisions in the rabbit.

*Marginal nucleus of superior cerebellar peduncle*

The gray associated with the superior cerebellar peduncle (figs. 11 and 12) in the opossum consists of encircling neurons and interstitial cells associated with the bundle as it turns down from the cerebellum into the isthmus region and proceeds forward to its decussation. Much of this gray is of an undifferentiated type, of the same general character as that of the surrounding area, and the appearance of a nucleus may be nothing more than a concentration of the adjacent cells as the fibers pass through the area. However, there are occasional larger, multipolar cells of the type of nucleus mesencephalicus pro-

fundus, which are partially embedded in the bundle and partly concentrated along its ventromedial border. They merge into the scattered gray of the dorsolateral tegmental nucleus and the caudodorsal end of nucleus mesencephalicus profundus and presumably specifically correspond to the marginal nucleus described for other forms.

### *Cuneiform area*

There is a wedge-shaped area of intermingled fibers and spindle-shaped cells which has been termed the cuneiform area (figs. 7 to 9). It lies ventromedial to the inferior colliculus and just external to the radiations of Meynert which bound the periventricular area. It is thus in the course of descending efferent tectal paths. It extends through practically all inferior collicular levels and thus is in the plane of entrance of lateral lemniscus fibers to this portion of the midbrain roof. It appears to receive fibers of this system and so to serve as a correlation area.

## MIDLINE NUCLEAR GROUPS

### *Linear nuclear gray*

The term linear nuclear group has been applied by Castaldi to the rows of cells arranged dorsoventrally in the region of the raphé, ventral to the central gray. Usually in mammals such linear groups fall into rostral, middle, and caudal divisions and these divisions are represented in the opossum.

The rostral division of the linear cell group (fig. 2) in this mammal appears at the cephalic end of the mesencephalon, dorsal to the supramammillary decussation or commissure of Forel. It lies near the midline, occupying the region between the two medial longitudinal fasciculi. Its dorsal tip gradually extends into the ventromedial portion of the ventral part of the central gray and its ventral tip reaches a line drawn approximately across the dorsal borders of the magnocellular portions of the two red nuclei. Slightly farther caudalward its ventral portion disappears and its dorsal part is replaced by the cephalic end of the Edinger-Westphal nucleus.

The intermediate division of the linear group (nucleus linearis intermedialis or centralis, fig. 6) appears in planes through the oculomotor nuclei, ventromedial to these centers and medial and ventromedial to the medial longitudinal fasciculi. At such levels there is a ventral tegmental decussation and the linear group approaches its upper border. With the appearance of the superior cerebellar decussation, the intermediate division of the linear group disappears, its dorsal portion being replaced by the caudal linear nucleus.

The caudal linear nucleus begins rostrally as a small mass of cells replacing the dorsal portion of the intermediate linear nucleus and overlying the decussating fibers of the superior cerebellar crossing (fig. 7). Caudal to this decussation the nuclear mass (figs. 8 to 11) spreads ventralward along the raphé and is ultimately continuous with the pontine raphé. Its cells are more regularly linearly arranged and somewhat more deeply stained than are those of the rostral and intermediate linear nuclei.

*Interstitial nucleus of commissure of Forel*

Intermingled with crossing fibers of the commissure of Forel (supramammillary or retroinfundibular decussation) are intercalate cells (figs. 2 and 3). They cap over the front end of the decussating fascicles and stream down toward the supramammillary nucleus along the course of that fornix component which is approaching the decussation. Such cells are intermingled, behind the plane of the mammillary body, with larger neurons having the general character of tegmental gray. Both the larger and smaller cells of the interstitial nucleus tend to continue lateralward toward substantia nigra and the red nucleus, but the cellular connections between the gray around the commissure and these more lateral regions of the tegmentum are not so marked in the opossum as in many other mammals. As the commissure fibers disappear from the field, their interstitial nucleus is replaced by undifferentiated central gray. This occurs in planes near the frontal pole of the magnocellular part of the red nucleus. The habenulo-peduncular tracts descend to the interpeduncular nucleus caudal to the commissure of Forel and its associated interstitial nucleus.

*Interpeduncular nucleus*

This nucleus (figs. 7 to 10) extends from planes through the caudal pole of pars reticulata of substantia nigra to the end of the mesencephalon. Rostrally it consists of more centrally located strands of cells bordered on either side by smaller patches of gray intermingled with the large fascicles of the habenulo-peduncular tract, which enter this nucleus at its rostral tip. Farther caudalward, in planes of transition between the oculomotor and trochlear nuclei, the interpeduncular gray has collected in strands on the dorsal side of the nucleus (fig. 8) and the fiber bundles have been confined largely to its periphery and its ventral portion. Behind this plane the arrangement again becomes diffuse and, towards the caudal end of the nucleus, the fascicles have largely disappeared and the area is represented by a more or less continuous mass of gray. Throughout its extent, as

its name implies, the interpeduncular nucleus is situated on the ventral surface of the brain between the two cerebral peduncles. For the most part its cells are small with occasional intermingled medium-sized neurons. They have relatively conspicuously stained Nissl granules.

## BASAL MIDBRAIN GRAY

### *Substantia nigra*

In the opossum, substantia nigra consists of the three parts typical for mammals — pars lateralis, pars compacta and pars reticulata. Pars lateralis (figs. 3 to 5) begins very near the frontal end of the complex in planes through the caudal pole of the mammillary body and extends to levels behind the medial geniculate nucleus. Rostrally, it is directly continuous with and indistinguishable from pars compacta and keeps this relation until planes cutting the more caudal part of the medial geniculate are reached. Through these levels it lies ventral and ventromedial to the medial geniculate nucleus but extends dorsally along the course of nigro-tectal fibers immediately behind this nucleus and shortly thereafter terminates. Throughout its extent, pars lateralis consists of medium-sized to fairly large, deeply staining, multipolar neurons, which resemble in general cell character and in size the neurons of pars compacta.

The rostral tip of pars compacta (figs. 2 to 7) extends farthest forward of any part of substantia nigra, appearing a few sections in front of the cephalic tip of pars lateralis. It has also the greatest caudal extent of any part of the complex, disappearing behind pars reticulata in planes passing through the rostral end of the interpeduncular nucleus. Near its rostral tip, pars compacta is not delimitable from pars lateralis, lying against this latter portion of substantia nigra. It increases gradually on its medial side so that it approaches the nucleus of the basal optic root and, behind that nucleus, extends along the peduncle medialward to almost the ventral surface of the brain. It is more sharply definable from the nucleus of the basal optic root, however, than in many other mammals. Behind the plane of the medial geniculate nucleus, the hitherto rather small pars compacta increases considerably in size and is here definitely separated from pars lateralis. After the disappearance of pars lateralis, pars compacta spreads somewhat lateralward along the peduncle but never reaches the lateral surface of the brain. As the interpeduncular nucleus is approached, pars compacta decreases rather rapidly and then disappears from the field. It resembles pars lateralis closely in cell type.

As a distinct nuclear group, pars reticulata (figs. 3 to 6) begins considerably farther caudalward than either of the other parts of substantia nigra, although occasional rare neurons in the course

of the peduncle may represent rostral extensions of this gray. It disappears in front of the caudal end of pars compacta, in planes in which the latter nucleus is beginning to decrease in size. Throughout, it shows no special characteristics, being composed of cells typical of substantia nigra but intercalated in the cerebral peduncle.

*Nucleus of basal optic root*

The nucleus of the basal optic root (figs. 3 and 4) is situated directly medial to the cerebral peduncle, close to the surface of the mesencephalon. It is triangular in general outline, with the apex directed dorsalward, and is comparatively well developed in these forms. Its cells are medium-sized to small, the former being rather deeply stained, vary from spindle-shaped to triangular in outline and are obviously multipolar. The nucleus lies in a plane entirely medial to the medial tip of pars compacta of substantia nigra. Its rostral pole lies immediately behind the mammillary body. The nucleus disappears just in front of the caudal pole of the medial geniculate nucleus.

## SUMMARY

1. The periventricular region falls into dorsal, lateral and ventral portions. The dorsal is largely tectal, the lateral is undifferentiated and the ventral is subdivisible into a series of nuclear groups surrounded by undifferentiated gray. Of such groups the eye muscle nuclei, the nucleus of Darkschewitsch, the dorsal tegmental nucleus, the laterodorsal tegmental nucleus, and the dorsal nucleus of the raphé are differentiable in mammals.

2. Of the midtegmental group, the red nucleus is the most clearly differentiated. Its magnocellular portion is prominent through most of the superior collicular levels and in appearance resembles greatly the red nucleus in certain submammalian forms. It is surrounded by clusters of tegmental cells which are particularly well developed dorsolaterally in levels through the caudal part of the red nucleus and grade over into the gray associated with the superior cerebellar peduncle. Such collections of cells represent portions of the primitive mesencephalic tegmental gray (nucleus tegmentalis or reticularis superior mesencephali, Ariëns Kappers, Huber and Crosby, '36) which have not been included within the encapsulating fibers of the superior cerebellar peduncle and

thus become a part of the red nucleus proper. The interstitial nucleus of the medial longitudinal fasciculus is relatively clearly developed in this marsupial but the annular nucleus has a very limited representation. Nucleus medialis profundus is actually beyond the limits of the midbrain block in the opossum, being confined to the isthmus and upper trigeminal levels. The pretectal nucleus as recognized by Tsai ('25) and its caudal continuation as described by Bodian ('40) have been recognized and are labeled in the photomicrographs.

3. Among the midline nuclear groups the linear nucleus is relatively feebly represented although rostral, intermediate and caudal portions were identified. The interstitial nucleus of the commissure of Forel shows cellular continuity with the red nucleus and substantia nigra, the orientation of the cells suggesting that they are intercalated along fiber fascicles. The interpeduncular nucleus extends throughout much of the base of the midbrain in the midline, being quite clearly delimited from the surrounding gray but without any particular pattern of nuclear differentiation.

4. At the base of the midbrain, substantia nigra overlies and, in part, intermingles with the cerebral peduncle. The three portions — pars compacta, pars reticulata, and pars lateralis — described for various mammals by Rioch ('29 a) and others are distinguishable. Pars compacta is relatively well developed and both it and pars reticulata are present throughout the length of the midbrain. Pars lateralis is not large but is easily differentiable, lying at first ventral and then caudal to the medial geniculate nucleus along the course of the tectal fibers. A small nucleus of the basal optic root is recognizable.

## PLATES 1 TO 6

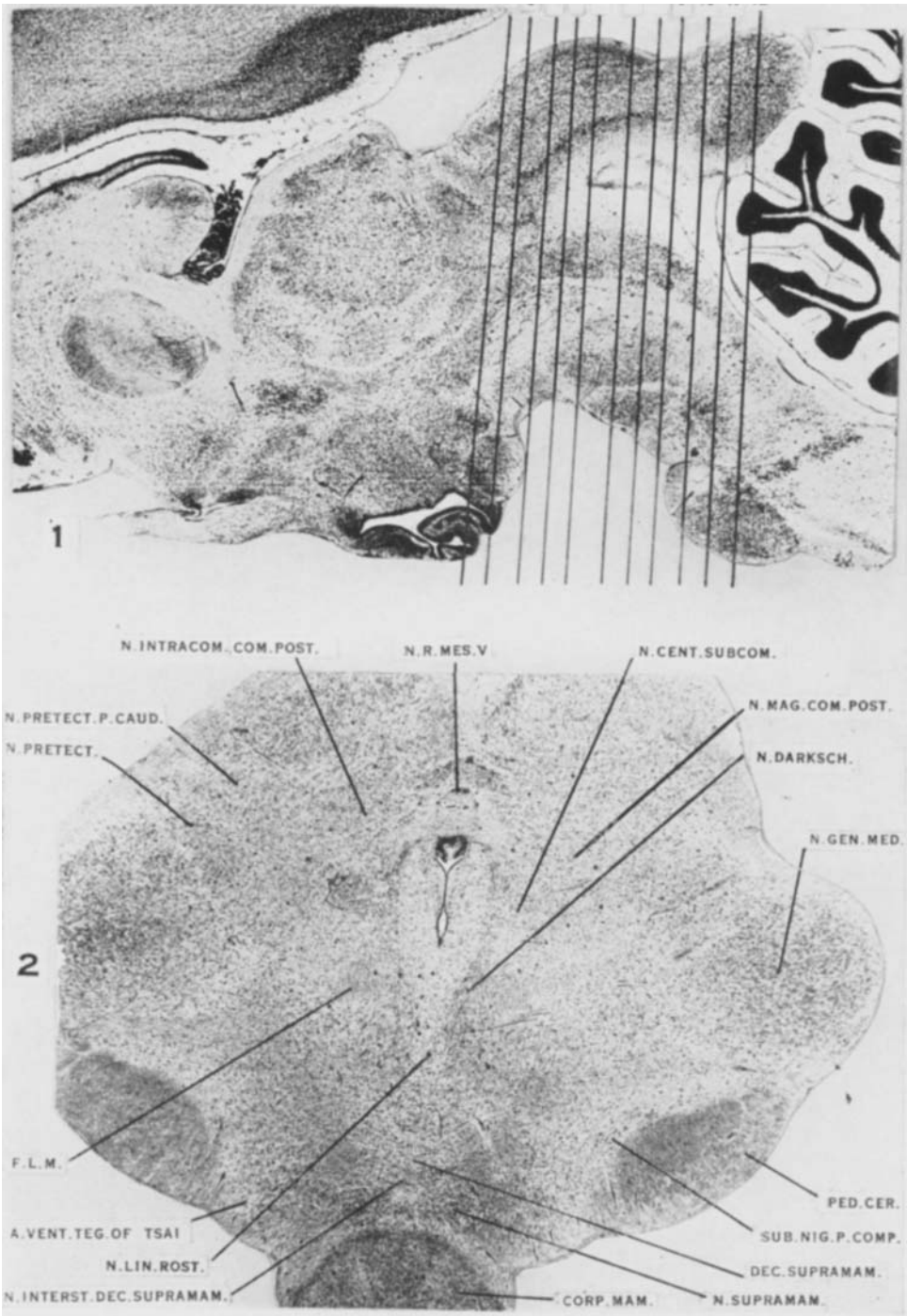
### EXPLANATION OF FIGURES

Figs. 1 to 12 Photomicrographs of sections of the midbrain of the opossum.

Fig. 1 Sagittal section illustrating the planes of section of figures 2 to 12. Toluidin blue preparation. × 8.

Figs. 2 to 12 Photomicrographs of transverse sections in planes indicated in figure 1. Toluidin blue preparations. × 13.

PLATE 1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N. PRETECT.
F. L. M.
A. VENT. TEG. OF TSAI
N. LIN. ROST.
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CORP. MAM.
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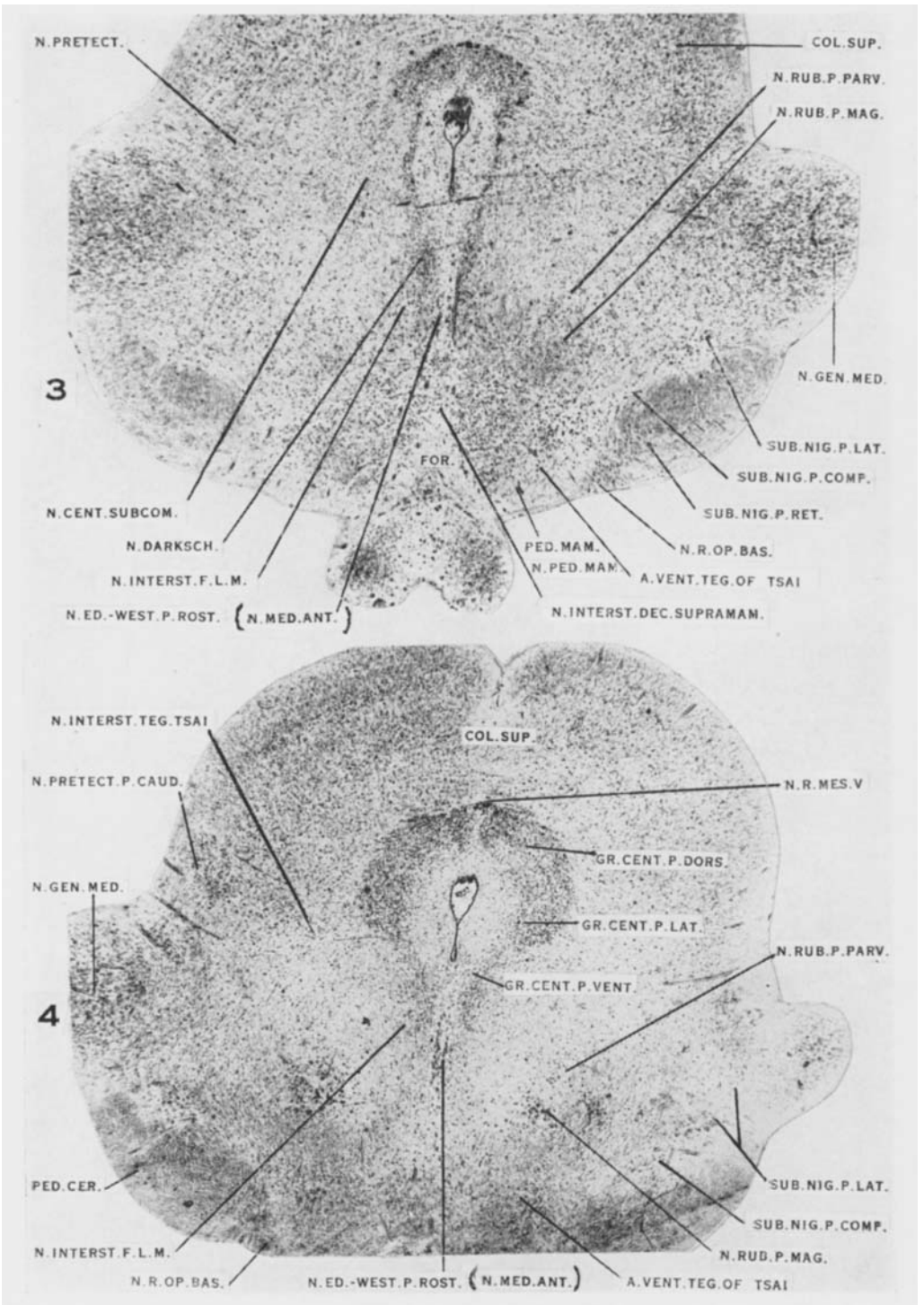
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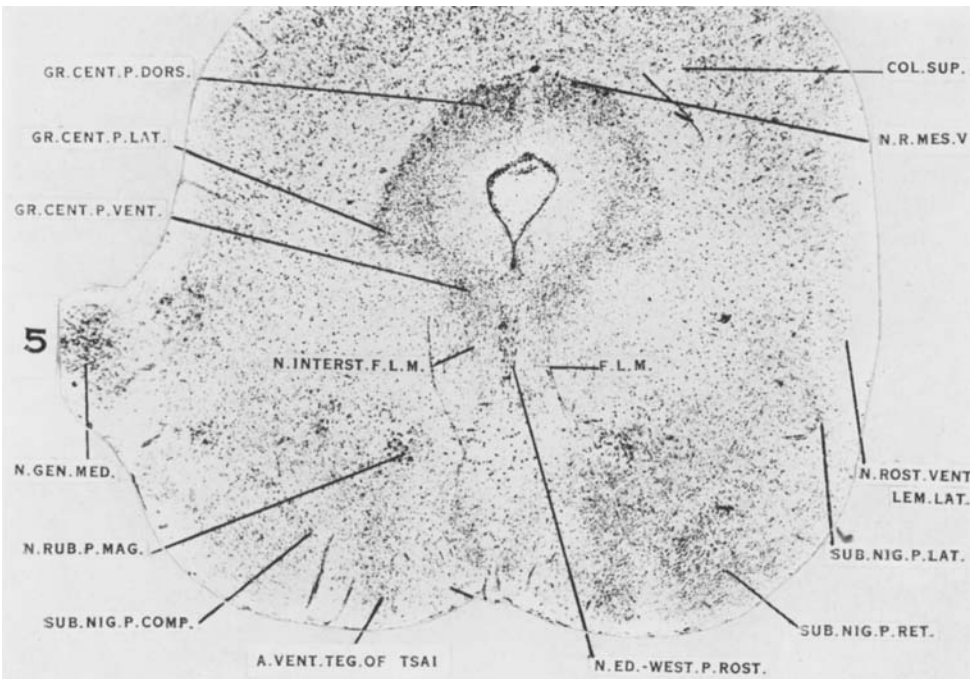
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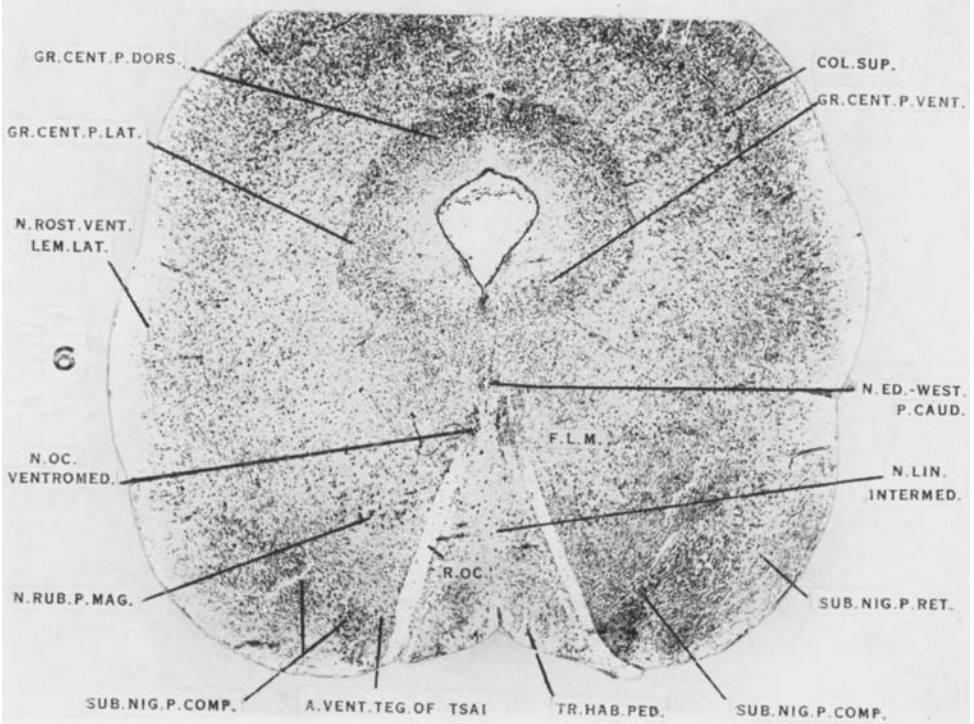
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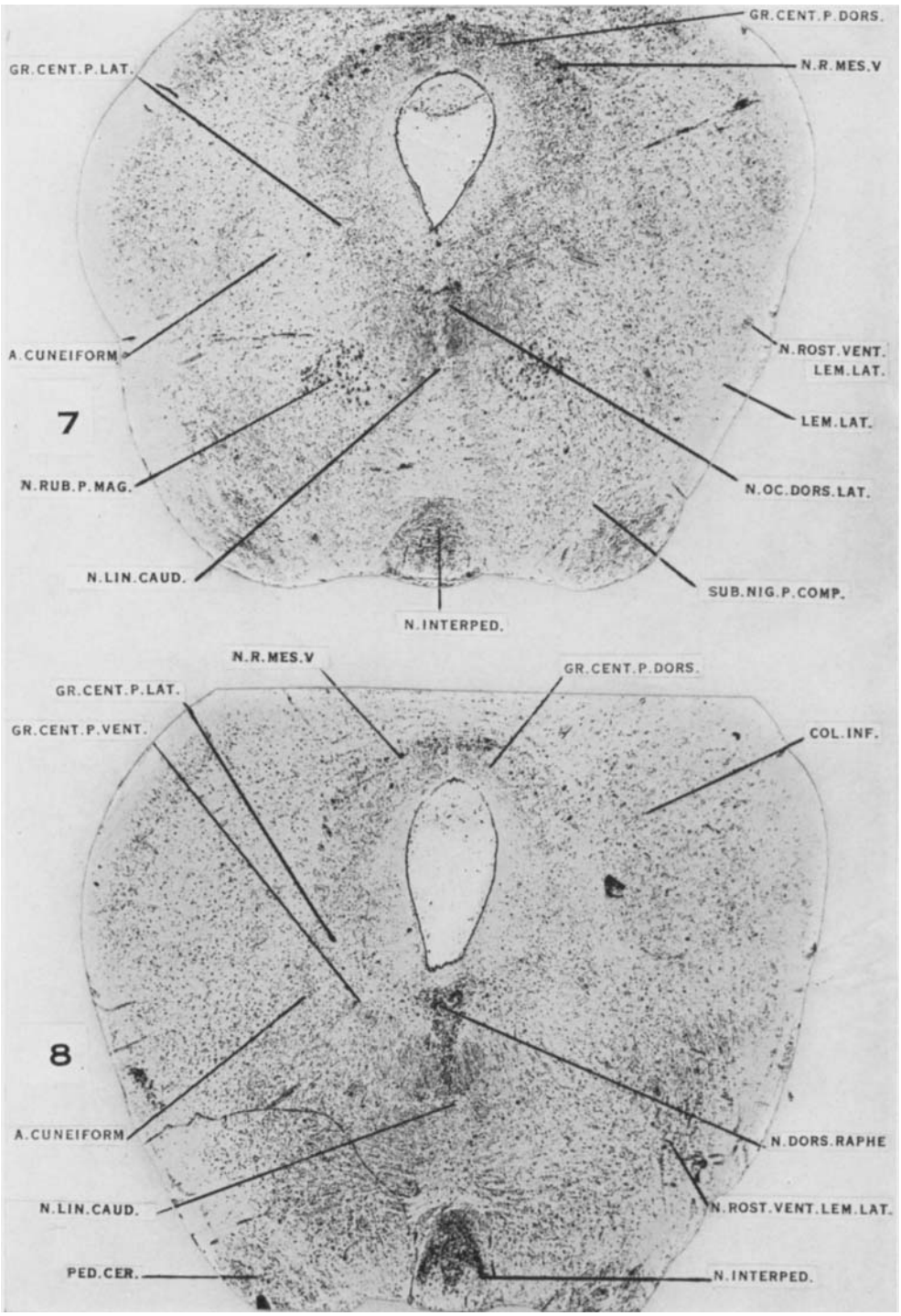
PLATE 4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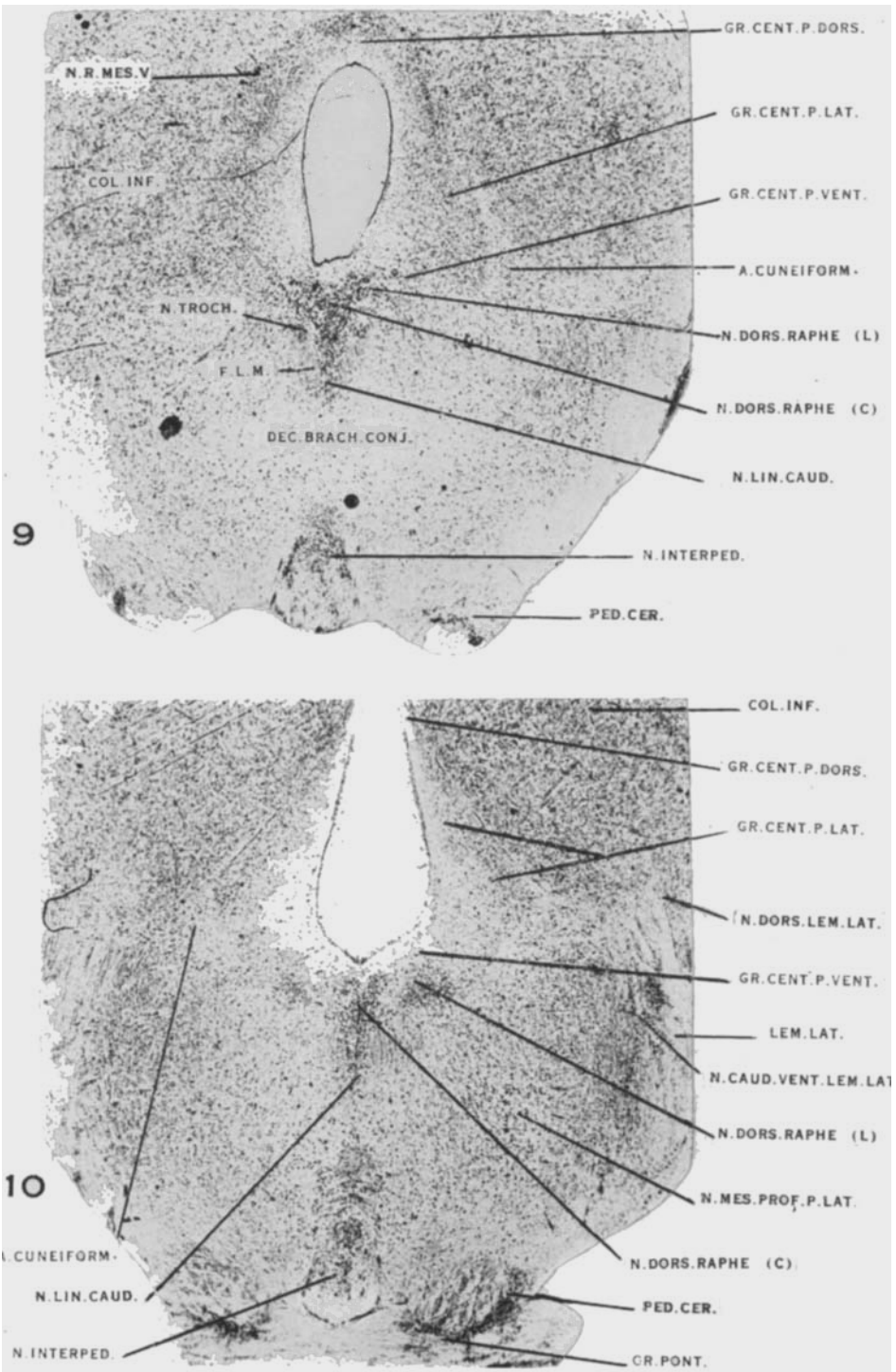
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N.DORS.RAPHE (C)
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9
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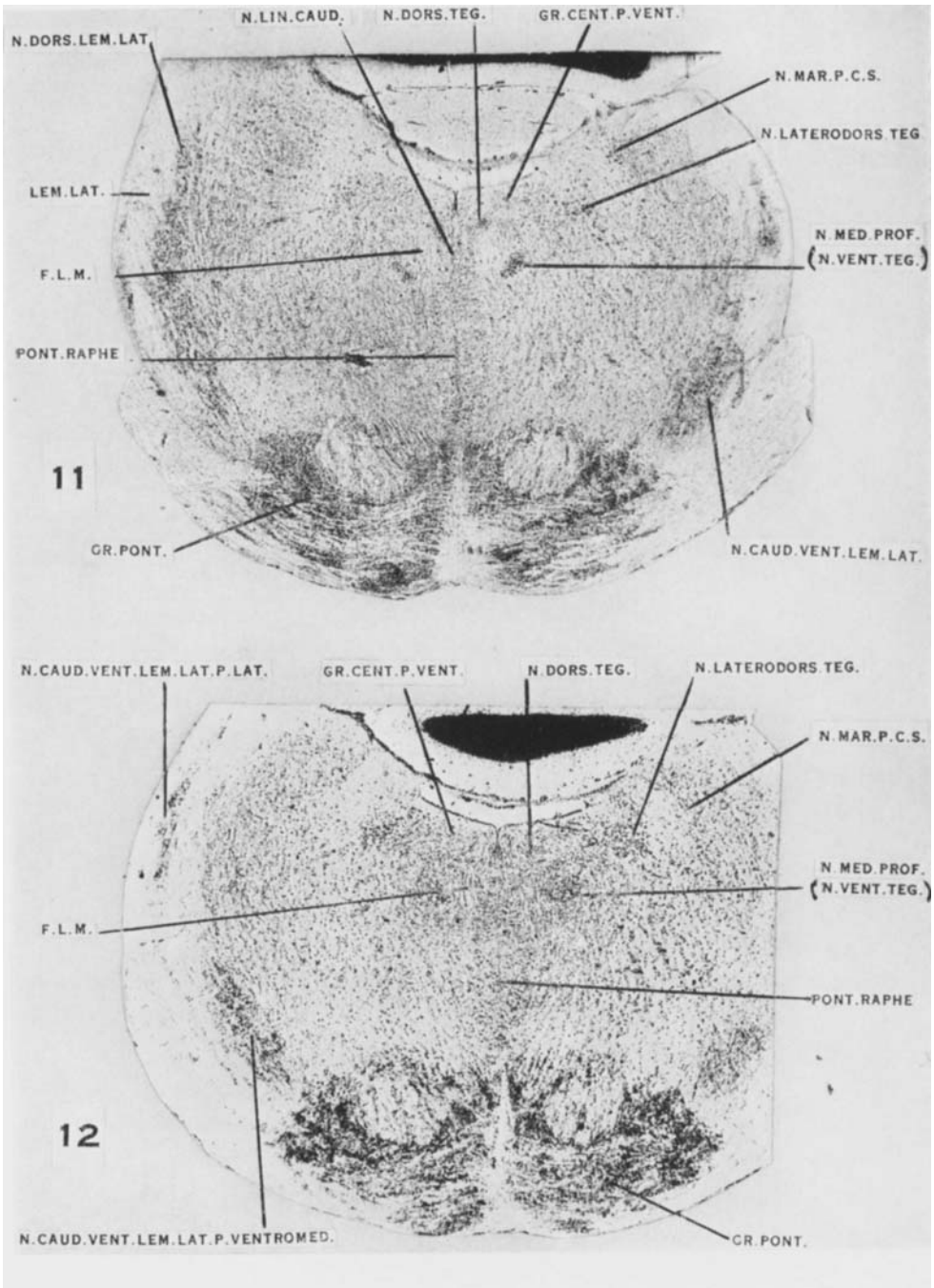
CR.PONT.

PLATE 6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