

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

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TWENTY-SIX PLATES (TWENTY-SIX FIGURES)

INTRODUCTION

The material used for this study of the midbrain of the 16 cm. pig (*Sus scrofa*), the adult sheep (*Ovis aries*) and the old horse (*Equus caballus*) consists of serially cut, transverse, toluidin blue sections. For the generous grant which made possible this research the writer wishes to express grateful acknowledgment to the Horace H. Rackham School of Graduate Studies of the University of Michigan.

Very little literature dealing with the ungulate midbrain has come to our attention. Papers by Solnitzsky ('38 and '39) deal with the dorsal thalamic, subthalamic, and hypothalamic regions of the pig brain; they contain accounts of the pretectal regions, substantia nigra and the rostral tip of the red nucleus. Rose ('42 b) has found that the pretectal nucleus in the sheep is represented by two groups of cells. Le Gros Clark ('26) observed that the Edinger-Westphal nucleus in the sheep was little differentiated, and in the pig the cells were only slightly different from the small medial raphé cells with which they become continuous anteriorly. The Edinger-Westphal nucleus in the pig is mostly a midline structure with only occasional bilateral clumping. Tsuchida ('06) found no Edinger-Westphal nucleus in the sheep and in the horse a few scattered cells only. He observed no nucleus medianus anterior and no true nucleus of Perlia; in the horse no nucleus of

Darkschewitsch nor nucleus of the posterior commissure were present, but in the sheep the nucleus of Darkschewitsch is weakly represented in spite of a large medial longitudinal fasciculus. He described the oculomotor nucleus as poorly differentiated into secondary groupings in the horse and the sheep. The oculomotor nucleus goes over into the trochlear nucleus without a break in the sheep, and in the horse the trochlear nucleus lies on the ventral aspect of the medial longitudinal fasciculus. Tsuchida stated that the eye-muscle nuclei in the goat are similar to those in the horse and the sheep, and the pig is like the other ungulates. The gross configuration of the sheep brain, including the midbrain, is illustrated in various texts, e.g., those of Burkholder ('12), Fiske ('13), Herrick and Crosby ('18), Ranson ('40 and other editions) and others.

There are certain variations in the development of the nuclear groups of the midbrain of the horse as compared to their homologues in the pig and the sheep. Some of these are due to species differences and some to the fact that the comparisons are based on brains of a fetal pig, an adult sheep, and an aged horse. Very little information concerning the midbrain centers in the horse is available in the literature. Van Valkenburg ('11) called attention to certain relations of the cells of the mesencephalic root of the trigeminal nerve, and Tsuchida ('06) and Vermeulen ('14) pointed out the unusual position of the trochlear nucleus ventral to the medial longitudinal fasciculus.

PART I. THE PIG

THE PERIVENTRICULAR GROUPS

General areas of periventricular gray

The central gray is divisible into dorsal, lateral and ventral portions. The dorsal portion (figs. 2 to 8) extends from the diencephalic-mesencephalic boundary to the caudal end of the inferior colliculus. Rostrally its lateral part differentiates into the medial portion of the dorsal nucleus of the posterior commissure. Throughout superior

collicular levels it constitutes the periventricular layer of the optic tectum and at inferior collicular levels it is directly continuous with the central nucleus of the inferior colliculus. The lateral division of the central gray (figs. 2 to 8) begins rostrally in the same planes as the dorsal part and disappears as the isthmus is attained. Throughout its extent it shows no special differentiation but is somewhat less clearly demarcated from the dorsal and ventral portions than in the adult forms studied. The ventral division of the central gray (figs. 2 to 8) in this embryo pig, as in various adult mammals, shows major differentiation of the central gray. In addition to the oculomotor and trochlear nuclei, it contains the relatively evident nucleus of Darkschewitsch, the dorsal nucleus of the raphé, the dorsal tegmental nucleus and the dorsolateral tegmental nucleus, all of which will be described separately. Otherwise it is represented by relatively undifferentiated central gray except for a lateral condensation of its cells throughout the rostral half of the mesencephalon, particularly at levels through the oculomotor complex. The cells are of the small, multipolar variety characteristic of undifferentiated gray.

Nuclear groups associated with posterior commissure

Three special portions of the nucleus of the posterior commissure can be recognized — the magnocellular, the central subcommissural and the intracommissural parts. The nucleus (fig. 1) appears in front of the decussating fibers as a mass of cells capping their rostral extreme. As the fibers begin to cross and turn ventralward, the nucleus is represented on both the medial and lateral borders of the commissure. The medial portion, *pars centralis subcommissuralis*, is a differentiation of the lateral part of the periventricular gray and is relatively large and clearly developed in planes through the crossing of the commissure which cut also the pretectal nucleus and the nucleus of the basal optic root. Laterally the magnocellular part of the nucleus of the posterior commissure is not so sharply separated from the surrounding tegmental gray, although an approximate boundary can be made. Behind the decussation the medial and lateral portions of the nucleus fuse into a common mass which encircles the posterior border of the commissural fibers. These cells are small and not differentially stained but somewhat more closely arranged than the surrounding central gray. Extending among the commissural fibers into the midline and across it are scattered clusters of cells and individual neurons which represent the intracommissural portion of the nucleus of the commissure.

Nucleus of Darkschewitsch

This nucleus (fig. 1) is very poorly developed in the material studied. It is present in planes which show the nucleus of the posterior commissure lying on either side of the commissural fibers and which pass through the pretectal nucleus and the nucleus of the basal optic root. It lies dorsomedial to the interstitial nucleus of the medial longitudinal fasciculus, within the lateral part of the ventral division of the periventricular gray. It consists of medium-sized, elongated, fairly deeply staining neurons, relatively few in number and showing no special arrangement.

Eye-muscle nuclei

Oculomotor complex. This complex appears caudally in planes cutting the superior colliculus dorsally and the caudal end of the interpeduncular nucleus and the pontine gray ventrally. In approximately the same levels lies the less differentiated frontal portion of the dorsal nucleus of the raphé. The complex extends forward to planes near the rostral pole of the tectal region which pass through the caudal part of the interstitial nucleus of the medial longitudinal fasciculus, the red nucleus and substantia nigra. This oculomotor complex is secondarily divisible into the chief oculomotor nucleus, which consists of a central nucleus of Perlia and medial and lateral oculomotor nuclei, and the rostral and the caudal Edinger-Westphal nuclei. It is probable that the lateral portion of the chief nucleus is comparable, in general, to the dorsolateral oculomotor nucleus of other mammals and that the medial represents the ventromedial oculomotor cell group, but at this age the pattern does not exactly correspond to that typical for most adult mammalian forms.

The lateral or dorsolateral oculomotor nucleus (fig. 4) and the medial or ventromedial oculomotor nucleus (fig. 4) tend, at their rostral (fig. 3) and caudal poles, to run into a common nuclear mass, which overlies the medial longitudinal fasciculus but is not continuous with the trochlear nucleus. Traced forward, the lateral oculomotor nucleus overlies the medial longitudinal fasciculus as a relatively discrete cell group until planes near the rostral tip of the interpeduncular nucleus, where it appears to fuse into a common mass with the medial portion of the complex. In those caudal planes in which the medial oculomotor nucleus is first distinct from the lateral oculomotor gray, it is an elongated column of cells medial to the medial longitudinal fasciculus. It tends, followed frontally, to separate into dorsal and ventral portions, but still farther forward loses the ventral part and ultimately fuses into the common mass mentioned previously. In cell type it is a typical somatic motor nucleus.

The central nucleus of *Perlia* (fig. 4) is relatively poorly differentiated at this age. It appears near the caudal end of the oculomotor complex in planes in which both lateral and medial oculomotor nuclei occur, and extends for only a short distance. It lies in the midplane between the two lateral nuclei and is represented by somewhat scattered neurons which tend to grade over into those of the lateral nucleus, but are of a somewhat smaller size.

The Edinger-Westphal complex is divided into rostral and caudal portions, the caudal portion representing the region to which the term Edinger-Westphal nucleus is always applied and the rostral part constituting the nucleus medianus anterior of Panegrossi, or the rostral end of the Edinger-Westphal nucleus of Zweig ('21). The caudal part of the Edinger-Westphal nucleus (fig. 3) lies at levels through the middle and the rostral pole of the oculomotor complex but is slightly behind the caudal end of the medial geniculate nucleus. This portion extends in front of the main oculomotor complex and the interpeduncular nucleus, passing over, rostrally and ventrorostally, into the cephalic portion of the Edinger-Westphal complex. Throughout its extent, the caudal end of the Edinger-Westphal gray is completely paired, although there may be slight interconnecting cell strands between the nuclei of the two sides. Its neurons are the typical preganglionic type and are relatively numerous, the nucleus appearing rather well developed, in comparison with the general differentiation of the gray in this embryonic pig brain.

The rostral end of the Edinger-Westphal nucleus (fig. 2) extends forward from its fusion with the caudal part of the complex between the highly developed caudal interstitial nuclei of the medial longitudinal fasciculus until near the diencephalic-mesencephalic boundary, at which level it is replaced by the rostral end of the linear nucleus. For the most part, the mass is somewhat indistinctly differentiated. It has a median position and its neurons exhibit a tendency toward longitudinal orientation in the transverse sections. Occasionally the cells show some concentration on either side of the midline, a condition suggestive of a possible tendency toward pairing. The neurons are rather more elongated and slightly less characteristically preganglionic in type than those of the caudal Edinger-Westphal nucleus. This appearance may be due to a difference in their orientation with reference to the plane of the section.

Trochlear gray. The trochlear nucleus of the fetal pig (fig. 5) occupies the position usual for it in many mammals (although not in the horse), lying dorsal to and partly embedded within the medial longitudinal fasciculus. It is entirely separated from the oculomotor complex, several sections intervening between the caudal end of the oculomotor nuclear group and the rostral pole of the trochlear nucleus.

In this respect it differs from the homologous gray of the horse and the sheep. It shows no clearly separated caudal or accessory trochlear nucleus, as was found in the horse. It is composed of groups of neurons which vary in number at different levels and which are typical multipolar cells resembling very closely those of the oculomotor complex, both as to size and general appearance.

Dorsal nucleus of raphé

The dorsal nucleus of the raphé (figs. 5 and 6) begins rostrally in planes through the caudal end of the oculomotor complex and extends caudally slightly behind the trochlear nucleus. Its rostral and caudal portions are represented by scattered cells which pass, without demarcation, into the less differentiated central gray, but its midportion shows the subdivisions characteristic of the dorsal nucleus of the raphé in mammalian forms, although such subdivisions are not so well differentiated as in some adult mammals. In planes through the trochlear nucleus, a central portion and lateral wings, are differentiable in the dorsal nucleus of the raphé. The central portion is represented first by its most ventral extension (fig. 5) but, slightly farther caudalward, spreads dorsally so that a long, bar-like central disk with an enlarged dorsal part (continuous with the lateral wings) may be recognized (fig. 6). This configuration is evident in planes toward the caudal pole of the trochlear nucleus and persists for only a short distance. Behind that level, the dorsal nucleus of the raphé is represented by a small central area lying between the dorsal tegmental nuclei. With the ventral extension of the ventricle (fig. 7), the caudal pole of the dorsal nucleus of the raphé fades out into the paired periventricular gray.

The characteristic cells of the dorsal nucleus of the raphé are relatively deeply staining neurons of slightly smaller size than those constituting the trochlear nucleus. Toward the less differentiated poles of the nucleus, the cells become smaller and less specifically stained.

Laterodorsal tegmental nucleus

In planes near the caudal pole of the dorsal tegmental nucleus, the laterodorsal tegmental nucleus (fig. 7) encircles the former nucleus dorsally and laterally. From this point forward, it occupies the dorsolateral part of the ventral division of the central gray, being separated from the dorsal nucleus of the raphé by the dorsal tegmental nucleus. Its limits are ill-defined at this age, the nuclear mass being recognizable by the presence of intermingled larger cells among the less differentiated central gray. Cells of this type extend through the

fiber bundles bounding the central gray into the adjoining tegmental field (fig. 7), in the manner customary for this nuclear mass in mammals, but this extension of cells is less marked than in the older mammals studied thus far. Behind the dorsal tegmental nucleus, the lateral part of the laterodorsal tegmental nucleus comes into relation with the mesencephalic root of V, suggesting the development in this region of the primordial nucleus of locus coeruleus described in adult ungulates (fig. 8). On the whole, the complex is not as yet well differentiated at this age. Rostrally, it fades into the general ventral part of the periventricular gray in planes behind the caudal pole of the trochlear nucleus.

Dorsal tegmental nucleus

The dorsal tegmental nucleus is best differentiated in planes which cut the inferior colliculus and the caudal pole of the superior colliculus dorsally and the pontine gray ventrally (fig. 7). At such levels it is a round to oval mass of small, not very deeply stained but relatively closely arranged neurons, lying between the medial longitudinal fasciculus ventrally and the laterodorsal tegmental nucleus dorsally and laterally. It fits into the inner curve of the latter nuclear gray. Medial to it at this plane lies the ventricle, from which it is separated by a small amount of undifferentiated gray, and ventrolateral to it are the radiations of Meynert, which intervene between the periventricular and the tegmental gray. Caudal to this plane, the dorsal tegmental nucleus gradually decreases in size, disappearing in the isthmus, its caudal pole not being sharply delimited from the undifferentiated gray of the upper pons. Rostrally from the plane described, it also decreases in size, lying somewhat nearer to the medial longitudinal fasciculus at its frontal pole and bounded medially by the caudal extension of the dorsal nucleus of the raphé. The dorsal tegmental nucleus of the pig has the relations usual for that nucleus in mammals but it is somewhat less clearly defined than in certain of the adult forms described.

Nucleus of mesencephalic root of V

The rostral end of the nucleus of the mesencephalic root of V is almost undifferentiated in the brain of the 16 cm. pig, only rare clusters of cells being found in or near the periventricular border at oculomotor levels (fig. 4). Such clusters appear to be composed, in part, of multipolar neurons and the evidence that they actually contribute to the mesencephalic root of V is lacking. At levels through the trochlear nucleus, these cells of the mesencephalic root of V are rather more regularly present, but they are far from numerous.

Many of those in the caudal half of the midbrain appear to be unipolar but occasional cells are obviously bipolar. Many sections show no cells of this type, but if they are present they are in clusters of three or four neurons, sometimes at the border of the periventricular area, sometimes slightly lateral and again within the periventricular gray (fig. 6). At the level of entrance of the fifth nerve (fig. 8), there are groups of cells associated with the mesencephalic root of V, ventrolateral to the lateral angle of the ventricle at the edge of the periventricular gray, but even here, there is no marked representation of this nucleus except for a limited extent, where the cells are numerous. This trigeminal portion is the best represented group in the series studied. It is obvious that in our material of the 16 cm. pig, the nucleus of the mesencephalic root of V is poorly differentiated except at trigeminal levels, although the motor nucleus of V is quite well developed. In the guinea pig material, Castaldi ('24) found that the nucleus of the mesencephalic root of V tended to develop with the differentiation of the motor nucleus of V.

MIDTEGMENTAL NUCLEAR GROUPS

Nuclear groups associated with medial longitudinal fasciculus

The interstitial nucleus of the medial longitudinal fasciculus is unusually well represented in the pig material of this age and is more than usually interstitial with respect to the fiber fascicles (figs. 1, 2). It is found in planes through the pretectal nucleus and the nucleus of the basal optic root, as a mass of neurons intercalated in the course of the accumulating fascicles of the medial longitudinal fasciculus. It can be followed caudalward in relationship with this fasciculus and overlying and surrounding the fiber complex to planes through the caudal Edinger-Westphal nucleus, through which levels it gradually disappears. Its cells are the typical multipolar, medium-sized neurons. Behind the interstitial nucleus of the medial longitudinal fasciculus there is a tendency for cells to line up along the border of the fasciculus and, at some levels through the trochlear complex, a nucleus corresponding to the annular nucleus of Castaldi ('23), which also is interstitial to the fibers of the fasciculus, can be seen.

Red nucleus

In the pig series studied, the red nucleus extends for about 2.7 mm. It lies at the rostral end of the midbrain, at the mesencephalic-diencephalic boundary, and extends caudalward to planes through the central nucleus of Perlia (figs. 1 to 4). Throughout its extent it has a midtegmental location. It is actually and proportionately

small, so that the two red nuclei appear relatively widely separated and lie at considerable distances from substantia nigra. The area ordinarily occupied by the red nucleus is filled largely with undifferentiated gray. Although there are foreshadowings of parvocellular and magnocellular portions, there is no clean-cut division between the two. However, the caudal end of the nucleus has rather marked magnocellular characteristics. At the rostral pole of the complex, the cells are medium-sized but, almost immediately, scattered, larger cells of the smaller magnocellular type begin to make their appearance. The area occupied by the nucleus and its cellular content increase as the mass is followed caudalward and, in those planes which extend through the nucleus Darkschewitsch, the red nucleus is an oval mass of cells of intermingled cell types. As the caudal end of the posterior commissure is reached, the red nucleus tends to show secondary cell masses, which had some representation even rostral to this level. Thereafter, into planes through the Edinger-Westphal nucleus, there are groupings and regroupings of cell masses of the red nucleus associated apparently with the passing of fiber fascicles. There is a tendency for the large cells to clump together and the smaller and medium-sized neurons to form discrete clusters. In such groupings, the dorsal and dorsomedial cell masses are composed chiefly of medium-sized and small cells, and so are suggestive of a poorly differentiated pars parvocellularis. The encircling ventral and ventrolateral groups (frequently with a tendency toward a crescent shape) consist mainly of larger neurons, foreshadowing a pars magnocellularis. Behind the level of the Edinger-Westphal nucleus, the cells within the red nucleus are more uniformly distributed, the mass then apparently consisting of a caudal extension of the ventrolateral magnocellular portion. The caudal end of the red nucleus is rounded off by the encapsulating fibers of the superior cerebellar peduncle.

Deep mesencephalic gray (nucleus mesencephalicus profundus)

A considerable part of the tegmental gray, other than that in the red nucleus and in the interstitial nucleus of the medial longitudinal fasciculus, is represented by masses of relatively undifferentiated neurons which show no nuclear grouping, so that at this stage of development, considerable portions of the area have the appearance of being occupied by almost undifferentiated gray (figs. 3 to 8). However, in planes through the magnocellular part of the red nucleus, cells resembling those of this latter nuclear mass are found among the fibers forming its capsule and dorsal and dorsolateral and occasionally ventrolateral to it. They show no constant pattern, varying

somewhat from section to section as to cell number and position, but they are representative of the masses of deep mesencephalic gray to which the terms of pars dorsalis, pars lateralis and pars ventralis of nucleus mesencephalicus profundus have been applied in many mammals. As the caudal end of the red nucleus is approached, for the most part these masses of gray disappear, except for an occasional neuron.

Ventral tegmental area and nucleus of mammillary peduncle

As has been stated elsewhere in this paper, the interpeduncular field at the rostral end of the midbrain is represented in this embryonic pig material by undifferentiated gray bordered on either side by the mammillary peduncle and the nucleus of the basal optic root (see figs. 1 to 3, A. vent. teg. of Tsai). As the rostral undifferentiated end of the interpeduncular nucleus comes into the field and the caudal pole of the nucleus of the basal optic root is approached, the front end of the ventral tegmental area of Tsai makes its appearance. This area extends caudalward until it is replaced by the pontine gray. Thus it is very large in the pig, having both a long rostrocaudal and a fairly wide mediolateral extent. In this respect it shows closest resemblance to the homologous gray in the rabbit. In relationship with it run the fibers of the mammillary peduncle (figs. 2 and 3). The cells immediately clustered around these fibers, in the dorsal portion of the ventral tegmental area of Tsai, may be regarded as the homologue of the nucleus of the mammillary peduncle described for other forms (Papez, '23; Fox, '41). This nucleus spreads lateralward with the fibers of the peduncle but never extends beyond the limits of the ventral tegmental area. The area appears to be, in part at least, a region of passage of fiber bundles; consequently its neurons, which vary from a medium-sized to small, and are chiefly multipolar, do not show any specific nuclear arrangement. The cells constituting the nucleus of the mammillary peduncle are distinguishable from the rest of the area by their more intimate grouping dorsal to the fiber fascicles, and may represent nothing more at this stage than a condensation of the nuclear gray of the region. The interstitial cells of the commissure of Forel (fig. 2) pass over, without sharp demarcation, into this ventral tegmental area.

Nucleus medialis profundus

This nucleus (fig. 6) lies in planes which cut the superior and inferior colliculi dorsally and the pontine gray ventrally. Thus it is found at the transition region between mesencephalon and pons. It occupies the usual position ventral to the medial longitudinal

fasciculus in the tegmental gray and consists of a patch of multipolar, relatively small, deeply staining neurons, which persist for about .4 mm. Nucleus medialis profundus is delimited, in the pig material available, by a definite capsule of medullated fibers, which separates it sharply from the surrounding gray.

Marginal nucleus of the superior cerebellar peduncle

As the superior cerebellar peduncle rides down through the field toward its decussation at levels of the inferior colliculus, it is surrounded by gray, much of which is undifferentiated in character, although occasional larger multipolar cells can be discerned (fig. 8). These latter cells follow down along the peduncle toward the scattered larger multipolar neurons of the tegmental gray, lateral and caudal to the red nucleus. Obviously at this stage of development, the marginal nucleus of the superior cerebellar peduncle is not yet well developed.

Cuneiform area

The name cuneiform area has been applied to an irregularly rhomboid-shaped region internal to the inferior colliculus but separated from it by the fascicles descending from the efferent layer of the optic tectum (fig. 7). Thus it lies in the course of efferent tectal tracts. Ventrolateral and lateral to it is the lateral lemniscus with its associated gray. Even in cell preparations the fibers of the lateral lemniscus can be traced into the cuneiform area and descending fascicles from the tectum can be seen to pass through the field. That the area is a region of passage of fiber bundles is evident, but the amount of actual synapse here must be left to a study of suitably prepared sections. Among the fiber fascicles are rather deeply staining, small to medium-sized multipolar neurons which are differentiable from the surrounding gray by their arrangement and by their staining properties.

Certain pretectal and subtectal components of tegmentum

Pretectal area. The pretectal area (see also Rose, '43) lies medial and dorsomedial to the pretectal nucleus, and dorsal to the posterior commissure and indistinctly separated from the superior collicular gray (fig. 1). The pretectal area merges with the tectal gray deep to stratum opticum, although, throughout its extent, it is composed of medium-sized cells intermingled in small part with larger and smaller elements but showing no specific nuclear character which differentiates it from the cells making up this portion of the tectal gray.

Pretectal nucleus. The pretectal nucleus (figs. 1 to 3) appears at caudal diencephalic levels overlying the medial geniculate nucleus but indistinctly separated from the surface of the diencephalon by the scattered larger cells in the course of optic fibers, which constitute the large-celled nucleus of the optic tract (fig. 1). It lies lateral and ventrolateral to the pretectal area and, with the appearance of the superior colliculus, it is situated ventral to this midbrain area. Gradually its cells spread dorsalward to intermingle with those of stratum griseum intermediale.

In the adult pig material studied by Solnitzky ('38), a (large-celled) nucleus of the optic tract and a pretectal nucleus were identified, the latter corresponding to the area pretectalis of the present account. The former cell mass corresponds to both the large-celled nucleus of the optic tract and the pretectal area described for the embryonic pig material. Solnitzky has not differentiated between the various descriptions of the pretectal nucleus and makes no mention of the confusion in terminology current in the literature. Recently, Rose ('43) has described the pretectal groups in the sheep. For further homologies, the account of the literature given at the end of this series of papers should be consulted.

Nuclear gray associated with lateral lemniscus. From planes through the superior olivary nucleus to those through the base of the inferior colliculus, the lateral lemniscus is accompanied in course by intercalate cells and masses of gray to which the general designation of nuclei of the lateral lemniscus may be applied. As it proceeds forward from inferior collicular levels toward the medial geniculate nucleus, such gray gradually disappears, to reappear only in planes immediately caudal to the latter nucleus. This gray associated with the lateral lemniscus may be subdivided for purposes of description into a dorsal nucleus, a caudal ventral nucleus, and a rostral ventral nucleus of the lemniscus.

The dorsal nucleus of the lateral lemniscus is a representative in the pig of nucleus isthmi of lower forms and to it the name of parabigeminal nucleus is often applied. It consists of medium-sized cells and slightly smaller neurons located at the extreme caudal pole of the inferior colliculus (fig. 8).

The caudal ventral nucleus of the lateral lemniscus has a ventromedial, a lateral portion, and a dorsal projection that is divisible into a caudodorsal and a rostradorsal part. Medium-sized, multipolar neurons, scattered throughout the course of the tract from the superior olivary nucleus to inferior collicular levels, constitute the intrafascicular or ventromedial part of lateral lemniscus gray (figs. 6 to 8); these cells may be scattered or they may be massed in fairly large groups. The lateral portion lies at inferior collicular levels as an

accumulation of gray near the ventral border of the lateral lemniscus and on the surface of the isthmus. The ventromedial portion extends dorsalward to become intermingled with the rostradorsal part, which is distinguishable from the ventromedial portion through the presence within it of larger, more deeply stained neurons and by its more intimate relations with the inferior collicular gray. The ventromedial portion of the caudal ventral nucleus differs somewhat from the remainder of the nucleus in cell type, containing medium-sized, more deeply staining neurons. This portion disappears in planes through the oculomotor complex, well behind the caudal pole of the medial geniculate nucleus. The caudodorsal and the rostradorsal divisions project toward the caudoventral base of the inferior colliculus and are separated from the surface by a molecular layer. They are large enough to produce an eminence on the lateral brain wall in the isthmus region, a relation reminiscent of the condition found in reptilian and avian forms. In this series, the main mass has been termed the caudodorsal portion (figs. 6 and 7) and its continuation forward under the inferior colliculus, the rostradorsal part (fig. 6).

The rostral ventral nucleus of the lateral lemniscus appears slightly behind the caudal end of the medial geniculate nucleus, along the course of lateral lemniscus fibers but not continuous with the other nuclei of this lemniscus system (figs. 4 and 5). It consists of more or less scattered intercalate cells which grade over without any sharp demarcation into the central nucleus of the medial geniculate.

MIDLINE NUCLEAR GROUPS

Linear nucleus

In the pig material studied, rostral and caudal portions of the linear nuclear group (see Castaldi, '23, for this group in the guinea pig) are recognizable but no intermediate or central portion could be identified. The rostral linear nucleus (fig. 1) appears at the diencephalic-mesencephalic boundary as a poorly differentiated row of deeper staining cells on either side of the midline. Followed caudalward, these become a trifle more prominent but then pass over into a more or less median mass of cells, which shows some indication of linear pattern but which fades out above the commissure of Forel and the rostral end of the Edinger-Westphal nucleus. From that point caudalward, until the level of the superior cerebellar decussation is reached, the midline gray, above the interpeduncular nucleus and below the oculomotor complex, is represented only by scattered, undifferentiated cell clusters, which show no evidence of linear arrangement. In levels through the caudal end of the oculomotor complex and the trochlear nucleus, dorsal to the superior cerebellar decus-

sation, there is a very poorly delimited caudal linear nucleus, which passes by undifferentiated gray into the median nucleus of the pontine raphé.

Interstitial nucleus of commissure of Forel

The commissure of Forel in the pig material is relatively large and has a marked rostrocaudal extent. It appears in the caudal end of the diencephalon in a supramammillary position and extends back approximately to planes through the nucleus of the basal optic root. The fibers are intermingled and accompanied in their course lateralward by the undifferentiated gray constituting the nucleus of the commissure (fig. 2). This gray passes over, without sharp delimitation and in company with fascicles of this decussating system, into the ventral tegmental area of Tsai, pars compacta of substantia nigra, and the medial border of the red nucleus. Moreover, there is no sharp limit to be set between it and the undifferentiated gray which constitutes the greater portion of the tegmental area of the midbrain.

Gray associated with ansulate commissure and superior cerebellar decussation

In planes through the caudal end of the oculomotor complex and the interpeduncular nucleus, a crossing of the tecto-bulbar and tecto-spinal systems occurs dorsal to the interpeduncular nucleus. Associated with this commissure, which is usually termed the ansulate commissure, are scattered neurons of the central undifferentiated gray, which in part overlie the crossing fibers and in part intermingle with them. These may be considered as an interstitial nucleus of the commissure (fig. 3). Similarly, in the superior cerebellar decussation, there are, in and near the midline, clusters of neurons which are intermingled with the crossing fascicles of the system (fig. 5). These neurons grade over into the surrounding gray of the region. They are not comparable to the so-called nucleus of the superior cerebellar peduncle (fig. 8) but represent undifferentiated central gray which, with the low degree of medullation exhibited by the crossing fibers, has not moved lateralward out of the midline.

Interpeduncular nucleus

On the whole, the interpeduncular nucleus (figs. 3 and 4) has a poorly differentiated rostral pole in the fetal pig. This cell mass does not make its appearance until considerably behind the caudal border of the mammillary body, the front end of the basal midbrain area being occupied by undifferentiated gray. It extends caudalward to the mesencephalic-pontine boundary, where it is replaced by the pontine

gray. The interpeduncular nucleus in the pig forms an eminence on the ventral surface and extends forward so that there is a pocket between it and the base of the midbrain, a type of foramen caecum. In front of this pocket, there is no clear differentiation of the nucleus. In this eminence formed by the interpeduncular nucleus, a central or median portion and lateral portions of the nuclear mass are recognizable (fig. 4). The central portion is bordered in front, dorsally and caudally by fiber bundles, the dorsal bundles being separated from foramen caecum by the undifferentiated gray which surrounds this pocket. At the rostral end of the interpeduncular nucleus, the habenulo-peduncular tracts lie lateral to the midportion of this nuclear gray but, in sections through the oculomotor complex and the magnocellular portion of the red nucleus, they have apparently intermingled with this gray and the lateral portions of the interpeduncular nucleus make their appearance on either side of the central mass. The mammillary peduncle overlies the lateral part of the interpeduncular nucleus. In front of this nucleus, it passes through the lateral tegmental area toward the mammillary body. As the caudal end of the interpeduncular nucleus is reached, the lateral part of this nucleus disappears and the medial part forms a horseshoe-shaped mass overlying the capsule of fibers which ultimately delimits the caudal pole of this nuclear gray.

The cells of the medial part of the interpeduncular nucleus are small, relatively undifferentiated neurons and there is no definite arrangement of cells and fibers such as is characteristic of it in some mammalian forms. The cells of the lateral part of the interpeduncular nucleus are larger, multipolar, and slightly more scattered in arrangement.

BASAL MIDBRAIN GRAY

Substantia nigra

Substantia nigra extends throughout the length of the mesencephalon and forward into the extreme caudal pole of the diencephalon, rostral to the front end of the red nucleus. It has the usual relations to the cerebral peduncle and consists of the three parts—pars reticulata, pars compacta, and pars lateralis—characteristic of mammals in general. Of these three, pars compacta is the most poorly developed.

Pars reticulata (figs. 1 to 4) extends throughout the length of substantia nigra. In the fetal pig it consists partly of characteristic multipolar neurons which are of a size intermediate between that of the medium-sized and the larger cells of the red nucleus, and partly of undifferentiated gray. As in other mammals, the cells are inter-

calated in the course of the fibers constituting the cerebral peduncle. They have certain peculiarities, the most marked of which is their relatively peripheral position, for some of them approach fairly near the ventral surface of the brain. Slightly behind the rostral appearance of pars reticulata, the more differentiated cells form a relatively large mass in the lateral half of the cerebral peduncle, with scattered representatives medialward, although the number of cells varies from level to level. This undifferentiated gray is found in almost equal amounts on the medial side of the peduncle. In planes through nucleus medianus anterior (rostral portion of the Edinger-Westphal complex) and behind that nucleus, the differentiated gray of pars reticulata appears to be more evenly distributed among the peduncular fibers. It still remains fairly large in amount, with some variation from level to level, until near the caudal pole of substantia nigra, and persists until it is replaced by pontine fibers. Dorsally, the differentiated portion of pars reticulata grades over without distinct separation into pars compacta at such levels as this latter portion has representation.

Pars compacta (figs. 1 to 4) begins slightly behind the rostral pole of pars reticulata as a small group of multipolar cells of similar type, which widens out into a narrow band overlying the peduncle. This band is continued caudalward in similar relations but, as the caudal pole of the red nucleus is reached, the number of cells becomes greatly reduced. Throughout much of the remaining extent of the midbrain, it is represented by intermittent cell clusters indistinctly separated from pars reticulata and varying in position from level to level without any constant pattern. Toward the caudal end of substantia nigra, there is a gradual increase in pars compacta, particularly ventromedially, and ultimately it becomes rather well developed.

The pars lateralis of substantia nigra (figs. 2 to 4) is relatively large compared with other parts of this nuclear mass and has a considerable rostrocaudal extent. Rostrally it begins behind the front end of the other two portions of the complex along the lateral border of the peduncle, ventral to the medial geniculate nucleus and the lateral extension of zona incerta. Behind zona incerta it increases in size, still lying ventral to the medial geniculate nucleus. As this latter nucleus reduces in size, pars lateralis increases somewhat and, near the caudal pole of the medial geniculate, extends dorsolateralward toward it, obviously along the course of fiber fascicles. Behind the caudal end of the medial geniculate nucleus, in planes through the oculomotor complex, pars lateralis lies ventral to and not sharply separated from the rostral nucleus of the lateral lemniscus. It continues until planes near the caudal pole of the

oculomotor complex dorsally and the pontine gray ventrally, disappearing in front of the caudal nucleus of the lateral lemniscus. Pars lateralis is composed of somewhat less differentiated cells than those comprising pars compacta. At least they are less deeply stained and tend to be more variable in type.

Nucleus of basal optic root

The nucleus of the basal optic root is quite prominent in the embryonic pig material (figs. 1 and 2). It appears in planes through the rostral end of the mesencephalon, cutting the posterior commissure dorsally and the region immediately caudal to the mammillary body ventrally, and extends caudward to levels through the caudal third of the posterior commissure and the rostral pole of the interpeduncular nucleus. Thus it lies completely in front of the oculomotor complex. It is on the medial side of the cerebral peduncle, extending dorsalward, from near the brain surface, along the medial border of this fiber mass. It spreads out dorsally into the lateral border of the lateral tegmental area of Tsai and up toward the commissure of Forel, the intercalate cells of which tend to fuse with its upper tip. They are multipolar cells, slightly smaller than those constituting substantia nigra, but in many ways resembling such neurons. They are not very closely arranged but intermingle with the fiber fascicles of the basal optic root, the arrangement being more dense toward the periphery than in the more dorsal part of the nucleus.

PART II. THE SHEEP

THE PERIVENTRICULAR GROUPS

General areas of periventricular gray

The periventricular gray is, as usual, divisible into dorsal, lateral and ventral portions. The dorsal portion (figs. 12 to 16) is co-existent with the optic tectum. The lateral portion (figs. 9, 12 to 16) extends from the rostral end of the mesencephalon to the isthmus, disappearing at the caudal border of the inferior colliculus. The ventral portion begins at the mesencephalic-diencephalic boundary and extends back into the isthmus, where it is represented by the periventricular gray of the upper end of the pons. The dorsal portion belongs to the tectum of the midbrain and need not receive further discussion here. The lateral portion is continuous with the chief nucleus of the inferior colliculus, dorsocaudally, and contributes in small part to the more medial portion of the nucleus of the posterior commissure. Most of the differentiation occurs in the ventral portion

(figs. 11 to 15) in the sheep as in other mammals and the nuclear groups represented in this region will be considered in the following paragraphs.

Nuclear groups associated with posterior commissure

There are three special subdivisions of the nuclear gray associated with the posterior commissure — a pars intracommissuralis, a pars magnocellularis and a pars centralis subcommissuralis. The nucleus of the posterior commissure (figs. 9 and 10) lies over the rostral face and surrounds the lateral extension of the system, fading out behind the crossing fibers into the general tegmental gray of the area. It is well developed in the sheep, being best seen in transverse planes which cut the pretectal nucleus, to which it lies ventral but separated in part by the commissural fibers. The central subcommissural portion of the nucleus is rather poorly developed in the sheep. This nucleus consists of cells of the general undifferentiated gray of the area intermingled with certain larger multipolar neurons resembling the larger tegmental cells which form its magnocellular portion. The intracommissural part of the nucleus (figs. 9 and 10) has a bilateral representation in the sheep, no cells being found in the midline. In general, it resembles in cellular character the less differentiated neurons of the remainder of the nucleus, its distinguishing characteristic being the position of its cells among the fibers.

Nucleus of Darkschewitsch

The nucleus of Darkschewitsch (figs. 9 and 10) lies in the ventral part of the periventricular gray, dorsal to the medial longitudinal fasciculus and dorsomedial to the interstitial nucleus of the fasciculus. Its rostral pole begins slightly behind the frontal tip of the interstitial nucleus and its caudal pole terminates in approximately the same plane as does the latter gray. Rostrally and caudally it is not very sharply differentiated but its midportion is a fairly clear cut, round to oval mass of slightly more deeply stained, closely arranged neurons.

Eye-muscle nuclei

Oculomotor complex. To the oculomotor complex must be allocated nucleus medianus anterior (or the rostral Edinger-Westphal nucleus), the caudal Edinger-Westphal nucleus and the chief oculomotor nuclei. Nucleus medianus anterior or the rostral Edinger-Westphal nucleus (fig. 10) appears at the diencephalic-mesencephalic boundary in planes which cut the posterior commissure dorsally and the interpeduncular fossa ventrally. At such levels it lies beneath the ventral tip of the

third ventricle and dorsal to the commissure of Forel, being intermingled with the less deeply stained, more nearly oval cells of the rostral linear nucleus. Its neurons resemble those of the caudal Edinger-Westphal nucleus and appear to be of preganglionic type. This patch of cells tends to have a median position, although at some levels there are faint indications of a pairing of the groups such as is characteristic of the nucleus in some mammals. As the gray mass is followed caudalward, through planes which pass through the nucleus of Darkschewitsch and also cut the interstitial nucleus of the medial longitudinal fasciculus, it increases somewhat in length and, through the rostral pole of the red nucleus, passes over without definite demarcation into the caudal Edinger-Westphal nucleus. In general the rostral Edinger-Westphal nucleus has a marked frontocaudal extent in the sheep as compared with its homologue in many mammals.

The caudal end of the Edinger-Westphal nucleus (fig. 11) is V-shaped, showing the marked tendency toward pairing which characterizes it in higher forms. In this respect it resembles the corresponding nucleus in certain carnivores. It appears just rostral to the plane of the chief oculomotor nucleus and extends caudalward above this latter complex for some distance. It is composed of typical preganglionic neurons and has the relations to be expected in this type of mammal.

The chief oculomotor complex in sheep, in its secondary subdivisions, suggests the conditions found in other ungulates, but is less easily compared with the relations in other mammals. Rostrally, it makes its appearance on the medial side of the medial longitudinal fasciculus as a single mass of neurons (fig. 11) of typical efferent type. This mass is soon supplemented by a secondary cell group which lies immediately lateral to it, so that the complex appears to be divided into medial and lateral portions (fig. 12 right). Still farther caudalward, as these nuclei have elongated, their ventral tips have a tendency to differentiate further and the medial group particularly shows a dorsal and a ventral portion. Then the ventral tips and the lateral portion of the nucleus disappear from the field. However, the medial part passes over directly into the trochlear nucleus (fig. 12 right). It probably corresponds in general to the ventromedial oculomotor nucleus of other forms and the lateral division to the dorsolateral oculomotor nucleus, but there is no real evidence to present in favor of this interpretation.

Trochlear gray. The trochlear nucleus (figs. 12 to 14) is large and well circumscribed and lies within the periventricular gray above the medial longitudinal fasciculus. Rostrally it is continuous with the

medial portion of the oculomotor nucleus (fig. 12, right) and caudally it disappears in planes which cut the superior colliculus and the most rostral end of the inferior colliculus dorsally and the caudal pole of the interpeduncular nucleus ventrally. Its relations differ in certain interesting respects from those in the horse, notably in the position of the nucleus dorsal to the medial longitudinal fasciculus (compare figs. 12 to 14 with fig. 21) rather than ventral to it, in its continuity with the medial part of the oculomotor complex rather than with the lateral portion, and finally, in the absence of accessory trochlear nuclei. It should be stressed that the cells in this nucleus are numerous but of a medium-sized, somatic efferent type, comparable to those of the chief oculomotor nucleus.

Dorsal nucleus of raphé

The dorsal nucleus of the raphé appears rostrally in planes through the middle part of the trochlear nucleus, which it overlies, and extends caudalward into the isthmus to levels through nucleus medialis profundus. Its frontal pole, a more or less scattered cluster of cells directly above the trochlear nucleus, soon differentiates into a middle portion and lateral wings (fig. 14). The middle portion has a dorsal tip, a round or oval intermediate or central part, and a ventral portion. These parts continue for some distance caudalward, but, behind the trochlear nucleus, a slightly different pattern is seen. The lateral wings begin to break up into secondary groups and the dorsal and ventral tips of the middle portion disappear. Then the nucleus becomes elongated, appearing as paired columns of cells near the midline, and these columns persist to its caudal pole (fig. 15). They represent the paired central portion which has been described in the caudal end of the nuclear mass in various mammals. In general the cells of the dorsal nucleus of the raphé are characterized by their deep staining and their rather definite grouping, so that the nuclear complex stands out from the surrounding undifferentiated gray. This is clearly evident in the photomicrographs. The constituent neurons are medium-sized and, in general, more closely arranged in the middle portion than in the lateral wings.

Laterodorsal tegmental nucleus

The laterodorsal tegmental nucleus (figs. 15 to 17) extends from the caudal end of the mesencephalon through the isthmus to the level of entrance of the trigeminal roots. Rostrally, it occupies the greater portion of the ventral part of the periventricular gray (fig. 15) and gradually extends through the surrounding fibers into the underlying

tegmentum. In such planes (fig. 15), the laterodorsal tegmental nucleus lies rostral to the dorsal tegmental nucleus, but, with the appearance of the latter, occupies a position dorsomedial, dorsal and lateral to it (fig. 16). The lateral portion of the laterodorsal tegmental nucleus extends toward the nucleus of the mesencephalic root of V and, as these groups are traced caudalward through the isthmus, they become particularly intimately related (fig. 17) and, near trigeminal levels, the cells of the two nuclei are somewhat intermingled. This caudal lateral part of the laterodorsal tegmental nucleus represents here a primordial nucleus of locus coeruleus, although no pigment has been demonstrated. The medial part of the laterodorsal tegmental nucleus decreases with the increase in size of the dorsal tegmental nucleus and tends to fade out at lower levels of the isthmus. The neurons of the laterodorsal tegmental nucleus are characteristically medium-sized, multipolar, dark staining neurons, which are intermingled with smaller cells of the general type of undifferentiated gray.

Dorsal tegmental nucleus

The dorsal tegmental nucleus (figs. 16 and 17) makes its appearance about the level of transition of the mesencephalon to the isthmus. It begins as a small, round cell mass (fig. 16), as seen in transverse sections, in the midst of the medial part of the laterodorsal tegmental nucleus and dorsal to the medial longitudinal fasciculus. Followed caudalward through the isthmus, it increases rapidly in size until it occupies a considerable proportion of the medial half of the ventral part of the periventricular gray, still retaining its round or oval cross-sectional outline (fig. 17). As the level of entrance of the trigeminal nerve is approached, the nucleus decreases in size and disappears from the field. This cell mass stands out very clearly in contrast to the surrounding gray by reason of the close arrangement of its small, medium-stained neurons and its rather definite outline.

Nucleus of mesencephalic root of V

The nucleus of the mesencephalic root of V is poorly developed in the sheep as compared with that of other ungulates and of many other mammals as well. In planes through the posterior commissure (figs. 9 and 10), single cells or clusters of two or three neurons occur along the lateral part of the periventricular gray. Behind the commissure, small clusters are found in a similar position. These may vary from six or eight neurons to three or four in a single field (figs. 11 and 12). Behind the oculomotor level, the cells of the

mesencephalic root of V become even further reduced, so that through the trochlear nucleus (figs. 13 and 14) only occasional cells or small clusters of neurons of this type are seen, and some sections show no cells at all. Behind the trochlear nucleus, in the isthmus, the cells of the mesencephalic root of V remain few in number until the caudal end of the inferior colliculus is approached (fig. 16), then there is a gradual increase in such cells along the lateral border of the ventricle at the level of entrance of the trigeminal root (no figures this far caudalward). Comparison of the nucleus of the mesencephalic root of V of the sheep with that of other mammals, and particularly of the horse, shows that this nucleus in the sheep is not only reduced in size but consists of smaller neurons. Deeper staining and somewhat lighter staining neurons are seen in this ungulate, the latter having possibly more than a single process. For the most part, these cells tend to follow the line of the periventricular gray. In planes through the laterodorsal tegmental nucleus, they lie close to its lateral portion, but not so intimately intermingled as in some mammals.

MIDTEGMENTAL NUCLEAR GROUPS

Nuclear groups associated with medial longitudinal fasciculus

The interstitial nucleus of the medial longitudinal fasciculus (figs. 9 and 10) begins at the caudal end of the diencephalon and extends to planes through the rostral part of the chief oculomotor nucleus and the front end of the fasciculus. It begins slightly rostral to the frontal tip of the nucleus of Darkschewitsch, but both terminate in approximately the same plane. Throughout, the interstitial nucleus lies over the fasciculus, and, in some planes, is slightly intermingled with it. Thus it occupies a position in the tegmental gray, ventrolateral to the nucleus of Darkschewitsch (fig. 9). The interstitial nucleus of the medial longitudinal fasciculus has medium-sized cells intermingled with neurons which resemble in type the larger cells found elsewhere in the deep tegmental gray.

The annular nucleus (fig. 15) is not very well developed in the sheep, being best represented at levels through the trochlear nucleus, where clusters of cells border the fasciculus, particularly medially and ventromedially, and occasionally intermingle with its fibers. Other traces of such a nucleus are found occasionally at isthmus levels.

Red nucleus

The red nucleus (figs. 9 to 11) begins in the caudal end of the diencephalon of the sheep. Its rostral tip lies medial to zona incerta and consists of scattered clusters of cells or single neurons which

represent the parvocellular portion of the nucleus. Very shortly behind this rostral tip, scattered cells of the magnocellular type appear (fig. 9) and the nuclear mass increases slowly in size and in cell constituents. At planes which cut the front end of the rostral Edinger-Westphal nucleus, or nucleus medianus anterior, and the interstitial nucleus of the medial longitudinal fasciculus, the red nucleus is a fairly circumscribed gray mass, consisting of intermingled cells of the parvocellular and magnocellular types, that is, very large and medium-sized neurons. In planes just rostral to the chief oculomotor complex (fig. 10), the cells of the red nucleus have spread medialward almost to the midline and the mass is poorly circumscribed. The emerging oculomotor rootlets cut through the nucleus and tend to divide it into secondary groups, as do other fibers of passage. There is no sharp line of demarcation, even in planes through the chief oculomotor nucleus, between the parvocellular and magnocellular portions, but there is some tendency for the dorsal part of the nucleus to be parvocellular and the ventral portion to be magnocellular (fig. 11). At levels through the central nucleus of Perlia, the parvocellular constituents are fairly numerous, but behind that level they become confined more particularly to the medial border of the nucleus and then disappear from the field. The magnocellular portion persists slightly behind the parvocellular part but has disappeared before the caudal end of the oculomotor complex is reached. A rather definite capsule of fibers encircles the red nucleus caudally (fig. 12) and extends forward along its caudal half, but rostrally the nuclear limits are very indistinct.

The cells of the magnocellular portion of the red nucleus are conspicuously large, almost giant cells, with many widespread dendritic processes and deeply staining Nissl granules. The neurons allocated to the parvocellular part are medium-sized and small, less deeply stained, and much less conspicuous. Actually, there is a graded series of cells in the red nucleus of the sheep, represented at one end of the scale by relatively small, inconspicuous multipolar neurons and at the other end by huge multipolar cells.

Deep mesencephalic gray (nucleus mesencephalicus profundus)

The limits of the red nucleus are not sharply defined and cells of its magnocellular type tend to spread out in the tegmental gray and to be intermingled with the fibers which partially encapsulate it. The surrounding tegmental areas contain medium-sized, non-differentially stained neurons not arranged in nuclear masses. At some levels, however, there are clusters of large cells in the tegmentum dorsal and occasionally dorsolateral to the red nucleus, and resembling its

magnocellular component. These cells are relatively very small in number, and are scarcely to be regarded as a definite pars dorsalis of nucleus mesencephalicus profundus lateralis. Between the red nucleus and substantia nigra there are scattered cells which are of about the size of those of substantia nigra and might be allocated to this tegmental gray (see fig. 11). Caudal to the red nucleus in planes through the superior cerebellar decussation, there is a relatively marked development of pars lateralis of nucleus mesencephalicus profundus. This persists for a considerable distance, becoming fused with the nucleus of the superior cerebellar peduncle in midtrochlear planes. Through approximately the same levels, but particularly at the rostral end of the trochlear complex, there are considerable clusters of large neurons which form a caudal portion of pars dorsalis of nucleus mesencephalicus profundus. The accumulation of tegmental cells behind and at the crossing of the superior cerebellar peduncle almost assumes the character of a distinct nuclear mass, constituting, as it were, a caudal magnocellular red nucleus. Its relation to the nucleus of the superior cerebellar peduncle is particularly important.

Ventral tegmental area and nucleus of mammillary peduncle

The rostral tip of the ventral tegmental area (figs. 9 to 11) lies lateral to the caudal end of the mammillary body and medial to the cerebral peduncle. Behind the mammillary gray, it occupies the region above the interpeduncular fossa between the two peduncles until the appearance of the interpeduncular nucleus and then is bounded medially by this nuclear gray. It fades out as pontine areas are approached. In the sheep, as in the other ungulates, it is largely a region of passage of fibers, between the bundles of which is scattered, largely undifferentiated gray. Among the fibers of passage are those constituting the mammillary peduncle (figs. 9 to 11). The spindle-shaped, darker staining, small neurons of the ventral tegmental area, which are intimately associated with this peduncle and possibly in synaptic relationship with it (see also Fox, '41), have been termed by Papez ('23) the interstitial nucleus of the peduncle and are so designated in the photomicrographs.

Nucleus medialis profundus

Nucleus medialis profundus (figs. 15, 16) is situated in the tegmental region of the midbrain, somewhat ventral to the medial longitudinal fasciculus. Its rostral pole (fig. 15) is in planes through the caudal part of the dorsal nucleus of the raphé and is not only ventral, but slightly ventrolateral, to the medial longitudinal fasciculus, from

which it is separated by a considerable space. It extends caudodorsalward through the tegmentum so that its caudal pole (fig. 16) approaches the ventrolateral side of the fasciculus, in planes which cut the rostral end of the dorsal tegmental nucleus. It is a columnar mass of cells showing a rounded outline in cross section. Its constituent neurons are fairly small, deeply stained and closely arranged. The surrounding capsule is not so large as it is in some mammals.

Marginal nucleus of superior cerebellar peduncle

This nucleus (figs. 15 to 17) is a mass of gray composed of medium-sized and larger tegmental cells (the latter of the type of pars lateralis of nucleus mesencephalicus profundus) which encircles the superior cerebellar peduncle in its course through the isthmus and forward to the level of its crossing in the midbrain. At the level of the decussation, the marginal nucleus passes over, without demarcation, into the well developed pars lateralis of nucleus mesencephalicus profundus (fig. 14), which caps the lateral border of the crossing fibers. Both of these nuclear masses, and the large-celled portion of the red nucleus as well, are phylogenetic derivatives of nucleus reticularis superior mesencephali of lower forms (Ariëns Kappers, Huber and Crosby, '36) and all of them are recipients of efferent cerebellar fibers, with this difference: that the red nucleus receives contralateral and the other nuclei, to a considerable extent, homolateral fibers.

Cuneiform area

The cuneiform area (figs. 14 to 16) is situated between the ventromedial border of the inferior colliculus and the periventricular gray, continuing throughout the extent of the inferior colliculus until its dorsalmost, deeply buried tip is approached. This cuneiform area consists of a wedge-shaped mass of intermingled cells and fibers; the cells are irregularly triangular, dark staining, medium-sized, multipolar neurons intermingled with larger cells of the general type of efferent tegmental neurons. The fiber fascicles are partly fibers of passage and partly in synapse directly or by collaterals with cells of the area. They are, in general, of two categories — efferent tectal fibers and branches of bundles constituting the lateral lemniscus.

Certain pretectal and subtectal components of tegmentum

Pretectal nucleus. The pretectal nucleus (figs. 9, 10) lies dorsal to the posterior commissure rostrally, and extends into the front end of the collicular eminence in relationship with stratum griseum intermediale of the optic tectum. At this front end, it is fairly easily

delimited from the surrounding gray, notably the dorsal nucleus of the posterior commissure, but toward its caudal pole it fuses with the tectal gray so that no specific limits can be set. Its cells are medium-sized, with occasional smaller neurons, and show no special staining characteristics. In general, they resemble the tectal gray with which they are intermingled. The nucleus here described is the nucleus pretectalis posterior of Rose ('42 b).

Pretectal area. Between the pretectal nucleus and the posterior commissure is a poorly defined area which over-rides the commissure and extends caudalward into relationship with the deep layers of the optic tectum. This is the area pretectalis (fig. 10) or area pretectalis medialis of Rose ('42 b).

Rose ('42) has identified three pretectal groups in this ungulate. In addition to area pretectalis medialis, he described a nucleus pretectalis anterior and a nucleus pretectalis posterior. In view of Rose's recent description and photographs, no further description need be given here except to state that the region labelled nucleus pretectalis on figures 9 and 10 of this paper appears to correspond to his nucleus pretectalis anterior.

Nuclear gray associated with lateral lemniscus. The nuclei of the lateral lemniscus may be subdivided for purposes of description into a caudal ventral nucleus, a rostral ventral nucleus, and a dorsal nucleus. The caudal ventral nucleus extends from the upper pons along the course of the lateral lemniscus to levels through the caudal end of the midbrain. For the most part, the ventromedial division is intrafascicular (figs. 15 to 17), although there is some clustering of cells just as there is in rodents (fig. 16). The intrafascicular ventromedial portion consists of multipolar, deeply staining neurons. Such neurons occur singly or occasionally in clusters or rows between the fascicles of the lateral lemniscus or adjacent to its borders. A small mass of gray close to the surface of the lower midbrain region constitutes a pars lateralis (fig. 16) of the caudal ventral nucleus. This portion has smaller more closely arranged cells and is adjacent to the lateral lemniscus rather than intercalated directly in its course. The dorsal tip of the ventromedial portion passes over dorsally into the ventrolateral edge of the marginal nucleus of the superior cerebellar peduncle and continues along the fibers of the lateral lemniscus which turn into the cuneiform area.

The dorsal portion of the caudal ventral nucleus of the lateral lemniscus (figs. 15 and 16) shows a larger caudodorsal group and a smaller, less distinct rostradorsal portion. The caudodorsal part (fig. 16) appears in the upper isthmus, internal to the dorsally running lateral lemniscus fibers as these sweep toward the inferior colliculus. It consists of a mass of small to medium-sized, rather

deeply staining and rather closely arranged neurons which, with associated fiber tracts, form an eminence on the brain wall. As the fibers enter the inferior colliculus, the caudodorsal group narrows down to a strand of interstitial cells which continue forward underneath the inferior colliculus along the ascending bundles of the lateral lemniscus. This rostral extension constitutes the rostradorsal portion of the caudal ventral nucleus (fig. 15). It disappears as the inferior colliculus loses its relationship to the surface and becomes buried beneath the superior collicular gray.

The rostral ventral nucleus of the lateral lemniscus (fig. 15) makes its appearance caudally in planes through the inferior colliculus and the rostradorsal nucleus of the lateral lemniscus and extends forward along the associated fiber bundles until the caudal border of the medial geniculate is approached. Its frontal pole is very attenuated, the main mass of the nucleus disappearing in planes through the caudal end of the oculomotor nucleus. It is a typical intercalated nucleus, consisting of rather small, deeply stained cells interspersed among the fiber fascicles.

The dorsal nucleus of the lateral lemniscus is the most caudal of the nuclei associated with this fiber tract. It is located dorsolateral to the marginal nucleus of the superior cerebellar peduncle, making a slight bulge on the lateral surface of the brain stem just ventral to the emerging roots of the trochlear nerve. The neurons are small, rather deeply staining and closely packed, so that they make a neat little group in this particular ungulate. This fact is particularly well illustrated in figure 17. The dorsal nucleus of the lateral lemniscus is probably better in the sheep than in the other ungulates studied in this series.

MIDLINE NUCLEAR GROUPS

Linear nucleus

The linear gray shows the usual divisions into rostral, intermediate or central and caudal portions. Of these, the caudal is the best developed and the intermediate the least developed. The rostral linear group (figs. 9 and 10) appears at the diencephalic-mesencephalic boundary line and extends back to the caudal border of the commissure of Forel. It consists of gray strands in the midline, occasionally wholly median in position and sometimes suggesting bilateral representation. These cells are intermingled and, in part, replaced by nucleus medianus anterior, or the rostral Edinger-Westphal nucleus, and by the interstitial nucleus of the commissure of Forel. They are small, and, on the whole, inconspicuous. The intermediate or central portion of the linear nucleus (figs. 11 and 12), because of the

presence of the ansulate commissure and the tegmental decussations, all of which are large, has a very limited representation in the sheep, actually consisting of clusters of cells between the major commissure masses and occasional neurons caught among the decussating fibers. As the decussation of the superior cerebellar peduncle is reached, behind the tegmental crossings, the linear nucleus becomes more prominent. This caudal portion of the cell group (figs. 13 to 15) occupies the midline region from the lower border of the medial longitudinal fasciculus to the upper border of the inferior cerebellar decussation, passing over caudally without demarcation into the median raphé of the pons. It consists of rather closely arranged, fairly deeply stained neurons, which in some planes show a tendency toward a bilateral arrangement.

Interstitial nucleus of commissure of Forel

The interstitial nucleus of the commissure of Forel (figs. 9 and 10 K) consists of gray surrounding the crossing fibers and intermingled among the fascicles. This gray extends across the midline so that there is continuity of the interstitial gray of the two sides. Dorsally, it passes over into the rostral end of the linear nucleus and laterally it is continued out along the spreading fibers to substantia nigra, the nucleus of the basal optic root, and the red nucleus, and merges with the surrounding tegmental gray. In general, it follows the course of distribution of the crossing fibers constituting the commissural system. It consists of smaller, undifferentially stained neurons similar to those of the surrounding areas.

Interpeduncular nucleus

The interpeduncular nucleus (figs. 12 to 14) appears rostrally in planes caudal to the Edinger-Westphal nucleus and through the caudal pole of the red nucleus. It extends backward until it is replaced by pontine gray. The sheep, then, belongs to the group of mammals in which no differentiated interpeduncular nucleus is demonstrable at the rostral end of the mesencephalon. This nucleus consists of a rounded mass of smaller, more closely arranged neurons, which constitute its central nucleus, and bordering lateral strands of slightly larger, more deeply stained, less closely arranged cells. These lateral strands sometimes join above the central nucleus and at other times are broken up into distinct clusters. As the caudal end of the nucleus is approached, the lateral portion disappears and the central part remains as a triangularly-shaped mass of gray, which is ultimately replaced by the tegmental area of the pons.

BASAL MIDBRAIN GRAY

Substantia nigra

Substantia nigra (figs. 9 to 14) makes its appearance at the most caudal end of the diencephalon and continues until it is replaced by the pontine gray.

Pars compacta (figs. 9 to 14) is present throughout the extent of the nuclear mass, although it varies in development at different levels. Slightly behind its diencephalic pole, it extends lateralward (fig. 9) from the more medial position which it had previously held, to form a band of cells along the upper margin of the peduncle. This band soon becomes very irregular and forms swirls and half circles which are so intermingled with the adjacent tegmental gray as to make the outlines of the nucleus practically indistinguishable (figs. 10 to 12). As the caudal part of the medial geniculate nucleus is approached, this lateral portion of pars compacta passes over into a pars lateralis (figs. 10 and 11). Behind pars lateralis of substantia nigra, pars compacta becomes greatly reduced and, toward its caudal pole, is represented by a band of cells overlying the medial border of the peduncle (figs. 13 and 14).

Pars reticulata of substantia nigra (figs. 9 to 13) has approximately the same forward extent as has pars compacta, but disappears caudally, excepting for occasional cells, in planes through the caudal end of the red nucleus. Through superior collicular levels, it is relatively well developed (figs. 10 to 12), consisting of numerous rows of neurons intercalated among the fiber fascicles and passing over without demarcation into pars compacta. It tends to occupy chiefly the inner half of the peduncle.

Pars lateralis (figs. 10 and 11) is not large in the sheep. It appears in continuity with the lateral extension of pars compacta, in planes toward the caudal end of the medial geniculate nucleus (fig. 11), and extends dorsalward as this latter nucleus gradually disappears from the field. Its cells resemble those of pars compacta but are somewhat differently oriented because they obviously lie along the course of fiber fascicles.

In general, the cells of substantia nigra are distinctly smaller than those of the red nucleus and are slightly smaller than the oculomotor neurons. They are relatively deep staining and no pigmentation has been demonstrated in the material available.

Nucleus of basal optic root

The nucleus of the basal optic root (fig. 11) appears medial to the cerebral peduncle in planes through nucleus medianus anterior

or the rostral Edinger-Westphal nucleus. It can be followed caudalward to planes which cut the caudal Edinger-Westphal nucleus just in front of the chief oculomotor complex. It is very closely intermingled with the medial border of substantia nigra at this level, and no sharp line of demarcation can be drawn between them in the cell material. Its cells resemble those of substantia nigra but are oriented in the course of the basal optic root and can be followed dorsalward, from near the brain surface, along the ventral tegmental area to beyond the upper border of substantia nigra.

PART III. THE HORSE

THE PERIVENTRICULAR GROUPS

General areas of periventricular gray

The midbrain periventricular gray in the horse shows a division into the three portions—dorsal, lateral and ventral—which have been found throughout the midbrain series. The dorsal division (figs. 18 to 24), which extends from the caudal border of the posterior commissure to levels through the inferior colliculus, has two rather special characteristics in the horse. The first of these is its intimate relation rostrally with the differentiated ingrowing ependymal layer which constitutes the relatively highly developed subcommissural organ. The other peculiarity of the dorsal portion of the periventricular gray in the horse is the marked evidence of its bilateral origin. In this animal, the middorsal portion of the aqueduct extends toward the brain surface and the dorsal part of the periventricular gray is represented on either side of the midline, but without cellular fusion, for a very considerable part of its extent. In planes through the trochlear nucleus, the gray on the two sides fuses across the midline (figs. 22 and 23), forming cell bands interspersed with crossing commissural fibers. Since this pars dorsalis actually belongs with the optic tectum, it need not be discussed further here.

Pars lateralis (figs. 18 to 24) begins at the plane of the posterior commissure and extends to inferior collicular levels, where it becomes continuous with the central nucleus of the inferior colliculus. Rostrally, it shows a differentiation into a more medial portion consisting of neurons linearly arranged along the course of the tectal division of the dorsal longitudinal fasciculus of Schütze, or the diencephalic-mesencephalic periventricular system, a dorsolateral portion which is the central subcommissural part of the nucleus of the posterior commissure, and a ventrolateral portion (fig. 19, z) which corresponds to nucleus centralis lateralis of the rodent (see Gillilan, '43 a). These several subdivisions are found only at the front end of the area, all

of them disappearing in approximately the same plane, which is the caudal end of the nucleus of the posterior commissure.

The ventral part of the midbrain periventricular gray (figs. 18 to 23) shows in the horse, as in other mammals, the major differentiation of this general region. In addition to scattered cells, the following nuclear groups characteristic for this area in mammals have been recognized.

Nuclear groups associated with posterior commissure

The intracommissural portion of the nucleus of the posterior commissure (fig. 19) is relatively poorly developed in the horse, although the commissural system itself is unusually large and consists of very heavily medullated fibers. Its cells, which resemble those of pars magnocellularis are arranged in rows between the fibers. Laterally, the intracommissural and magnocellular portions of the nucleus merge.

The nuclear gray associated with the posterior commissure, (figs. 18 and 19) is large and relatively well organized in the horse, a fact in keeping with the marked development of this fiber system. It surrounds the laterally extending fibers of the system rostrally, caudally, medially and laterally. The medial cells, termed pars centralis subcommissuralis, actually represent a differentiation of pars lateralis of the periventricular gray. The rest of the nucleus lies within the tegmental areas of the mid-brain, at its greatest extent reaching almost half-way to the lateral surface. Its relation to the tegmentum is indicated not only by its position, but also by its cell type. Its constituent neurons are, for the most part, medium-sized, multipolar cells but intermingled with these, among the spreading fibers of the commissure, are occasional very large, deeply stained multipolar neurons comparable in appearance with those constituting nucleus mesencephalicus profundus and the magnocellular part of the red nucleus. These give to this lateral portion of the nucleus the designation of pars magnocellularis. It should be noted that there is an intimate relation of certain cells of the nucleus of the mesencephalic root of V to the innermost fascicles of the posterior commissure (see figs. 18 and 19). The nuclear gray related with the posterior commissure extends from the caudal end of the diencephalon, just rostral to its associated fiber systems, to planes through the caudal pole of the Edinger-Westphal complex.

Nucleus of Darkschewitsch

The magnocellular portion of the nucleus of the posterior commissure and the Darkschewitsch nucleus lie in the same transverse planes, but the former extends farther forward and farther caudalward

than does the latter. The Darkschewitsch nucleus (not illustrated) is situated in the central gray, dorsal to the medial longitudinal fasciculus and medial and slightly dorsal to the interstitial nucleus of this fasciculus. In the transverse series, it is approximately oval in outline in planes in which it is best developed, fading out as scattered cells rostrally and caudally. It consists of elongated multipolar neurons slightly smaller than those constituting the magnocellular part of the nucleus of the posterior commissure.

Eye-muscle nuclei

Oculomotor complex. The Edinger-Westphal complex, and more particularly its caudal portion, is very well developed in the horse. The rostral end of this nuclear mass, also termed nucleus medianus anterior, appears in sections passing through the nucleus of Darkschewitsch and the parvocellular portion of the red nucleus. It replaces the scattered gray which represents the poorly differentiated rostral part of the linear nucleus, with which its cells are actually intermingled, but is differentiable through the preganglionic character of its constituent neurons. It is an unpaired nuclear group situated in the midline, ventral to the medial longitudinal fasciculus and immediately rostral to the chief oculomotor complex. It is continuous dorsally and dorsocaudally with the caudal portion of the Edinger-Westphal nucleus at planes which pass through the rostral tip of the chief oculomotor nucleus.

The caudal part of the Edinger-Westphal complex (figs. 19 and 20) forms, with its fellow of the opposite side, a V-shaped mass which shows then marked indications of bilateral development, but is not completely paired. It has the characteristic preganglionic appearance and a relatively great extent, overriding the chief oculomotor nucleus and continuing medial to it for many sections. It does not terminate until about the caudal third of the oculomotor complex is reached.

The chief oculomotor gray does not lend itself to sharp differentiation into secondary nuclear masses in the horse. Rostrally, immediately behind the front end of the Edinger-Westphal complex, a ventromedial oculomotor nucleus appears internal to the medial longitudinal fasciculus (figs. 19 and 20). Slightly farther caudalward a cluster of similar efferent neurons, dorsal to the fasciculus but continuous with the ventromedial group, may be regarded as a poorly differentiated dorsolateral oculomotor nucleus (fig. 21). In planes behind the nucleus of Darkschewitsch, the chief oculomotor gray is less well organized, for cells of the type characterizing it not only border the fasciculus medially and dorsally, but extend down among its fascicles, occurring either as single neurons or in small clusters. Some of these

clusters even lie along the ventral and ventrolateral surfaces of the bundle. This condition persists for some distance. However, as the caudal end of the Edinger-Westphal complex is approached, the chief oculomotor nucleus appears to be represented largely by cells overlying the medial longitudinal fasciculus. Such cells may be considered as constituting another representative of a dorsolateral oculomotor nucleus. Behind the Edinger-Westphal complex, as the trochlear levels are approached, there is a second intermingling of neurons with the fascicles of the medial longitudinal fasciculus. Through such interstitial neurons, the dorsolateral oculomotor nucleus is directly continuous with the trochlear nucleus, which lies ventral to the medial longitudinal fasciculus. In these more rostral planes, in which the cells of the oculomotor complex are intermingled with the fibers of the medial longitudinal fasciculus, scattered neurons of the oculomotor type intermingled with smaller neurons occur in the midline, representing a very poorly developed fusion of the ventromedial oculomotor gray of the two sides (fig. 21). This probably corresponds to the paramedian oculomotor nucleus of Le Gros Clark ('26) or the central nucleus of Perlia (1889). Behind the level of such fusion in a median position, but dorsomedial to the rest of the oculomotor gray, is a small cluster of small and medium-sized cells which presumably constitutes a caudal central nucleus, such as was described by Tsuchida ('06). Le Gros Clark ('26) called attention to the fact that in *Tarsius* the cells of the caudal central nucleus resembled those of the Edinger-Westphal nucleus, though possibly a little larger, suggesting "a similar physiological significance." However, in *Galago*, this same observer found neurons in this region approximating those of the lateral (or dorsolateral) oculomotor nucleus.

Trochlear gray. The trochlear nucleus (fig. 22) lies in planes cutting the superior colliculus dorsally and the interpeduncular nucleus and the rostral end of the superior cerebellar decussation ventrally. In the series studied, the planes are not quite at right angles to the long axis of the brain. It has the unusual position previously described for it in the horse by Tsuchida ('06) and Vermeulen ('14), that is, it is ventral to the medial longitudinal fasciculus. As was stated previously, it is continuous with the dorsolateral portion of the oculomotor complex through cell bands intermingled with fascicles of the medial longitudinal fasciculus. The trochlear nucleus is large and fairly compact and, even in the cell preparations, root fibers can be traced dorsally around the ventricle to decussate in the anterior medullary velum. In the material studied, its neurons are typical multipolar efferent neurons, but appear slightly larger than those of the chief oculomotor complex. In the absence of

horizontal series, it is impossible to state positively that this variation may not be due to differences in cell orientation.

The main right trochlear nucleus extends for approximately 5 mm. and then disappears rather abruptly from the field. After an interval of about $1\frac{1}{2}$ mm., an accessory right trochlear nucleus (fig. 23) may be seen lying in the midst of the medial longitudinal fasciculus, dorsal, as well as caudal, to the position of the main trochlear mass. It consists of a rather clearly demarcated cluster of neurons which persists for a short distance. The series studied shows also an accessory trochlear nucleus on the left, of approximately comparable size and similar relations; due probably to the tilt of the series, the two accessory nuclei are not visible in the same sections.

Dorsal nucleus of raphé

Rostrally, the central portion of the dorsal nucleus of the raphé is a somewhat poorly delimited V-shaped mass of neurons (figs. 21 and 22). Throughout trochlear levels it becomes a larger, easily definable, conspicuously stained cell mass, Y-shaped in outline, occupying the midregion of the ventral portion of the periventricular gray. At such levels, the nucleus is continued laterally into relatively widespread, wing-shaped portions which may be called the lateral wings of the dorsal nucleus of the raphé (figs. 23 and 24). The nucleus retains this general character through rostral portions of the isthmus, but as the aqueduct begins to widen out into the fourth ventricle, the lateral wings disappear and the central part begins in its ventral portion, so that it soon assumes a V-shaped outline (fig. 25). Its caudal portion is represented only by two very short rows of neurons.

Laterodorsal tegmental nucleus

The laterodorsal tegmental nucleus belongs partly to the mesencephalon and partly to the pons. Its rostral pole appears in planes through the accessory trochlear nucleus, and its caudal pole is found at the level of entrance of the trigeminal nerve. Throughout its extent, there is a tendency for differentiation into a medial and a lateral portion, the latter being characterized by the presence of some pigment in the neurons, particularly caudally, and by a more intimate relation with the nucleus of the mesencephalic root of V. It is this lateral portion (figs. 25 and 26), and most particularly its caudal part, which is to be regarded especially as homologous with the nucleus of locus coeruleus (or substantia ferruginea) of primates.

At its rostral end (fig. 24), the laterodorsal tegmental nucleus appears in the ventral portion of the central gray immediately lateral

to the lateral wings of the dorsal nucleus of the raphé and not sharply separated from them. Its cells extend ventrolaterally beyond the confines of the periventricular gray into the tegmentum. Even at such levels, an occasional pigmented cell is found in the lateral part of the nuclear mass. With the appearance of the dorsal tegmental nucleus, the laterodorsal tegmental nucleus encircles it dorsally and externally, and, at about the same levels, increases on its lateral side. With the greater development of the dorsal tegmental nucleus in more caudal planes, the medial part of the laterodorsal tegmental nucleus becomes still further reduced and is represented only by scattered gray as the levels of the trigeminal nucleus are approached. The outer part of the laterodorsal tegmental nucleus shows an increase in pigment-containing cells throughout the level of the dorsal tegmental nucleus and tends to approach the cells of the nucleus of the mesencephalic root of V, the two masses being to some extent intermingled. Not all of the cells of this lateral portion are pigment-bearing and the relation to the nucleus of the mesencephalic root of V is not so intimate as in primates. However, this lateral portion, or at least its more caudal part, may be regarded as the forerunner of the nucleus of locus coeruleus of the primate brain. Both the cells having pigment and those which are pigment-free are multipolar in character and deeply staining. The larger neurons of the laterodorsal tegmental nucleus are smaller than those of the nucleus of the mesencephalic root of V. They are intermediate in size between the cells of the marginal nucleus of the superior cerebellar peduncle and the larger tegmental cells belonging to nucleus mesencephalicus profundus, with both of which gray masses they are somewhat intermingled.

Dorsal tegmental nucleus

The dorsal tegmental nucleus (figs. 25 and 26) begins at the level of the inferior colliculus caudal to the plane of the accessory trochlear nucleus and extends through the isthmus to near the rostral pole of the motor trigeminal nucleus. Rostrally and caudally the outlines of the nuclear mass are somewhat indistinct, but most of it is fairly well delimited from the surrounding gray through the smaller, less deeply staining character of its constituent neurons. Reconstructed sagittally, it is an elliptical mass of cells bounded dorsomedially, through much of its extent, by the dorsal nucleus of the raphé and bordered laterally and dorsolaterally throughout by the laterodorsal tegmental nucleus. It lies, then, within the ventral portion of the periventricular gray, dorsal to the medial longitudinal fasciculus. In general relations, it resembles closely the homologous gray of other mammals.

Nucleus of mesencephalic root of V

It is not the purpose of the present report to consider in detail the nuclear grouping or the finer cellular character of the neurons constituting the nucleus of the mesencephalic root of V, nor is it possible to contribute at this time to the knowledge of the function of these neurons. The work of Weinberg ('28), Sheinin ('30) and Castaldi ('26, etc.) have provided very considerable information with regard to the structure, relations and grouping of these neurons. These papers have also presented the pertinent literature and discussed from varying points of view the function of these cells. However, since the nucleus of the mesencephalic root of V has not been described for the horse and since such material is not readily available, there are certain general considerations which might well be presented. In the first place, the cells are extraordinarily numerous and exceedingly large in the horse, so large in fact that they are visible macroscopically in preparations stained with toluidin blue. They are found at practically all levels from the region of entrance of the motor root of the trigeminal to the mesencephalic-diencephalic boundary, some of them being intermingled with the fascicles of the posterior commissure (figs. 18 to 26). Many of them lie in the deep tectal gray just external to the periventricular region; others extend down along the borders of the periventricular gray into the tegmentum of the midbrain. Scattered cells of this type are found in the periventricular gray, in the inferior collicular gray (fig. 24), and among the fascicles of the intertectal and the posterior commissures (figs. 18 and 19). None of them to date has been seen in either the oculomotor or trochlear nuclei, as Weinberg ('28) found to be the case in man. Although they are scattered almost continuously over so wide an area, there are three regions in which they are particularly numerous. The most caudal of these is immediately rostral to the entrance of the trigeminal roots. At such planes, they are intimately related with the nucleus of locus coeruleus (figs. 25 and 26), the neurons of the two cell masses frequently intermingling. A second accumulation is found at upper isthmus levels near the region of decussation of the trochlear roots. Here the cells of the mesencephalic root of V lie in intimate relation with the crossing trochlear fibers (fig. 25). The third, most rostral group of cells of this nucleus is at superior collicular levels where the oculomotor fibers are arising from the chief oculomotor nucleus (fig. 21).

With very few exceptions, the cells of the nucleus of the mesencephalic root of V are large, egg-shaped, unipolar neurons, with fine Nissl granules and a round or oval nucleus situated near the middle of the cell body. They certainly resemble closely the cells constituting the semilunar ganglion.

MIDTEGMENTAL NUCLEAR GROUPS

Nuclear groups associated with medial longitudinal fasciculus

Various nuclei of the brain stem are associated with the medial longitudinal fasciculus, either as contributors of fascicles to it or as recipients of fibers from it, or both. Most of these nuclei have other functions which determine their general classification, but there are two cell groups which are so closely related to this fiber system that they are referred to as nuclei of the medial longitudinal fasciculus. These are the interstitial nucleus of the fasciculus and the annular nucleus.

The interstitial nucleus of the medial longitudinal fasciculus (fig. 18) is found in the horse at levels through the nucleus of Darkschewitsch, overlapping the latter nucleus rostrally and caudally for a short distance. It consists of somewhat scattered neurons overlying the medial longitudinal fasciculus and, to some slight extent, intermingled with its fascicles. This places it in the tegmental gray, lateral and slightly ventrolateral to the nucleus of Darkschewitsch. The cells of the interstitial nucleus are multipolar neurons of the same general type as those constituting the various portions of nucleus mesencephalicus profundus and the magnocellular part of the red nucleus. It is probable that they are phylogenetic derivatives of the same general tegmental gray.

The annular nucleus, as described by Castaldi ('26) for the guinea pig, consists of a wreath-like arrangement of neurons surrounding the medial longitudinal fasciculus and somewhat intermingled with its constituent fibers (figs. 23 and 24). At levels through the trochlear nucleus of the horse, neurons of the same general type and in close relation to the medial longitudinal fasciculus may be seen (fig. 23). However, these are in clusters and do not completely encircle the fasciculus. They disappear in planes through the dorsal tegmental nucleus. On the whole, then, the annular nucleus may be said to have representation in the caudal end of the mesencephalon and the isthmus region in the horse, but to be lacking, except as individual scattered neurons, at other levels. These cells are smaller than those of the interstitial nucleus and less deeply stained; presumably they, too, serve interstitial functions.

Red nucleus

Although the red nucleus in the horse shows parvocellular and magnocellular portions, the magnocellular part far overbalances in size, extent, and neuron number the parvocellular division.

The parvocellular portion of the red nucleus (figs. 18 to 20) appears at the caudal end of the diencephalon, directly medial to zona incerta

and in front of the mammillary body. Its rostral pole is very indistinct, fading out into the general gray of the subthalamus. Even at this plane, it is intermingled with scattered large cells, which appear to represent the rostral tip of the magnocellular portion. As the sections are traced rostrocaudalward, the outlines of the red nucleus become somewhat more distinct, although the nucleus is never so sharply delimited at frontal levels as is the case in some forms. Cells of the parvocellular type are present within the red nucleus to planes just behind the interstitial nucleus of the medial longitudinal fasciculus. Throughout its extent, then, the parvocellular part is intermingled with the magnocellular portion of the nucleus, but its pattern varies from level to level. Usually cells of this type are found along the dorsomedial border of the red nucleus in a position comparable to that occupied by the parvocellular portion in many other mammals. However, through the caudal end of the parvocellular portion, on the dorsolateral border of the red nucleus, a cluster of small neurons (fig. 19) intermingled with very tiny cells suggests the carnivore nucleus minimus. Similar clusters of small and tiny cells occur at some levels medial to the main mass of the red nucleus and at others ventral to it. The cells of the parvocellular part of the red nucleus are characteristically medium-sized, multipolar neurons with smaller, less deeply staining Nissl granules than those found in the magnocellular division. The very tiny cells are triangular to spindle-shaped and somewhat deeply staining.

The magnocellular portion of the red nucleus (figs. 18 to 20) in the horse occurs throughout the whole extent of the nuclear complex. Rostrally, as has been noted, it is intermingled with the parvocellular portion, but, in planes slightly behind the interstitial nucleus of the medial longitudinal fasciculus, it constitutes practically all of the red nucleus. Its cells are large, multipolar efferent neurons relatively numerous and the most conspicuously stained elements in the midbrain.

Rostrally, the red nucleus is almost circular in outline in the transverse series studied. As the planes of the oculomotor nucleus are reached, it is divided into a medial and a lateral portion by a large fiber bundle which cuts diagonally through it to reach the ventral surface of the tegmentum. As the parvocellular portion disappears, the nuclear outline decreases and the mass becomes oval. Beyond this point, the cell group gradually shifts toward the midline, so that it is crossed by oculomotor fibers. These fascicles penetrate even to its lateral border. It disappears slightly rostral to the caudal end of the oculomotor complex, in the plane of the sections studied. Its caudal pole is encapsulated by the decussated fibers of the superior cerebellar peduncle (fig. 21). For some sections before its disappearance, the red nucleus is represented only by scattered neurons.

Deep mesencephalic gray (nucleus mesencephalicus profundus)

The term nucleus mesencephalicus profundus is applied to neurons of the type of the magnocellular portion of the red nucleus which are scattered as individual elements or in smaller or larger clusters throughout the tegmental gray but are not included within the encapsulating fibers of the red nuclear complex. Nucleus mesencephalicus profundus shows some particularly interesting relationships in the horse. Far rostralward, it is represented by scattered neurons of the tegmental type situated in the gray dorsal and lateral to the red nucleus. Such neurons are rarely in clusters and are not numerous. In planes through the main portion of the oculomotor complex, except rarely, no neurons of this type appear. As the caudal end of the red nucleus is approached, scattered cells reappear behind the red nucleus. They represent a pars lateralis of nucleus mesencephalicus profundus (fig. 22). As the cells increase in number in sections through the superior cerebellar decussation, this pars lateralis is unusually well represented, its size and appearance almost suggesting a caudal red nucleus (figs. 23 and 24). As the fibers of the superior cerebellar peduncle are traced dorsolateralward, in levels through the caudal end of the decussation, the cells of pars lateralis blend with the marginal nucleus of the superior cerebellar peduncle (fig. 26). Behind the decussation the cells representative of nucleus mesencephalicus profundus again become very scanty and, through the isthmus, there is only an occasional neuron of this type. In the horse, more than in any other form thus far considered, there is a marked concentration of nucleus mesencephalicus profundus at inferior collicular levels which suggests a caudal division of the red nucleus.

Ventral tegmental area and nucleus of mammillary peduncle

The ventral tegmental area of Tsai (fig. 21) is very poorly developed in the horse. So far as it is present at all, it is made up of scattered neurons medial to substantia nigra. In planes rostral to the interpeduncular nucleus, most of this field is occupied by fiber fascicles. With the appearance of the latter nucleus, the ventral tegmental area serves chiefly as an interstitial nucleus of the mammillary peduncle (figs. 19 to 23), which is relatively large in the horse. At levels through the interpeduncular and the trochlear nuclei, this interstitial nucleus has a V-shape, one limb of the V overlying substantia nigra and the other extending more directly dorsalward. Otherwise it is an elongated cluster of neurons in close relationship to the peduncle. The constituent cells are medium-sized, deep staining and multipolar of varying outline, the shapes depending somewhat on the orientation of the cells with reference to the fiber fascicles.

Nucleus medialis profundus

Nucleus medialis profundus is conspicuous in the horse. It is found at isthmus levels and in the caudal end of the mesencephalon, in a position ventral and, more caudally, lateral to the medial longitudinal fasciculus. Its rostral pole appears behind the trochlear nucleus in planes through the midportion of the dorsal tegmental nucleus. Rostrally, it consists of a single compact mass of neurons beneath the medial longitudinal fasciculus. This relationship is maintained until the lower end of the nuclear mass is approached, then the cells spread lateralward and two clusters of neurons are found, one cluster lateral and the other slightly ventrolateral to the medial longitudinal fasciculus (see fig. 25). These persist for a few sections and then disappear from the field. The cells constituting nucleus medialis profundus are fairly large, deeply staining, multipolar neurons with cell bodies which appear polygonal in the transverse series. They have round to oval nuclei, which are excentric in position, and coarse, densely massed, deeply staining Nissl granules.

Marginal nucleus of superior cerebellar peduncle

This cell mass extends from the place of entrance of the superior cerebellar peduncle into the isthmus gray, to the caudal lateral part of nucleus mesencephalicus profundus which overlies the lateral border of the superior cerebellar decussation at inferior collicular levels. It passes over, without demarcation, into this latter gray mass. The marginal nucleus is relatively well developed in the horse (figs. 25 and 26), surrounding the peduncle fibers on both sides in their forward course and forming also an interstitial nucleus for their passage. Medially, it grades over into the laterodorsal tegmental nucleus and toward the cuneiform area. This nucleus is composed of neurons similar to those constituting nucleus mesencephalicus profundus pars lateralis and functionally is probably of the same general character. The exaggeration of the caudal lateral part of nucleus mesencephalicus profundus is in line with the marked development of the marginal nucleus.

Cuneiform area

The term cuneiform area has been applied by Castaldi ('23) and others to a small region of neurons and fibers of passage situated ventral to the inferior colliculus, lateral to the periventricular gray, and medial and dorsomedial to the dorsal nucleus of the lateral lemniscus and its accompanying fiber fascicles (fig. 24). It appears to be a region of interrelation between tectal fibers and collaterals of the lateral lemniscus. Its neurons are small and non-differentially stained. In the horse, they are fairly evenly distributed among the fibers of passage. In ungulates, this region is not well developed.

Certain pretectal and subtectal components of tegmentum

Pretectal nucleus. The term pretectal has been applied to various areas at the caudodorsal portion of the diencephalon and the rostral end of the midbrain. In the present account, we are using the term pretectal nucleus for the mesencephalic gray which underlies the rostral end of the superior collicular eminence, rostral and then lateral to the tectum proper (figs. 19 and 20). This region is essentially mesencephalic. It corresponds to the pretectal area of Rioch ('31), Ingram, Hannet and Ranson ('32), Barris, Ingram and Ranson ('35), Papez ('32) and Magoun and Ranson ('35). It is the pretectum illustrated in the Ariëns Kappers, Huber and Crosby ('36) text, where the various terminologies are also discussed. This nucleus in the horse begins in planes through the pineal recess just lateral to the pineal stalk. Almost immediately, it lies beneath the eminence which is designated the superior colliculus or anterior quadrigeminal body in gross preparations of the brain. It rapidly becomes an ovoid mass of cells, which, with the appearance of the tectal gray, shifts to the lateral part of the collicular eminence. In this region, it lies in relatively close approximation to stratum griseum mediale or intermediale of the optic tectum. Toward its caudal pole, it narrows down and is represented by a smaller oval mass which probably corresponds to the caudal part of the pretectal nucleus as described by Bodian ('39). Ultimately it fades out into stratum griseum intermediale without any sharp line of demarcation between the two areas.

Its neurons are small to medium-size and resemble similar cells found within the tectal layer. Consequently, it is difficult to distinguish the pretectal nucleus from the tectal gray as the contour of the nucleus is lost.

Pretectal area. A poorly defined mass of gray overriding the posterior commissure and becoming continuous with the deep portions of the optic tectum constitutes a pretectal area or area pretectalis of Rose.

Nucleus "X." This nucleus (figs. 20 to 22) is a very prominent mass of gray found at the lateral border of stratum griseum profundum or centrale of the optic tectum but within the tegmentum. It lies in the pathway of both afferent and efferent tracts to the optic tectum, being bounded laterally by entering bundles and ventromedially by outgoing paths. It appears rostrally in planes immediately caudal to the nucleus of the posterior commissure, but farther lateralward in the field than that nuclear group, and ventral to the pretectal nucleus (see fig. 20, X). Caudalward it disappears by becoming incorporated within stratum griseum profundum of the

optic tectum, at planes through the rostral tip of the trochlear nucleus. It consists of large, deeply stained multipolar neurons intermingled with smaller multipolar cells. At some levels the large-celled elements predominate and at others the small cells form a conspicuous part of the mass. In transverse sections the outline of the nucleus is distinctly circular until it begins to blend with the deep layer of the optic tectum. This nuclear condensation belongs in general to the sub- and pretectal masses of gray which are intermediate between the optic tectum and the underlying tegmentum and which find representation also in the pretectal nucleus, the nucleus of the posterior commissure, and certain nuclei of the lateral lemniscus. It is probably in general homologous with the nucleus interstitialis tegmenti identified in the opossum by Tsai ('25) and Woodburne ('43).

Nuclear gray associated with the lateral lemniscus. Along the course of the lateral lemniscus from the superior olivary levels to the medial geniculate, there are considerable masses of gray which belong to the general category of nuclei of the lateral lemniscus. Many of these are more or less continuous with each other through scattered neurons, but the following major groups have been recognized: the dorsal nuclear group; the caudal ventral nuclear group, which has a ventromedial, a caudodorsal and a rostradorsal portion; and a rostral ventral group.

The dorsal nucleus of the lateral lemniscus appears at the most caudal levels and is similar to that found in the other ungulates and rodents. The cells are small, intermingled with occasional larger neurons, and they appear just dorsolateral to the marginal nucleus of the superior cerebellar peduncle (fig. 26).

The caudal ventral nuclear group is represented in the horse by the ventromedial (intrafascicular), the caudodorsal and the rostradorsal portion, no trace of a lateral part being present. The intrafascicular portion (figs. 25 and 26) consists of deeply staining multipolar neurons extending from the superior olivary level forward along the ascending fascicles of the lateral lemniscus to the upper isthmus region. It serves largely as an interstitial nucleus, the cells lying in small clusters along the medial border of the bundle and among the fiber fascicles. It is well developed in the horse.

The dorsal extension of the nucleus of the lateral lemniscus finds its chief representation in its caudodorsal portion. This part of the nucleus appears in the isthmus and extends forward to merge with the inferior collicular gray, but it is not so well developed as in some mammals. In front of the main distribution of the lateral lemniscus to the inferior colliculus, as the bundle proceeds forward toward the diencephalon, but still at lower midbrain levels, narrow bands of cells

and scattered neurons accompany it for a considerable distance as a rostral extension of the dorsal part. These lie immediately at the base of the inferior colliculus, near the lateral surface of the midbrain, and have been termed the rostrrodorsal division (fig. 25).

The rostral ventral nucleus of the lateral lemniscus (figs. 21, 22 to 24) is a small mass of gray along the course of the lateral lemniscus from planes through the accessory trochlear nucleus to medial geniculate levels where it becomes continuous with this diencephalic gray. Throughout its extent, the rostral ventral nucleus lies near the mid-lateral surface of the mesencephalon, intermingled with the fibers of the accompanying fascicles.

The cells of the caudal ventral nucleus are medium-sized relatively deeply stained, and consequently somewhat conspicuous multipolar neurons. Those constituting the rostral ventral nucleus are slightly smaller, somewhat less deeply stained, and correspondingly less conspicuous. The neurons forming the caudo-dorsal portion of the caudal ventral nucleus are still smaller, on the whole, than those of the more ventral group, although they show an intermingling of small and medium-sized neurons at some levels. They resemble to a considerable degree the cells forming the capsule around the chief nucleus of the inferior colliculus. Their relations suggest that they bear somewhat the same relation to the inferior colliculus that the pretectal area does to the optic tectum. The rostro-dorsal portion of the caudal ventral nucleus shows a similar intermingling of smaller and slightly larger, more deeply stained neurons, but with possibly a greater preponderance of the larger cells than is found in the caudo-dorsal portion of this nuclear complex.

MIDLINE NUCLEAR GROUPS

Linear nuclear gray

The linear nuclear group shows the three subdivisions — rostral, intermediate and caudal — which are characteristic for it in mammals in general. Of these three portions, the caudal is the best developed. The rostral linear nucleus (fig. 18) is found at the diencephalic-mesencephalic boundary, in front of the Edinger-Westphal complex and rostral and then dorsal to the commissure of Forel. It is represented by a median group of scattered, medium-sized neurons, somewhat linearly arranged, and displaced gradually by the rostral portion of the Edinger-Westphal complex. A few of the neurons of this type continue caudalward above the commissure of Forel and behind that commissure pass imperceptibly into the intermediate or central linear group. This latter division (figs. 19 and 20) extends from a position between the two medial longitudinal fasciculi to the ventral tegmental area. In its

dorsal portion, the cells tend to be arranged in rows, but its ventral part is broken up at many levels by the crossing fascicles of the ansulate commissure. These scattered representatives of the linear group found among the commissural bundle may be regarded as an interstitial nucleus of this commissure. With the appearance of the ventral tegmental and dorsal tegmental decussations, the linear gray is still further reduced, but behind the crossing of these fiber systems this gray increases again and, through the level of decussation of the cerebellar peduncle, it is fairly considerable in amount. At such levels it overlies the decussation and is represented as clusters of gray among the crossing bundles. This portion of the linear gray belongs to the caudal division of the complex (fig. 23). Behind the level of the superior cerebellar peduncle the linear nucleus passes over without demarcation into the median raphé of the pons.

Interstitial nucleus of commissure of Forel

The interstitial nucleus of the commissure of Forel is very poorly developed in the horse. It is represented by scattered gray immediately rostral to the crossing of the fibers, and then by neurons extending outward toward the red nucleus, substantia nigra and the nucleus of the basal optic root along the course of the laterally running fascicles.

Gray associated with ansulate commissure and superior cerebellar decussation

In planes through the oculomotor complex and the rostral tip of the interpeduncular nucleus, a group of cells of the undifferentiated gray of the region is found mingled with and partly overlying the tectobulbar and tecto-spinal fibers which cross in the ansulate commissure. This interstitial nucleus of the ansulate commissure (fig. 19) is primarily a midline structure associated with the decussating fibers.

Farther caudalward another midline group of cells occurs in the course of the decussation of the superior cerebellar peduncle (figs. 21 to 24). This interstitial nucleus is first noticeable at levels through the capsule of the red nucleus (see fig. 21), but it is most marked caudally (figs. 23 and 24). The larger number of neurons found in this interstitial nucleus, together with the conspicuous nucleus mesencephalicus profundus and the marginal nucleus of the superior cerebellar peduncle, is a fact worth noting, and they emphasize the functional possibilities of the brachium conjunctivum.

Interpeduncular nucleus

The interpeduncular nucleus (figs. 21 to 24) makes its appearance relatively far caudalward in the horse, its rostral pole appearing through the caudal end of the oculomotor complex, unless one is to allocate to this nuclear gray, scattered clusters of cells situated at various levels farther forward but in no instance forming a continuous mass of neurons. The nucleus disappears as the mesencephalon passes over into pontine gray. In planes in which it is well developed, it forms a somewhat rounded mass overlying the interpeduncular fossa and, at certain levels, differentiable into a central core of very fine oval neurons and lateral portions of slightly larger, more scattered, somewhat deeper staining, multipolar cells. Both portions of the nucleus are interrupted by fiber fascicles.

BASAL MIDBRAIN GRAY

Substantia nigra

Substantia nigra extends from the caudal end of the diencephalon through the midbrain levels to planes at which it is replaced by pontine gray. It is secondarily divisible into pars compacta, pars reticulata and pars lateralis. At the diencephalic-mesencephalic boundary, substantia nigra is represented by a band of neurons overlying the peduncle fibers and by scattered cells of similar type interspersed among these fibers almost to the surface of the midbrain. The scattered neurons among the peduncle fibers obviously represent pars reticulata (figs. 19 to 21). Such a pars reticulata occurs throughout the midbrain but is less well developed and less near the surface caudally than rostrally. The band of cells overlying the peduncle is secondarily divisible into an internal and an external portion, frontally, and shows this division through planes including the trochlear nucleus, although the two parts are connected by cell strands. The internal portion is represented throughout the whole midbrain region and its relations to the nucleus of the basal optic root and to the peduncle definitely place it as belonging to pars compacta (figs. 19 to 24). The external portion is immediately adjacent to the medial side of the cortico-tectal system, which is easily recognizable because of its size and the configuration of the peduncle even in the cell material. With the appearance of pars lateralis of substantia nigra (fig. 21) lateral to the cortico-tectal tract and extending dorsalward behind the medial geniculate nucleus, this external portion comes into cell continuity with it, thus being intermediate in position and in relations between pars compacta and pars lateralis of substantia nigra as found in other mammals. Only a study of fiber connections can determine to which portion of substantia nigra the external portion should be allocated.

Lateral to the cortico-tectal tract, in planes immediately rostral to the caudal pole of the medial geniculate nucleus, a group of cells makes its appearance. Caudalward, it can be followed along the course of nigro-tectal and tecto-nigral connections. In such planes it lies immediately behind the medial geniculate nucleus, in the tegmental region of the midbrain. It constitutes a pars lateralis of substantia nigra (fig. 21).

All portions of substantia nigra are composed of multipolar, relatively deeply stained neurons, which in size and form are very similar throughout. They are considerably smaller than the large cells in the midbrain tegmentum, including those of the red nucleus. In occasional cells in pars lateralis and in the external portion of pars compacta, pigment may be found. Usually this occupies only a part of the cell, the remainder still showing Nissl granules and the other structures typical of the neurons.

Nucleus of basal optic root

In approximately the plane of the rostral end of the Edinger-Westphal nucleus, the nucleus of the basal optic root makes its appearance. It lies medial to the cerebral peduncle and ventromedial to substantia nigra, from which mass of gray it is not sharply differentiable. It has no great rostrocaudal extent, disappearing from the field in the series studied in front of the chief oculomotor complex. It consists of rather deeply staining, triangularly-shaped neurons lying along the course of the fibers of the basal optic root and continuing dorsolaterally over the medial border of substantia nigra. Its relations are similar to those in carnivores.

MODIFICATIONS OF THE VENTRICULAR EPENDYMA

Subcommissural organ

In the dorsal wall of the aqueduct, beneath the posterior commissure, there is a conspicuous modification of the ependyma which marks the position of the subcommissural organ (fig. 19). It consists of ingrowths of tube-like structures which are lined by two types of cells. One of these is a typical columnar cell as seen in cross section, with an oval nucleus near the base of the cell and basophilic staining granules. Some of the cells show traces of cilia, apparently with basal nodules. It has the general character of the chief cells described in many organs. The other is a round or oval cell with a smaller, more deeply stained, centrally-located nucleus and a cytoplasm which appears to be slightly acidophilic. The presence of these two types of cells, which may represent stages in the life history of a single

cell, together with the rich blood supply to the region, suggests a possible secretory function for this area. Studies are under way to determine whether it has a glandular character. Caudal to the level of the posterior commissure the ependyma still shows outgrowths along the dorsal walls of the ventricle throughout most of the mid-brain area. In the material available for study, which is not specifically stained for gland cells, the more caudal outgrowths appear to show less of the acidophilic staining element.

SUMMARY

It seems more valuable to compare the relations found in the tegmentum of the horse with those seen in the corresponding regions of the sheep and the pig. In this way some idea of the pattern common to ungulates may be obtained.

The nucleus of the posterior commissure is well developed in all ungulates, and best demarcated in the horse. The intra-commissural portion is well developed in the pig and crosses the midline. It is bilateral in the sheep and poorly developed in the horse. The nucleus of Darkschewitsch is not sharply delimited rostrally and caudally and less clearly differentiated in the pig than in other ungulates.

All the ungulates studied show a modification in the secondary subdivisions of the chief oculomotor complex, which in the sheep and the pig tends to show lateral and medial, rather than dorsolateral and ventromedial, portions. The trochlear nucleus is continuous with the ventromedial portion of the oculomotor nucleus in the sheep and with the dorsolateral part in the horse. Continuity between the two nuclei is established in the horse by scattered cells through the medial longitudinal fasciculus, the trochlear nucleus lying ventral to this bundle. In the sheep, pig and horse, nucleus medianus anterior, or the rostral Edinger-Westphal complex, is unpaired, although in every case hints of pairing are present. The caudal Edinger-Westphal is completely paired in the pig and V-shaped in the sheep and horse.

The dorsal nucleus of the raphé is well developed in adult ungulates and shows the typical parts. Although identifiable, the secondary subdivisions are less clear-cut in the fetal pig

material. The dorsal tegmental nucleus in these forms has relations characteristic for it in other mammals. It is less well defined in the pig material studied, but it is especially clear in the adult sheep. The laterodorsal tegmental nucleus is poorly defined in the fetal pig, with less extension into underlying tegmental gray, and there is no marked separation of it into medial and lateral portions. In the sheep, it is well developed and the cells of the lateral part are intermingled with those of the nucleus of the mesencephalic root of V. The laterodorsal tegmental nucleus of the horse resembles that of the sheep, but in its lateral portion there are cells containing pigment, so that this part might be designated the nucleus of locus coeruleus.

The midtegmental nuclear groups are more clearly delimited in the adult than in the fetal ungulate material, although not always larger. The interstitial nucleus of the medial longitudinal fasciculus is unusually well represented in the fetal pig and directly comparable to that of other mammals including the horse and the sheep. Traces of an annular nucleus are found in all three species, being best developed at trochlear levels.

The red nucleus is predominately magnocellular, this portion being present in all except the extreme rostral part of the nuclear complex. Large and small-celled parts are not clearly circumscribed, as there are various transitional types between the two extremes. In the horse, medially and ventrally situated clusters of tiny neurons suggest the nucleus minimus of carnivores. In general, in the fetal pig, the red nucleus is distinctly small compared with the total tegmental area. In adult ungulates, it occupies a very considerable portion of the tegmentum. The red nuclei of the two sides approach each other at the mid-line, and small clusters of scattered cells spread out into surrounding tegmental gray so that the boundaries of the nuclear masses are indefinite. Clusters of cells behind the caudal pole of the red nucleus at the level of the superior cerebellar decussation suggest a caudal red nucleus. These cell groups are formed by accumulations of

neurons which are continuous with the gray constituting the marginal nucleus of the superior cerebellar peduncle in the sheep. There is little representation of nucleus mesencephalicus profundus in the rostral part of the ungulate midbrain.

Attention is called to the mass of gray in the horse and the sheep representing the interstitial area described by Tsai ('25) in the opossum. This area appears to be a subtectal differentiation related to afferent and efferent tectal paths.

Nucleus medialis profundus is recognizable in all three ungulates studied, but is particularly interesting in the horse because of its separation on each side of the brain into two subdivisions, a lateral and a ventrolateral. The ventral tegmental area is well represented in the pig, possibly suggesting a fetal rather than an adult condition.

The pretectal area has been identified in its usual relations in the pig, the sheep and the horse. The nuclear groups described as nuclei of the lateral lemniscus in other mammals are relatively large in ungulates. The caudodorsal portion of the dorsal nucleus is well differentiated, forming an eminence on the brain wall in the isthmus region. This eminence is best developed in the pig and here, particularly, suggests the nucleus isthmi of lower forms. Pars lateralis of the caudal ventral nucleus of the lateral lemniscus is lacking in the horse and poorly represented in the other ungulates.

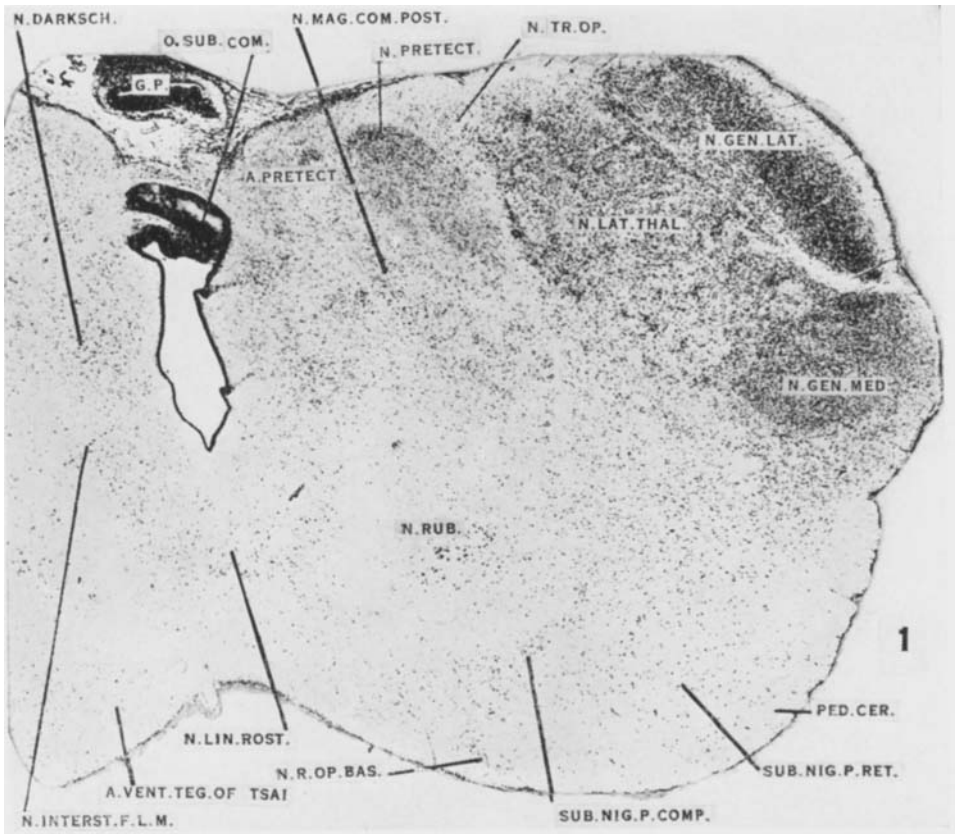
The linear nuclear group has the usual subdivision in the sheep and the horse. Its caudal portion is largest and the intermediate portion most poorly developed in these ungulates. In the pig, in the region of the intermediate portion and the rostral part of the caudal linear group, the gray has not taken on a linear arrangement, but remains in an undifferentiated condition serving as interstitial gray for the ansulate commissure and the decussation of the superior cerebellar peduncle.

The rostral end of the interpeduncle nucleus begins relatively far back in all ungulates, even in the fetal pig, usually appearing in planes through the caudal end of the oculomotor complex. It extends to the beginning of the pons. In all un-

gulates studied, it shows secondary differentiation into a central mass of smaller cells and a lateral portion composed of larger multipolar neurons. Pars reticulata of substantia nigra is present throughout most of the rostrocaudal extent of the cerebral peduncle, having an interstitial position with relation to the fibers. In adult ungulates the distribution of gray is fairly uniform, with some of the groups extending out to the periphery. Pars lateralis of substantia nigra is relatively large in the fetal pig material. It is closely related to the external portion of pars compacta in the sheep and the horse, and is less well developed in these ungulates. In the horse, some cells of pars lateralis and a few neurons in the related pars compacta contain pigment. Pars compacta of substantia nigra is more irregular in ungulates in general, particularly in the horse and the sheep, than in some other mammals and is somewhat smaller caudally. There is a separation of pars compacta into an external portion adjacent to the cortico-tectal system and an internal portion more intimately related to the nucleus of the basal optic root. The nucleus of the basal optic root is relatively clearly defined in the fetal pig material, but, although differentiable in other ungulates, tends to grade over without sharp demarcation into substantia nigra.

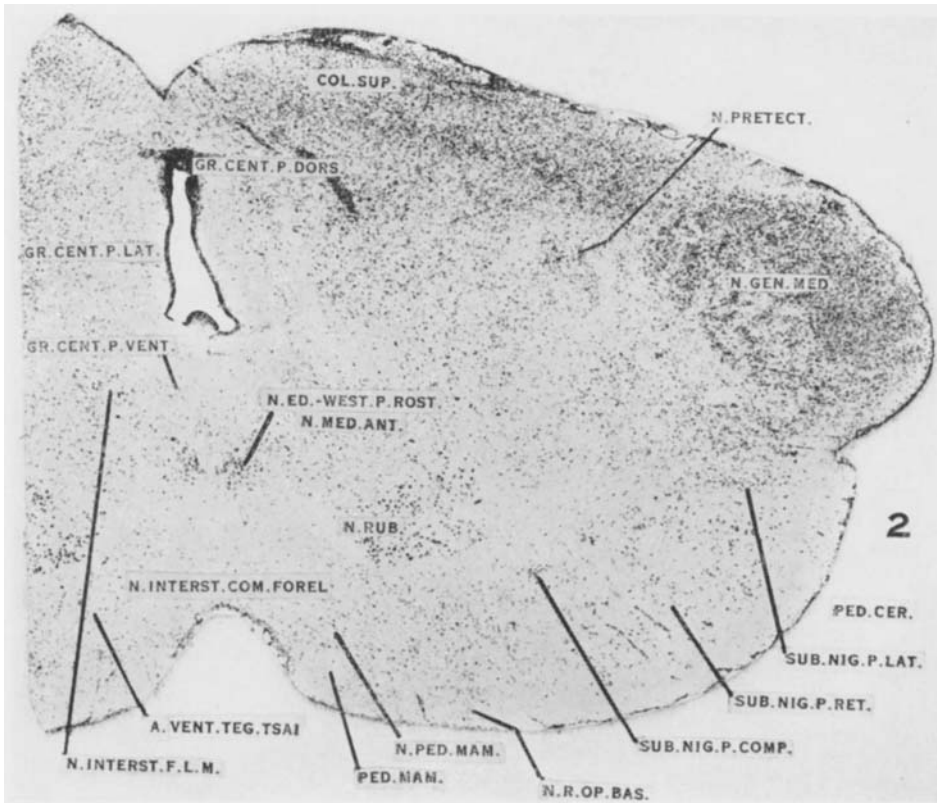
Figs. 1 to 8 Transverse sections of brain
from a 16 cm. fetal pig. Toluidin blue. $\times 20$.

PLATE 1



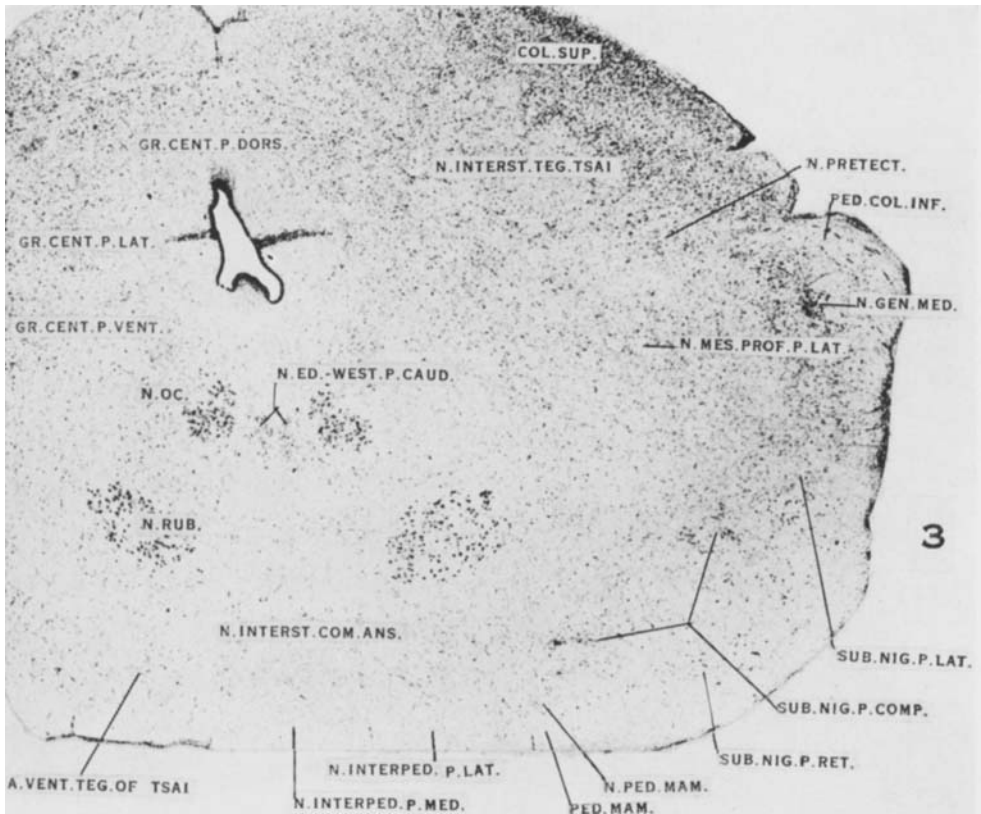
1 Through the extreme rostral mesencephalon, showing the pretectal groups dorsally and the red nucleus, substantia nigra and the nucleus of the basal optic root ventrally.

PLATE 2



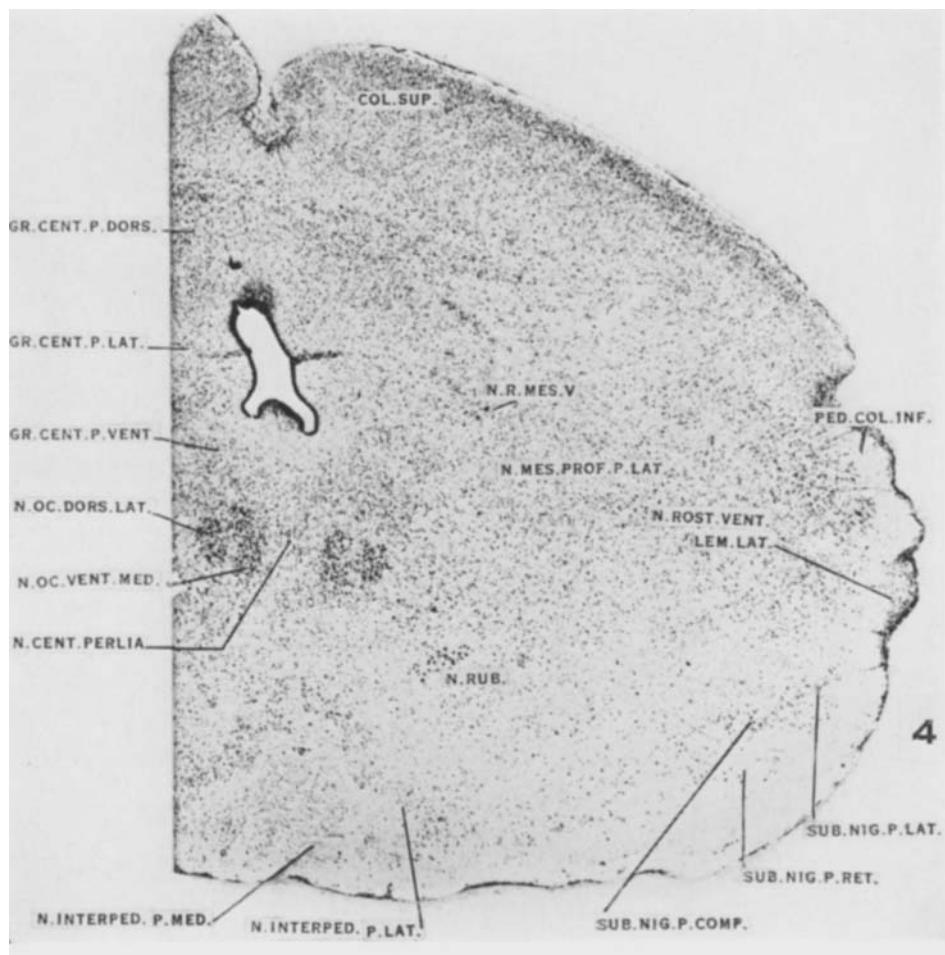
2 Fig. Through the rostral Edinger-Westphal nucleus.

PLATE 3



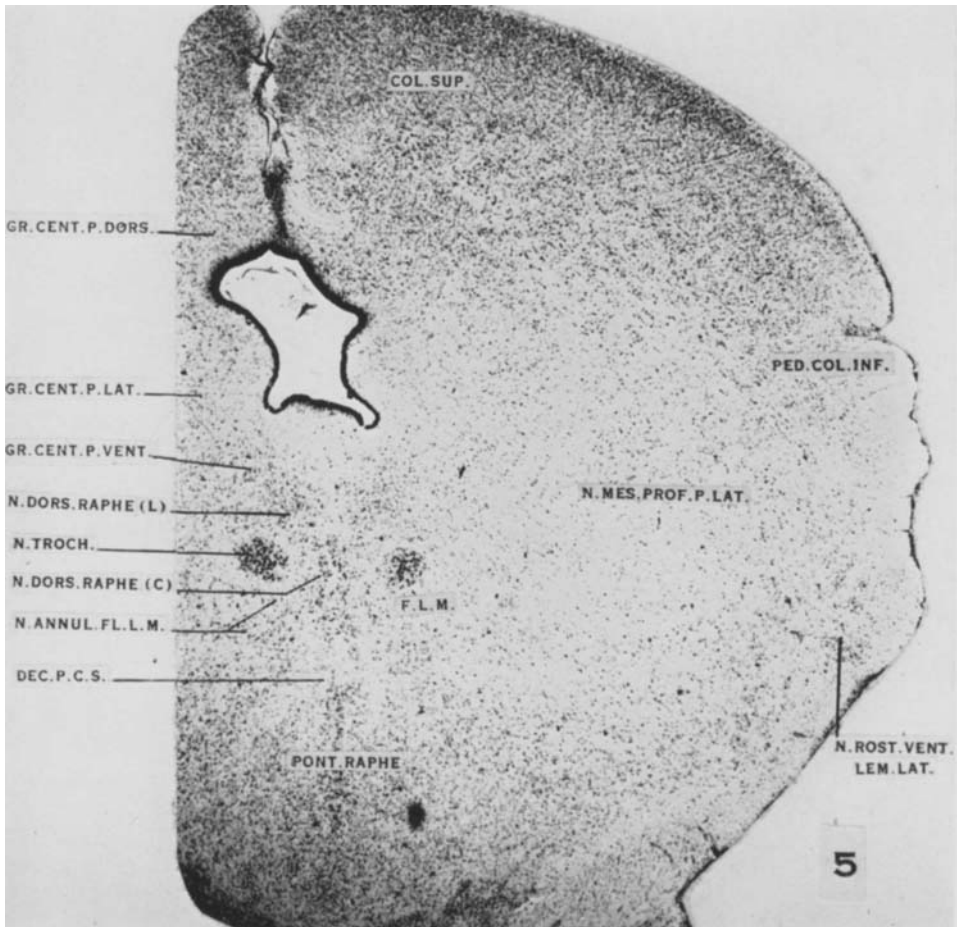
3 Fig. Through the caudal Edinger-Westphal and the oculomotor nuclei.

PLATE 4



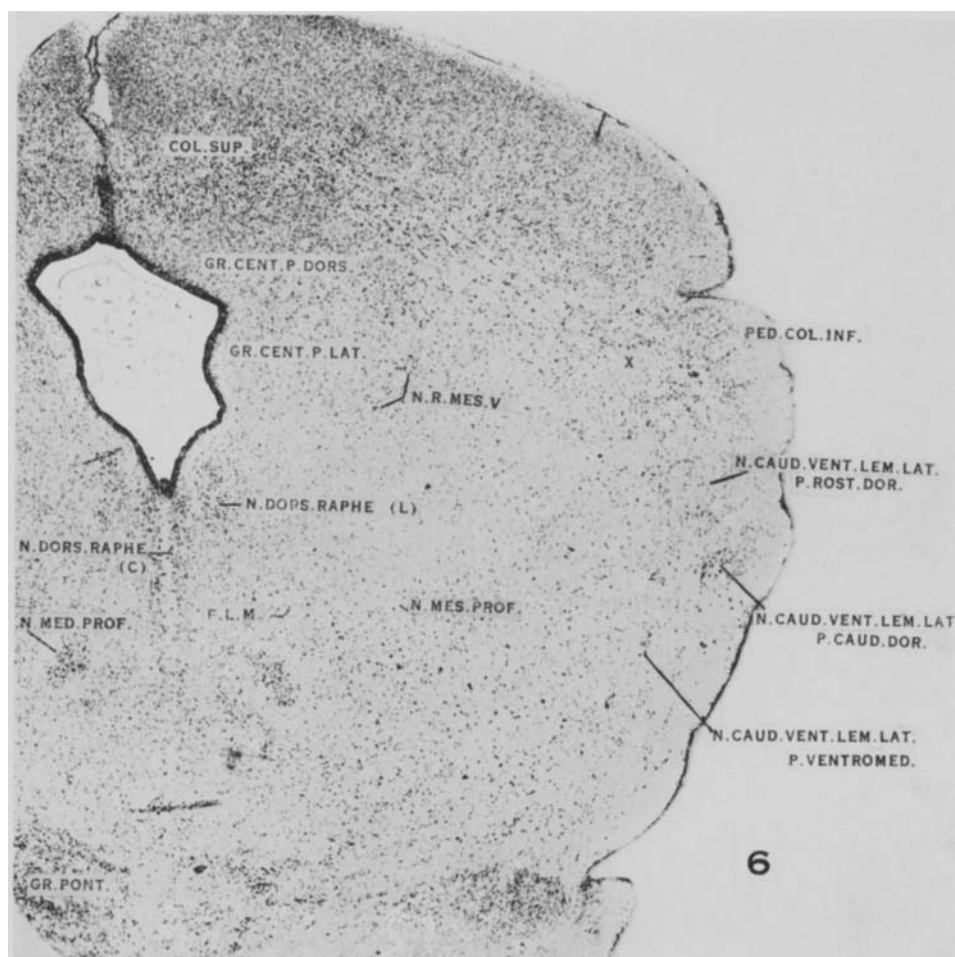
4 Fig. Through the oculomotor and interpeduncular nuclei.

PLATE 5



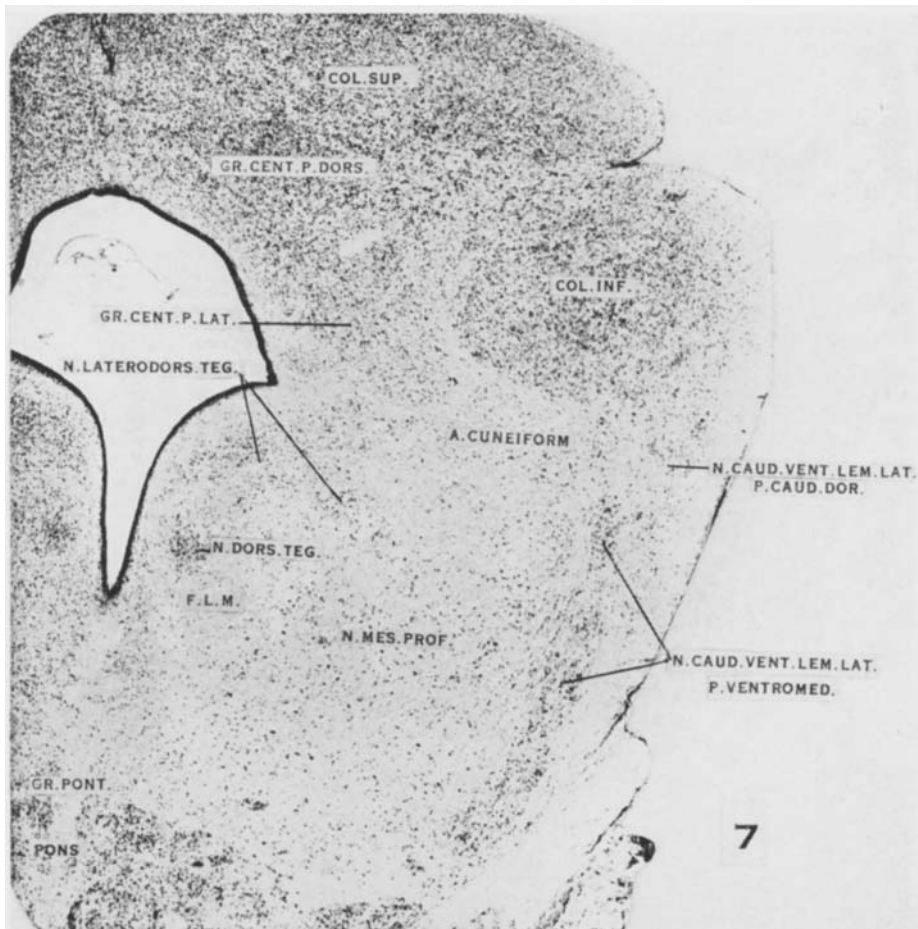
5 Fig. Through the trochlear nucleus and the dorsal nucleus of the raphé.

PLATE 6



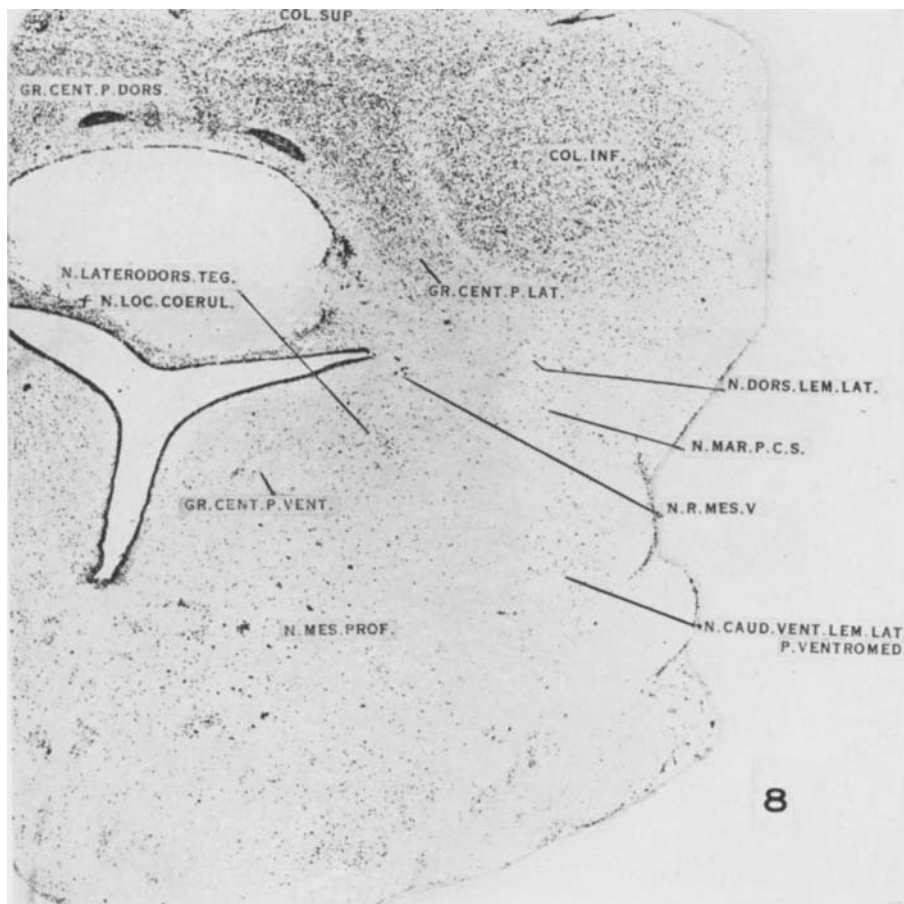
6 Fig. Through nucleus medialis profundus and the nuclei of the lateral lemniscus.

PLATE 7



7 Fig. Through the dorsal tegmental nucleus and the nuclei of the lateral lemniscus.

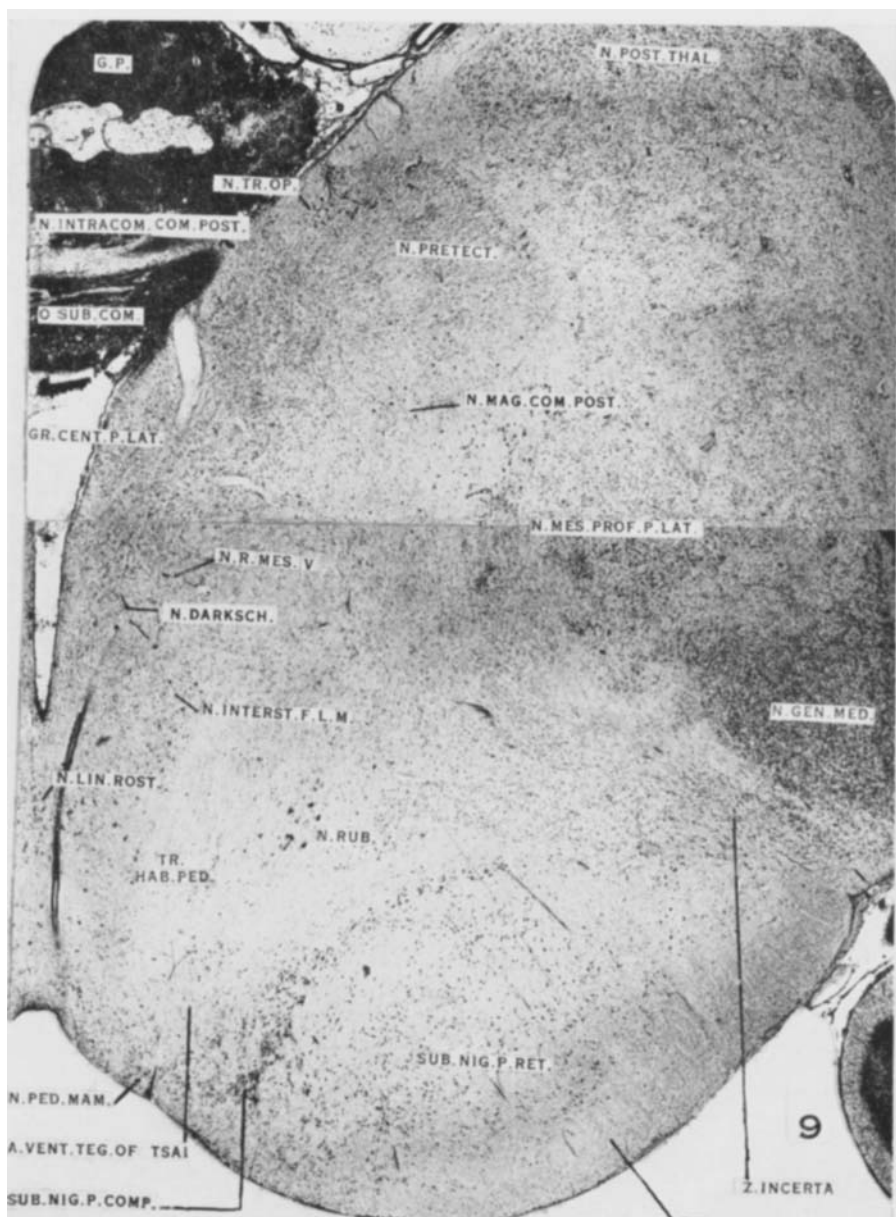
PLATE 8



8 Fig. Through the caudal portions of the nuclei of the lateral lemniscus.

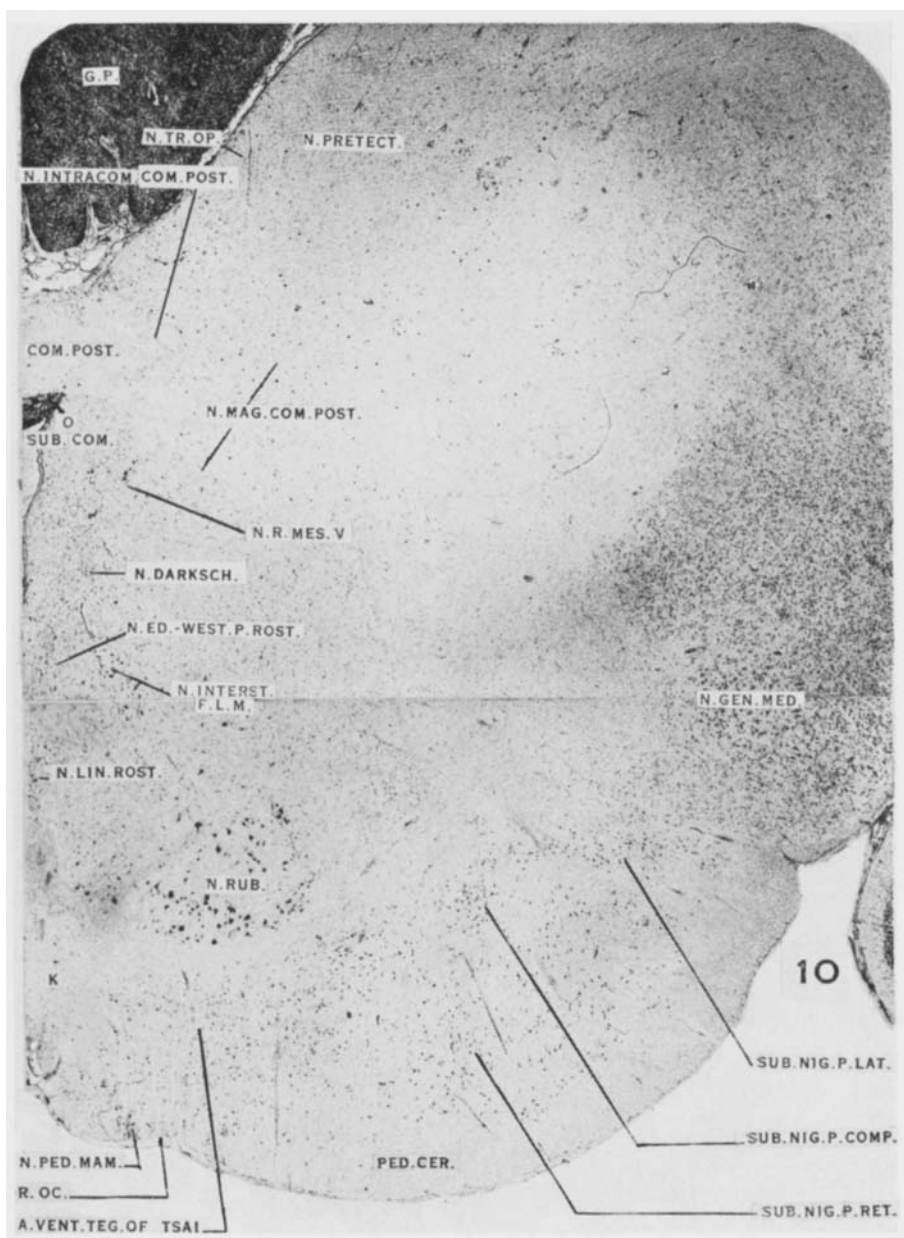
Figs. 9 to 17 Transverse sections of an adult sheep brain. Toluidin blue. $\times 10$.

PLATE 9



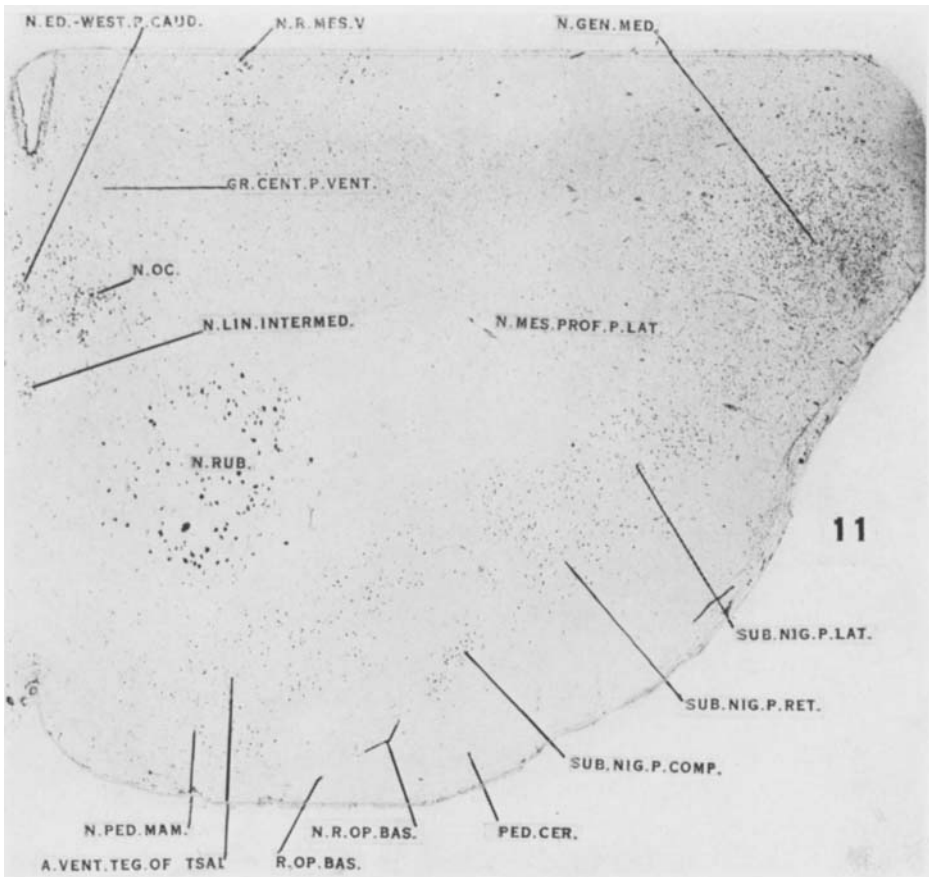
9 Sheep. Through the mesencephalo-diencephalic boundary, illustrating the pretectal nucleus and the subcommissural organ.

PLATE 10



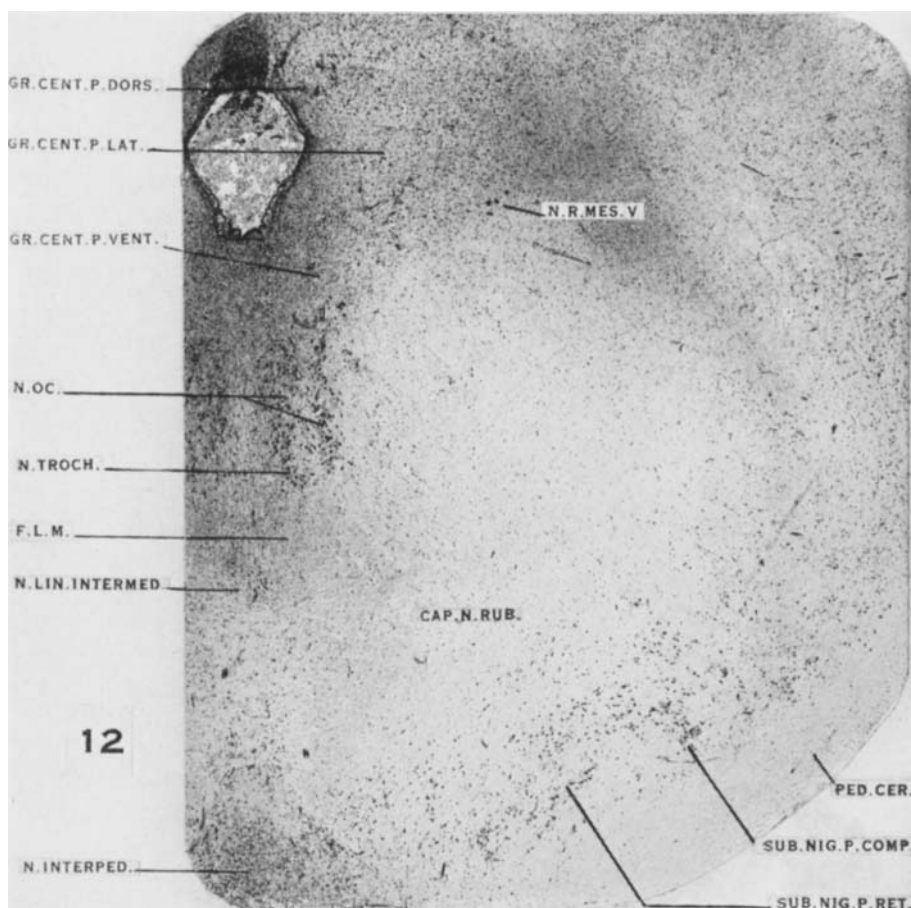
10 Sheep. Rostral mesencephalon showing the nuclei of the posterior commissure and the rostral Edinger-Westphal nucleus.

PLATE 11



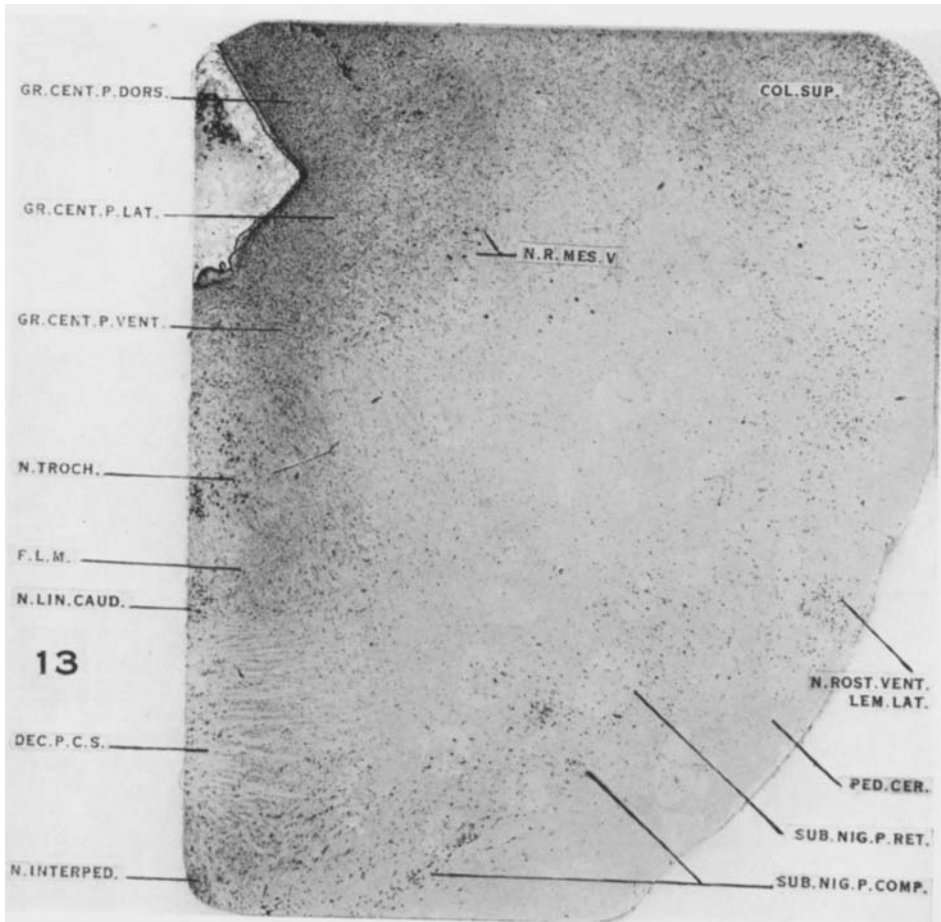
11 Sheep. Through the caudal Edinger-Westphal and oculomotor nuclei.

PLATE 12



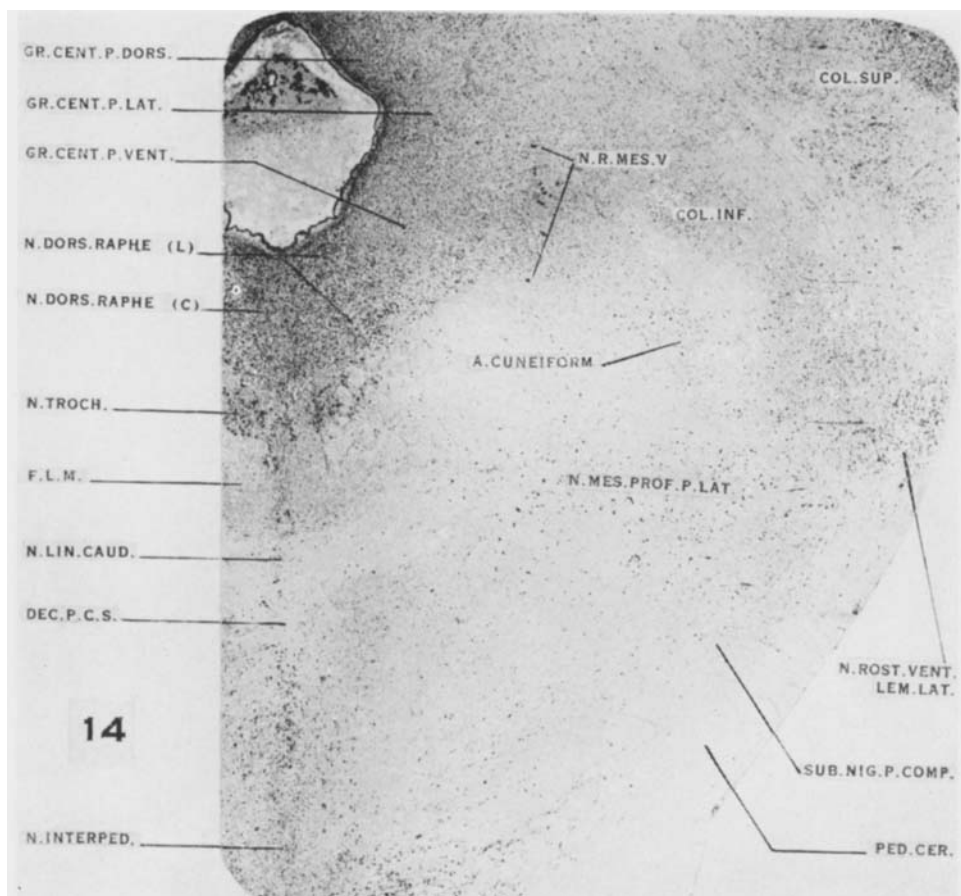
12 Sheep. This figure shows the continuity between the ventromedial division of the oculomotor nucleus and nucleus trochlearis.

PLATE 13



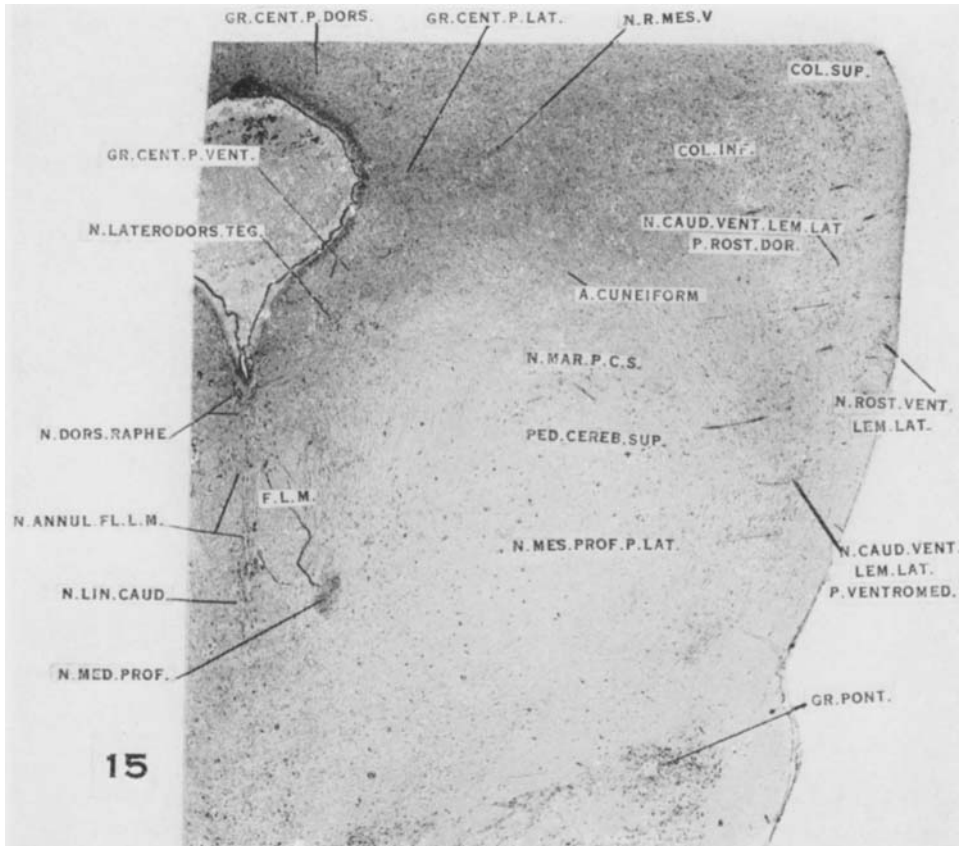
13 Sheep. Through the trochlear nucleus and the rostral ventral nucleus of the lateral lemniscus.

PLATE 14



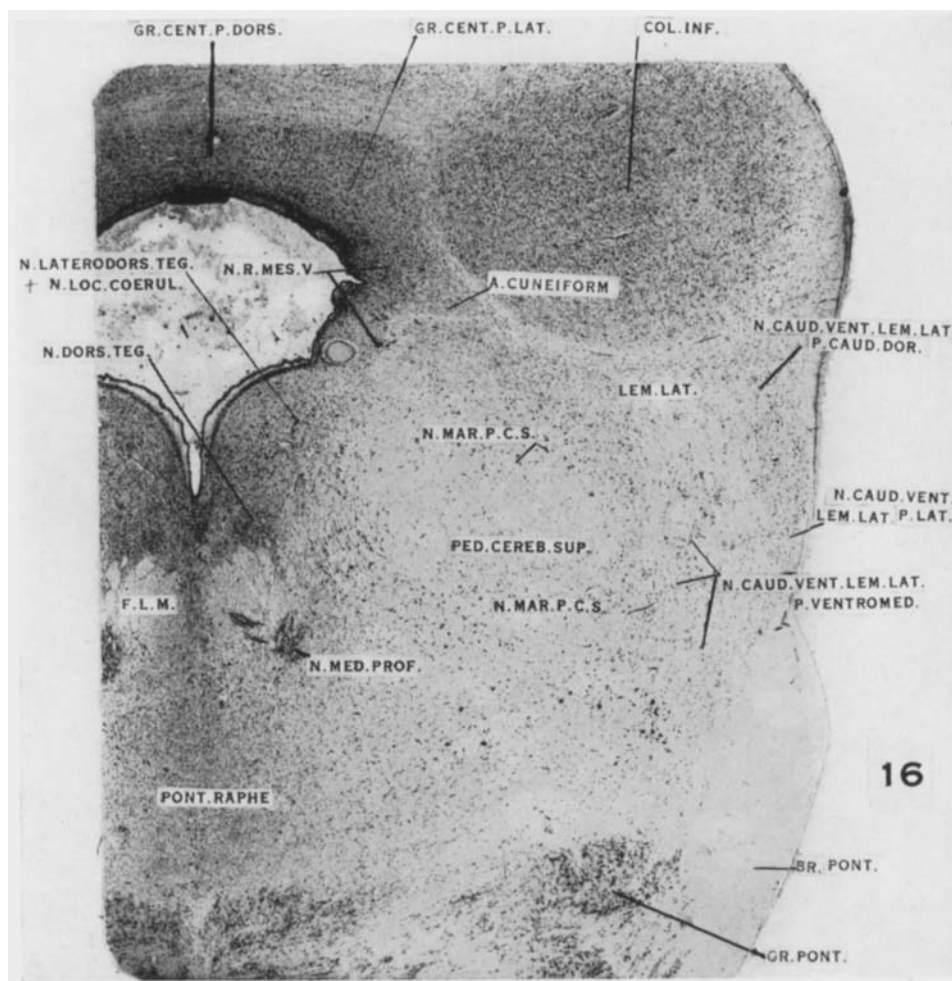
14 Sheep. Through the trochlear nucleus and the dorsal nucleus of the raphé.

PLATE 15



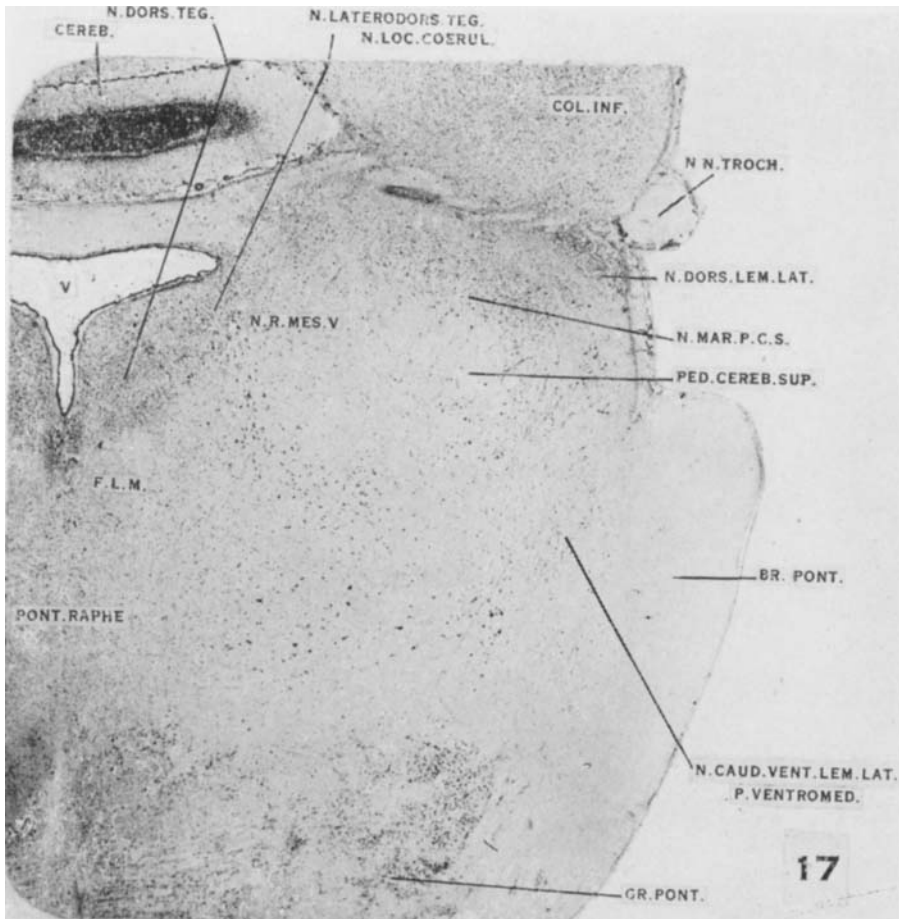
15 Sheep. Through nucleus medialis profundus and the nuclei of the lateral lemniscus.

PLATE 16



16 Sheep. Through the same nuclear groups as figure 15 but farther caudalward.

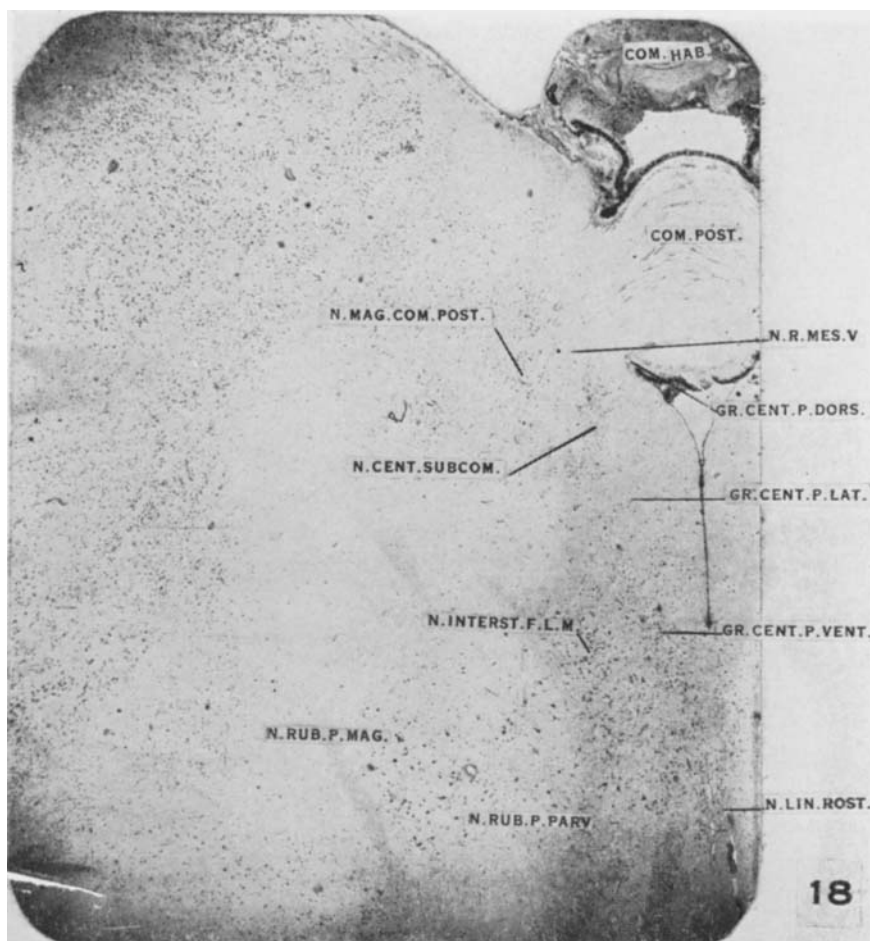
PLATE 17



17 Sheep. Through the roots of the trochlear nerve and the dorsal nucleus of the lateral lemniscus.

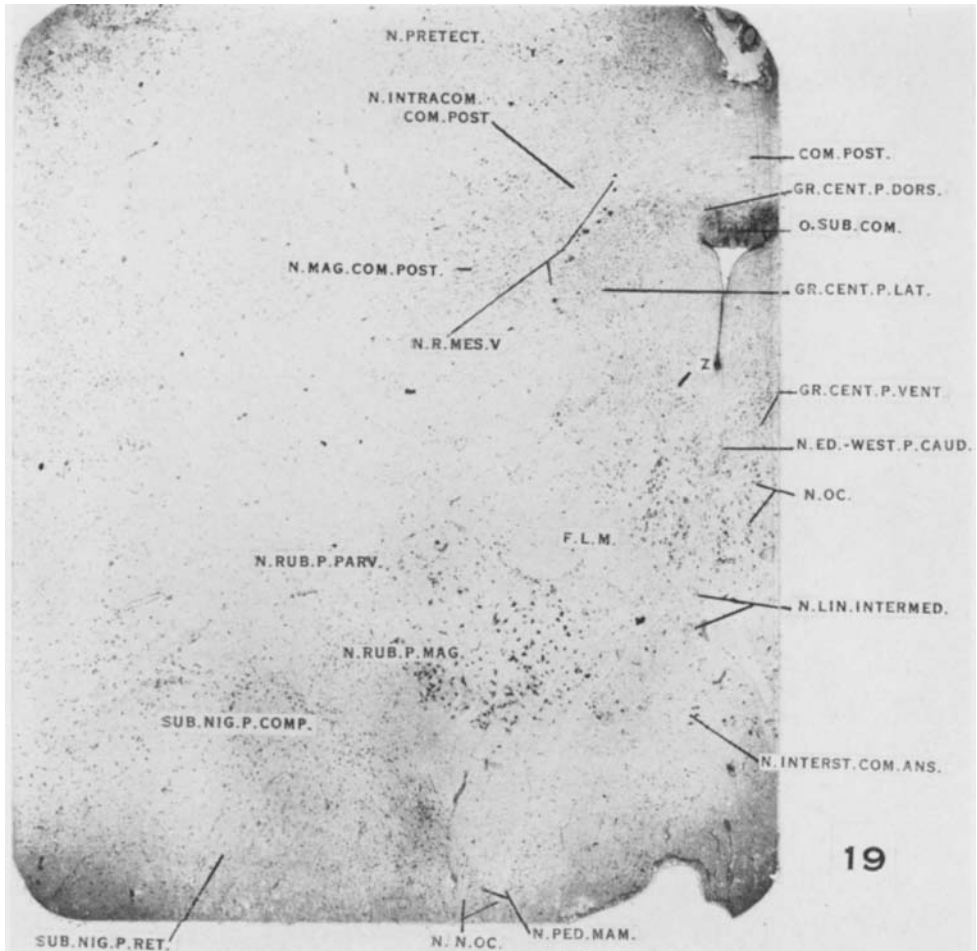
Figs. 18 to 26 Transverse sections of the adult
horse brain. Toluidin blue. $\times 7.5$.

PLATE 18



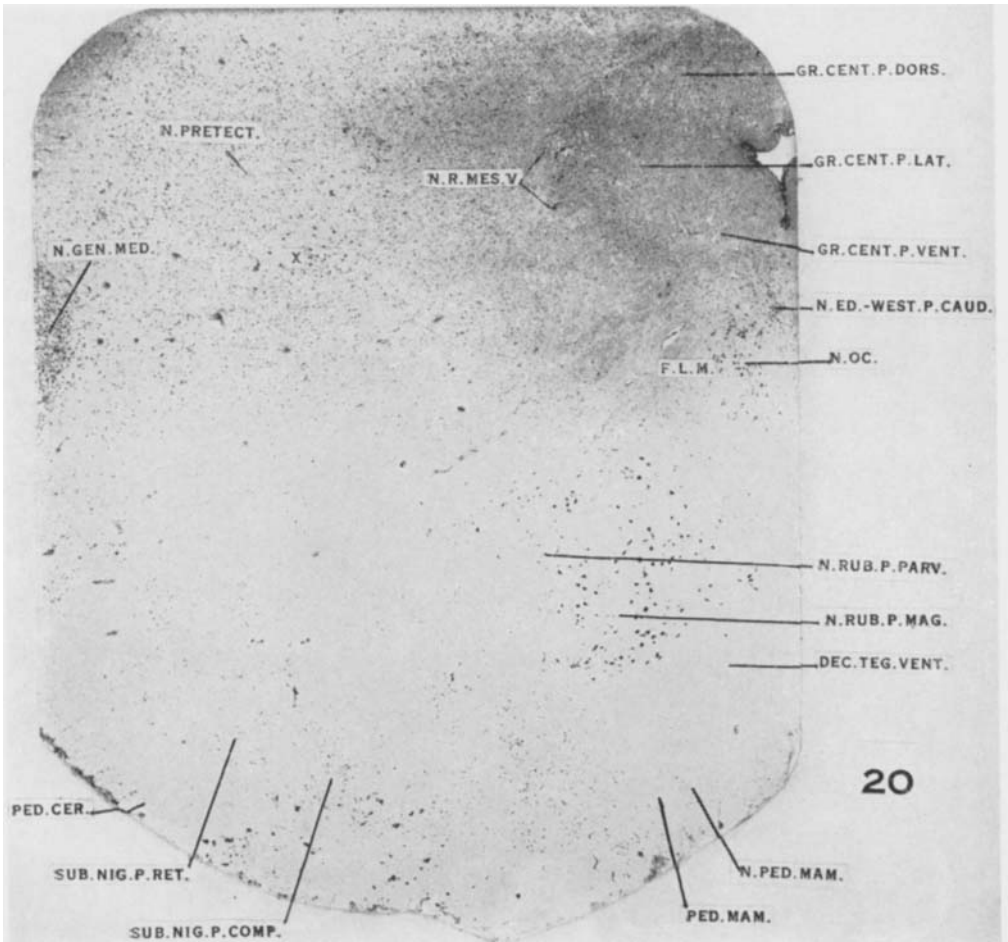
18 Horse. Through the habenular and posterior commissures and the nucleus of the posterior commissure.

PLATE 19



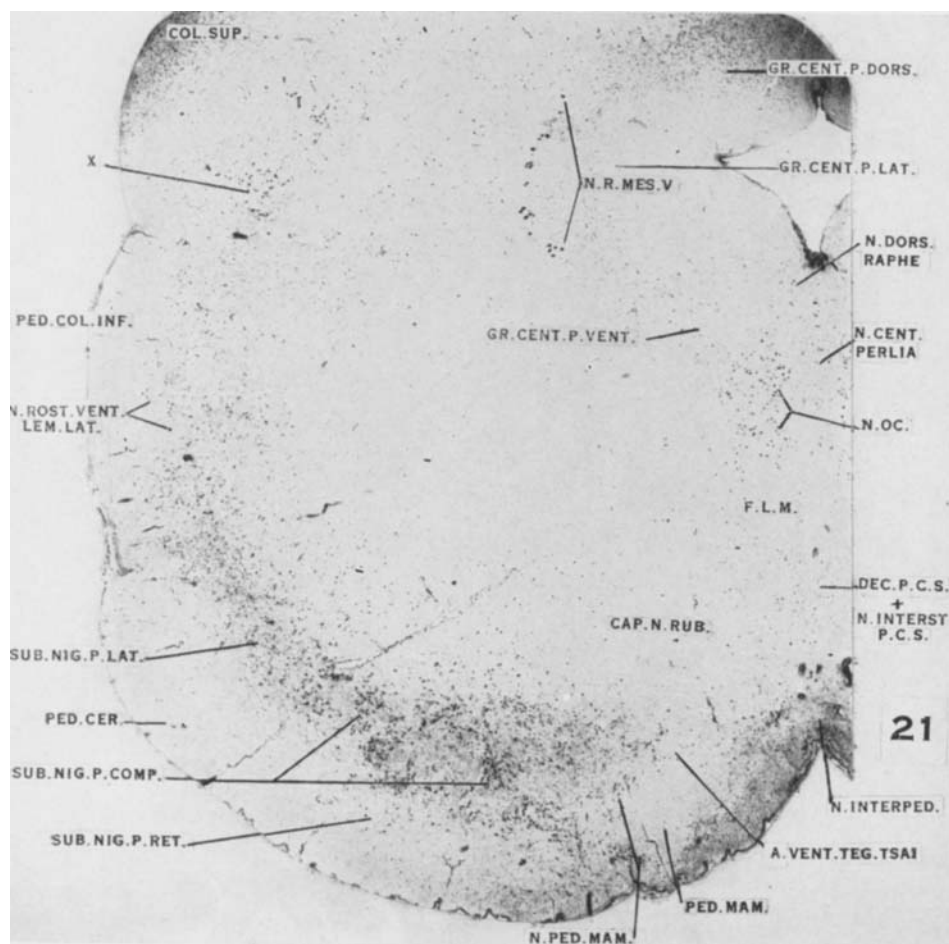
19 Horse. Rostral mesencephalon showing the nuclei of the posterior commissure, the nucleus of the mesencephalic root of V, the caudal Edinger-Westphal and the oculomotor nuclei. The subcommissural organ should be noted here.

PLATE 20



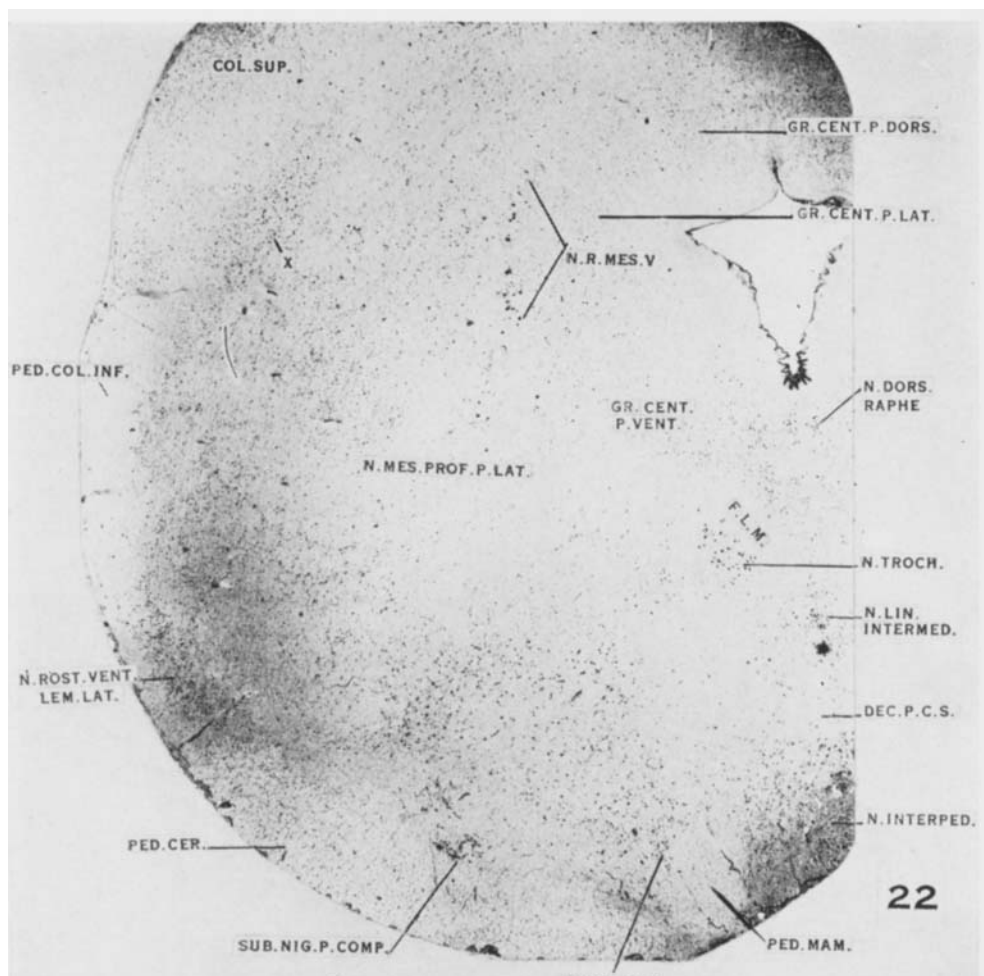
20 Horse. Through the oculomotor complex and the red nucleus.

PLATE 21



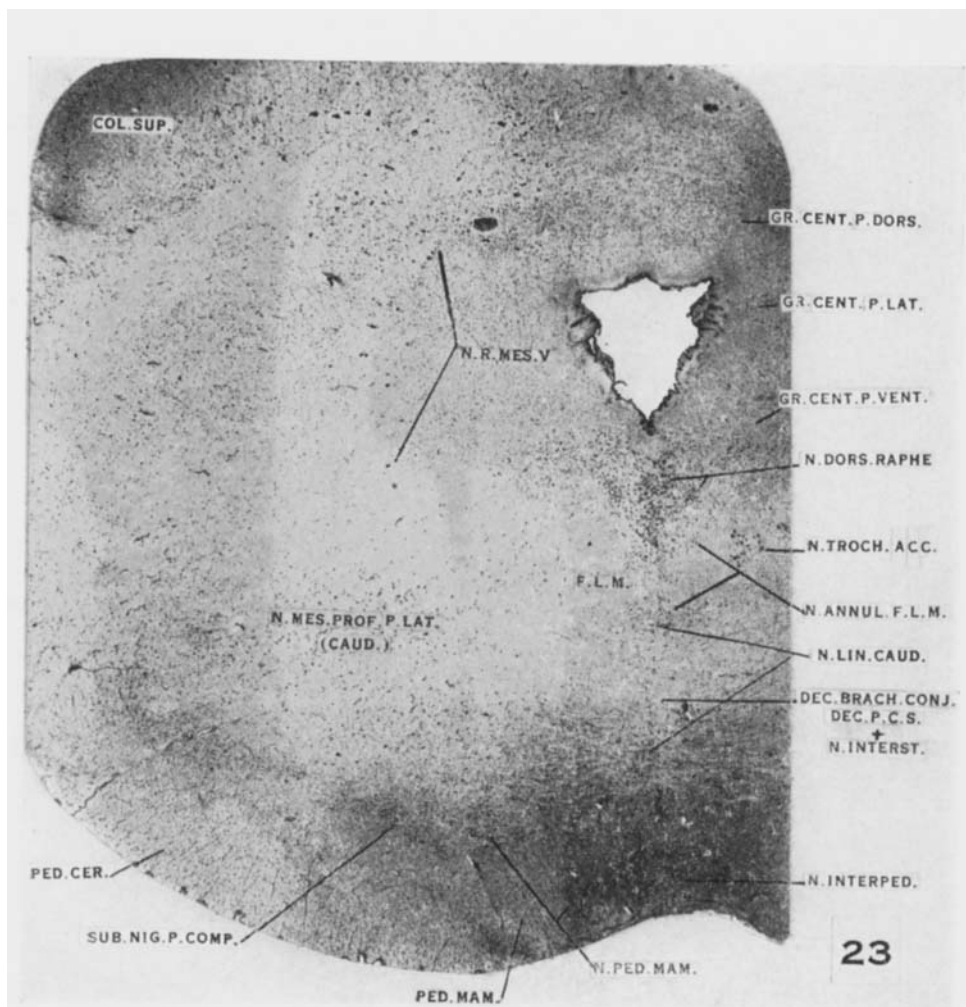
21 Horse. Through the oculomotor complex including the central nucleus of Perlia and the capsule of the red nucleus. Nucleus X is very evident at this level, as is the nucleus of the mesencephalic root of V.

PLATE 22



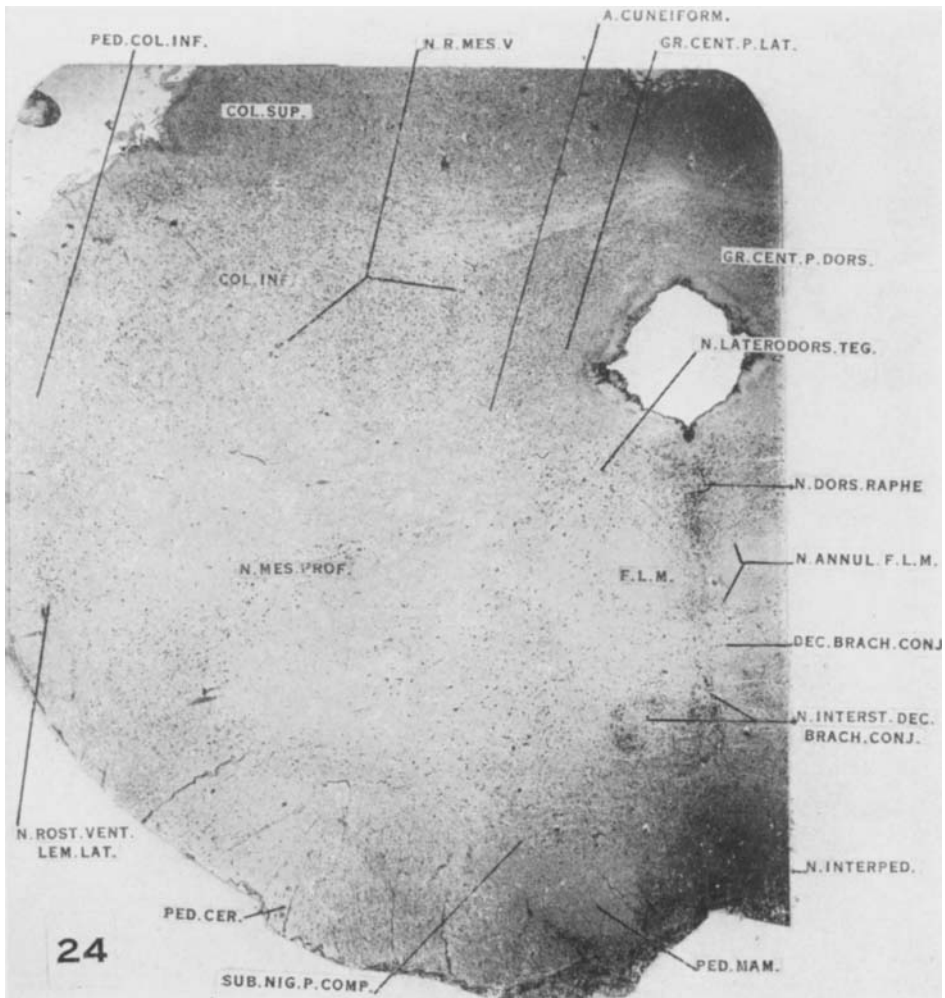
22 Horse. Through the rostral tip of the dorsal nucleus of the raphe and the interpeduncular nucleus. This section shows the trochlear nucleus in its position ventral to the medial longitudinal fasciculus.

PLATE 23



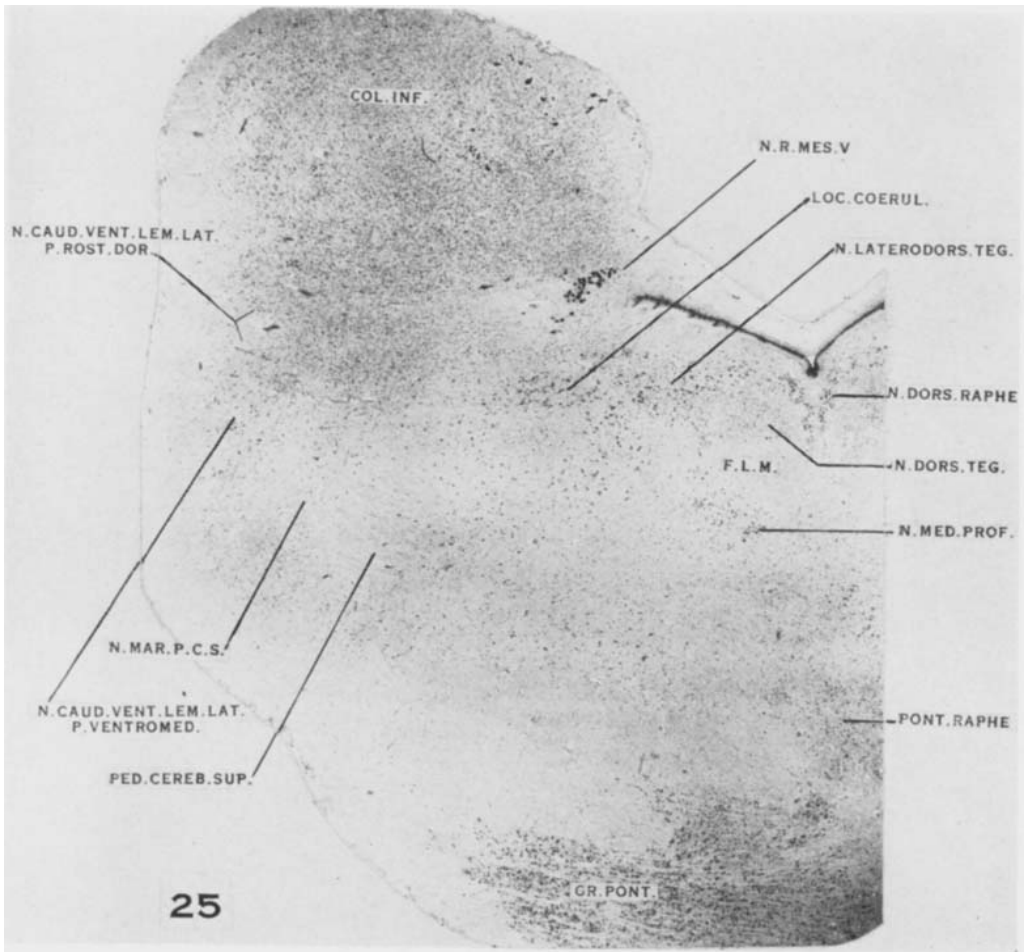
23 Horse. Through the right accessory trochlear nucleus. The large nucleus mesencephalicus profundus, nucleus of the mesencephalic root of V and the dorsal nucleus of the raphe are well marked here.

PLATE 24



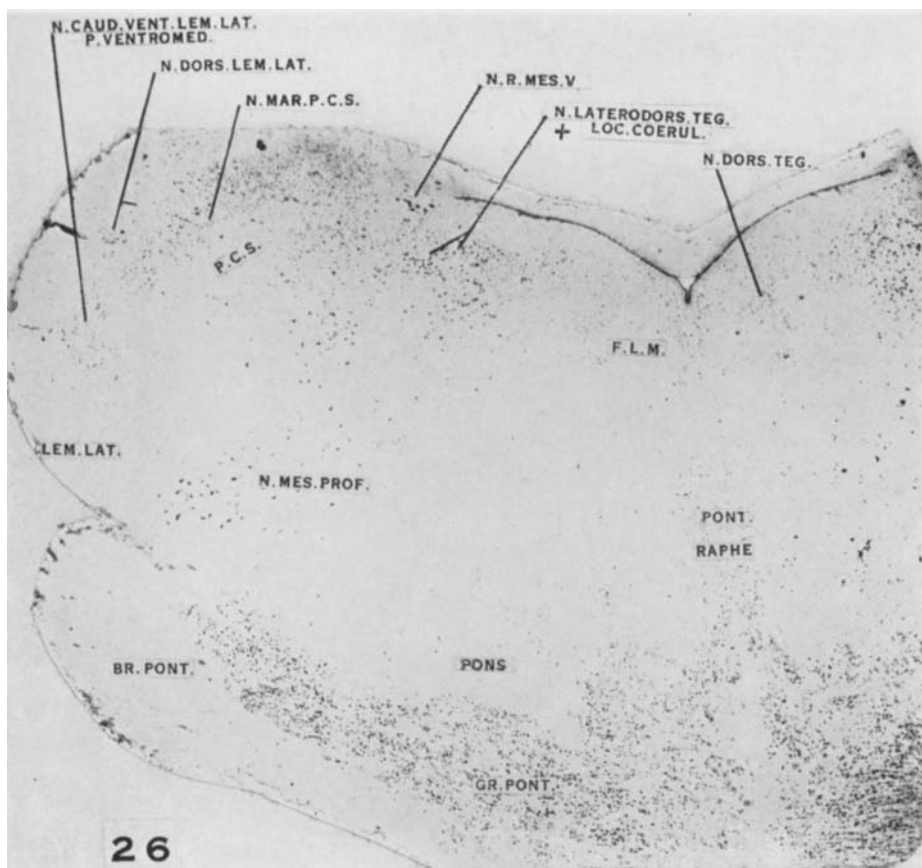
24 Horse. Note nucleus mesencephalicus profundus and the interstitial nucleus of the brachium conjunctivum. Cells belonging to the nucleus of the mesencephalic root of V are in the center of the inferior collicular gray.

PLATE 25



25 Horse. Through the nuclei of the lateral lemniscus. The nucleus of the mesencephalic root of V is especially large here, and locus coeruleus contains pigmented cells. A small annular nucleus of the medial longitudinal fasciculus is present.

PLATE 26



26 Horse. Through the dorsal nucleus of the lateral lemniscus.