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

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SEVEN PLATES (ELEVEN FIGURES)

INTRODUCTION

The midbrain of the armadillo has received little consideration from comparative neurologists, although the pretectal nucleus was described by Papez ('32) in his study of the diencephalon of this form. The general development of the nervous system in this mammal had been considered much earlier by Newman and Patterson ('10). Papez called attention to the fact that in many ways the brain of the armadillo (Tatusia novemcincta) resembles that of insectivores and this study, in general, confirms that conclusion, although the armadillo brain shows less evidence of compression than does that of the short-tailed shrew (Blarina brevicauda).

The material on which this account is based consists of a complete series of sections transversely-cut and stained with toluidin blue. The illustrations are in the form of photomicrographs taken at a magnification of 10 for the cross sections and 11 and 3 for the orientation figures.

THE PERIVENTRICULAR GROUPS

General areas of periventricular gray

The periventricular areas begin rostrally at the line between the diencephalon and the mesencephalon. The region (figs. 3 to 9) is divisible into the usual dorsal, lateral and ventral portions. The dorsal portion (figs. 3 to 7) extends caudalward to inferior collicular levels, being continuous there with the outermost layers of this part

of the tectum. Pars dorsalis forms the periventricular layer of the superior colliculus also. The lateral portion of the periventricular gray is directly continuous caudally with the chief nucleus of the inferior colliculus (figs. 8 and 9) and disappears at the beginning of the isthmus region. In addition to this relation to the inferior colliculus, pars lateralis shows a differentiation near its rostral end, the central subcommissural part of the nucleus of the posterior commissure (fig. 2). The ventral part of the periventricular gray (figs. 2 to 11) extends throughout the length of the mesencephalon, grading over rostrally and caudally into the diencephalic and pontine gray respectively. This ventral portion in the armadillo, as in the opossum, is the most differentiated part of the periventricular gray, exhibiting the same nuclear groups as were described for the marsupial brain, namely: the nuclei of the eye-muscle nerves, the nucleus of Darkschewitsch, the dorsal nucleus of the raphé, and the dorsal tegmental and laterodorsal tegmental nuclei. Between these more specialized areas is somewhat scattered, relatively undifferentiated gray, which is also allocated to pars ventralis.

Nuclear groups associated with posterior commissure

The nucleus of the posterior commissure (figs. 2 and 3) appears at the diencephalic-mesencephalic transition just rostral to the decussating fibers and ventral and ventromedial to the pretectal nucleus. With the appearance of the commissural fibers, it is separable into two parts, a lateral portion, which lies within the tegmentum of the midbrain, and a medial portion, which is a differentiated lateral part of the lateral periventricular area and constitutes a central, subcommissural part of the nucleus. Caudal to the commissure, the medial and lateral parts fuse into a single nucleus, which soon disappears. The dorsolateral part of the nucleus is made up of neurons which are only slightly larger than those forming the rest of the nucleus and show no special cellular characteristics as compared with those of other adjoining nuclei, but the limits are fairly easily determined because of a thinning out of the cells at the nuclear boundaries. This portion represents the magnocellular part of the nucleus of the commissure. The central subcommissural nucleus of the posterior commissure is differentiable from the remaining pars lateralis of the periventricular gray through the somewhat closer arrangement, deeper staining and rather larger size of its constituent neurons.

The intracommissural portion of the nucleus of the posterior commissure (fig. 2) is formed by the neurons scattered among the closely packed fiber fascicles of the posterior commissure. These cells do not extend to the midline.

Nucleus of Darkschewitsch

The nucleus of Darkschewitsch (fig. 2) is small and poorly defined in the armadillo. In the material available it has not been possible to determine the exact caudal or rostral limits and it is clear-cut in only about three sections. Within the rostral portion of pars ventralis of the periventricular gray the nucleus of Darkschewitsch lies dorsomedial to the interstitial nucleus of the medial longitudinal fasciculus and to the fasciculus and very close to the plane cutting the front end of the Edinger-Westphal complex. This nucleus of Darkschewitsch consists of spindle-shaped, deeply staining, small neurons, the nuclear mass tending to assume somewhat oval outlines where its limits can be ascertained.

Eye-muscle nuclei

As might be expected in an animal with eyes as small as those of the armadillo, the eye-muscle nuclei are poorly developed, the reduction in the chief oculomotor complex being the most marked.

Oculomotor complex. The chief oculomotor nucleus (fig. 5A) extends through planes which include the caudal third of the red nucleus, the two nuclear masses terminating caudally at approximately the same level. Its rostral tip is found in planes through the caudal end of the medial geniculate nucleus. Frontally (fig. 5A), the cells of the chief oculomotor nucleus are very few in number and do not form a discrete nuclear group, but are intermingled with those constituting the caudal nucleus of the Edinger-Westphal complex. They are differentiable from these latter, however, by their typically somatic efferent character and by their more lateral extent. As the oculomotor group is traced caudalward, the neurons accumulate into a single cell cluster which does not show separation into the ventromedial and dorsolateral portions typical for many mammals. A small subdivision represented only by scattered cells appears in the midline in the periventricular gray and extends to the caudal end of the oculomotor complex. This is a poorly differentiated component corresponding to the caudal central oculomotor nucleus of other mammals (Le Gros Clark, '26). Scattered cells belonging to the oculomotor complex are interspersed among the bundles of the medial longitudinal fasciculus. The caudal end of the oculomotor complex overlaps medially the rostral pole of the trochlear nucleus (fig. 6).

A nucleus medianus anterior, or rostral part of the Edinger-Westphal nucleus (Le Gros Clark, '26, and others), and a caudal or chief Edinger-Westphal nucleus have been identified in the armadillo. The rostral end of the Edinger-Westphal gray (fig. 3)

appears as an unpaired midline group of typical preganglionic neurons intermingled with a poorly developed rostral part of the linear complex in planes through the diencephalic-mesencephalic transition. From this level, the rostral Edinger-Westphal nucleus extends caudalward and slightly dorsalward to become continuous dorsally with the caudal Edinger-Westphal nucleus in planes in front of the chief oculomotor gray and just behind the caudal pole of the nucleus of Darkschewitsch.

The caudal Edinger-Westphal nucleus (figs. 4, 5, 5A) extends back in the periventricular gray until it is replaced by the central nucleus of the chief oculomotor complex. Like the rostral portion, it is a mass of unpaired preganglionic neurons although a blood vessel passing through it tends, at certain levels, to separate it into two parts. As was stated previously, it is somewhat intermingled medially with neurons of the chief oculomotor complex.

Trochlear gray. The trochlear nucleus (fig. 6), which appears lateral to the caudal tip of the chief oculomotor nuclear gray, indents the medial longitudinal fasciculus in the manner typical for many mammals. Other cells of similar somatic efferent type are found among the bundles of the medial longitudinal fasciculus and, toward the caudal end of the complex, a small cluster of cells lies ventral to this fasciculus, foreshadowing the condition seen in the horse. The material available suggests that the cells constituting the trochlear nucleus are slightly larger than those of the chief oculomotor nucleus and that the whole trochlear complex is somewhat better organized.

Dorsal nucleus of raphé

The dorsal nucleus of the raphé (figs. 6 to 10) is well developed in the armadillo, having all the major subdivisions typical for this mass in mammals (see particularly fig. 7). Thus a more central mass, having a separated ventral group, and lateral wings have been recognized. The central mass, consisting of round to oval, deep-staining and fairly closely arranged neurons, extends throughout the length of the dorsal nucleus of the raphé. Through the isthmus region it overrides a more linearly arranged ventral group, composed of two rows of deeply stained cells. The lateral wings (supratrochlear nuclei of Zweig, '21, and others) make their appearance as paired cell clusters slightly behind the rostral pole of the central nucleus, as part of the dorsal nucleus of the raphé. They increase rapidly in size as they are followed caudally and, at their greatest extent, occupy the larger portion of the medial half of the ventral periventricular gray. They disappear as the isthmus is reached, somewhat behind the frontal tip of the ventral group of the central part of the dorsal nucleus of the raphé. These lateral wings are composed of neurons

slightly larger than those of the surrounding periventricular gray and somewhat more deeply stained.

Laterodorsal tegmental nucleus

The laterodorsal tegmental nucleus (figs. 8 to 11) extends from planes which cut the inferior colliculus dorsally and the pontine gray ventrally to trigeminal levels. It is represented rostrally by a few larger, more deeply stained cells scattered through the ventral part of the periventricular region, external to the lateral wings of the dorsal nucleus of the raphé and also into the tegmentum. As the lateral wings disappear caudalward, the laterodorsal nucleus increases in size and spreads medialward, occupying a large part of the ventral periventricular region. The laterodorsal tegmental nucleus overlaps the dorsal tegmental nucleus dorsally and laterally. This relation exists until the caudal end of the latter nucleus is reached. As the pontine regions are approached, the laterodorsal tegmental nucleus shows a fairly definite separation into a lateral part, which is intermingled with the scattered cells of the nucleus of the mesencephalic root of V and borders on the root, and a more medial, diffuse portion. The medial part then disappears, but the lateral portion (figs. 10 and 11), which is a forerunner of the nucleus of locus coeruleus, persists into trigeminal levels. For most of their extent through the isthmus, the cells of the laterodorsal tegmental nucleus spread beyond the periventricular gray into the underlying tegmentum.

Dorsal tegmental nucleus

The dorsal tegmental nucleus (figs. 9 and 10) is a column of very small neurons, almost circular in cross sectional outline, which lies between the midline and the laterodorsal tegmental nucleus in the ventral part of the periventricular gray of the isthmus. It is overlapped, throughout most of its extent, by the laterodorsal tegmental nucleus, but is clearly differentiable from this latter by differences in cell size. Its neurons are very compactly arranged.

Nucleus of mesencephalic root of V

The nucleus of the mesencephalic root of V has representation from planes through the level of entrance of the trigeminal nerve (figs. 11 to 4) to those rostral to the chief oculomotor nucleus and caudal to the posterior commissure. Caudally its cells are intermingled on the medial side of the root, with neurons forming the lateral part of nucleus laterodorsalis tegmenti. Other cells lie lateral to the root in the region of the isthmus. The cells of the nucleus of the mesen-

cephalic root of V are differentiable from those of the laterodorsal tegmental nucleus through their distinctly oval outline. Throughout the caudal portion of inferior collicular levels, the nucleus of the mesencephalic root of V is represented by relatively few, scattered neurons lying along the inner border of the inferior colliculus. As trochlear levels are approached, however, the cells of the nucleus become more numerous and they are found not only along the periventricular gray but within this gray and, in some instances, embedded in the inferior colliculus. There is a marked increase in the neurons through superior collicular levels (fig. 4) where the cells are found in rather large clusters along the edge of the periventricular gray, occasionally in or near the midline and sometimes closely approaching the chief oculomotor nucleus. The most rostral cells lie in front of the chief oculomotor nucleus, in planes which still pass through the Edinger-Westphal complex. They all have disappeared, however, before planes through the posterior commissure are reached. The cells of the nucleus of the mesencephalic root of V in the armadillo have an appearance typical of the homologous neurons in other forms, although they are not so outstandingly large as in many other mammals and are particularly inclined to be smaller in regions of fusion with nucleus laterodorsalis tegmenti.

MIDTEGMENTAL NUCLEAR GROUPS

Nuclear groups associated with medial longitudinal fasciculus

The interstitial nucleus of the medial longitudinal fasciculus (figs. 2 to 4) has a marked rostrocaudal extent in the armadillo. Its frontal pole appears at the diencephalic-mesencephalic boundary and its caudal end is found in planes through the rostral portion of the interpeduncular nucleus. It consists of deeply staining neurons approaching in size those constituting the red nucleus. In no field do these cells show a distinct nuclear arrangement but lie dorsal to and among the bundles of the medial longitudinal fasciculus. The caudal part of the nucleus is less well represented than its frontal portion.

The second nucleus associated with the medial longitudinal fasciculus, the annular nucleus, is very poorly developed in the armadillo. Traces of such a nucleus occur in the form of small cell clusters, which do not form a complete ring about the fasciculus in any one section. These clusters are more prominent at trochlear and posttrochlear levels (figs. 6 and 7), but they grade over into the periventricular gray and the linear nucleus, and their neurons intermingle with the fibers of the fasciculus. The cells constituting the annular nucleus are medium-sized, deeply staining multipolar neurons.

Red nucleus

The red nucleus (figs. 3 to 5) is predominantly magnocellular, with smaller neurons, singly or in clusters, intermingled with the larger cells at all levels. A cap, chiefly of small cells, fits over the rostral pole of the nucleus (fig. 3) but larger elements predominate for most of its extent, being most numerous in its caudal portion (figs. 4 and 5). It extends from planes which cut the beginning of the tectal commissure dorsally and the caudal end of the mammillary body ventrally to a level through the caudal pole of superior colliculus dorsally and the interpeduncular nucleus ventrally. A feature in which it resembles the red nucleus of submammalian forms, and that will be described later for the embryonic pig, is the marked distance between the red nuclei of the two sides. Both large and small cells are multipolar, the former being of the efferent type which characterizes the motor tegmentum.

Deep mesencephalic gray (nucleus mesencephalicus profundus)

The tegmentum in the armadillo, as in the opossum, contains single cells and clusters of larger neurons other than those constituting the more generally recognized nuclear groups, such as the red nucleus and the interstitial nucleus of the medial longitudinal fasciculus. To these larger elements, the general name of nucleus mesencephalicus profundus (formatio reticularis mesencephali of Rauber, 1893, Dejerine, '01, and others; nucleus lateralis profundus mesencephali of Castaldi, '23) has been more specifically applied. They are interspersed among smaller cells which constitute the great undifferentiated mass of mesencephalic reticular gray. Such less differentiated gray occurs in large amounts in the armadillo tegmentum, although, throughout the whole extent of the midbrain, occasional large cells may be seen. Near the rostral end of the mesencephalon, a small cluster of neurons, beginning in front of the red nucleus, constitutes a pars dorsalis of nucleus mesencephalicus profundus (fig. 3). This persists for only a short distance and then gives way to occasional large cells, which become slightly more numerous as the caudal end of the red nucleus is approached. Caudal and caudoventral to the plane of the latter nucleus, typical large neurons, scattered at the sides of the superior cerebellar decussation, represent a pars lateralis and a pars ventralis of nucleus mesencephalicus profundus, the more considerable accumulation occurring lateral to the decussating fibers (fig. 6). Pars lateralis is well represented at some levels of the isthmus and grades over into scattered cells, which follow upward along the superior cerebellar peduncle. The latter approach the nucleus of this

peduncle, which consists of small neurons, intermingled with somewhat larger, deeper staining cells. These deeper staining cells are, on the whole, smaller than those of nucleus mesencephalicus profundus pars lateralis and there is no direct nuclear continuity. The largest cells of nucleus mesencephalicus profundus are to be found in these caudal and lateral portions and at the extreme rostral end of the tegmentum.

Cells paralleling the course of efferent tectal bundles, as these emerge from the superior colliculus lateral to the periventricular gray, represent, in the armadillo as in the opossum, the nucleus interstitialis tegmenti of Tsai. This is an area in which the cells of the tegmentum are linearly arranged along efferent tectal tracts. Its particular significance, if any, is not at present understood.

Marginal nucleus of superior cerebellar peduncle

The marginal nucleus of the superior cerebellar peduncle (figs. 9 and 10) consists of scattered cells on both sides of the peduncle with the neurons showing a somewhat closer arrangement laterally than medially. These cells follow down along the peduncle through the tegmental gray of the midbrain, to intermingle with the cells of pars lateralis of nucleus mesencephalicus profundus at planes through the decussation of the peduncle (fig. 6). They are deeply staining, multipolar neurons of a somewhat smaller size than those constituting the associated portion of nucleus mesencephalicus profundus. Scattered among them are smaller, undifferentially stained cells.

Cuneiform area

The cuneiform area (figs. 6 to 8) extends throughout inferior collicular levels, lying between the inferior colliculus laterally and the periventricular gray, and particularly the nucleus of the mesencephalic root of V, medially. Ventrally it merges into the underlying tegmental gray, so that the cuneiform outline, which led to its designation, is not so clear in the armadillo as in many mammals. This area is obviously a region of passage of fiber fascicles as well as a possible correlation center, with efferent bundles from the optic tectum intermingling with fibers from the lateral lemniscus.

Ventral tegmental area and nucleus of mammillary peduncle

The ventral tegmental area of Tsai ('25) is represented in the armadillo by scattered gray. This appears rostrally in the region between the caudal end of the mammillary body and substantia nigra (fig. 3), at which level it grades over, without demarcation, into the

interstitial nucleus of the commissure of Forel. Here the mammillary peduncle separates it from the ventral surface of the brain. Substantia nigra and then, for some distance, the nucleus of the basal optic root form the lateral boundary of this area. With the appearance of the interpeduncular nucleus, the ventral tegmental area is bounded medially by this cell mass and dorsally by the ventral tegmental decussation (fig. 4) and then the decussation of the superior cerebellar peduncle (fig. 5). It is crossed dorsoventrally, beginning at its caudal pole, by the mammillary peduncle and its associated nuclear gray. The nucleus of the mammillary peduncle (figs. 4 and 5) is of a typical interstitial type with spindle-shaped neurons, which surround the peduncle on all sides until it approaches the surface of the brain. The remainder of the ventral tegmental area shows no special differentiation.

Nucleus medialis profundus of Castaldi ('23)
Nucleus ventralis tegmenti of von Gudden

This nucleus (fig. 8) is a fairly distinct oval mass of medium-sized to quite large, deeply stained neurons among which are scattered a few small cells. It appears rostrally in planes considerably behind the trochlear nucleus and extends for some distance through the isthmus. It lies, throughout its extent, ventral to the medial longitudinal fasciculus in the position typical for it in mammals.

Certain pretectal and subtectal components of tegmentum

Pretectal area. The pretectal area has been described by Papez ('32) for the armadillo and such description need not be repeated here since our material documents his description (fig. 2). This area corresponds to the area pretectalis medialis recently described by Rose ('42 b) for the sheep.

Pretectal nucleus. The pretectal nucleus (fig. 2) of the armadillo was described by Papez ('32). Its position and extent have been verified. It appears at habenular levels and extends caudalward into the midbrain, lying between the medial geniculate nucleus and the optic tectum near the lateral surface of the brain, close to the optic tract. Throughout much of its extent, it is ventrolateral to the optic tectum but remains relatively discretely delimited from this region at its caudal pole. It is a columnar mass, almost circular in cross section, well circumscribed and composed of rather small to medium-sized neurons.

Nuclear gray associated with lateral lemniscus. The nuclei of the lateral lemniscus fall into a caudal ventral (figs. 6 to 11), a rostral ventral (fig. 5) and a dorsal nucleus (figs. 8 and 9) in the armadillo.

The caudal ventral nucleus is represented by intrafascicular neurons intermingled with fibers of the lateral lemniscus from planes through the superior olivary nucleus to approximately the upper borders of the midbrain. Caudally, cells of this type accumulate at some levels in clusters along the bundle and may be regarded as representing a ventromedial portion of the caudal ventral nucleus. No pars lateralis of this caudal ventral nucleus, such as has been described for rodents, was identified in the armadillo. Immediately behind the medial geniculate nucleus, a slight increase in the cells associated with the lateral lemniscus and the appearance of somewhat larger neurons mark the position of the rostral ventral nucleus of the lateral lemniscus. This latter nucleus passes over without demarcation into the medial geniculate nucleus. The dorsal nucleus of the lateral lemniscus may be divided, for purposes of description, into a caudodorsal portion, which corresponds to nucleus isthmi of lower forms and to the cell mass usually designated as the dorsal nucleus of the lateral lemniscus in man, and into a rostrodorsal portion. The caudodorsal part (fig. 9) lies in the isthmus, where it overlaps the superior cerebellar peduncle and its associated nucleus. It shows no marked differentiation and, on the whole, is poorly developed. The rostrodorsal part (fig. 8) of the dorsal nucleus of the lateral lemniscus lies at the base of the inferior colliculus in the region where the lateral lemniscus is spreading out to envelop this portion of the tectum. This rostrodorsal division is poorly developed, consisting merely of a few scattered neurons intermingled with lemnisci fibers.

MIDLINE NUCLEAR GROUPS

Linear nuclear gray

This nuclear gray described for the rodent brain by Castaldi ('23) is only poorly represented in the midbrain of the armadillo, although rostral, intermediate and caudal portions can be recognized. The rostral group is directly continuous with the diencephalic periventricular gray. Its few, scattered neurons are intermingled with the rostral Edinger-Westphal nucleus and overlie the interstitial nucleus of the commissure of Forel. Followed rostrocaudally they are completely substituted for by the rostral Edinger-Westphal nucleus. Behind the interstitial nucleus of the commissure of Forel, the linear nucleus spreads ventrally to form a poorly represented intermediate group. This intermediate portion of the linear nuclear gray consists of clusters of small neurons, not showing a definite linear arrangement, situated on either side of the midline. As the rostral end of the superior cerebellar decussation comes into the field. the linear group practically disappears, only to reappear as the caudal

part of the linear nucleus, in a position dorsal to the superior cerebellar decussation and ventral to the very long dorsal tegmental decussation. This caudal portion spreads dorsalward behind the latter decussation and, as the crossing of the superior cerebellar peduncles disappears, extends ventralward to become continuous with the interpeduncular nucleus. Then it passes over, as does the interpeduncular nucleus, into the gray of the median pontine raphé.

The cells of the rostral portion of the nucleus (fig. 3) are small, dark-staining neurons oriented dorsoventrally in the course of the periventricular fibers. Those of the intermediate group (fig. 5A) do not show such definite orientation and, on the whole, are somewhat less deeply stained and slightly more oval in outline. In the caudal part (figs. 6 to 8) there is an intermingling of small cells resembling those of the rostral portion with somewhat larger, more deeply staining neurons.

Interstitial nucleus of commissure of Forel

The interstitial nucleus of the commissure of Forel (fig. 2) is intercalated along the course of the commissural fibers, which appear at the diencephalic-mesencephalic transition and extend into the beginning of the mesencephalon. Through midportions of the commissure, cells of the interstitial nucleus occur in the midline and, throughout the extent of this decussation, follow lateralward along its distributing fibers. Thus they grade over ventrolaterally into the nucleus of the basal optic root and the more medial part of pars compacta of substantia nigra. Dorsolaterally they can be followed as far as the red nucleus. In the diencephalic-mesencephalic transition area, the cells of the interstitial nucleus of the commissure of Forel extend down toward the mammillary gray. The cells are small to medium-sized and undifferentially stained neurons.

Interpeduncular nucleus

The interpeduncular nucleus (figs. 4 to 7) is found from a plane behind the caudal pole of the trochlear nucleus, which cuts the inferior colliculus dorsally and the pontine fibers ventrally, to a plane through the caudal pole of the medial geniculate nucleus. Rostrally the interpeduncular nucleus consists of an almost undifferentiated mass of gray, which gradually becomes more compact dorsally, thereafter assuming a toadstool shape. Caudally it is an oval mass capped by a semicircular band of gray. It passes over into the median pontine raphé without any clear demarcation between the two areas. The cells of the interpeduncular nucleus for the most part are small to medium-sized and deep staining, with the band described above consisting of still smaller neurons.

BASAL MIDBRAIN GRAY

Substantia nigra

The rostral end of substantia nigra lies in the caudal part of the diencephalon (fig. 2), in planes which pass through the habenula dorsally and the mammillary body ventrally. In this region, both pars reticulata and pars compacta are represented. The tip of pars reticulata extends slightly oral to that of pars compacta. Pars compacta (figs. 2 to 5) increases along the medial half of the peduncle and is not sharply separated either from the increased pars reticulata or from the nucleus of the basal optic root (fig. 3). In planes through the caudal pole of the medial geniculate nucleus, both pars compacta and pars reticulata decrease and then spread out over the width of the peduncle (fig. 3), at this level lying ventral to the caudal tip of pars lateralis. Behind this plane, pars compacta and pars reticulata gradually disappear. At the caudal end of the complex, both of these portions of substantia nigra are slightly better developed laterally than medially. They disappear (fig. 5) as the pontine gray comes into the field, pars compacta persisting slightly behind pars reticulata.

Pars lateralis of substantia nigra (figs. 3 to 5) begins rostrally just behind the frontal tip of the remainder of the complex, in planes which pass through the pretectal nucleus and the rostral end of the optic tectum dorsally and the mammillary body ventrally. It grades over into the lateral portion of pars reticulata frontally. As the caudal pole of the medial geniculate nucleus is reached, the cells decrease somewhat in number in pars lateralis, which finds representation in an accumulation of gray ventral to the medial geniculate nucleus. Neurons of this portion of substantia nigra are found among the fiber fascicles extending toward the tectum beneath (fig. 3) and then behind (figs. 4 and 5) the medial geniculate nucleus.

The neurons constituting the three portions of substantia nigra in the armadillo are dark staining, multipolar cells, distinctly smaller than those forming the magnocellular portion of the red nucleus. Some intermingling of small cells occurs.

Nucleus of basal optic root

This nucleus (fig. 3) is small and indistinctly delimited in the armadillo. It is situated at the rostral end of the mesencephalon medial to substantia nigra, from which it is poorly delimited. It is most easily recognized in those planes in which fibers of the basal optic root may be traced into it. Its neurons extend upward along the fascicles of the root for a short distance toward the ventral tegmental area. The constituent neurons of the nucleus of the basal optic root resemble closely those of substantia nigra.

SUMMARY

Since the general discussion at the end of this series of papers compares the development of the various centers of the midbrain through a wide series of mammals, it will be necessary here to call attention only to certain special characteristics of the tegmentum of the midbrain and the isthmus in the armadillo.

In the periventricular area, the dorsal nucleus of the raphé is relatively well differentiated and has the main subdivisions characteristic of this nuclear mass in mammals. The dorsal tegmental nucleus is a small-celled column of gray with typical position and relations. Nucleus laterodorsalis tegmenti, which lies rostral to the dorsal tegmental nucleus and extends to planes caudal to it, encircles it laterally and dorsally. This laterodorsal nucleus shows a relatively definite separation into medial and lateral parts, with the lateral portion in close relation to the cells of the nucleus of the mesencephalic root of V. This position suggests a primordial nucleus of locus coeruleus, although the cells are unpigmented. The oculomotor and trochlear nuclei supplying striated muscle are small, a condition in conformity with the size of the eyes in this animal. Surprisingly enough, the Edinger-Westphal complex is well developed.

The midtegmental regions in the armadillo show a fairly small red nucleus separated from its fellow of the other side by a considerable distance. There is no clearly delimitable parvocellular portion although the frontal part of the nucleus has a cap of small cells. The caudal end of the nucleus is almost entirely magnocellular. The various divisions of nucleus mesencephalic profundus are not particularly well developed except rostrally and caudally. An accumulation of such cells, lateral to the decussation of the superior cerebellar peduncle and approaching its marginal nucleus, stands out rather prominently. The interstitial nucleus of the medial longitudinal fasciculus has a marked rostrocaudal extent in the armadillo.

The interpeduncular nucleus is present throughout the midbrain, although not sharply separable from the pontine tegmental gray. Otherwise, the midline tegmental area is poorly differentiated in the midbrain of the armadillo. The findings on the pretectal area and the pretectal nucleus document those of Papez ('32).

Substantia nigra has the three portions typical of this gray in mammals, but, like the red nucleus, is not so large as in certain other forms. Medially it is poorly delimited from the nucleus of the basal optic root.

PLATES 1 TO 7

EXPLANATION OF FIGURES

1 Photograph of the midbrain and isthmus of the armadillo illustrating the planes of section of figures 2 to 11. × 11.

1A Photograph of a midsagittal view of the brain of the armadillo. × 3.

2 to 11 Photomicrographs of transverse sections of the midbrain and isthmus in planes indicated in figure 1. Toluidin blue preparation. × 10.

5A An enlargement of the region involving the caudal part of the Edinger-Westphal nucleus at the level illustrated in figure 5. Toluidin blue preparation × 60.

PLATE 1

PLATE 2

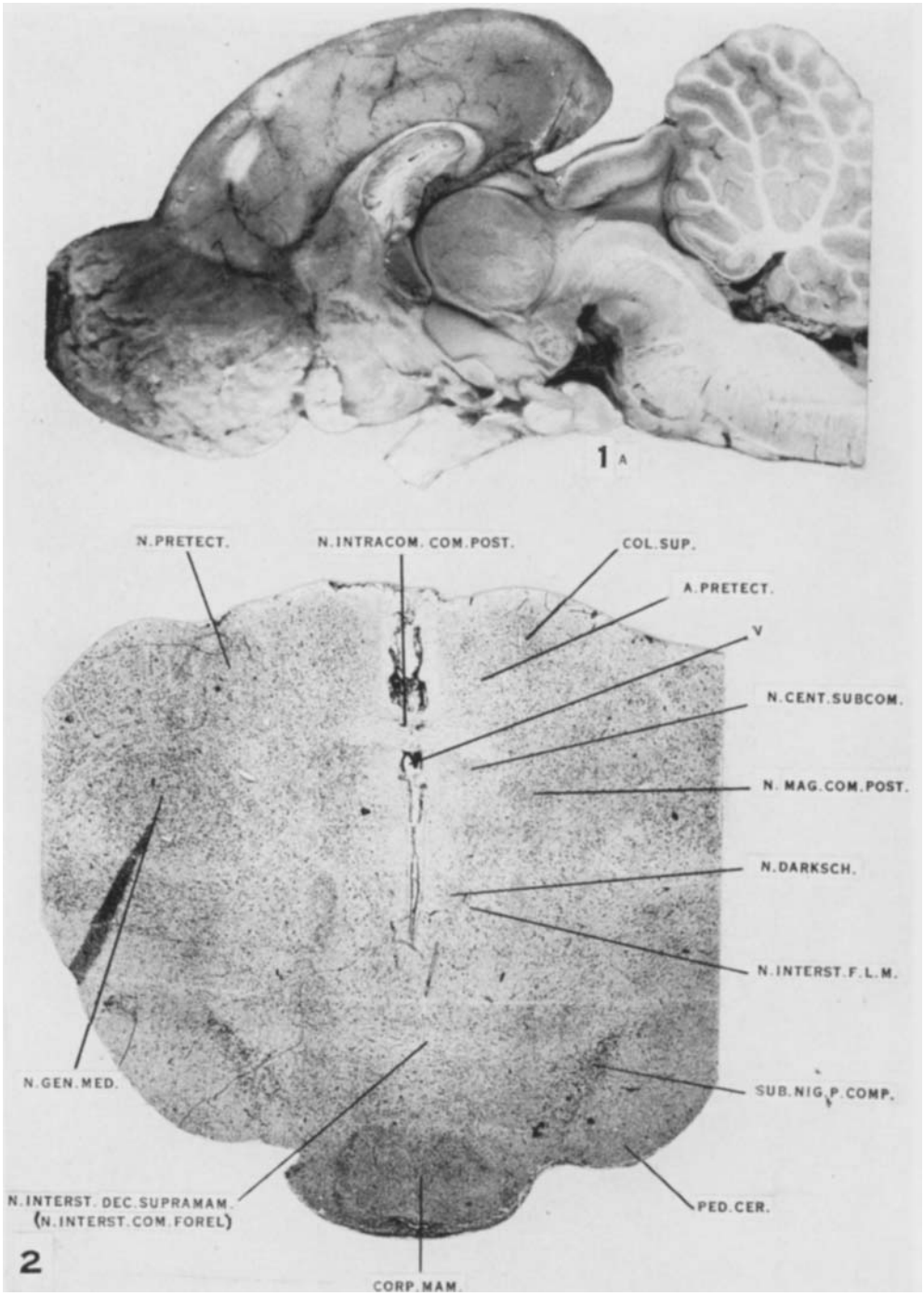
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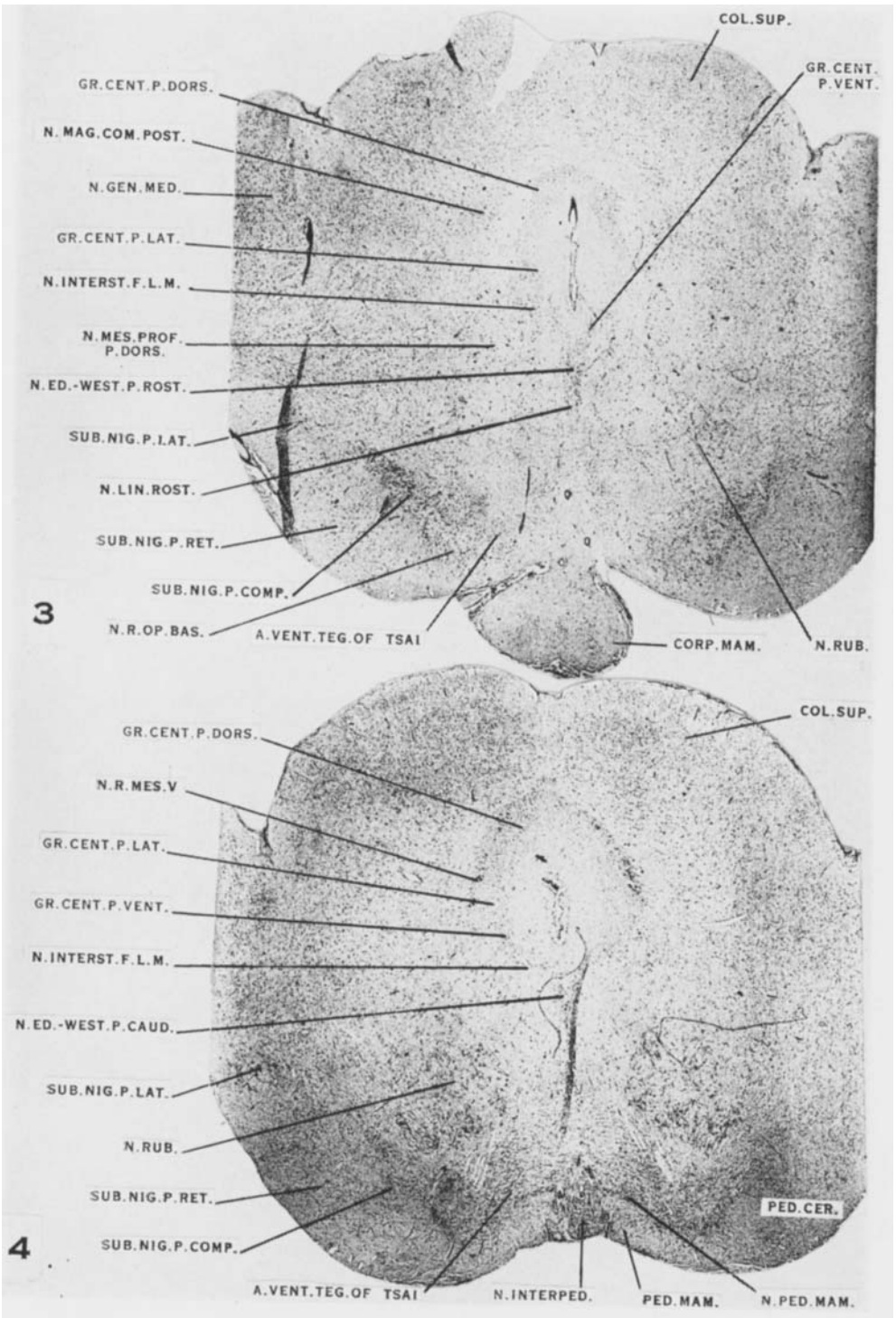
PLATE 3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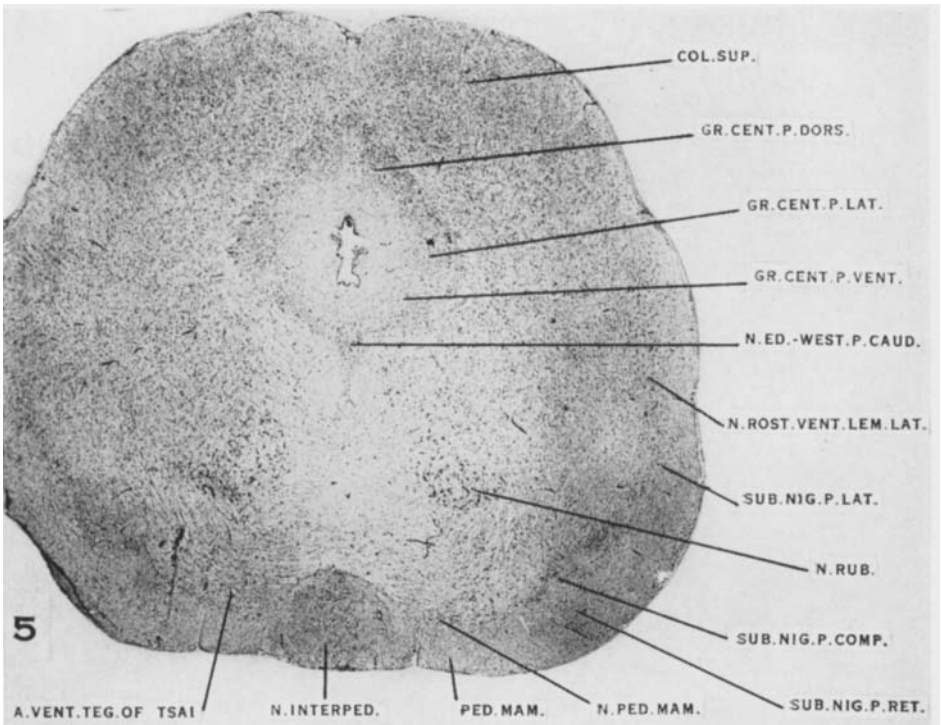
SUB.NIG.P.LAT.
N.LIN.ROST.
SUB.NIG.P.RET.
SUB.NIG.P.COMP.
3
N.R.OP.BAS.
A.VENT.TEG.OF TSAI
CORP.MAM.
N.RUB.
COL.SUP.
GR.CENT.P.DORS.
N.R.MES.V
GR.CENT.P.LAT.
GR.CENT.P.VENT.
N.INTERST.F.L.M.
N.ED.-WEST.P.CAUD.
SUB.NIG.P.LAT.
N.RUB.
SUB.NIG.P.RET.
PED.CER.
4
SUB.NIG.P.COMP.
A.VENT.TEG.OF TSAI
N.INTERPED.
PED.MAM.
N.PED.MAM.

PLATE 4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GR.CENT.P.DORS.
GR.CENT.P.LAT.
GR.CENT.P.VENT.
N.ED.-WEST.P.CAUD.
N.ROST.VENT.LEM.LAT.
SUB.NIG.P.LAT.
N.RUB.
SUB.NIG.P.COMP.
SUB.NIG.P.RET.
5
A.VENT.TEG.OF TSAI
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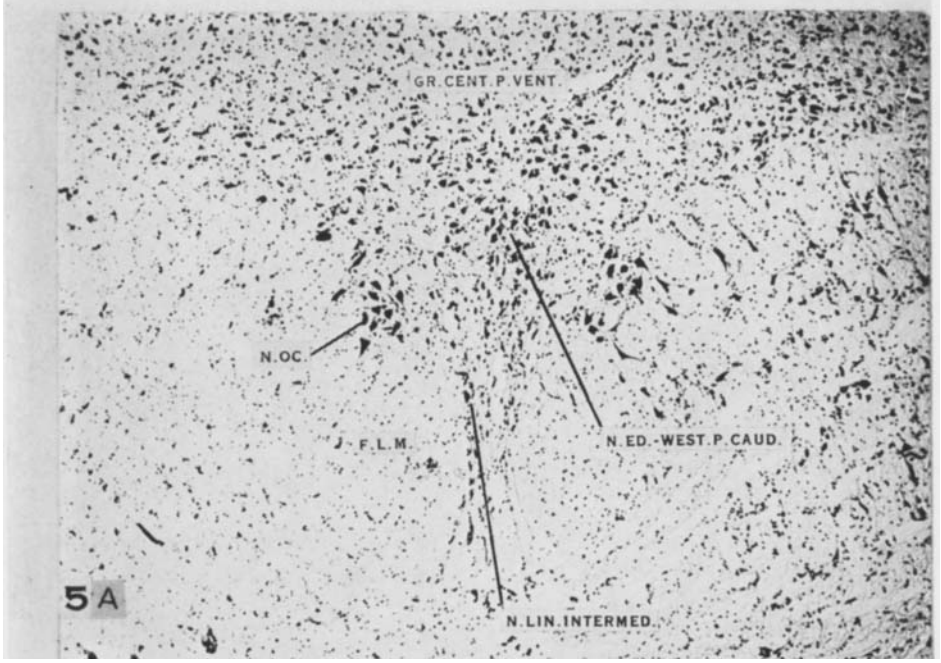
PED.MAM.
N.PED.MAM.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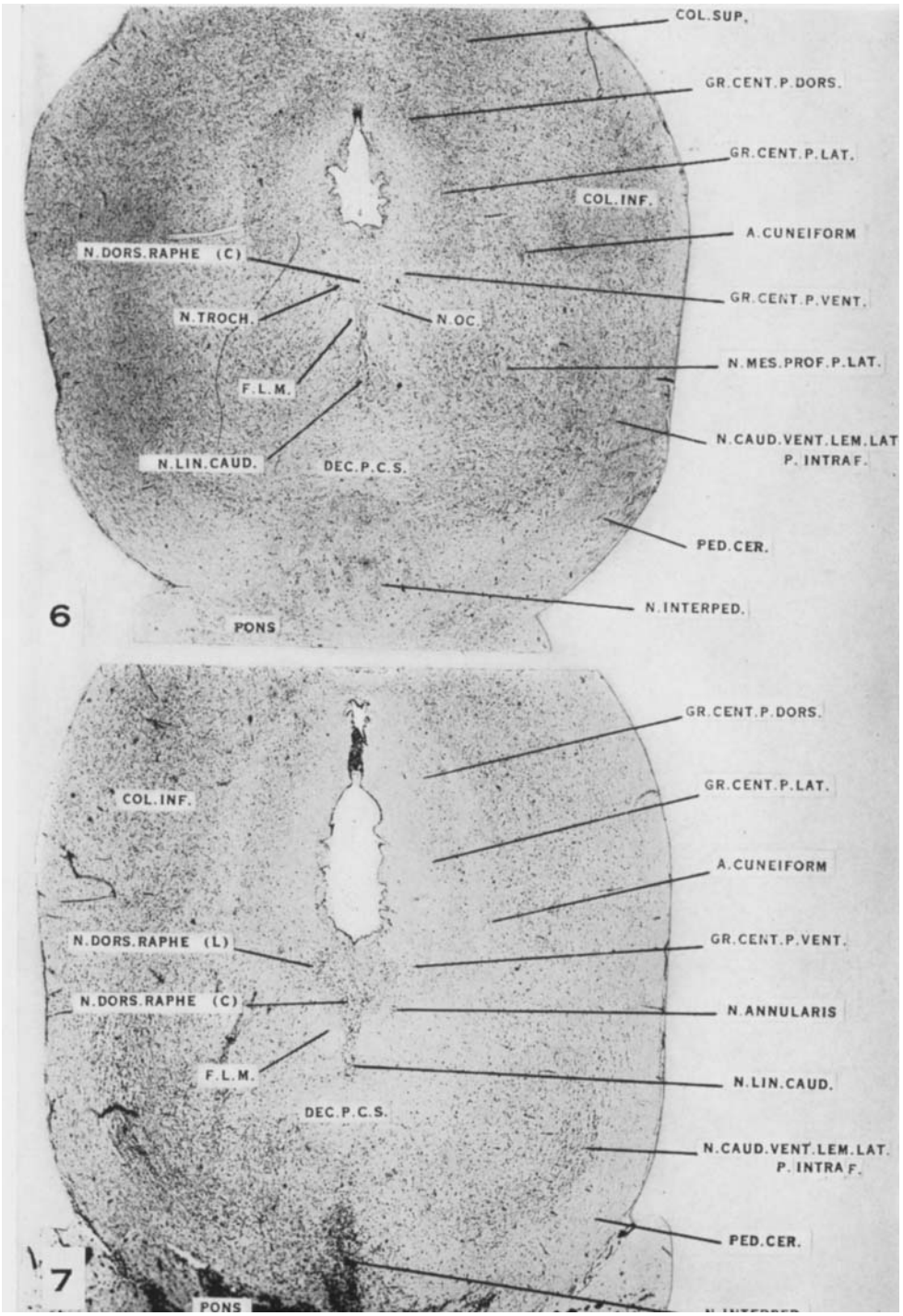
F.L.M.
N.ED.-WEST.P.CAUD.
5A
N.LIN.INTERMED.

PLATE 5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GR.CENT.P.DORS.
GR.CENT.P.LAT.
COL.INF.
A.CUNEIFORM
N.DORS.RAPHE (C)
GR.CENT.P.VENT.
N.TROCH.
N.OC.
N.MES.PROF.P.LAT.
F.L.M.
N.CAUD.VENT.LEM.LAT
P. INTRAF.
N.LIN.CAUD.
DEC.P.C.S.
PED.CER.
N.INTERPED.
6
PONS
GR.CENT.P.DORS.
COL.INF.
GR.CENT.P.LAT.
A.CUNEIFORM
N.DORS.RAPHE (L)
GR.CENT.P.VENT.
N.DORS.RAPHE (C)
N.ANNULARIS
F.L.M.
N.LIN.CAUD.
DEC.P.C.S.
N.CAUD.VENT.LEM.LAT.
P. INTRA F.
PED.CER.
7
PONS

PLATE 6

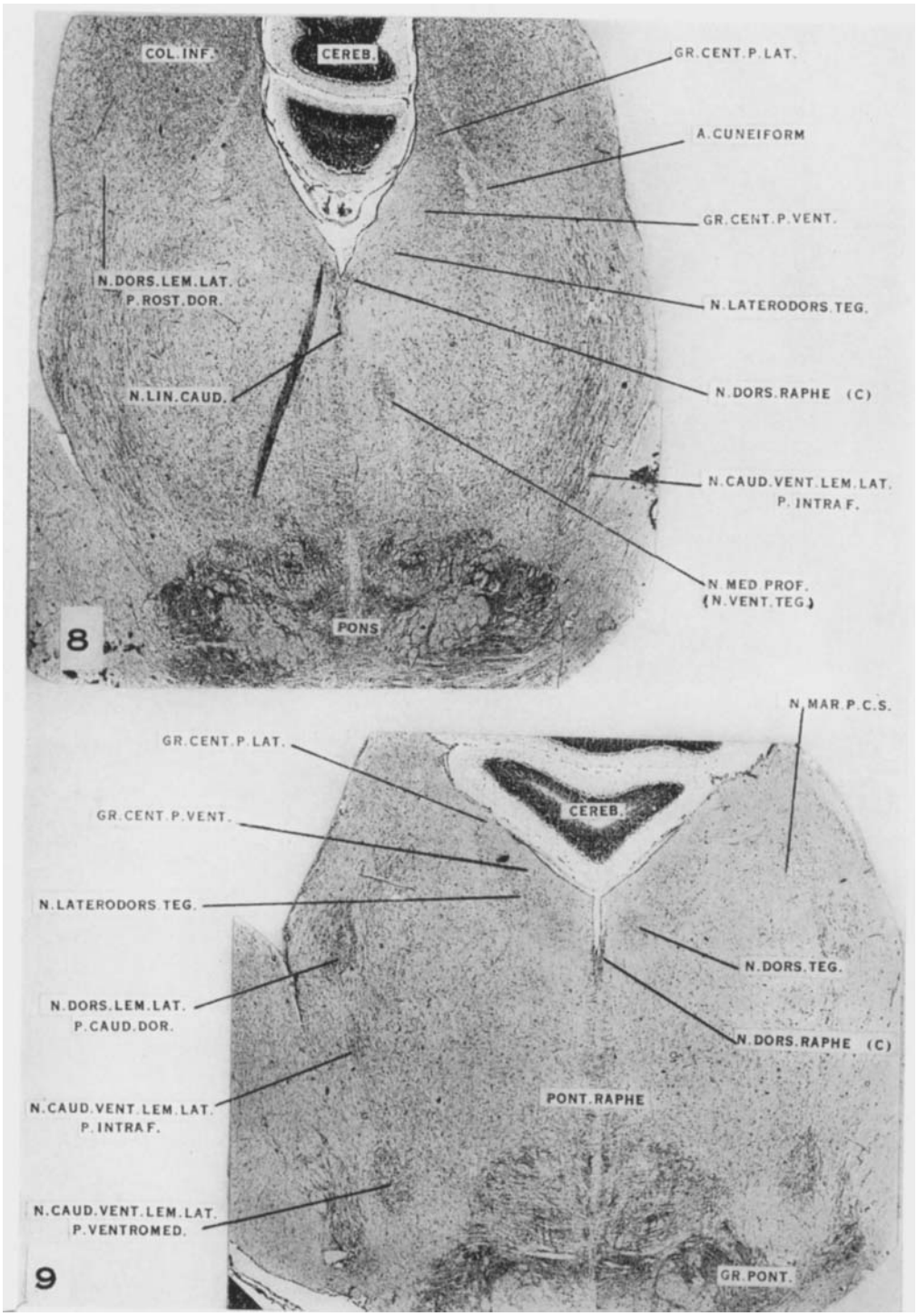
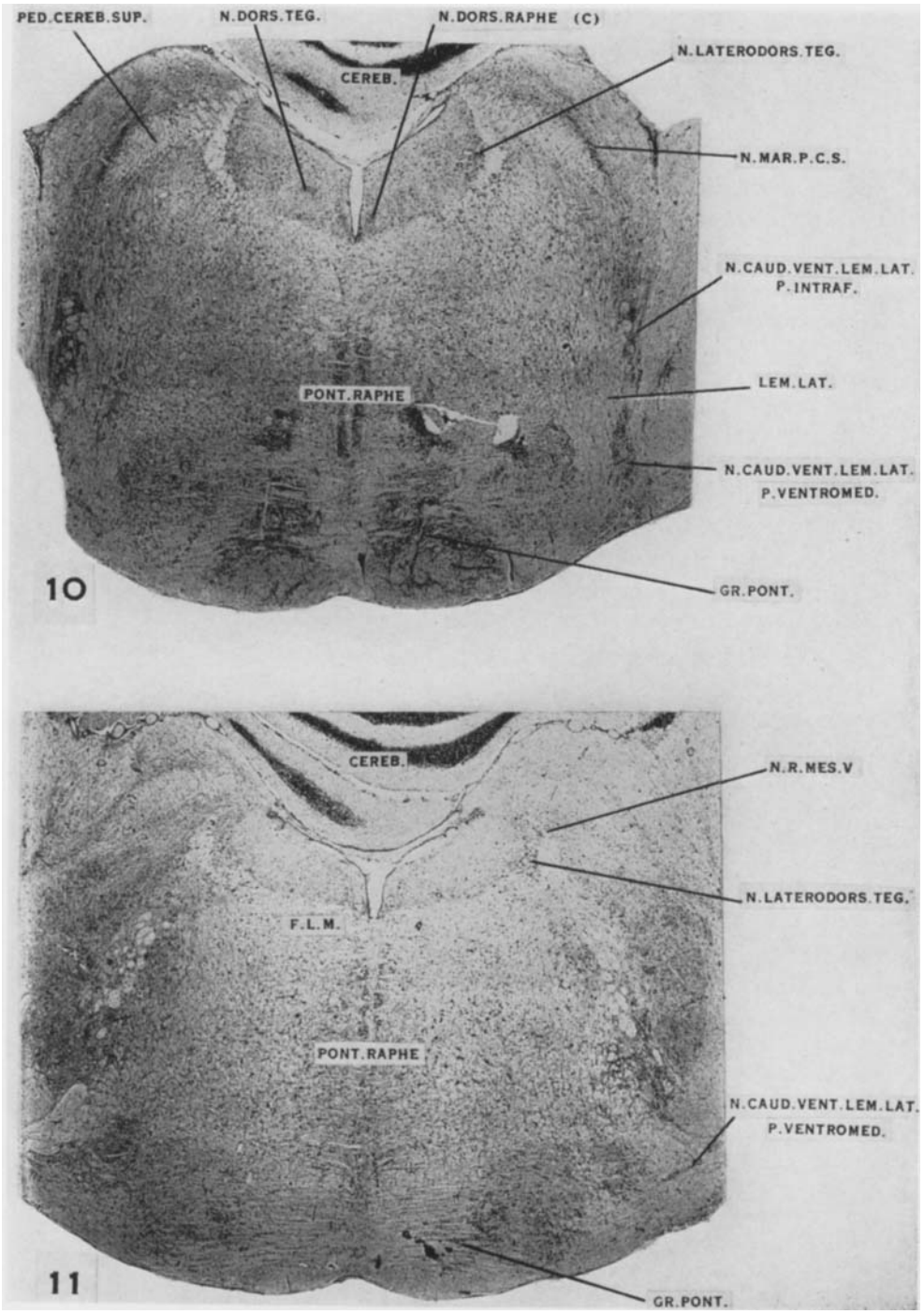

COL. INF.
CEREB.
GR. CENT. P. LAT.
A. CUNEIFORM
GR. CENT. P. VENT.
N. DORS. LEM. LAT.
P. ROST. DOR.
N. LATERODORS. TEG.
N. LIN. CAUD.
N. DORS. RAPHE (C)
N. CAUD. VENT. LEM. LAT.
P. INTRA F.
N. MED PROF.
(N. VENT. TEG.)
PONS
8
N. MAR. P. C. S.
GR. CENT. P. LAT.
GR. CENT. P. VENT.
CEREB.
N. LATERODORS. TEG.
N. DORS. TEG.
N. DORS. LEM. LAT.
P. CAUD. DOR.
N. DORS. RAPHE (C)
N. CAUD. VENT. LEM. LAT.
P. INTRA F.
PONT. RAPHE
N. CAUD. VENT. LEM. LAT.
P. VENTROMED.
GR. PONT.
9

PLATE 7


PED.CEREB.SUP.
N.DORS.TEG.
N.DORS.RAPHE (C)
CEREB.
N.LATERODORS.TEG.
N.MAR.P.C.S.
N.CAUD.VENT.LEM.LAT.
P.INTRAF.
LEM.LAT.
PONT.RAPHE
N.CAUD.VENT.LEM.LAT.
P.VENTROMED.
GR.PONT.
10
CEREB.
N.R.MES.V
N.LATERODORS.TEG.
F.L.M.
PONT.RAPHE
N.CAUD.VENT.LEM.LAT.
P.VENTROMED.
GR.PONT.
11