

*Anatomy. — The cellmasses in the telencephalon and diencephalon of the Rattle Snake, Crotalus atrox.* By FR. J. WARNER, M.D. (Communicated by Prof. C. U. ARIËNS KAPPERS.)

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The study of the brain of this snake was undertaken with the object of forming a basis of comparison of the ophidian brain with that of the other reptiles, the data concerning the brain of snakes being very scanty.

The central nervous relations in these animals have never been described systematically. A. MEYER ('92, '95) has made some interesting observations on the arrangements of the cells in the cortex, RABL—RÜCKHARD ('94) briefly described the fornix system, EDINGER ('96, '99) gave us some notes on the brain of *Tropidonotus natrix*; KAPPERS and THEUNISSEN ('08) gave a drawing of the forebrain commissures and cortex in *Zamenis*, DE LANGE ('11) produced photographs of the Cobra and Boa constrictor brain and a wax reconstruction of the forebrain of *Eunectes murinus*, VAN VALKENBURG ('11) gave us a minute description of the mesencephalic trigeminus nucleus in *Eunectes* and KAPPERS ('20) a drawing of this root in *Boa constrictor*. Finally ROSE ('23) gave a description of the cortex and striatum in *Tropidonotus natrix* and *Boa constrictor*.

Apart from these scattered notes no data are available on this subject.

In the following pages the fore- and tweenbrain of the rattlesnake will be compared especially with the lizard's brain, the *Lacertilia* being the nearest relatives of the *Ophidia*.

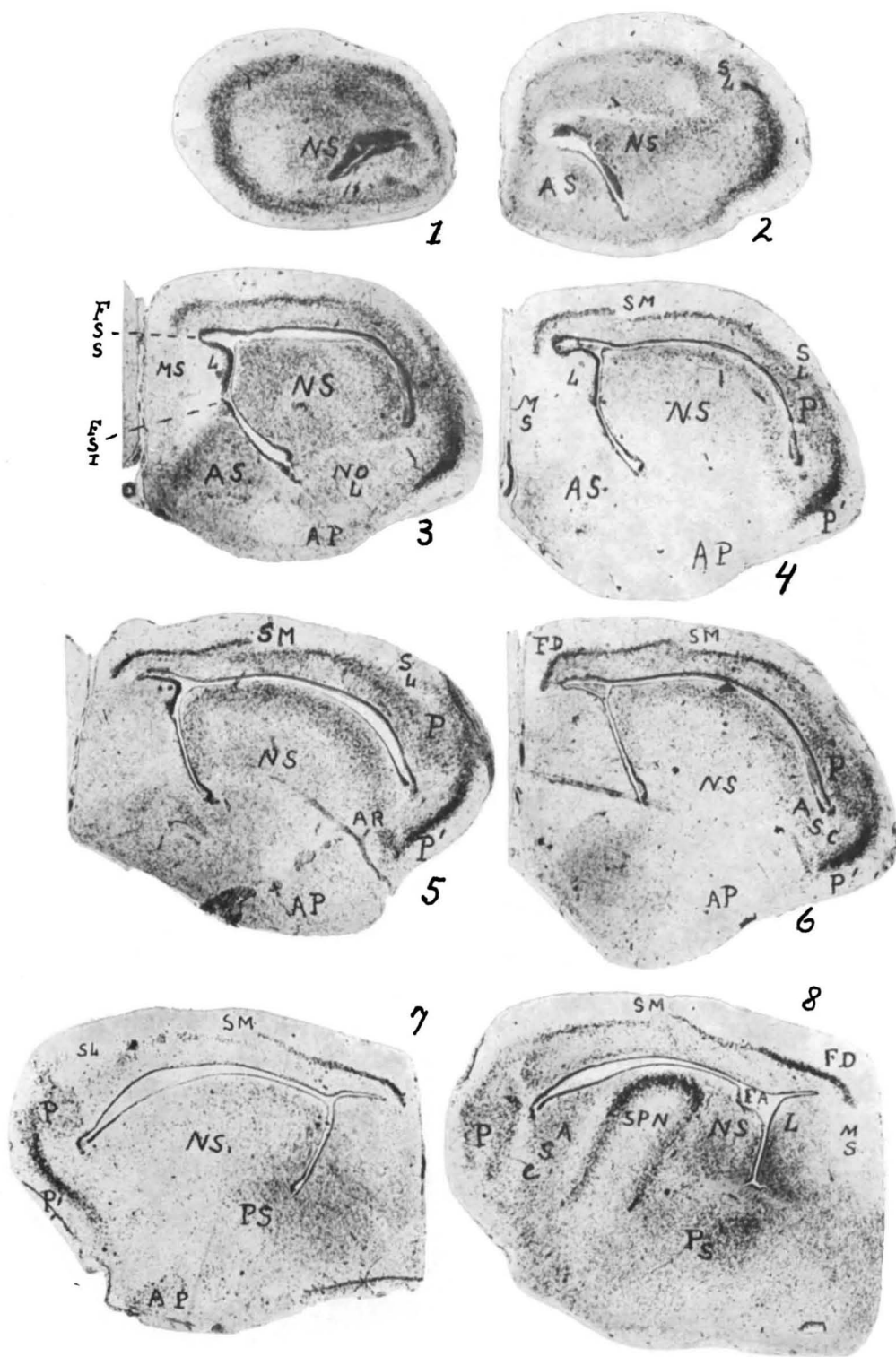
For this purpose a transverse and a sagittal series of the brain of *Crotalus atrox* were stained with the Nissl method, and the most instructive sections photographed.

### *Telencephalon.*

In its most frontal part (fig. 1 and 2) the forebrain is surrounded on all sides by a cortical layer, the cortex of the lobus olfactorius anterior, the cells of which are more crowded on the lateral side. The olfactory ventricle is a small oblique split in the ventro-medial part. The ventro-medial intraventricular protrusion (A.S.) continues further backward (fig. 3 and 4) in what may be *the nucleus accumbens septi* of other authors. (KAPPERS, DE LANGE, HERRICK, CROSBY). The larger dorso-lateral intraventricular protrusion (N.S.) continues backward in the neostriatum and may be compared to the crus epirhnicum of the striatum as described by HIS in mammalian embryos, lying on the dorso-lateral side of the

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PLATE I.



olfactory ventricle. In fig. 2 its cells show a continuity with the dorsal cortex cells (cf. also fig. 3 FREDERIKSE).

While in fig. 1 the cortex is still practically continuous in fig. 2 the condition has changed in so far as in the cortical layer a distinct break is visible on the dorso-lateral side (*superpositio lateralis*, S.L.). This superposition of layers at the lateral side remains along the whole hemisphere and only disappears near the caudal pole (fig. 11 and 13). In fig. 2 the medial cortex is still continuous from the basis to the top of the brain. This, however, changes in fig. 3, where the real *septum* develops between the *fissura septalis superior* (F. S. S.), its limit with the cortex, and the *fiss. septalis inferior* (F. S. I.), its limit with the nucleus accumbens. The cells of the septum are less crowded than those of the nucl. accumbens and can be divided in a larger medial (M. S.) and smaller but denser lateral group (L), as described in other reptiles (HERRICK, RÖTHIG, CROSBY, FREDERIKSE). The medial group is not sharply separated from the deeper medio-dorsal cortex cells.

This may be the reason that some authors (JOHNSTON, HERRICK) accepted the presence of an undifferentiated primordium hippocampi between the hippocampus proper and the septum. It seems more justified however to consider this as a part of the septum in Reptiles.

The neostriatum N.S. is quite distinct in fig. 3 and 4, being separated dorsally and laterally from the cortex. The lateral cortex plate does no more continue in its laminated arrangement in the ventral wall of the hemisphere. Its cortical arrangement ends with the more crowded layer P', visible already in the preceding sections. These crowded cells are covered by a deeper zonal layer than the other parts of the cortex. The basis of the brain, the *area parolfactoria* (A. P., ROSE's field S) contains widely scattered cells, more or less separated from the neostriatum by fiber tracts (pale spots), while part of them form the nucl. tr. olfactorius lateralis (N.O.L.) of CROSBY. The arrangement of the cells in the nucl. accumbens is very much the same as in the neostriatum.

Whereas the dorso-medial cortex layer is still continuous in fig. 3, fig. 4 shows a new feature by the occurrence of *superpositio medialis* (S.M.), establishing a break between the medio-dorsal cortex layer and the dorsal one. The type of cells in both is still very much the same here, but further backward the cells in the medial part of the medial cortex keep a smaller size, while those in its dorsal part as those in the dorsal layer are larger and less crowded. Figures 5 and 6, show the same but are interesting on account of the sharp limitation of the lower lateral cortex, from the cells of the area parolfactoria by an artery (A.R.) penetrating into the neostriatum (N.S.). In these figures the nucl. accumbens septi, though still present, is no more so distinct as it is more frontally (especially in fig. 3).

In the neostriatum the dorso-lateral cells are larger and form a cap on the smaller central cells. The larger cells are very evident near the

sulc. superstriatalis of HINES or pallio-striatal angle (angulo-striatal cells, A. S. C. fig. 6). The cortex between this angle and the superpositio lateralis shows a striking thickening (P=area praepiriformis communis of ROSE), not present more ventrally with the darkly stained and more crowded cells of the ventro-lateral cortex (P').

This thickening of the cortex already starts frontally (cf. fig. 3 and the sagittal section in fig. 19) and continues until the end of the attachment of the archistriatum to the pallium. Its occurrence apparently has to do with the origin of the cortico-striatic connections (cf. also W. HERMAN) that may arise from the deeper larger cells of this thickening (P), usually called the piriform cortex, perhaps better called praepiriform cortex (ROSE).

Fig. 8 shows the spherical or rather horseshoelike nucleus (S P.N.) of the archistriatum. It appears however, that also the angulo-striatal cellgroup (A.S.C.) forms part of the archistriatum. Its increase coincides with the decrease of the neostriatum. In this figure (8) the ventrally crowded cells P' of the lateral cortex have gone, but the thicker lateral cortex P remains as far backward as the archistriatum (ROSE's K) with its angulo-striatal nucleus is attached to the cortex<sup>1)</sup> (cf. fig. 8—13). More scattered cells, representing CROSBY's diagonal band (D. B. fig. 9) extend from this cortex into the area parolfactoria.

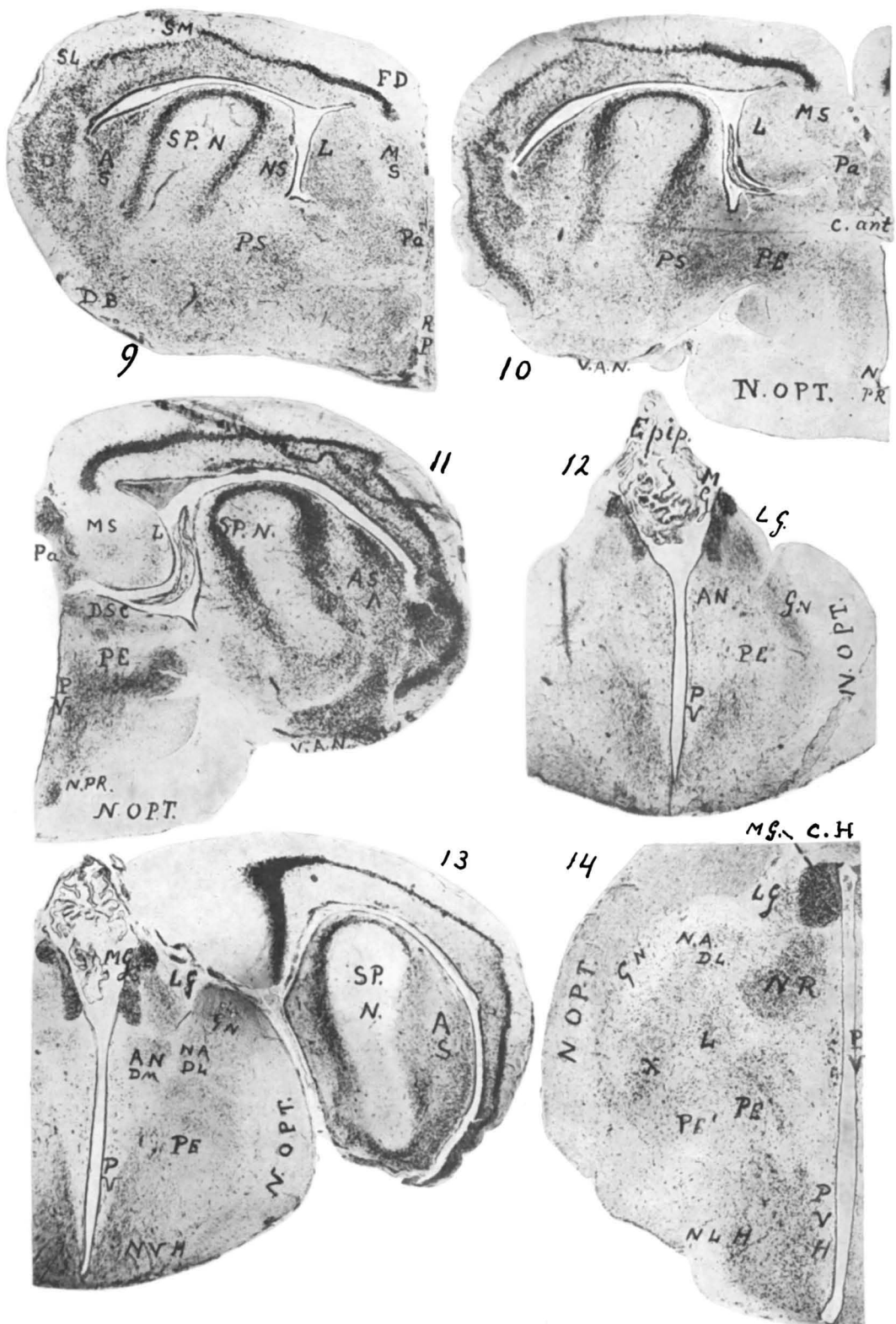
In fig. 8 and 9 the last rest of the neostriatum N.S. is visible, its limit with the archistriatum being indicated by the *archi-neostriatal fissure* (F.A.) occurring also in *Varanus salvator* (KAPPERS) and *Var. bengalensis* (ROSE<sup>2)</sup>). Underneath it the paleostriatum P.S. (ROSE's field H l.c. fig. 23) is seen. Fig. 10 and 11 show its continuity with the peduncular nucleus (P. E.).

In fig. 9—11 in addition to the medial and lateral septum nuclei underneath the medial one another group of cells occurs adjacent to the commissura anterior (c.a.). This is the *paraterminal nucleus* of FREDERIKSE, thus named as it appears right in front of the lamina terminalis. The commissura anterior seems to divide the paraterminal nucleus in a supra- and infra-commissural part, the latter continuing in the dorsal superficial cells (D.S.C. fig. 11) of the tuberculum anterius thalami ventralis of HERRICK (see below).

In fig. 11, in which the lower opening of the spherical archistriatum nucleus is closed a new group of cells occurs underneath it at the basis, the nucleus ventro-medialis of CROSBY and HINES, the ventral amygdaloid nucleus of CAIRNEY which is continuous with the angulo-striatal nucleus

<sup>1)</sup> Also FREDERIKSE in his Atlas of the lizards brain gave a photograph of the connection of the lateral (his piriform) cortex with the large lateral cells of the archistriatum (see his fig. 9). According to HINES the connection of the piriform cortex with the peripheral cells of the neostriatum is a secondary one only arising in a later stage of development in *Sphenodon*.

<sup>2)</sup> Not designated though in his figure 23.



of the archistriatum (cf. FREDERIKSE's cortex lateralis<sup>1</sup>) joining the archistriatum, l.c. fig. 10). In this snake this nucleus is well limited from the lateral cortex.

Where the foramen Monroi opens from right to the left (fig. 11) a large part of the septum continues over the foramen. It seems as if also a part of the paraterminal nucleus continues in the supraforminal septum, together with the caudal continuations of the medial and lateral septum nuclei. A closer examination however shows that the continuation of the paraterminal nucleus in the supraforaminal septum is only scanty, the supraforaminal or fimbrial septum consisting practically only from the medial and lateral septum nuclei, which soon fuse (cf. fig. 13, where this fimbrial part is much reduced).

In fig. 19 I give a sagittal section of the forebrain, showing the relation of the neostriatum (N.S.) and archistriatum, its spherical nucleus (S.P.N.) as well as its angulo-striatal cells. The archistriatum is limited from the neostriatum by the fiss. archi-neostriatica (F.A.N.). Underneath both the area parolfactoria (A.P.) and part of the paleostriatum are seen. Frontally the superpositio lateralis (S.L.) the thick piriform cortex (P) and the thinner, more crowded cells of the ventro-lateral cortex (P') are seen. Somewhat behind the latter, separated from it by a pale spot the nucleus olfactorius lateralis (N.O.L.) of CROSBY.

#### *Diencephalon.*

In the most frontal part of the *diencephalon* on the level of the foramen Monroi in the tuberculum anterius thalami ventralis of HERRICK, we may distinguish some dorsal superficial cells (fig. 11: D.S.C.) from larger deeper cells (P.E.), the latter extending from the telo-diencephalic bridge to the centre of this region bordering there immediately on the periventricular nucleus (P.V.). The deeper cells are the caudal continuation of the paleostriatum (P.S., fig. 10) and remain related to the forebrain peduncle as first described by KAPPERS and THEUNISSEN (1908). More caudally the superficial cells increase in number and gather in the nucleus striae thalamicae dorsalis, which again continues in the lateral cellgroup of the ganglion habenulae (fig. 12 L.G.), the medial group of which (M.G.) consists of more crowded cells (fig. 12). In the same figure a new group of cells (G.N.) appears lying in the concavity of the optic tract lateral to the lateral habenular nucleus and more ventrally. Medially to this *geniculate ganglion*, underneath the gangl. habenulae, the cells form a more or less defined group A.N. which may be homologous to the nucl. anterior thalami of the Lizard (cf. FREDERIKSE) continuing into the nucl. anterior dorso-medialis of HUBER and CROSBY (fig. 13 A.N.D.M.).

<sup>1</sup>) Whether this nucleus may be considered as a derivative of the lower end of the cortex lateralis, I do not know. Miss HINES as well as FREDERIKSE observed connections of this nucleus with the lateral cortex.

This nucleus is smaller and less separated from the rotundus nucleus as in Lizards.

More caudally (fig. 13), the geniculate nucleus becomes less compact extending further medially, but it may be well distinguished from the anterior dorso-lateral nucleus (N.A.D.L.), appearing in these sections (fig. 13 and 14).

Among the peduncular cells of these sections some very large ones occur. The ganglia habenulae are very evident in fig. 13, the lateral nucleus as well as the medial one, the latter showing a constriction in its upper half, due to the bundle of the habenular commissure.

More backward (fig. 14) the lateral habenular ganglion decreases, while the medial one, covered here by the habenular commissure (C.H.), increases. The large more circumscribed *nucleus rotundus* has taken the place of the medial anterior nucleus. In the lateral cell masses of the thalamus two groups may be observed, one consisting of larger cells (G.N.) laying against the optic tract and a larger group of slightly smaller cells medially to it, the nucl. anterior dorso-lateralis (N.A.D.L.) of HUBER and CROSBY (nucl. anterior lateralis of FREDERIKSE, l.c. fig. 15). Another group, ventrally to the latter, wedging in between the suprapeduncular and rotundus nucleus may correspond to the lateral nucleus of DE LANGE and FREDERIKSE (L, not to be identified with the lateral thalamic nucleus of mammals). Laterally to the peduncle (P.E.) itself, there is another group, indicated by X, the character of which is not clear to me. It seems to correspond to FREDERIKSE's nucl. suprapeduncularis (cf. l.c. fig. 17 and 18) but further backward continues into the nucl. of the basal optic tract (cf. my fig. 15 and 16).

The hypothalamus appears in this section and shows a large mass of cells, divided in a lateral (N.L.H.) and medial periventricular group (P.V.H.), the latter being continuous with the large peduncular cells (P.E.).

Fig. 15, a section through the posterior commissure and the subcommissural organ shows, in addition to the thickened ependyma of the latter the more ventral secreting ependymal proliferation (S.E.) described by KAPPERS, CHARLTON and CRAIGIE in other Sauropsida. Cytotectonically this region shows various changes. The nucl. rotundus (N.R.) has become thinner and higher. Whereas in the lizard the greatest diameter of the rotundus nucleus in this region is the horizontal one, here it is the vertical one. In both however its ventro-lateral edge extends further laterally than the dorsal part of the nucleus. The rotundus nucleus is passed laterally by the fasc. retroflexus which is surrounded by the *perifascicular cellgroup*<sup>1)</sup> of HUBER and CROSBY the cells of which are less crowded (P.F.).

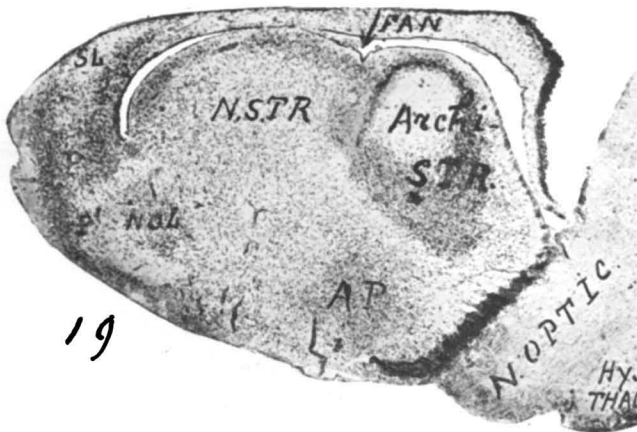
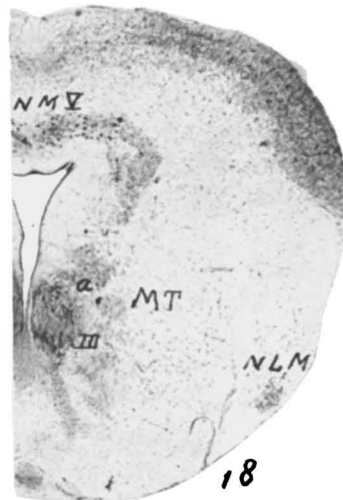
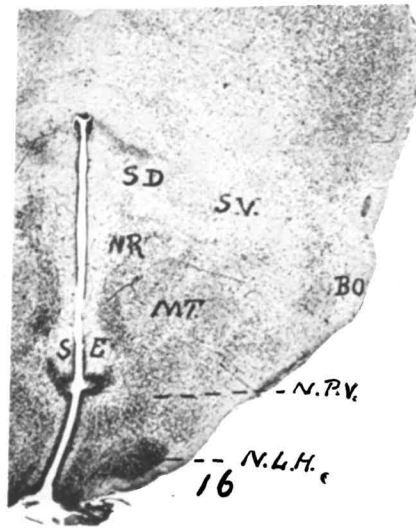
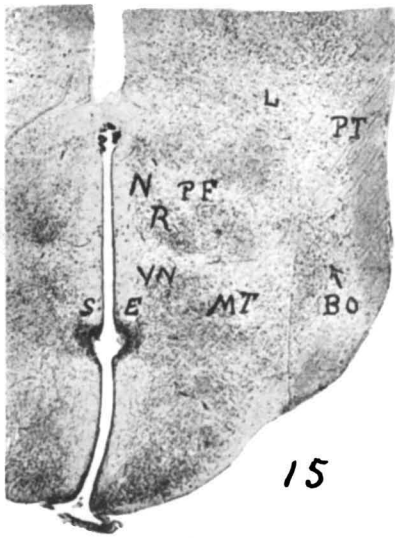
The large periventricular cells, so numerous still in fig. 14, have gone, the periventricular region above the secreting ependyma being quite pale.

<sup>1)</sup> Possibly the perifascicular cellgroup is a more loosely arranged part of the rotundus, its cells being dispersed by the fasciculus retroflexus.



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PLATE III.





Dorsolaterally to this ependymal spot immediately below the nucl. rotundus the cells are more numerous. This cellgroup may correspond to FREDERIKSE's ventral nucleus (V.N.), with which name no homology with the ventral thalamic nucleus is involved. Perhaps it is homologous to the *nucleus centralis a* in the cat as figured by WINKLER and POTTER in their atlas (l.c. plate XI). Especially the relations of this large celled nucleus in the lizard are in favor of this homology. Whether or not it corresponds to the nucl. diagonalis described by HUBER and CROSBY in the Alligator I dare not say.

The reticular cells of the mesencephalic tegmentum have appeared, and this level, (M. T.), more pronounced in fig. 16, marks the beginning of the mesencephalic tegmentum.

In the hypothalamus many cells occur. In fig. 15 they do not show a differentiation in groups as they do more frontally (fig. 14) and caudally (fig. 16). Dorso-laterally to the tegmentum a cellgroup occurs separated from the periphery by the optic fiber tract. This cellgroup (B. O.), related to the cellgroup X in figure 14, is the nucleus of the *basal optic tract*, so conspicuous in *Crotalus horridus americana* and also in this animal. In fig. 15 between this nucleus and the tectum another large celled nucleus occurs: the *nucl. praetectalis*, bordering mediodorsally, under the tectum, on the *lenticiform nucleus* of EDINGER and KAPPERS (L).

Fig. 16 contains the caudal end of the rotundus nucleus (N. R.) next the fasciculus retroflexus. As also the nucleus perifascicularis (P. F. fig. 15) ends here. This seems to prove that the latter really is closely associated with the former.

The posterior commissure is surrounded dorsally and ventrally by cells but only the ventral ones form a real nucleus (S. D.) homologous perhaps to the dorsal or medial spiriform nucleus of the lizard, as described by FREDERIKSE (l.c. fig. 17), but smaller. Laterally (more clearly at the left side of the section) it borders on cells (S. V.) larger as a group than the dorsal spiriform nucleus but less crowded. Whether or not this is the homologue of the ventral or lateral spiriform nucleus is difficult to tell.

The periventricular cells underneath the region in which in the preceding figure the ventral or central nucleus occurred continue along the ependyma (*filiiform nucleus* of WINKLER and POTTER) into the periventricular hypothalamic nucleus (N. P. V.).

These are the main cellgroups of the diencephalon and praetectal region. Comparing them to the lizard, a striking difference is found in the smaller size of the anterior and especially of the rotundus nucleus, the latter of which is the homologue of the ventro-medial group of mammals. Whether this is to be correlated with the lack of extremities in snakes (the ventro-medial nuclear group in mammals being the lemniscus group for the head as well as for the body) is possible, but needs further control. Correlated with the smaller size of this cellgroup in the snake is the relatively smaller size of the neo-striatum in these animals. In *Varanus* (DE LANGE,

W. HERMAN) the neostriatum forms more, in *Crotalus* less than two thirds of the striatal complex. Yet the reduction in the neostriatum is less than in the anterior-rotundus nuclei.

The *midbrain* of this animal shows the same general features as in other Reptiles. Fig. 17 passes through the posterior part of the hypothalamus and shows the caudal end of the basal optic nucleus. Cells of origin (F. L. P. M.) of the medial longitudinal bundle are seen underneath the aquaeductus Sylvii.

Also the nucleus ruber, so well described by DE LANGE is seen in fig. 17 (N. Ru.). In the roof of the midbrain (laterally) a few cells (M. V.) of the mesencephalic trigeminus nucleus are lying. Most of the cells of this nucleus, are crowded in more caudal levels (cf. fig. 18) near the midline, as described by VAN VALKENBURG. Its most caudal group, coinciding with the end of the tectum, only occupies the dorsal midline in which sometimes 15 cells are seen in one section.

In fig. 18 large cells of the oculomotor nucleus (III) are seen and, dorso-laterally to the longitudinal fascicle, the smaller accessory cells of EDINGER—WESTPHAL (a), which however are not as numerous here and do not form such a distinct accessory nucleus as in lizards, *Varanus* especially (cf. KAPPERS).

At the lateral periphery a new cellgroup (N.L.M.) occurs belonging to the lateral lemniscus system: the lateral mesencephalic nucleus, comparable to the semilunar nucleus described in birds by MESDAG, KAPPERS, HUBER and CROSBY.

An interesting feature of this brain is the small size of the ganglion isthmi, that hardly protrudes. As this ganglion is so well developed in *Lacerta* (FREDERIKSE) *Varanus* and still more so *Chamaeleon* (KAPPERS, SHANKLIN) its reduction (as that of the cerebellum) may be due to the simple static relations in snakes, the ganglion isthmi forming the frontal pole of the static area of the oblongata, and establishing a link of this area with the tectum opticum.

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