A STUDY OF THE ANURAN DIENCEPHALON

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TWENTY FIGURES

The group of vertebrates on which the present study is based has profoundly influenced, directly or indirectly, the progress of the biological sciences. The word-wide distribution and abundance of the group, and the ease with which its members are managed, have made these animals especially useful as laboratory specimens.

The present research deals primarily with the diencephalon. Even in such a rather limited area the intricacies of the cellular pattern and fiber connections make it extremely hazardous to reach definite, undisputed conclusions.

This paper would not be complete without an expression of the heartfelt gratitude of the author for the patient guidance, constant encouragement and assistance given to him by Professor E. C. Crosby. To the University of Puerto Rico and to the Horace H. Rackham School of Graduate Studies, the author will be ever grateful for the financial aid which permitted the completion of this study.

MATERIALS

The author has been very fortunate to have at his disposal all the amphibian material contained in the extremely valuable Huber Neurological Collection of the University of Michi-

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gan. Ten series of Rana catesbiana and Rana pipiens, cut in three different planes and stained with toluidine blue and by the Weigert, Weil or pyridine-silver methods, were consistently used as the basis for the research. In addition, two series of Hyla sp., one in transverse and the other in sagittal section and both stained with toluidine blue, were studied. The author prepared three series of the brain of Rana pipiens, all cut in transverse planes and stained with toluidine blue, pyridine-silver or by Weil's method.

From the collection of slides belonging to Dr. C. J. Herrick, some of which were prepared by the late Dr. P. S. McKibben, several other series were, on occasion, studied in search of details lacking in the other material available. Thus, it was possible in almost every instance to check the limits of a given nuclear group or the course of a specific bundle of fibers in various planes and in several kinds of preparations.

REVIEW OF THE LITERATURE

The literature of the amphibian brain, especially that on tailed forms, is fairly abundant. A detailed analysis of all the published accounts which in one way or another are concerned with the amphibian diencephalon would be lengthy without adding to the present description. However, for the sake of completeness, a brief chronological review of the more important contributions will be given. Pertinent references to the literature will be made with the presentation of the results.

The gross aspect of the nervous system of Rana pipiens and some microscopical details of unstained sections of it were given by Wyman in 1853. Reissner (1864), Stieda (1875), Köppen (1888), Edinger (1893) and Ramón (1896) filled in details which were very ably put together by Gaupp (1899) in his excellent book on the anatomy of the frog. The last mentioned author supplemented the earlier work greatly from his own research, so that actually his account may be considered as the line of departure for modern investigators in the field.

During the present century Rubaschkin ('03), Ariëns Kappers and Hammer ('18) and Röthig ('23, '26, '27) have produced papers dealing exclusively with the anuran brain. Outstanding among all contributions are those resulting from the monumental life-time research of C. Judson Herrick which have had a great influence, not only in clarifying the structure of the brain of urodeles but also in the whole field of neuroanatomy. The comprehensive reference book by Ariëns Kappers ('20–'21), particularly in its more recent, up-to-date English version (Ariëns Kappers, Huber and Crosby, '36), has been an invaluable source book throughout the whole investigation.

NUCLEAR PATTERN

Nuclei of the epithalamus

Dorsal habenular nucleus (nucleus parvus of Reissner, 1864; ganglion habenulae of Osborn, 1888; Gaupp, 1899, and others). In three species of anurans the right and left dorsal habenular nuclei are not exactly alike in shape and, to a slight extent, differ in size. For convenience, therefore, they will be considered separately.

Right dorsal habenular nucleus. This nucleus occupies approximately the rostral one-third (R. catesbiana) to one-half (Hyla sp. and R. pipiens) of the dorsal region of the diencephalon. In Hyla sp. it begins rostrally as a cluster of cells close to the dorsal angle of the ventricular wall. Spinalwards it assumes a roughly oval to heart-shaped outline. A band, 3 to 4 cells thick, forms its periphery but the central part of the nucleus is practically devoid of cells. Except for the difference in rostrocaudal extent, the nucleus in R. catesbiana and R. pipiens shows the same characteristics. It is, however, more elongated dorsoventrally in the former amphibian than in Hyla sp. (figs. 3, 4 and 7).

Left dorsal habenular nucleus. In Hyla sp. the nucleus (not figured) begins slightly behind the rostral limit of the dorsal diencephalic region lying dorsal to nucleus dorsomedialis anterior. Caudalward, it is oval in shape with a dense band

of cells forming a rind around a central portion in which a few cells are seen. It soon enlarges and, at about one-fourth of its length, a second portion of the nucleus begins to appear. This lateral division resembles the medial division and replaces the latter at about three-fifths of the way caudad through the habenula. It continues alone until the end of the dorsal habenular region. The same duplication of structure of the left dorsal habenular nucleus has been observed in R. catesbiana (fig. 3) and R. pipiens. However, due to the reduction of the dorsal habenular region in these forms, the second or lateral division of the nucleus is actually seen ventrolateral to the more medially placed anterior portion (figs. 4 and 11). The lateral division, then, appears after the medial is fully formed and extends farther spinalward (figs. 7 and 10). In general, the cells of the dorsal habenular nucleus are medium-sized, oval to round, with coarse granulations. Some cells forming the rind of the nucleus have their processes directed toward the almost cell-free center. In fiber preparations, this center is occupied by medullated and nonmedullated fibers, some coming from other nuclei, others arising from the peripheral band of cells forming the outer part of the nucleus (Gaupp, 1899; Rubaschkin, '03).

It is evident from the above description that the dorsal habenular nucleus in the three species of tailless amphibians studied shows marked asymmetry. The right nucleus is single and not so long as the left. The latter has a medial and a lateral division, and extends farther caudally. Each nucleus is found ventromedial to stria medullaris, between the fibers of the stria and the point where tela choroidea is continuous with the ependyma of the third ventricle.

The dorsal habenular nucleus appears to be somewhat better differentiated in Hyla. In Rana (figs. 3 and 4) it is separated from the ventral by the sulcus intrahabenularis of Herrick ('33). In all cases, it presses against the ventricular wall making a definite elevation inside the ventricle.

Ventral habenular nucleus (subhabenular area, Ariëns Kappers and Hammer, '18; Röthig, '23). In Hyla the first cells of

the ventral habenular nucleus appear just rostral to the beginning of the dorsal habenular nucleus. After the latter nucleus appears, the ventral nucleus is seen as a fairly compact mass of cells dorsal to sulcus subhabenularis or sulcus dorsalis thalami (see Herrick, '17). Because of the asymmetry of the dorsal habenular nucleus, the left ventral habenular nucleus takes a position ventrolateral to the former, but the right ventral nucleus is truly ventral. Both right and left ventral habenular nuclei are about the same size and both may be roughly divided into a medial and a lateral portion. This division is more apparent about halfway through their rostrocaudal extent, the two portions being less distinguishable both rostrally and caudally. As seen in silver preparations of R. catesbiana, this separation of the cell groups of the ventral habenular nucleus into two parts is caused by the fibers of the habenulo-peduncular tract passing downward and backward between them. The medial division of the ventral habenular nucleus lies almost directly dorsal to the subhabenular sulcus. It is small cephalad, enlarges caudally, and tapers off to end about midway of the rostrocaudal extent of the diencephalon. The lateral division, which is actually dorsolateral to it, is fairly large rostrally but then becomes coextensive with the medial, so that for a short distance before its termination no definite boundary can be established between them.

In R. catesbiana the ventral habenular nucleus (figs. 1, 2, 3, 4 and 12) shows more or less the same relations. It extends for one-third of the length of the diencephalon; its caudalmost tip is shown in figure 7. As is the case with the dorsal habenular nucleus, the ventral nucleus is more elongated dorsoventrally than in Hyla, and the separation into medial and lateral divisions is sharper than in the latter form. The lateral division of the right ventral habenular nucleus is shown in part in figure 6. In general, the ventral habenular nucleus of R. pipiens is similar to the one just described, the only difference being that the right nucleus begins rostral to the right dorsal habenular nucleus and is slightly longer than the left ventral

habenular nucleus. The cells of the ventral habenular nucleus are generally large, with fine granulations. They are not packed together but form a loose mass roughly oval to round in cross-section.

The cell masses of the anuran epithalamus, except for the asymmetry noted, can be directly compared with the corresponding groups of Necturus and Ambystoma (Herrick, '17, '33, '35). From the studies of Crosby ('17), Huber and Crosby ('26), Kuhlenbeck ('31) and others, on the reptilian brain, it seems probable that the medial and the lateral habenular nuclei of those forms are equivalent to the dorsal and the ventral nuclei, respectively, of the present account.

Nuclei of the thalamus

In the description of these nuclei the terminology employed by Huber and Crosby ('26) in their account of the thalamus of Alligator mississippiensis, and which has been generally accepted by other authors, has been followed as far as possible.

Nucleus dorsomedialis anterior. This is a rather small group of cells, not over 200 μ in length, wedged in between the ventral habenular and the ventral thalamic regions, in the anterior end of the diencephalon (fig. 1). In Hyla this nucleus appears close to the ependyma of the third ventricle, slightly dorsomedial to the caudal part of the bed nucleus of the hippocampal commissure, which is a well-defined cell mass in the region posterior to the interventricular foramen. The number of its cells increases caudally and the nucleus assumes an oblique position, with its lateral tip more ventral than its medial end. At about three-fourths of the length from its front tip, the ventrolateral part of the nucleus is somewhat obscured by the beginnings of nucleus dorsolateralis anterior. From here spinalwards the latter nucleus increases in size and the dorsomedial nucleus is reduced until, finally, its former position is practically filled by the dorsolateral nucleus. Two species of Rana (figs. 1 to 3) show, in general, the

same relationships. The cells of the dorsomedial nucleus are small to medium-sized and do not stain very densely. Their processes are directed laterally.

The only connections definitely traced to nucleus dorsomedialis anterior are the olfacto-thalamic tract from the bed nucleus of the hippocampal commissure (fig. 10) and the thalamo-habenular fibers to the habenular nuclei (fig. 14). It is interconnected with the anterior dorsolateral nucleus and probably with nucleus rotundus. Possibly some of the fibers of the anterior strio-thalamic tract also reach this nucleus. The nucleus, as described above, forms at least a part of area dorsalis of Röthig ('23, anurans) and of pars optica thalami as that term was employed by Herrick in 1917. The latter author suggested ('33, p. 219) that it is probably the primordium of the anterior dorsomedial nucleus described by Huber and Crosby ('26) in the alligator, and this is apparently the case.

Nucleus dorsolateralis anterior. This nucleus is also short, being approximately the same length as is the dorsomedial nucleus. Whereas the dorsomedial nucleus began medially, near the ependyma, the anterior end of the dorsolateral nucleus is first seen in the lateral part of the field. In all forms studied, it appears either slightly ventral or immediately caudal to the ventrolateral part of the dorsomedial nucleus (figs. 2, 3, 6 and 8). From its beginning the dorsolateral nucleus increases in size both caudally and medially and gradually replaces the dorsomedial nucleus. Where fully developed, the nucleus is approximatey oval in cross-section. Its cells are fairly compact but not heaped together. They are medium to large in size and round in outline. The ventrolateral area of the ventral thalamus lies beneath nucleus dorsolateralis. Ventrolateral to it, near its caudal limit, are the cells of the lateral geniculate nucleus (fig. 3).

Nucleus dorsolateralis anterior is connected with the caudal part of the striatum, and possibly with the anterior entopeduncular nucleus, by tractus strio-thalamicus anterior (fig. 14, tr. str.-thal.). It is interconnected with nucleus rotundus

and nucleus dorsomedialis anterior. The lateral tecto-thalamic tract relates it to the roof of the midbrain. Probably it is equivalent to parts of both area dorsalis and area intermedia of Röthig ('23, '26). It is either a part of the nucleus of Bellonci or the rostralmost tip of the middle area of the dorsal thalamus of Ambystoma and Necturus (Herrick, '35, and elsewhere). Its reptilian counterpart has been described by several workers to whose papers the reader is referred in the Discussion.

Nucleus rotundus (pars media of Röthig, '23, '26; middle area of the dorsal thalamus, Herrick, '33, '35). The cell group thus designated is the largest and most sharply differentiated of the three cell masses forming the anterior part of the dorsal thalamus and may be considered as forming the intermediate area of the dorsolateral nucleus, replacing the latter from lateral to medial as the series are read spinalward (figs. 3 and 4). Nucleus rotundus is an oval to round, dense mass of cells. It is faintly separated from the ventral thalamus by a somewhat cell-free zone extending obliquely in a ventral and lateral direction from sulcus medius thalami (fig. 4) but is still in the dorsal thalamus, the boundary between the dorsal and the ventral thalamus also being oblique. Laterally it is bounded by a thin fiber layer which separates it from the lateral geniculate nucleus. The cephalic end of the nucleus rotundus is bounded dorsally by the cells of the ventral habenular region. Caudally, area subhabenularis appears between the two, forming a cap over the dorsomedial part of nucleus rotundus (left side of fig. 4).

Nucleus rotundus is more dense laterally, so that its medial portion consists of periventricular rows of cells alternating with fibers. The nucleus terminates caudally in a plane passing either through the anterior part or through the middle of the chiasma ridge, depending on the specimen. It has rich connections with the striatum through the intermediate strio-thalamic tract and with the midbrain tectum by the lateral tecto-thalamic (fig. 12) and by other pathways not thoroughly analyzed. Most of the ascending fibers from lower brain cen-

ters end in or around it. It is interconnected with the anterior dorsolateral and dorsomedial nuclei, the subhabenular area and the nuclei of the dorsocaudal part of the thalamus.

Area subhabenularis. In a plane at the level of the caudal one-fourth of the dorsal habenular nucleus, where the lateral portion of the left dorsal habenular nucleus is approximately half the size of the medial portion, a group of cells appears between the ventral habenular nucleus and nucleus rotundus (fig. 4, left side). These cells form the subhabenular area insofar as they lie beneath the habenulae. They extend for a short distance backward, and pass without sharp demilitation into the caudally lying posterocentral nucleus (figs. 6 and 7). The cells are thus wedged between three other nuclear masses. Except for some contributions to the tecto-thalamic and habenulo-tectal tracts, and some fibers to nucleus rotundus, no other connections were traced to this cell group. The area subhabenularis of the present account is not the area of the same name described in anurans by some workers (Ariëns Kappers and Hammer, '18; Röthig, '23) but rather represents, at least in part, pars intercalaris of Gaupp (1899) and Herrick ('17, '33, '35), who in the 1935 paper related it to the dorsal thalamus. Its name was applied to the similarly situated nucleus in the reptilian diencephalon by Huber and Crosby ('26) and others.

Nucleus posterocentralis thalami. This is a very extensive cellular area occupying approximately the caudal one-third to one-half of the dorsal thalamus. It begins caudal to the area subhabenularis (right side of fig. 4) but very soon spreads dorsoventrally filling a much larger space than the latter between the caudal part of the dorsal habenular nucleus and nucleus rotundus (figs. 5 to 8). The last mentioned nuclear mass shifts gradually ventralward and simultaneously the posterocentral nucleus increases in size (fig. 6). Rostrally, nucleus posterocentralis thalami consists of a rather dense cell band extending obliquely so that its ventral part, in contact with nucleus rotundus, is more lateral than its dorsal portion. After the round nucleus terminates, nucleus postero-

centralis assumes a roughly oval shape slanting laterally. Its medial margin has 3 or 4 stripes of periventricular cells. The lateral border forms a more homogeneous mass of fairly large, rounded or oval cells with processes transversely directed. The nucleus is broader in Hyla. Ventrally it rests on the ventrolateral area of the ventral thalamus, from which it can be separated by sulcus medius thalami. Farther spinalward the nucleus is roughly spindle-shaped.

At about one-fifth of its length from its rostral end, a group of cells is seen to accumulate at the dorsolateral border of nucleus posterocentralis, which has been termed nucleus posterolateralis thalami (fig. 5). In levels where the latter nucleus is fully formed, the former nucleus is reduced to a narrow band of cells consisting mainly of relatively undifferentiated linearly arranged cells alternating with fiber bands. Near the termination of the posterocentral nucleus the posterolateral nucleus disappears from the field. The nucleus posterocentralis is reduced dorsoventrally; the space beneath is occupied by the rostral part of the midbrain tegmentum and the posterior commissure appears behind it.

The posterocentral nucleus contributes fibers to the medial strio-thalamic tract. It is related to the tectum and to lower centers by fiber bundles which have not as yet been fully analyzed and probably contributes fascicles to the postoptic commissural system. It belongs to the posterior area of urodeles (Herrick, '33, '35), and possibly represents the nucleus of the same name described by Huber and Crosby ('26, alligator), Cairney ('26, Sphenodon), and others. Röthig's ('23, '26) pars posterior probably includes both the posterocentral and posterolateral nuclei of the present study.

Nucleus posterolateralis thalami. The cell group forming the posterolateral nucleus of the dorsal thalamus first appears in planes through about the rostral one-fifth of nucleus posterocentralis. It is an approximately oval mass placed obliquely along the dorsolateral border of the latter nucleus (figs. 5 to 8). It increases considerably in size as it is fol-

lowed caudalward. As it does so, the posterocentral nucleus is reduced to a thin band of cells on its medial and ventral borders.

The posterolateral nucleus is larger in Rana than in Hyla, perhaps being better differentiated. In both cases it is bounded laterally by the fibers forming the peripheral white layer (stratum medullare superficiale, Gaupp, 1899).

The connections of the posterolateral nucleus are difficult to follow because of the intricate systems of fibers passing to the tectum and to the postoptic commissure from the area it occupies. For this reason it is almost impossible to establish with surety its homologies. As has been pointed out it is a part of the posterior area of urodeles. Herrick in 1935 referred to it in Ambystoma as "an undifferentiated field transitional to the tectum and motor tegmentum. It may contain the primordium of the mammalian metathalamus." As seen in sagittal sections (figs. 6, 9 and 10) the whole posterior region of the dorsal thalamus of anurans slants ventrally, so that its caudalmost tip is just in front of the most ventral cells forming the anterior tectal area. All the region dorsal to the caudal end of the dorsal thalamus and in front of the anterior tectal area has scattered cells in it, but apparently it consists mostly of optic and other types of fibers to the tectum and ascending fibers from the midbrain to the thalamus. Several nuclear masses have been identified in the corresponding region of the reptilian thalamus but their homology with the nucleus described above is uncertain and has to await further knowledge of the course of the fibers involved.

Area ventralis anterior. In both Rana and Hyla the rostralmost portion of the ventral thalamus is visible in a plane passing just caudal to the place where the preoptic recess opens into the third ventricle. It appears medial to the caudal part of the bed nucleus of the hippocampal commissure (fig. 1). Slightly farther caudalward the bed nucleus of this commissure disappears and then the cells of the ventral thalamus form a narrow band running obliquely between the ependyma

of the third ventricle and the amygdaloid area. Directly
dorsal to them are the very last cells of the medial septal
nucleus. Ventrally and caudally are large vesiculated cells
of the same type as seen in the magnocellular portion of the
preoptic region. The cephalic part of the ventral thalamus
thus shows an upward curve, so that for a short distance it
is in line with the dorsal thalamic region (fig. 8). This rostro-
dorsal portion of the ventral thalamus is replaced, after ap-
proximately 200 μ, by nucleus dorsomedialis anterior of the
dorsal thalamus; at the same time it is continuous with the
ventral thalamic region underneath the latter nucleus.

Area ventralis anterior extends caudoventralward under
the dorsomedial nucleus and, farther back, also under the ros-
tral end of nucleus rotundus. The number of vesiculated cells
first increases and then decreases. These cells are inter-
mingled with small, round or oval cells the processes of which,
as of those of the preceding type, are directed laterally. Pe-
ripheral to the anterior ventral area is a round mass, the
anterior entopeduncular nucleus. Ventrally and ventrome-
dially the area is bounded by the most dorsal cells of the
preoptic nuclei (fig. 2). Farther back, as the anterior ento-
peduncular nucleus disappears from the field, its lateral
boundary is formed by fiber tracts, mainly the lateral fore-
brain bundle. As nucleus rotundus makes its appearance, the
dorsomedial tip of the anterior ventral area is somewhat
wedged between it and the ependyma, but borders nucleus
rotundus ventrally (fig. 3). Approximately in the same plane,
and just ventrolateral to the anterior ventral area, a new
group of cells (described below as area ventromedialis) begins
to shape up dorsal to the medial forebrain bundle. From here
on caudalward the anterior ventral area is reduced in size. It
is separated from the ependyma by fibers, probably of the
medial olfacto-habenular system.

The anterior ventral area corresponds to the rostralmost
portion of Gaupp's (1899) pars media from which he and
Herrick ('10, and later) derive the bed nucleus of the hippo-
campal commissure. The latter author, however, applied the

term eminentia thalami to the same region of urodeles and found it reduced in frogs. The relations and position of this cellular area are very similar to those described by Huber and Crosby ('26) for Alligator mississipiensis and it is believed that it is homologous to the similarly designated area of that form.

Area ventrolateralis. This cell group is very indistinctly separated from the caudal portion of nucleus rotundus which it surrounds ventrolaterally. It is seen at a plane passing approximately through the caudal half of the habenular commissure, where the first cells of the subhabenular region come into view. In the same plane, the anterior ventral area forms the apex of a roughly triangular space of which the dorsolateral angle is formed by the cells of the ventrolateral area and the ventromedial angle by area ventromedialis (see below). The cells of area ventrolateralis are small, mostly round, arranged more or less in vertical rows with the processes transversely oriented. This cell mass grows considerably in size caudally, some of its more medial rows of cells reaching the ependyma (fig. 4). From its very beginning the area is bounded laterally by a somewhat cell-free zone, lateral and dorsal to which are the neurons forming the lateral geniculate complex. However, farther back the fiber layer is reduced, so that the ventromedial cells of the lateral geniculate are in contact with, and very indistinctly separable from, the lateral border of area ventrolateralis (fig. 5). At the same time, with the disappearance of the anterior ventral area the ventrolateral group extends medially to the ependyma, although this medial portion is made up of vertical rows of cells alternating with fibers and perhaps may be better considered as undifferentiated periventricular gray. Behind the plane of nucleus rotundus, the region dorsal to the ventrolateral area is occupied by nucleus posterocentralis (fig. 6). For a considerable distance there is very little change in the relationships of the different nuclei. At about the level of a plane passing through the caudal part of the chiasma, the lateral geniculate complex disappears. The ventrolateral

area continues for a short distance ventral to nucleus postero-
centralis, and then the whole ventral thalamic region passes
over into the tegmentum of the midbrain (fig. 6).

The ventrolateral area is probably the same as the area
externa of pars ventralis described by Röthig ('23). It cer-
tainly corresponds to the description given by Ariëns Kap-
pers ('20-'21) to a similar area in Crocodilia, from which the
term has been adopted. Probably it includes area triangularis
of Huber and Crosby ('26), Papez ('35) and others.

Area ventromedialis. This area forms a more or less round
mass of rather sparsely scattered but large vesiculated cells
(fig. 6) situated somewhat lateral to the anterior ventral
area, from which it is separated by fibers (fig. 3). Area ven-
tromedialis has a position dorsal to the medial forebrain bun-
dle (left side of fig. 4). Shanklin ('30) used the same name
for a cell mass similarly located in Chameleon vulgaris.
Papez ('35) called a comparably placed group nucleus supra-
peduncularis in Chelone midas.

The ventromedial area is bounded dorsally and dorsolater-
ally by area ventrolateralis where the latter appears (figs. 4
and 5). The dorsolateral tip of the medial preoptic nucleus
is medial to the ventromedial area, which in general is of
small diameter as seen in cross-section. Its cells are small
with some of the processes directed dorsoventrally. After the
anterior ventral area disappears, the ventrolateral area seems
to occupy all of the field. Farther back, however, area ven-
tromedialis is seen again, its medial portion formed by the
undifferentiated, periventricular type of arrangement of cells
and fibers mentioned in connection with the ventrolateral
area. Finally, the whole region assumes the same general ap-
pearance at about the level of the caudal part of the chiasma
ridge. In this plane it is not possible to distinguish between
lateral and medial ventral areas. The whole ventral tha-
lamic region is prolonged caudalward in this fashion to the
plane where the posterior recess (infundibular recess) opens
into the third ventricle. Here the gray of the ventral thalamus

is in the shape of a fan with its neurons arranged in rows running dorsomedially. Shortly behind this level the tegmentum of the midbrain begins.

Corpus geniculatum laterale. It is probable that even in Anura there are two different parts to the lateral geniculate body. The dorsal nucleus of the lateral geniculate is both dorsal and rostral in position. It is first seen dorsal to the anterior entopeduncular nucleus and lateral to nucleus dorsomedialis anterior, where it lies in the region medial and slightly ventral to the place where the caudal part of the hemisphere is about to become free from the diencephalon (fig. 2). It consists of a few bipolar, medium-sized cells arranged roughly in a row parallel to the periphery. It is bounded laterally and dorsally by the lateral cortico-habenular fibers. As the hemisphere wall separates from the diencephalon and the last mentioned tract joins stria medullaris, the cells of the dorsal nucleus approach the periphery (figs. 3, 9 and 12). Medial to them are fibers of the lateral olfacto-habenular tract which separate the nucleus indistinctly from nucleus dorsolateralis anterior. The field ventral to the dorsal nucleus begins at this plane to show the most anterior cells of the ventral nucleus of the lateral geniculate. Both dorsal and ventral nuclei are seen for a short distance in the same transverse plane, the former lying lateral to nucleus dorsolateralis anterior and the latter situated lateral to the ventrolateral part of nucleus rotundus. As the anterior dorsolateral nucleus is replaced by nucleus rotundus, the ventral nucleus of the lateral geniculate spreads upward. Actually, no line can be drawn separating the dorsal from the ventral nucleus at this level, but the cells of the latter are smaller and more compactly arranged. Caudal to this level only the ventral nucleus, which is larger both in number of cells and extent, is present.

The dorsal nucleus of the lateral geniculate receives a slender fascicle of fibers from the axial bundle of the optic tract (figs. 9 and 12) and is connected with the tectum. It is the same as Bellonci's (1888) nucleus anterior superior

corporis geniculati thalami, a term also used by Herrick in 1917 (p. 243) for this cell group in Necturus and the frog, and in 1925 for it in Ambystoma. From its relations to the other nuclei and fibers of the area, it appears to correspond to the differentiated lateral part of nucleus dorsolateralis anterior of Huber and Crosby ('26, fig. 6 b) about which they say (p. 124) : "This extension occurs as the optic tract, on its way to the tectum, swings lateral to the nucleus. The cells in the extension, while obviously of the same type and apparently belonging to nucleus dorsolateralis anterior, exhibit a certain massing which is suggestive of future nuclear differentiation. Furthermore this region appears to receive terminal fibers and collaterals from the optic tract. This differentiated portion of the nucleus dorsolateralis anterior may be forecasting an optic thalamic center of higher forms." Papez ('35) described a nucleus ovalis in the turtle (Chelone midas) which he related to nucleus anterior superior geniculati thalami described by Bellonci and Herrick, and to nucleus ovalis of Huber and Crosby and others. The oval nucleus which Huber and Crosby described in their 1926 paper, however, does not receive optic tract fibers, whereas the lateral extension of nucleus dorsolateralis anterior has such connections. Addens, in two papers on the homologies of the so-called nucleus of Bellonci in reptiles and mammals ('38) and selachians ('46), compares it with the oval nucleus of Huber and Crosby. To this the same objection may be raised, although Addens' nucleus of Bellonci is probably the same which Papez ('35) called nucleus ovoidalis.

The ventral nucleus, just caudal to the habenular commissure and in the rostral one-third of the chiasma, occupies a position lateral to nucleus rotundus (fig. 4). The diencephalic wall has here a low outward protuberance covered externally by the caudal pole of the hemisphere which contains the ventral nucleus of the lateral geniculate. Ventral to it is the small round group of cells forming the posterior entopeduncular nucleus. Superficially there are optic tract fibers, possibly of optico-geniculate character (fig. 9). At the be-

ginning of the posterocentral nucleus the ventral part of the lateral geniculate surrounds nucleus rotundus both laterally and ventrally (fig. 8) and comes in contact with the ventrolateral area, from which it is inseparable from here to its termination. At this same level, the peripheral white layer has increased in size and the posterior entopeduncular nucleus moved farther ventrally. The cells of the ventral nucleus of the lateral geniculate are roughly laminar in arrangement, although there is no wide fiber layer between them. Their processes extend for the most part in an obliquely dorsoventral direction. However, a few fibers, especially those more medially placed, have a transverse orientation. Farther caudal, the upper part of the nucleus is more clearly demarcated by fibers from nucleus posterocentralis. Gradually the ventral nucleus of the lateral geniculate begins to decrease in size. It is always in contact ventromedially with area ventrolateralis (left side of fig. 5). Its upper portion terminates first, the inferior part disappearing at about a plane passing through the caudal chiasma region. Roughly, the ventral nucleus of the lateral geniculate extends throughout the cranial half of the diencephalon, whereas the dorsal nucleus occupies only the rostral and dorsal fifth of this space. The ventral nucleus of the lateral geniculate corresponds to the lateral geniculate body as described by most authors. Its probable homology with the mammalian ventral nucleus has been suggested by Cairney ('26), Le Gros Clark ('32a) and Herrick ('33).

Nucleus entopeduncularis. The name as used here is applied to cells which lie either directly in the path of, or adjacent to, the two main divisions of the lateral forebrain bundle. Nucleus entopeduncularis is sharply divisible into an anterior, more dorsomedial portion and a posterior, more extensive ventrolateral group.

The anterior entopeduncular nucleus (fig. 1) begins just caudal and slightly ventral to the amygdaloid area. In a plane passing rostral to the chiasma, it is a roughly round, dense mass of cells partially split dorsoventrally by fibers (fig. 2).

It is located above the dorsolateral tip of the medial preoptic nucleus, lateral to the anterior ventral area and ventral to the dorsal nucleus of the lateral geniculate. Peripherally it is bounded by a white layer. In a cross-section of R. pipiens stained by Weil's method, it lies directly among the fibers of the dorsal division of the lateral forebrain bundle. Below and slightly lateral to it are the fibers of the ventral division of this bundle. It ends approximately at the level of the beginning of the chiasma ridge.

The anterior entopeduncular nucleus is referred to by Gaupp (1899) in- his description of the basal (lateral) forebrain bundle as an especially abundant cell mass back of the interventricular foramen associated with the commissural portion of the bundle. It is the bed nucleus of the decussation of the lateral forebrain bundle of Herrick's description of Ambystoma ('27), and, probably, corresponds to the nucleus of the dorsal supraoptic decussation described by Huber and Crosby ('26) in the alligator. The last mentioned term has been used by other workers on reptilian brains, including Papez ('35) who, however, stated that it corresponds ''with the nucleus labeled entopeduncularis by de Lange ('13) in Testudo graeca in his figure 32.'' The term employed by de Lange has therefore the priority.

The posterior entopeduncular nucleus is associated with the ventral division of the lateral forebrain bundle. Practically throughout the whole course of this bundle in the diencephalon, cells can be seen among its fibers, especially among those more dorsally placed. However, in a cross-section passing caudal to the habenular commissure, a group of cells begins to shape up below the ventral nucleus of the lateral geniculate and slightly ventrolateral to area ventrolateralis (fig. 4). These cells are just above the ventral division of the lateral forebrain bundle and close to the periphery. Farther caudalward the cells form a rounded group, although they are not so compact as those in the anterior entopeduncular nucleus. Still farther back, the cells are scattered, some located within the dorsolateral part of the bundle, others lat-

eral and dorsal to it (fig. 5). In this position they are very similar to the ento- and juxtapeduncular nuclei described and figured by Ariëns Kappers and Hammer ('18) for R. catesbiana. The group dwindles and reappears a few times, the cells among the fibers increasing as those outside decrease in number. Later a discontinuous ring of cells forms around the bundle, the whole structure being very diffuse as the midbrain level is reached. Horizontal sections of R. catesbiana stained for cells show both the anterior and the posterior entopeduncular nuclei and their relations.

Gaupp (1899) applied the term nucleus ventralis thalami to the rostral portion of the posterior entopeduncular nucleus, from which he believed the basal (lateral) forebrain bundle received fibers. Papez ('35) described the posterior entopeduncular nucleus in turtles and traced its homology in other reptiles.

Nuclei of the preoptic region and the hypothalamus

The terminology for the nuclear configuration of these areas has been adopted from the paper by Crosby and Woodburne ('40). Most of the findings agree with the report of these authors, so that the nuclei will be considered only very briefly. The description applies to R. catesbiana and Hyla. The only noticeable difference between the two is that the latter shows a greater migration of the cellular elements toward the periphery.

Nucleus periventricularis preopticus. This nucleus begins at the rostral end of the preoptic recess and then forms the most internal portion of the cells surrounding it (fig. 1). The neurons are arranged in 3 or 4 vertical rows bounded laterally by the uniformly scattered gray of the medial preoptic nucleus. In sections passing through the rostral portion of area ventralis anterior of the ventral thalamus, the periventricular preoptic nucleus begins to be replaced by the magnocellular preoptic nucleus. Caudal to the latter, in sections passing through the middle of nucleus rotundus, the peri-

ventricular preoptic nucleus reappears and continues back-
ward, decreasing in size as it does so, to the top of the
chiasma ridge (figs. 3 to 6).

Nucleus magnocellularis preopticus. This nucleus is
bounded both in front and behind by the periventricular
preoptic nucleus (fig. 6). It is found approximately one-third
of the way back from the rostral end of the preoptic area and
occupies only about one-fourth of the rostrocaudal extent of
the region (fig. 2). The large cells forming this nucleus were
seen also in area ventralis anterior, and, farther back, in area
ventromedialis (fig. 3). Nucleus magnocellularis preopticus
is a very conspicuous group, easy to identify in R. catesbiana
and R. pipiens but not so sharply defined in Hyla. In the last
mentioned specimen the cells are not very large and are more
or less intermingled with the medial preoptic gray, which in all
forms studied bounds the nucleus laterally.

Nucleus preopticus medialis. In sections slightly behind the
anterior portion of the preoptic recess, the gray forming the
medial preoptic nucleus appears lateral to the periventricular
preoptic nucleus (figs. 1 to 5). This gray is a rather broad,
homogeneous band of cells which increases in size dorsoven-
trally as the recess joins the third ventricle. Its lateral mar-
gin is irregular and forms the medial boundary for the cell-
free zone called the lateral preoptic area where fiber systems
run. The medial preoptic nucleus has a dorsolateral extension
which abuts against the ventromedial area. The nucleus is
present throughout the whole length of the preoptic region.
As the anterior hypothalamic region is approached over the
chiasma ridge, the nucleus is reduced in size and lies above
the rostral end of the ventral hypothalamic gray.

*Ventral hypothalamus. Anterior portion of the ventral hy-
pothalamic area.* In planes passing through the crest of the
chiasma ridge, Crosby and Woodburne ('40) located a dif-
ferentiated portion of the ventral hypothalamus which they
called nucleus suprachiasmaticus. This nucleus could not be
delimited in the available material and the general term of
anterior portion of the ventral hypothalamic area has been

given to the gray surrounding the ventral tip of the third ventricle (fig. 5). The caudal part of the preoptic gray overlies the cells of this rostralmost portion of the hypothalamus.

Nucleus periventricularis arcuatus. A short distance caudal to the above described area, the cells of the periventricularis arcuatus are arranged in two groups. There is a more medial group consisting of a single, somewhat discontinuous row of cells bordering the ependyma of the recess, and a broader lateral band of cells parallel to but external to the medial group. The thin strip of cells has a short extent, but the lateral band can be traced back to the caudal end of the infundibulum (figs. 6, 15 and 16).

Medial hypothalamic gray. At the rostral end of the infundibular recess there is a thin band of cells which runs almost parallel to the periventricular arcuate nucleus, and, swinging medially, is continuous with it ventrally. The neurons at the dorsolateral tip of this row of cells are more numerous, and the whole is separated from the arcuate nucleus by fibers. This is faintly shown but not labeled in figure 16, which was taken caudal to the plane referred to above. The arrangement is probably indicative of a lateral migration of the cells and the group extends but for a short distance. It is possible that this gray is the precursor of the medial hypothalamic area.

Dorsal hypothalamus. Beginning slightly caudal to the anterior end of the ventral hypothalamus, in transverse planes cutting through the caudal part of nucleus posterolateralis of the dorsal thalamus, the dorsal hypothalamic region is wedged between the ventral thalamus and the periventricular arcuate nucleus (figs. 6 and 16). From this point it extends back to the tegmentum of the midbrain. For the greatest part of its rostrocaudal extent, it is separated from the ventral hypothalamus by the intrahypothalamic sulcus and from the ventral thalamus by the thalamo-hypothalamic or ventral thalamic sulcus. The separation of the dorsal hypothalamic area into specific nuclear groups is rather difficult. It was possible, however, to recognize the elements forming

the primordia of some of the cell masses present in higher forms. The localization of these groups agrees with that of Crosby and Woodburne ('40) and their paper should be consulted for details.

FIBER CONNECTIONS

Stria medullaris

For convenience, the fiber tracts described herein comprise not only those belonging to the medullary stria proper, but also all the habenular connections which were identified in this study. A short summary of the tracts forming the stria is given at the end of this section. Most of the habenular connections have been previously described under different names by earlier workers. The comprehensive treatise by Ariëns Kappers, Huber and Crosby ('36) offers the best account of them and the terms employed in the description which follows have been adopted mostly from their text and from the various papers by Dr. C. J. Herrick including his recent book ('48) "The brain of the Tiger Salamander." The origin or termination of some of the tracts, which have been occasionally assigned to a specific cell group, are given tentatively and require verification by experimental methods.

Medial cortico-habenular tract. This tract of thinly medullated fibers passes from the primordium hippocampi into the stria medullaris caudal to the interventricular foramen (figs. 10, 13, and 17). Some fibers from the same region apparently relay in course in the bed nucleus of the hippocampal commissure.

Septo-habenular tract. In accordance with the account of Ariëns Kappers, Huber and Crosby ('36) fibers from the medial septal nucleus run laterally, ventrally, and caudally to join the stria.

Lateral cortico-habenular tract (Herrick, '10, and elsewhere). Fibers coming from the primordial piriforme and the more caudal part of the primordial general cortex collect at the lateral surface in the caudal region of the hemisphere.

From there they swing ventromedially and then dorsally at the place where the hemisphere wall and the diencephalon are about to separate (fig. 9). Some of the fibers cross immediately to the other side, forming the dorsalmost bundle of the habenular commissure (fig. 14). This crossing represents the so-called commissura superior telencephali (Ariëns Kappers and Hammer, '18; Röthig, '26). Other fibers from the primordium piriforme enter the dorsal habenular nucleus. Some of these fibers are collaterals of the commissural fibers. This tract is nonmedullated.

In cross-sections passing through the rostral part of the striatum a group of fibers is seen accumulating in the limiting zone between it and the overlaying piriform cortex. The fibers run medially and then ventrocaudally just lateral to the ependymal wall of the lateral ventricle, then, farther caudally, cross among the striatal cells to the ventral surface of the hemisphere wall. Here, in planes passing through the precommissural field, they are lost among the fibers of the lateral cortico-habenular and anterior olfacto-habenular tracts. Whether these fibers reach the habenular region is uncertain, but undoubtedly they are similar to the anterior lateral cortico-habenular tract described by Crosby ('17) and Huber and Crosby ('26). Although no nucleus of the lateral olfactory tract has been identified as such in the material studied, the piriform connections and the course followed by these fibers suggest their possible homology with the reptilian tract.

Anterior olfacto-habenular tract. Horizontal sections of the brain of R. catesbiana show that from the ventral, lateral and dorsolateral parts of the anterior olfactory nucleus, and to a small extent from the olfactory bulb, thinly medullated fibers pass caudally (fig. 9) to run with the lateral cortico-habenular tract before it enters stria medullaris (fig. 14). The fibers arising from the ventral part of the nucleus pass caudalward along the ventral surface of the hemisphere to the caudal pole where they swing dorsomedially to join the lateral cortico-habenular fibers (figs. 18 and 19). The fibers arising from the dorsolateral portion of the anterior olfac-

tory nucleus swing laterally and then follow a ventrocaudal
course paralleling the fibers of the lateral cortico-habenular
tract, which they join near the posterior pole of the hemi-
sphere. Between these two systems of fibers there is an in-
termediate group which arises from the lateral part of the
anterior olfactory nucleus and from the olfactory bulb. It
runs external to the lateral cortico-habenular tract and, turn-
ing around the caudal pole of the hemisphere, accompanies the
other tracts into the stria medullaris. There is very little
difference between this tract and the one described by Her-
rick ('27, '33) for Ambystoma and Necturus.

Amygdalo-habenular fibers. Fibers from the amygdaloid
area to the habenular region can be divided into two groups.
The more rostral fibers swing dorsally and medially to enter
stria medullaris. Slightly farther caudal there are other
amygdalo-habenular fibers (fig. 10) which, either before or
after crossing in the interamygdaloid commissure, pass di-
rectly to the habenular nuclei, apparently to its ventral nu-
cleus. The first group originates with the fibers of stria
terminalis, forming a component of it which joins the medul-
lary stria (figs. 13 and 17). The second group is a direct
amygdalo-habenular system. Taken together, these connec-
tions represent the tractus amygdalo-habenularis of Necturus
(Herrick, '33). In reptiles, however, only the component of
the terminal stria reaches the habenula (Cairney, '26, in
Sphenodon; Shanklin, '30, in Chameleon). So far as amygdalo-
habenular connections are concerned, the anurans occupy a
position intermediate between that of the urodeles and that
of the reptiles.

Medial olfacto-habenular tract. The rostral portion of the
periventricular preoptic nucleus sends unmedullated fibers
dorsally close to the ependyma of the ventricle to end in
the medial division of the ventral habenular nucleus (fig. 14).
From the medial preoptic nucleus fibers run laterally and then
anteriorly and dorsally to join the stria medullaris with which
they enter the dorsal habenular nucleus (figs. 10 and 14).
Thus, there are two possible routes for impulses passing from

the anterior preoptic region to the habenulae, the more medial one forming a periventricular system which ends directly in the ventral habenular nucleus; the intermediate route passing among the cells of the ventral and dorsal thalami medial to the lateral forebrain bundle to join the stria medullaris. The same division can be worked out in Necturus following the description of the medial olfacto-habenular tract given by Herrick ('33, p. 207). It was also observed and described in some turtles by Crosby and Woodburne ('40).

Lateral olfacto-habenular tract. From the medial preoptic nucleus and from the magnocellular preoptic nucleus medullated fibers run ventrolaterally to pass around the outside of the lateral forebrain bundle (figs. 14, 15, and 17). Some of the more caudal fibers slant dorsorostrally and after spreading out among the cells of the ventral nucleus of the lateral geniculate enter the stria medullaris (fig. 10). This tract is larger than either division of the medial olfacto-habenular and some of its fibers seem to cross to the contralateral dorsal habenular nucleus.

Thalamo-habenular fibers. This system of fibers has been variously described by workers (Ariëns Kappers and Hammer, '18; Röthig, '26; Herrick, '10) on the amphibian brain as sometimes coming from the ventral thalamus and sometimes from the dorsal thalamus. However, in pyridine-silver preparations of the brain of R. catesbiana, a more or less diffuse group of fibers courses between the anterior dorsomedial nucleus and the habenular region (fig. 14). The fibers are of medium medullation and enter both ventral and dorsal habenular nuclei. It is possible that some may cross to the other side. This agrees with Herrick's accounts in 1933 and 1948.

Hypothalamo-habenular fibers. These fibers form a part of an intricate system bordering the ependymal lining of the third ventricle, the periventricular system (figs. 14, 15, and 18), and coursing among the more medial cells of the thalamus. They arise from the region of the dorsal hypothalamus in scattered bundles. After they have passed the ventral tha-

lamus they collect close to the ventricular wall and in this position run dorsalward and forward to enter the ventro-medial side of the dorsal habenular nucleus. Before they reach the latter nucleus they are intermingled with the me-dial fibers of the medial olfacto-habenular tract. Fibers of hypothalamic origin were described by Crosby and Wood-burne ('40) as part of their medial olfacto-habenular tract, but whether they are comparable to the hypothalamo-habenu-lar system described here requires further investigation.

Habenulo-peduncular tract (Köppen, 1888; Gaupp, 1899, and others). The fibers of this tract, which are chiefly medul-lated but in part are unmedullated, come only from the ventral habenular nucleus (figs. 10 and 12). As they run ventrolat-eralward and caudalward they separate the cells of the ventral nucleus into a lateral and a medial group (fig. 15). As the fi-bers reach the caudal and ventral aspect of nucleus rotundus, they become intermingled with the lateral forebrain bundle. However, they pass obliquely through the bundle to reach the interpeduncular region of the midbrain, where they end, ap-parently, after crossing (Gaupp, 1899; Ariëns Kappers and Hammer, '18).

Habenulo-tectal tract (tractus ganglii habenulae ad mesen-cephalon, Edinger, 1893). Horizontal sections passing through the habenular region show a considerable number of fibers which come from most of the ventral surface of the habenular nuclei as well as from the caudal aspect of the dorsal habenu-lar nuclei (figs. 10 and 11). These fibers, partly medullated and partly unmedullated, pass almost straight back through the dorsomedial part of the posterocentral nucleus to reach the region of the posterior commissure. Some of the fibers cross in the commissure, but others continue behind it, al-though it was not possible to determine their exact termina-tion. Possibly some end in pretectal areas just back of the commissure.

The last two tracts are probably the main efferent paths from the habenular region, bringing into synaptic relation-ship the latter region with both tectum and tegmentum of the

midbrain. The prinicipal afferent (figs. 10 to 12) connections are those which make up stria medullaris. This bundle (fig. 14) is first seen at the tele-diencephalic junction, immediately in front of the interventricular foramen. In this position it contains medial cortico-habenular, septo-habenular and amygdalo-habenular fibers (see also the description of the stria terminalis). Slightly back of this plane the stria is joined by part of the lateral cortico-habenular and by the anterior olfacto-habenular tracts. The medullary stria then crosses to the forward end of the diencephalon where it occupies the dorsal tip of the epithalamus. Immediately it begins to receive fibers from the lateral and medial olfacto-habenular tracts. Some amygdalo-habenular fascicles, the periventricular fibers of the medial olfacto-habenular tract, the thalamo-habenular, and hypothalamo-habenular tracts do not enter the stria medullaris, so far as it could be determined, but end directly in the habenula. It is very probable that there are short internuclear fibers between the ventral and dorsal habenular nuclei. The central, almost cell-free, space within the dorsal habenular nucleus is a possible place of synapse for these internuclear fibers with the processes of the peripheral rind of cells forming the nucleus and with collaterals or terminal fibers of the incoming tracts (Rubaschkin, '03).

Medial forebrain bundle

This is one of the two great systems of fibers connecting the telencephalon with the middle and ventral diencephalic fields. Caudal to the olfactory bulb fibers of the medial forebrain bundle begin to collect along the periphery of the medial wall of the telencephalon. These myelinated fibers are arranged in two fairly distinct groups, each of which starts in a more or less definite area. One group of fascicles runs just inside the medial surface of the hemisphere; the other closer to the medial ventricular wall (figs. 18 to 20). Fibers of the medial division are seen in parasagittal sections arising from practically the whole rostrocaudal extent of primordium hippocampi. They form a broad sheet of fibers coursing ventro-

caudal to the precommissural area. In transverse sections through the hippocampal region some vertically running fibers are seen close to the medial surface of the hemisphere wall. Some of these fibers end among the cells of the medial septal nucleus and are believed to represent tractus olfactorius septi of Ariëns Kappers ('20–'21).

Fibers from the medial septal nucleus join the hippocampal fibers, the two together forming the medial division of the medial forebrain bundle, as they will be called hereafter (faisceau cortico-medialis of Ramón, 1896; pars posterior of Röthig, '26). This division is seen in cross-sections dorso-medial to the lateral septal nucleus. From here it proceeds caudalward. It undergoes a partial decussation in the anterior commissure (fig. 20), the crossing taking place rostral and ventral to that of the lateral division. It also lies rostral and ventral to the interventricular foramen. Crossed and uncrossed fibers enter the more dorsomedial side of the lateral preoptic area (fig. 14). They continue spinalward and, as the chiasma region is reached, they interlace with the fibers crossing in that field. They are shown as white longitudinal stripes in figure 10. Sagittal sections show that most of the fibers enter the infundibular region where they distribute to the periventricular arcuate nucleus. This is also shown in figures 15 and 16. Not all the fibers can be accounted for in this way; some of them probably pass on caudalward among the cells of the dorsal hypothalamus and perhaps to the tegmentum of the midbrain (fig. 10). The fibers seen closer to the ventricular wall of the hemisphere are best observed in horizontal sections passing below the primordium hippocampi (figs. 19 and 20). They originate from the ventromedial and the dorsomedial parts of the anterior olfactory nucleus. After collecting caudal to this nucleus, they run almost straight spinalward. They get some contributions from the accessory olfactory bulb, as seen in more ventral planes. Farther back, fibers from the lateral septal nucleus and probably from nucleus accumbens are added. All of these fascicles form the lateral division of the medial forebrain bundle

as it will be referred to hereafter (faisceau olfactif commissural of Ramón, 1896; pars anterior of Röthig, '26). Transverse sections through the precommissural field show this division as a rounded bundle lateral to the obliquely cut fibers of the medial division. On reaching the anterior commissure, the majority of the fibers cross over to the contralateral side rostral and slightly ventral to the amygdaloid commissure (figs. 13 and 20). Most of the fibers from the accessory olfactory bulb do not cross but, together with a few fibers from the ventromedial anterior olfactory nucleus, turn laterally to end, at least in part, in the amygdaloid area (shown but not labeled in fig. 20). The fibers ending in the amygdaloid area constitute an olfacto-amygdaloid tract. They are the lateralmost fibers of the lateral division, running practically next to the medial ventricular wall.

Crossed, and some uncrossed, fibers of the lateral division of the medial forebrain bundle enter the dorsolateral part of the lateral preoptic area (fig. 14). Here they lie medial and slightly ventromedial to the lateral forebrain bundle. They terminate among the cells of the medial preoptic and probably in the periventricular preoptic nuclei. To reach their terminations they interlace with the longitudinally running fibers of the medial division. Farther back, fibers of the lateral division end in the anterior part of the ventral hypothalamus (fig. 10).

The medial forebrain bundle has been described in the literature under a variety of names. Gaupp (1899) was probably the first to use the present term for the anuran bundle. In 1917 Herrick described it in Necturus and traced some of its fibers to the midbrain tegmentum in addition to fascicles to the hypothalamus. From its origin and distribution, the lateral division of the medial forebrain bundle appears to be homologous with the reptilian medial forebrain bundle of the literature (Crosby, '17; Shanklin, '30, and others) whereas the anuran medial division of the medial forebrain bundle is recognized in reptiles as a separate fascicle forming a part

of the fornix system (see the '26 paper by Huber and Crosby, p. 147, for a list of references which supply additional evidence for this comparison).

Stria terminalis

From the anterodorsal part of the nucleus amygdala, fibers pass medially accumulating dorsal to the crossed component of the lateral forebrain bundle and ventral to the hippocampal commissure (fig. 13). Slightly behind the latter commissure some of these fibers swing dorsally to join the medial cortico-habenular tract (figs. 10 and 17), in the medullary stria. These fibers represent, therefore, the terminal stria component to stria medullaris (Ariëns Kappers, Huber and Crosby, '36) and were described with the last mentioned system. At the same levels there are loose, unmedullated fibers between the two amygdalae (figs. 13 and 18, com. amygd.). They run ventral to the hippocampal commissure and somewhat intermingled with the crossed component of the lateral forebrain bundle, and probably represent commissura interepistriatica of Ariëns Kappers and Hammer ('18) or commissura amygdalarum of Herrick ('33).

Other fibers from the anterodorsal amygdala follow a downward and medial course (fig. 18, str. term.) to join a second group coming from medial and ventral areas of the same cell mass. This last mentioned group was described by Herrick ('21) as forming the dorsal olfactory projection tract. It is believed preferable, however, to consider them as a part of the terminal stria, since both groups originate from practically the same area. After the two components join, the tract so formed passes to the dorsomedial border of the lateral forebrain bundle, where either together with the latter, or with the lateral division of the medial forebrain bundle, it runs back to the crest of the chiasma ridge. At this level the fibers of stria terminalis pass ventromedially to end among the cells of the anterior part of the ventral hypothalamus (fig. 15). The tract probably corresponds to the preoptic por-

tion of stria terminalis (Crosby, '17, alligator) and to both tractus amygdalo-hypothalamicus anterior and tractus amygdalo-hypothalamicus medialis of Cairney ('26) in Sphenodon.

Lateral forebrain bundle

The lateral forebrain bundle of anurans was identified first by Reissner (1864) who referred to it as a circular bundle of longitudinal fibers. It was also described in some detail by Gaupp (1899) and, more recently, by Röthig ('26, '27). It is a system of ascending and descending fibers joining the striatal areas of the hemispheres with the dorsal thalamic region of the diencephalon and with the tegmentum of the midbrain. The material at hand does not permit the establishment of the direction of conduction of the different components of the bundle. Consequently, the terminology employed in naming these components has no definite relation to the direction in which they conduct, and is used merely to make comparisons easier.

For convenience, the description of the lateral forebrain bundle will start at its most rostral end, in the striatum. This area occupies the ventrolateral quadrant of the hemisphere wall and is separated from the overlying gray of the piriform primordium by a cell-free limiting zone. From the region back of the accessory olfactory bulb, the striatum extends caudalward and also ventralward around the ventricle. It ends on the medial ventricular surface next to the septal field. Beginning at the rostal end and continuing throughout the whole length of the striatum, fibers extend backward. The dorsofrontal portion of the striatum contributes but few fibers. The majority of the bundles accumulate in the lateral and ventrolateral margins of the striatum (fig. 9) internal to the descending olfactory tracts (fig. 19). In transverse planes passing in front of the hippocampal commissure, but back of the decussating medial division of the medial forebrain bundle, the fibers of the lateral forebrain bundle can be divided into two groups, dorsal and ventral. The ventral division comes from the front end of the striatum and at this level

is almost cross-cut. The dorsal division accumulates within the more caudal limits of the striatum and its fibers are sectioned tangentially. From this caudal striatal area there are fibers which course ventralward and medialward between the peripherally running ventral part of the anterior olfacto-habenular tract and the more deeply situated, cross-cut fibers of the ventral division of the lateral forebrain bundle. These fibers constitute the diagonal band of Broca, which ends in the septal and anterior preoptic regions. At the level immediately in front of the interventricular foramen, the lateral forebrain bundle occupies a position ventral and ventro-lateral to the amygdaloid gray, with which its more dorso-medial fibers intermingle (fig. 17). The external surface of the brain has, from this plane caudalward, a more or less definite elevation, the fascicular prominence of Gaupp (1899), inside of which runs the lateral forebrain bundle in its course through the diencephalon (figs. 1 to 5 and 13 to 16). Dorso-laterally the bundle is bounded by the fibers of the ventral olfactory projection tract; dorsally and dorsomedially are the bundles of stria terminalis. The region caudal and ven-tromedial to the amygdala, with which the fibers of the lateral forebrain bundle intermingle, represents a synaptic area for the decussation of the dorsal division of the bundle. In this respect it may be called a bed nucleus of the bundle (Herrick, '27), or, as has been pointed out in connection with the cell areas, it may be termed the anterior portion of the ento-peduncular nucleus. The dorsal division of the lateral fore-brain bundle begins to cross in a plane back of the inter-ventricular foramen (figs. 13 and 19). The fibers accumulate first at the dorsomedial side of the bundle. The decussation includes medullated and nonmedullated fibers, although some of the latter actually are true interamygdaloid connections. The hippocampal commissure is dorsal here and extends somewhat caudal to the crossings described above.

Dorsal division of the lateral forebrain bundle (thalamo-striatal component, Crosby, '17; Huber and Crosby, '26; dorsal peduncle, Ariëns Kappers, '20–'21; pars thalamica,

Röthig, '26). From the anterior entopeduncular nucleus crossed, and probably uncrossed, fibers pass dorsally and dorsocaudally (figs. 14 and 17). Whether these fibers have a synapse in the nucleus or merely pass through it has not been satisfactorily determined, although it is possible that some do synapse. In Weil preparations thinly medullated fibers can be seen to enter the anterior dorsolateral nucleus. This connection may well be taken to represent the anterior strio-thalamic tract described by Huber and Crosby ('26) in the alligator.

Coming from the same area of the anterior entopeduncular nucleus but running farther caudalward are thinly medullated fibers passing to the ventral aspect of nucleus rotundus (fig. 18, L.F.B. p. dors.), which belong to the intermediate strio-thalamic tract of Huber and Crosby ('26). Still farther back there are fascicles which, after intermingling with the cells on the medial aspect of nucleus rotundus, end in the posterocentral nucleus. These very loose fibers probably represent the homologue of the medial strio-thalamic tract of the authors mentioned above. These connections are comparable to the thalamo-frontal tracts of urodeles (Herrick, '17, '27, and elsewhere).

Ventral division of the lateral forebrain bundle (ventral peduncle, Ariëns Kappers, '20–'21; pars hypothalamica, peduncular fibers and tractus strio-tegmentalis et bulbaris of Röthig, '26). Most, if not all, of the medullated fibers of this division (fig. 20) come from the anterior and ventral portions of the striatum. So far as could be determined, they do not cross in the anterior commissure, nor is there any apparent synapse in the anterior entopeduncular nucleus. In the preoptic region this division is large and round in cross-section (fig. 14). To a great extent it is responsible for the formation of the fascicular eminence of Gaupp (1899). About halfway back in the preoptic region the fibers of the lateral olfacto-habenular tract swing dorsolaterally external to the bundle. Farther caudal the latter tract is covered on the outside by the axial and marginal bundles of the optic tract

passing to the lateral geniculate nucleus (fig. 15). Approximately at this same level there are scattered fascicles from the bundle to the anterior part of the ventral hypothalamus, as well as to the lateral hypothalamic gray farther caudalward (figs. 16 and 17, tr. str. hypoth.). These fibers passing from the ventral peduncle of the lateral forebrain bundle to the hypothalamus may be considered homologous to the strio-hypothalamic tract described by Huber and Crosby ('26) for Alligator mississippiensis, and by Röthig ('26) in R. fusca as pars hypothalamica. Back of the chiasma ridge the ventral peduncle is broken up, to a greater or lesser degree, into smaller fascicles (fig. 17). This happens in the region where the most anterior cells of the caudal entopeduncular nucleus are found. A group of these cells lies dorsal to the peduncle and is described and labeled by Ariëns Kappers and Hammer ('18) as nucleus juxtapeduncularis. The material studied is not favorable for determining whether the fibers synapse on these cells, but from this region caudalward the fascicles of the ventral peduncle follow at least three different courses. One group continues directly to the neurons forming the terminus of the entopeduncular complex at midbrain levels (figs. 16 and 17). These fibers probably represent tractus strio-tegmentalis ventralis of Huber and Crosby ('26) and at least a part of tractus strio-tegmentalis et bulbaris of Röthig ('26). Their origin, course and termination suggest the possibility that they may represent the precursors of the strio-nigral and strio-rubral fibers of higher forms (Beccari, '23; Huber and Crosby, '33; Papez, '35, and others). A second group of fibers of the ventral peduncle slant somewhat dorsally and medially to end in the front part of the general tegmental gray, as shown at A in figures 10 and 18. The third group consists of dorsally directed fibers (figs. 16 and 17) the terminations of which were not observed. Their course suggests that they may represent a strio-tectal pathway.

Herrick ('33, p. 168) gives an excellent analysis of the components of the lateral forebrain bundle of urodeles. The

reader is referred to that paper for the details but in general, they are comparable to the tracts described above for anurans.

Ventral olfactory projection tract

From the rostral and dorsolateral tip of the amygdaloid gray there are fine nonmedullated fibers passing down and back, lateral to the lateral forebrain bundle. At the rostral end of the fascicular eminence these fibers run just internal to the anterior olfacto-habenular tract, between it and the lateral forebrain bundle. They are shown very faintly in figure 13. After continuing caudalward for a short distance, these fibers enter the lateral preoptic area where they pass medially, interlacing with the caudally running fibers of the medial forebrain bundle. They constitute the ventral olfactory projection tract described by Crosby ('17, alligator) and Herrick ('21, various amphibians). They terminate near the cephalic end of the preoptic gray, the fibers entering the upper half of the lateral aspect of the medial preoptic nucleus (fig. 14). Near their origin in the anterior amygdaloid region the ventral olfactory projection tract fibers can be distinguished from the fibers of the diagonal band by the different course they pursue, the latter fibers run ventrally and forward, the former ventrally and backward.

Optic connections

The decussation of the optic nerves and the course of the optic tracts within the brain have been described by several investigators, notably by Wlassak (1893) in frogs and by Herrick ('25) in Ambystoma and the frog. Only a brief account will be given here of the findings in the material studied.

Basal optic root. After the decussation (fig. 9), this bundle turns immediately caudalward and somewhat dorsally, running along the periphery of the hypothalamus (fig. 16). On reaching the anterior part of the tegmentum it swings me-

dially and ends, at least in part, in a group of cells postero-lateral to the interpeduncular nucleus (fig. 9). The nucleus of termination of the basal optic root is the nucleus of the basal optic root of Huber and Crosby ('26) and the application of the same name to the anuran structure makes comparisons easier. In Herrick's latest reference ('48, pp. 36 and 221) he describes a "ventrolateral peduncular neuropil" of urodeles, which is the unspecialized primordium of the nucleus of the basal optic root, a visceral-gustatory nucleus, and several other neighboring structures.

Marginal bundle. The fibers constituting this bundle include by far the greatest number of incoming optic nerve fibers. After the decussation they spread fan-like on each side of the chiasma ridge. A majority of the fibers, making about two-thirds to four-fifths of the bundle, pass dorsocaudally to the di-mesencephalic junction. Upon reaching the anterior limits of the tectum, a part of the fibers course practically straight back (fig. 20, tr.op. marg. p. post.) and then swing medially to distribute on the posterior and medial surfaces of the optic layer (fig. 9). This fascicle is the one labeled fibrae opticae ventrales by Ariëns Kappers and Hammer ('18, figs. 11 and 12).

The remainder of the marginal bundle continues dorso-caudalward to end superficially, along the anterior and medial regions of the tectum (figs. 9, 11, 12, and 16). This portion of the marginal bundle is labeled by Ariëns Kappers and Hammer, fibrae opticae mediales ('18, fig. 11) and later fibrae opticae dorsales ('18, fig. 12). It is possible that collaterals of the marginal bundle enter the ventral nucleus of the lateral geniculate body (fig. 15). Huber and Crosby ('26) found the bundle in the alligator essentially as described above and, in addition, traced either stem or collateral fibers to the lateral portion of the anterior dorsolateral nucleus (dorsal nucleus of the lateral geniculate of the present account).

Axial bundle. These fibers run somewhat medial to the marginal bundle. There is, however, no sharp separation

between the two groups of fibers. The axial bundle as described here includes only those fibers which, instead of passing dorsocaudally as the marginal fibers do, run in a dorsal and slightly dorsofrontal direction (fig. 9). The fibers running dorsally are the more numerous and distribute to the ventral and ventrolateral aspect of the ventral nucleus of the lateral geniculate. The fibers passing dorsofrontally are relatively few, yet they can be followed on the lateral surface of the diencephalon almost to the superficial ditelencephalic sulcus (fig. 18). As they reach the level where the caudal hemisphere pole is about to separate from the diencephalon, they pass medialward to end among the few cells forming the dorsal nucleus of the lateral geniculate (figs. 12 and 15). It is very probable that these are the fibers that Osborn (1888, p. 82 and fig. 31) described without confirmation as passing directly to the hemisphere. No such connection was found in the material investigated nor were there any fibers traced from the lateral geniculate which could be taken as the optic radiations described by Herrick in 1925 (p. 463).

The axial bundle of reptiles (Huber and Crosby, '26) is much smaller and less clearly separated from the marginal tract than the comparable system in urodeles and it seems probable that the anuran axial bundle represents an intermediate stage between those of reptiles and urodeles. Frey ('38) described a hypothalamic optic bundle in amphibians, which he compared in part to the axial bundle of Wlassak, but which has connections with the small-celled part of the preoptic nucleus. No such bundle could be traced in the available material but further investigation of it would be desirable.

Other fiber connections of diencephalic centers

In parasagittal sections stained for fibers, in planes in which the stria medullaris turns into the epithalamic area, there are some scattered medullated fibers from the bed nucleus of the hippocampal commissure (tractus olfacto-thala-

micus, figs. 10 and 17) which, instead of joining the stria, pass back to end in the anterior dorsomedial nucleus. A few collaterals of the medial olfacto-habenular tract also reach the same nucleus. Herrick ('33) described in Necturus an olfacto-thalamic tract which he said is "a collateral connection of the stria medullaris with the neuropil of Bellonci at the rostral end of the dorsal thalamus." It is probable that this tract is the same as was described here for the anurans.

The preoptic tract described by Röthig ('26) was identified. It connects the preoptic and ventral hypothalamic areas after crossing above and slightly caudal to the optic fibers and is termed the preoptico-hypothalamic tract (figs. 15 and 16).

Just internal to the fibers of the marginal optic bundle there are rich connections from the stratum album centrale and possibly also from a mass of gray rostral to it, which pass almost straight forward to the lateral and posterior surfaces of nucleus rotundus and the anterior dorsolateral nucleus. This tecto-thalamic tract (fig. 17), the reptilian lateral tecto-thalamic fibers (Ariëns Kappers, Huber and Crosby, '36), is only a part of a great number of fascicles which join tectal and diencephalic areas. A dorsomedial group of tecto-thalamic connections, the dorsomedial tecto-thalamic tract (figs. 10 and 12) passes from the posterocentral and posterolateral nuclei to the tectum.

Fibers from both ventral and dorsal nuclei of the lateral geniculate body turn dorsocaudalward to the tectum (figs. 17 and 18). The majority of them come from the ventral nucleus, and in their course are mingled with fibers of the marginal bundle as well as with those of the lateral tecto-thalamic tract (figs. 11 and 12). These geniculo-tectal fibers do not form a compact tract, but rather a loose, broad layer, and in a general way are the forerunners of the geniculo-tectal tracts of reptiles (Shanklin, '30, and others). In sagittal sections, a considerable number of fibers can be seen running ventrocaudalward from the ventral nucleus of the lateral geniculate body. They are lost back of the chiasma ridge where they mingle with the postoptic commissure complex

(fig. 17). These fibers may represent the fasciculus geniculatus descendens of some authors (see Ariëns Kappers, Huber and Crosby, '36, p. 997).

The supraoptic or postoptic commissural system comprises a considerable number of unmedullated fibers (figs. 16 and 17), and two or three sharply defined medullated bundles (fig. 10) which can be seen in sagittal sections passing almost perpendicularly backward, internal to the optic tracts. They seem to connect dorsal thalamic areas with the ventral thalamus and hypothalamus. It is possible that there are crossed tecto-thalamic connections among the fibers. A careful analysis of the whole complex as well as of the ascending bulbo- and spino-thalamic tracts was considered inadvisable in the present study. It has been postponed until further knowledge is gained of the mesencephalic and rhombencephalic centers.

DISCUSSION

The literature on the anuran brain up to the present account makes no definite mention of the relation between a given side of the body and the asymmetry of the dorsal habenular nuclei. Gaupp (1899) and especially Röthig ('23) did notice the difference in structure of the nuclei of the two sides but failed to detect their difference in size. In 1936 Ariëns Kappers, Huber and Crosby said: "It is important to mention that the habenulo-peduncular tracts are of equal size on both sides as the habenulae are symmetrical in amphibians." This generalization probably can be attributed to the influence of the work of Herrick on the brains of urodeles, where apparently both nuclei are of the same size. It has been generally accepted that cyclostomes and elasmobranchs have asymmetrical habenulae, in the former the right and in the latter the left nuclei being the larger. In the dipnoan Ceratodus, Holmgren and van der Horst ('25) found both habenular nuclei of the same size, but most of the ganoids have asymmetrical habenulae (Ariëns Kappers, Huber and Crosby, '36). The condition in the

dipnoans and ganoids agrees, respectively, with the findings
in urodeles and anurans. Reference will be made later to
this similarity in the structure of the habenulae.

Various attempts to subdivide the anuran thalamus into
specific cell masses with more or less definite boundaries and
connections have been made. Gaupp (1899) and Röthig ('23),
among others, succeeeded, to a greater or lesser degree, in
this task, but failed to clarify the question of homologies.
With the great advance in the study of the brain of urodeles
brought about through the outstanding contributions of C.
J. Herrick, and a similar progress in the study of the rep-
tilian and avian brains as a result of the painstaking re-
searches of C. U. Ariëns Kappers ('29 and elsewhere), Huber
and Crosby ('26 and '33), Craigie ('28, '30, '32 and else-
where), Durward ('32), Kuhlenbeck ('31) and others, a
renewed attack on the problem has been made possible.

The present attempt at classification has been only par-
tially successful. There are some nuclear masses which can
be definitely compared to corresponding groups of higher
forms, but there are others in which the homologies are doubt-
ful. Nucleus dorsomedialis anterior is, at least, the pri-
mordium of the nucleus of that name in reptiles, and as such
represents the mammalian anteromedial nucleus (Le Gros
Clark, '32b; Ariëns Kappers, Huber and Crosby, '36). Al-
though a definite mammillo-thalamic tract or Vicq-d'Azyr
bundle has not been described for anurans, it may be repre-
sented by some of the fibers of the periventricular complex.

The reptilian nucleus dorsolateralis anterior has been com-
pared in part to the mammalian ventral nucleus (Ariëns
Kappers, Huber and Crosby, '36) and its presence in anurans
has been demonstrated in the preceding section. There is
no question about the homologies of nucleus rotundus of
Anura, Reptilia and Aves yet it is rather difficult to deter-
mine its mammalian counterpart. Probably it forms part of
the nucleus ventralis as suggested by Ingvar ('23), Le Gros
Clark ('32b), Huber and Crosby ('26), Cairney ('26), and
Ariëns Kappers, Huber and Crosby ('36). Both nucleus dor-

solateralis anterior and nucleus rotundus show many simi-
larities in structure and connections. In this respect they
certainly respond to the designation of "neothalamus" ap-
plied to the general area they occupy by Ariëns Kappers
and Hammer ('18). It is not impossible, therefore, that they
contain the primordia of more than one dorsal thalamic nu-
cleus of higher forms.

The posterocentral and posterolateral nuclei of anurans
probably represent the original gray matter from which all
the groups of reptilian postrotundal gray and nucleus re-
uniens evolved. It is doubtful whether they represent the
metathalamus of higher forms as suggested by Herrick ('35)
for the corresponding region of Ambystoma.

The ventral nucleus of the lateral geniculate is phylogeneti-
cally very old, having been described in the literature from
fishes to man. The dorsal nucleus of the lateral geniculate,
on the other hand, heretofore had been described as pres-
ent only in reptiles (Cairney, '26; Huber and Crosby, '33)
and higher forms. In anurans it is definitely a new structure
which lacks as yet structural differentiation, so that most
authors have included it with other nuclear groups. In
these forms its cells are seemingly in the process of pe-
ripheral migration. This is corroborated by the fact that in
alligator (also probably in turtles) the nucleus is merely an
extension from the anterior dorsolateral nucleus, although
in other reptiles (lizards) it is rather well defined.

Intimately associated with the ventral nucleus of the lat-
eral geniculate is the ventrolateral area. This cell mass prob-
ably includes also the reptilian area triangularis. Ariëns
Kappers, Huber and Crosby ('36) suggested that the two
areas may represent the mammalian zona incerta, and their
position and relations certainly indicate it, but later Crosby
and Woodburne (Encylopaedia Britannica) placed the ven-
trolateral area with nucleus rotundus and regarded the area
triangularis only as zona incerta. The anuran ventrolateral
area, is at the same time so indistinctly separated from the
caudal part of nucleus rotundus that, if the mammalian

homology of the latter nucleus holds, it may also contribute
to nucleus ventralis. As for the anterior ventral and ventro-
medial areas, they probably represent, in a general way, the
various cell groups which in mammals form the fields of Forel,
and perhaps the subthalamic nucleus. Nevertheless, these
latter areas need much further investigation before their
exact homologies can be given.

The entopeduncular complex, including both anterior and
posterior entopeduncular nuclei of the present description,
is believed to be differentiated clearly in the anurans. The
close relationship of both parts of the complex to the lateral
forebrain bundle suggests that the cells have migrated, un-
der the influence of impulses passing in the bundle, from
the general periventricular gray of the ventral thalamus as
it is found in the urodeles. The anterior and posterior ento-
peduncular nuclei are directly comparable to similar masses
found in reptiles, birds and mammals. The prolongation of
the posterior nucleus into the midbrain tegmentum suggests
the possibility that it may also contain the primordia of the
lateral part of the substantia nigra (Beccari, '23; Ariëns Kap-
pers, Huber and Crosby, '36, p. 986) and of the large-celled
part of the red nucleus.

The hypothalamus of anurans shows a definite advance
over that of the urodeles. Although it is still under the very
strong influence of the olfactory impulses brought mainly
by the medial forebrain bundle, its nuclear organization
shows the beginnings of practically all the reptilian nuclei
from which the complex avian and specialized mammalian
structures evolved.

Before closing this discussion of the anuran diencephalon,
attention is called to implication of some of the findings on
the phylogeny of the amphibians. During the course of this
investigation it became more and more evident that in basic
structure the anuran brain has departed rather radically from
that of the urodeles. Even after taking into consideration the
probably degenerate condition of the brain in some of the
tailed amphibians, and allowing for specialization in the

tailless forms, there is a pronounced advance in the nervous system of the latter over that of the former, pointing rather strikingly toward the reptilian type of brain. In recent years, Säve-Söderbergh ('35, '36) has brought out paleontolgical evidence tending to show that the Anura, together with the majority of the Reptilia, the Aves and the Mammalia, belong to the group Batrachomorpha, and that their labryinthodont ancestors were closely allied to the Crossopterygii. The same author pointed out, with evidence from other workers, that the urodeles fall definitely out of the evolutionary line represented by the Batrachomorpha and are very nearly related to the Dipnoi. In connection with the discussion of symmetry of the dorsal habenular nucleus, the similarity between dipnoans and urodeles has been mentioned. The progress of the anuran nuclei and connections leading toward the reptilian structural organization has been shown in the presentation of the results and need not be repeated here.

The discussion of the phylogeny of the amphibians, and even less the evaluation of the relative merits of the evidence at hand, falls completely outside the scope of this paper and the abilities of its author. It was considered useful to mention them because, from the very beginning of his neuroanatomical training, the writer has been thoroughly impressed by the great abundance of evidence for evolutionary development that is found in the study of the vertebrate nervous system.

SUMMARY AND CONCLUSIONS

1. The epithalamic region of anurans has a dorsal and a ventral habenular nucleus, the left dorsal nucleus being larger than the right. These nuclei are compared to the medial and lateral habenular nuclei of higher forms. They receive olfactory impulses through stria medullaris, are connected with the thalamus and tectum, and discharge to the interpeduncular nucleus by the habenulo-peduncular tract.

2. The thalamus can be divided into different nuclear masses comparable to those of reptiles. Outstanding among them are nucleus rotundus, connected with striatum and tectum, and possibly receiving ascending fibers from lower brain centers; the dorsal and ventral nuclei of the lateral geniculate, which receive either stem- or collateral fibers of the optic tracts and discharge mainly to the tectum; the ventrolateral area, closely associated with nucleus rotundus and the ventral nucleus of the lateral geniculate, and which probably represents a part of the mammalian ventral nucleus and zona incerta; and the entopeduncular complex, beginning to differentiate in these forms in close association with the lateral forebrain bundle, and from which a series of subthalamic nuclei of higher forms has probably evolved.

3. The preoptic and hypothalamic areas show an advance over the comparable areas in urodeles. They are under the influence of the olfactory impulses, but show progress toward the other types of centers found also in higher forms, mainly through the connections of the periventricular fiber complex, which probably relates the hypothalamic areas with the dorsal thalamus and the midbrain tegmentum.

The nuclear pattern and fiber connections of the anuran diencephalon have been analyzed and an effort has been made to correlate the findings of other workers in order to make easier the comparisons with both higher and lower forms. To accomplish this end, the terminology which has been adopted is the one most commonly applied to the given structure. Finally, some evidence has been presented which shows the closer similarity between the anuran and reptilian diencephalic area than between that of the anurans and the urodeles.

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ABBREVIATIONS

A., fascicles separating from lateral forebrain bundle

a.amygd., amygdaloid area

a.subhab., area subhabenularis

a.vent.ant., anterior ventral area

a.vent.ant.(begin.), beginning of anterior ventral area

a.ventrolat., ventrolateral area

a.ventromed., ventromedial area

c.opt., optic chiasm

com.amygd., commissura amygdalarum

com.hab., habenular commissure

com.hip., hippocampal commissure

com.post., posterior commissure

corp.gen.lat.p.dor., dorsal nucleus of lateral geniculate

corp.gen.lat.p.vent., ventral nucleus of lateral geniculate

dec.L.F.B.p.dor., decussation of the dorsal division of the lateral forebrain bundle

dec.M.F.B.p.lat., decussation of the lateral division of the medial forebrain bundle

dec.M.F.B.p.med., decussation of the medial division of the medial forebrain bundle

fasc.gen. desc., fasciculus geniculatus descendens

for.intervent., interventricular foramen

hypoth.vent.p.ant., anterior part of ventral hypothalamus

hypoth.dor., dorsal hypothalamus

infund., infundibulum

infund.rec., infundibular recess

L.F.B., lateral forebrain bundle

L.F.B.p.dor., dorsal division of lateral forebrain bundle

L.F.B.p.vent., ventral division of lateral forebrain bundle

M.F.B., medial forebrain bundle

M.F.B.p.lat., lateral division of medial forebrain bundle

M.F.B.p.med., medial division of medial forebrain bundle

N.opt., optic nerve

nuc.com.hip., bed nucleus of the hippocampal commissure

nuc.dorsolat.ant., nucleus dosolateralis anterior

nuc.dorsomed.ant., nucleus dorsomedialis anterior

nuc.entoped.ant., anterior entopeduncular nucleus

nuc.entoped.post., posterior entopeduncular nucleus

nuc.hab.dor., dorsal habenular nucleus

nuc.hab.vent., ventral habenular nucleus

nuc.hab.vent.p.caud., caudal part of ventral habenular nucleus

nuc.hab.vent.p.lat., lateral division of ventral habenular nucleus

nuc.mag.preopt., nucleus magnocellularis preopticus

nuc.med.sept., medial septal nucleus

nuc.perivent.arc., nucleus periventricularis arcuatus

nuc.perivent.preopt., nucleus periventricularis preopticus

nuc.post.-cent., nucleus posterocentralis

nuc.post.-lat., nucleus posterolateralis

nuc.preopt.lat., nucleus preopticus lateralis

nuc.preopt.med., nucleus preopticus medialis

nuc.rot., nucleus rotundus

perivent.syst., periventricular fiber system

post-op.com.syst., post-optic commissural system

preopt.rec., preoptic recess

prim.hip., primordium hippocampi

prom.chias., chiasma ridge

prom.fasc., fascicular prominence

s.dor., sulcus dorsalis thalami

s.intrahab., sulcus intrahabenularis

s.med., sulcus medialis thalami

s.subhab., sulcus subhabenularis

str.med., stria medullaris

str.term., stria terminalis

tr.amygd.-hab., amygdalo-habenular tract

tr.cort.-hab.lat., lateral cortico-habenular tract

tr.cort.-hab.med., medial cortico-habenular tract

tr.gen.-tect., geniculo-tectal tract

tr.hab.-ped., habenulo-peduncular tract

tr.hab.-tect., habenulo-tectal tract

tr.olf.-hab.ant., anterior olfacto-habenular tract

tr.olf.-hab.lat., lateral olfacto-habenular tract

tr.olf.-hab.med., medial olfacto-habenular tract

tr.olf.-hab.med.+lat., medial plus lateral olfacto-habenular tracts

tr.olf.-thal., olfacto-thalamic tract

tr.olf.vent., ventral olfactory projection tract

tr.op.axil., axillary optic bundle

tr.op.basal., basal optic root

tr.op.mar., marginal optic bundle

tr.op.mar.+axil., marginal plus axillary optic bundle

tr.op.mar.p.ant., anterior division of marginal optic bundle

tr.op.mar.p.post., posterior division of marginal optic bundle

tr.preop.-hypoth., preoptico-hypothalamic tract

tr.str.-hypoth., strio-hypothalamic tract

tr.str.-tect., strio-tectal tract

tr.str.-tegm., strio-tegmental tract

tr.str.-tegm.vent., ventral strio-tegmental tract

tr.str.-thal., strio-thalamic tracts

tr.tect.-thal., tecto-thalamic tracts

tr.thal.-hab., thalamo-habenular tract

vent.tert., third ventricle

PLATE 1

All figures are photomicrographs of sections of R. catesbiana.

1 Transverse section through the anteriormost portion of the diencephalon, series H61, showing the beginnings of the ventral habenular nucleus, nucleus dorsomedialis anterior and area ventralis anterior. The left side of the figure lies in a more rostral plane and shows nucleus medialis septi and the amygdaloid area. Toluidin blue. × 20.

2 Section of the same specimen as the preceding figure taken at the level of the beginnings of the right dorsal habenular nucleus and the dorsal nucleus of the lateral geniculate body. The anterior entopeduncular nucleus is shown as a well-defined mass of cells on the right side, which as before is farther caudad. Toluidin blue. × 20.
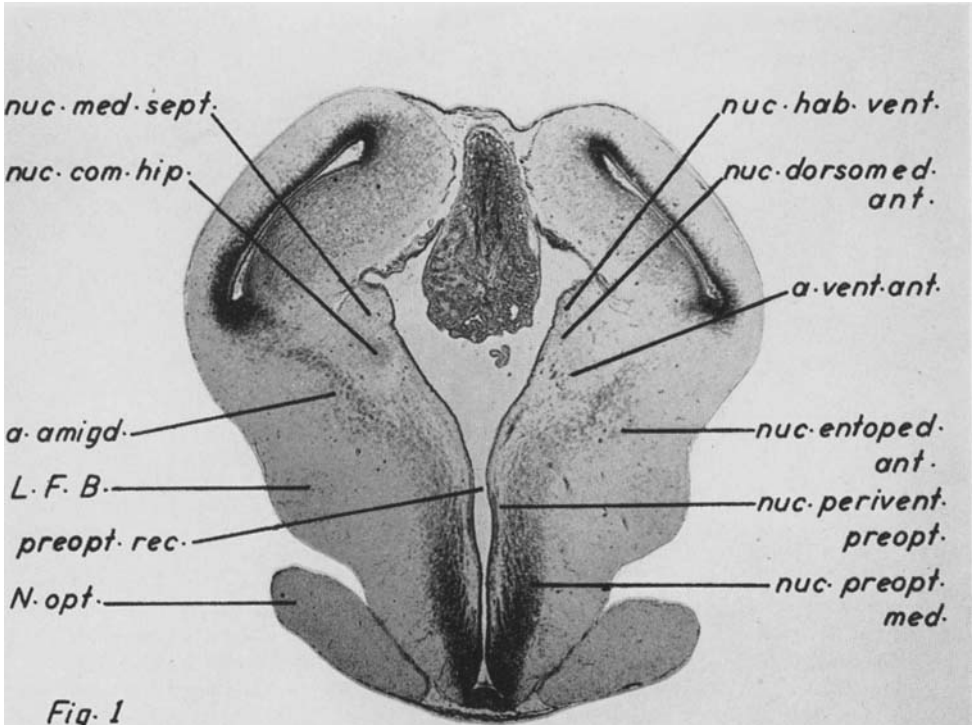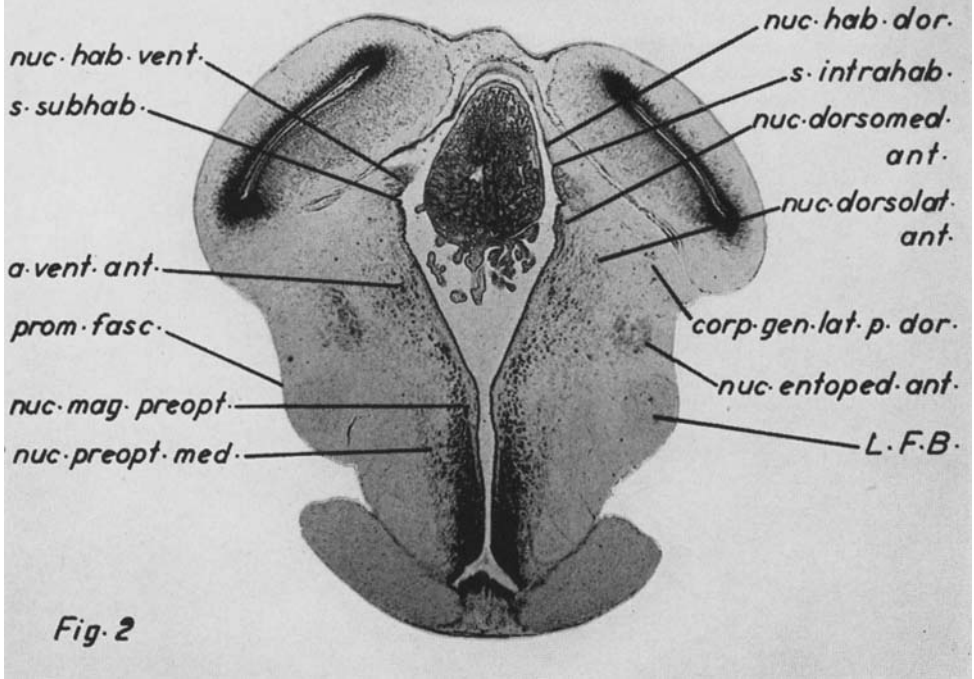
50

Fig. 1

Fig. 2

3   Transverse section of the diencephalon, series H61, immediately rostral to the optic chiasm. The relationships of nucleus rotundus with other nuclear masses are clearly shown, as well as the relative positions of the dorsal and ventral divisions of the lateral geniculate nucleus. Right side of the figure is more caudal than the left. Toluidin blue.   × 20.

4   Section through the beginning of the optic chiasm (approximately middle one-third of the diencephalon) of the same specimen as the preceding figure. The double structure of the left dorsal habenular nucleus is sharply defined. The caudal portion of nucleus rotundus is seen wedged laterally between nucleus posterocentralis and area ventrolateralis, ventrolateral to which lies the beginning of the posterior entopeduncular mass of cells. Toluidin blue.   × 20.
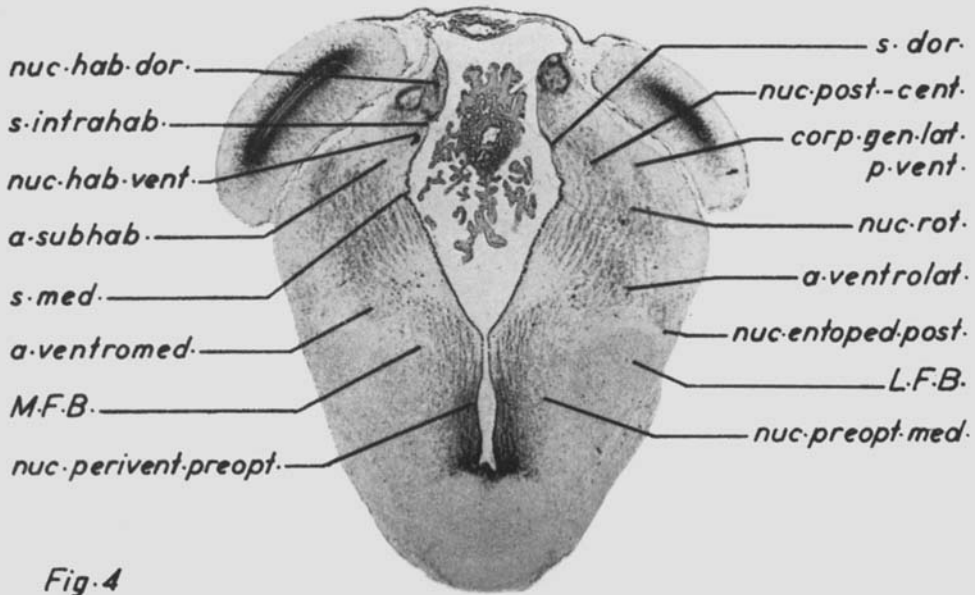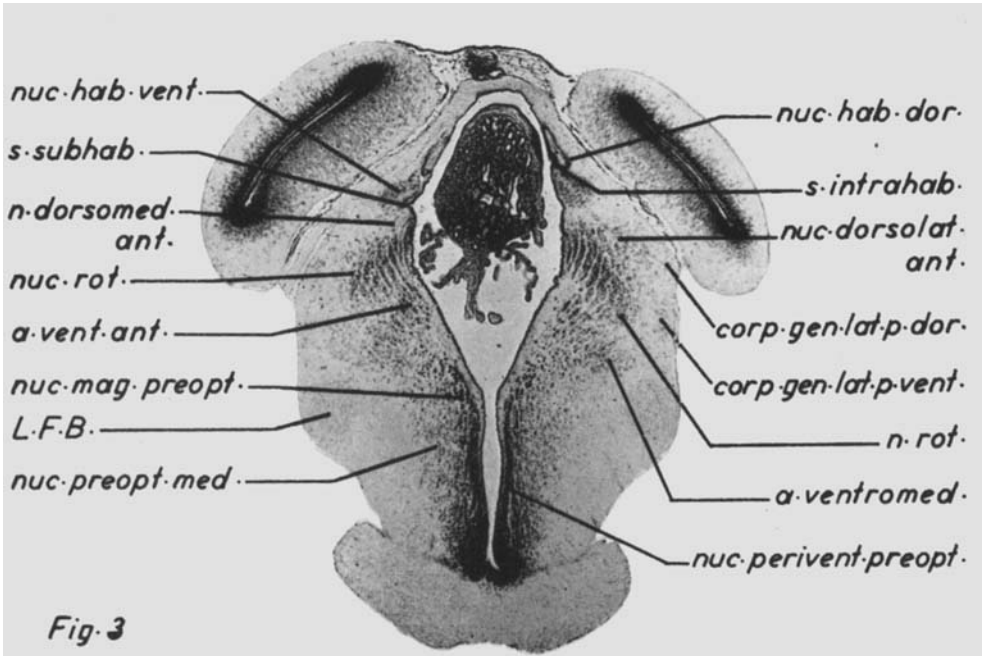
JOSE GUILLERMO FRONTERA

nuc·hab·vent·

s·subhab·

n·dorsomed·
ant·

nuc·rot·

a·vent·ant·

nuc·mag·preopt·

L·F·B·

nuc·preopt·med·

nuc·hab·dor·

s·intrahab·

nuc·dorsolat·
ant·

corp·gen·lat·p·dor·

corp·gen·lat·p·vent·

n·rot·

a·ventromed·

nuc·perivent·preopt·

Fig·3

nuc·hab·dor·

s·intrahab·

nuc·hab·vent·

a·subhab·

s·med·

a·ventromed·

M·F·B·

nuc·perivent·preopt·

s·dor·

nuc·post·-cent·

corp·gen·lat·
p·vent·

nuc·rot·

a·ventrolat·

nuc·entoped·post·

L·F·B·

nuc·preopt·med·

Fig·4

53

5   Transverse section of the diencephalon, series H61, passing caudal to the habenular commissure and through the anterior portion of the ventral hypothalamus.   Toluidin blue.   × 20.

6   Parasagittal section of the right side of the diencephalon, series H62, passing through the lateral division of the ventral habenular nucleus.   The plane of the section is slightly oblique to the vertical axis, so that the dorsal structures are more lateral than the ventral.   Nucleus magnocellularis preopticus is seen wedged between the anterior and posterior portions of the periventricular preoptic nucleus.   Toluidin blue.   × 20.
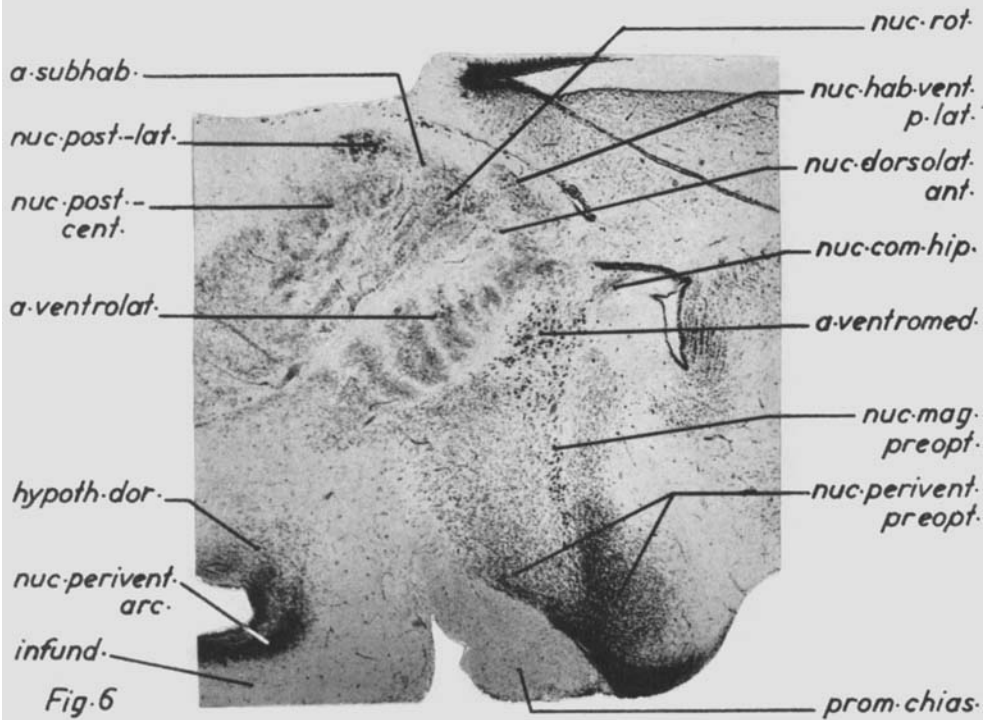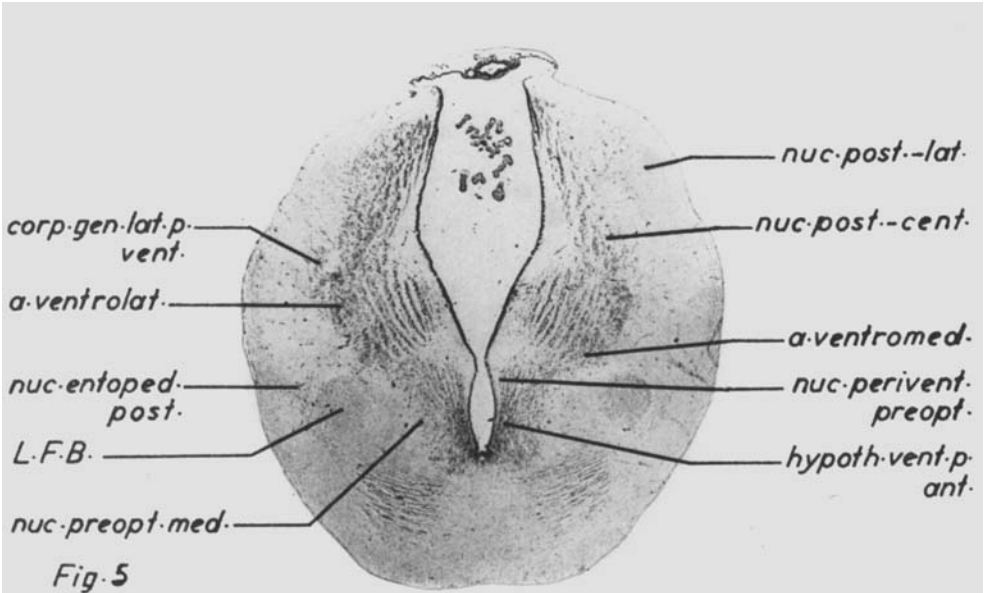
Fig. 5

Fig. 6

PLATE 4

7 Horizontal sections of the diencephalon, series H64. The left side of the section is more ventral than the right. The figure shows clearly the asymmetry of the dorsal habenular nuclei and the relative position of postero-central and posterolateral nuclei. Toluidin blue. × 20.

8 Horizontal section of the diencephalon of the same specimen as the preceding, taken at a more ventral plane. The anterior dorsomedial and dorsolateral nuclei are shown on the left side of the figure. Nucleus rotundus is seen caudal to nucleus dorsolateralis anterior and the ventral nucleus of the lateral geniculate body occupies a position lateral and rostrolateral to both. Toluidin blue. × 20.
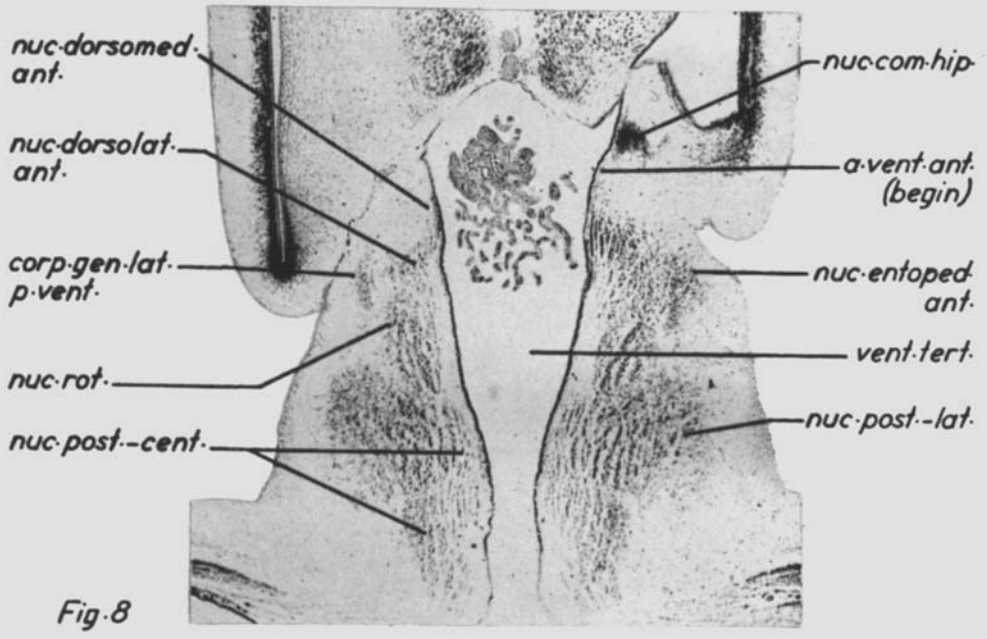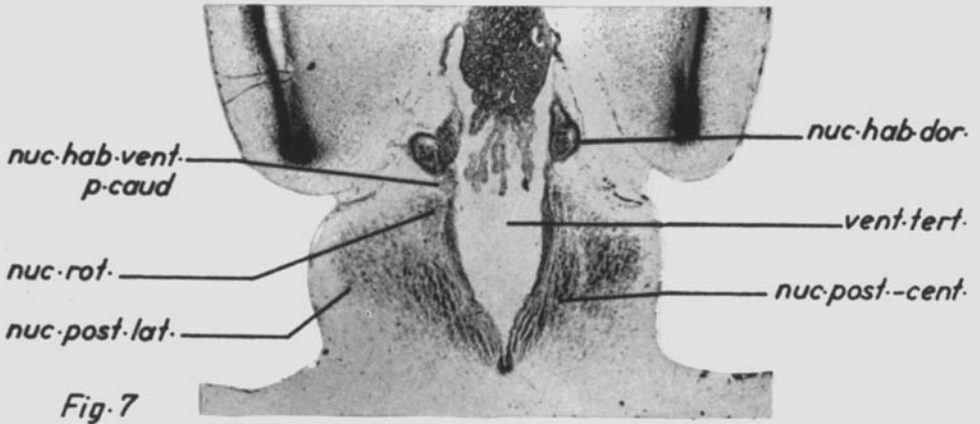
nuc·hab·vent·
p·caud

nuc·rot·

nuc·post·lat·

Fig·7

nuc·hab·dor·

vent·tert·

nuc·post.-cent·

nuc·dorsomed·
ant·

nuc·dorsolat·
ant·

corp·gen·lat·
p·vent·

nuc·rot·

nuc·post.-cent·

Fig·8

nuc·com·hip·

a·vent·ant·
(begin)

nuc·entoped·
ant·

vent·tert·

nuc·post.-lat·

9 Parasagittal section of the right side of the diencephalon, series H69. This figure is particularly useful in following the course of the more superficially running fibers of the optic tracts. The lateral cortico-habenular and anterior olfacto-habenular tracts are seen on their way to join stria medullaris. Weigert. × 20.

10 Section of the same specimen as in the preceding figure taken at a more medial plane on the left side. The lateral division of the left dorsal habenular nucleus is shown. The course of the medial forebrain bundle is shown in part. A group of fibers from the ventral peduncle of the lateral forebrain bundle is distributed at A to the front end of the general tegmental gray. Weigert. × 20.
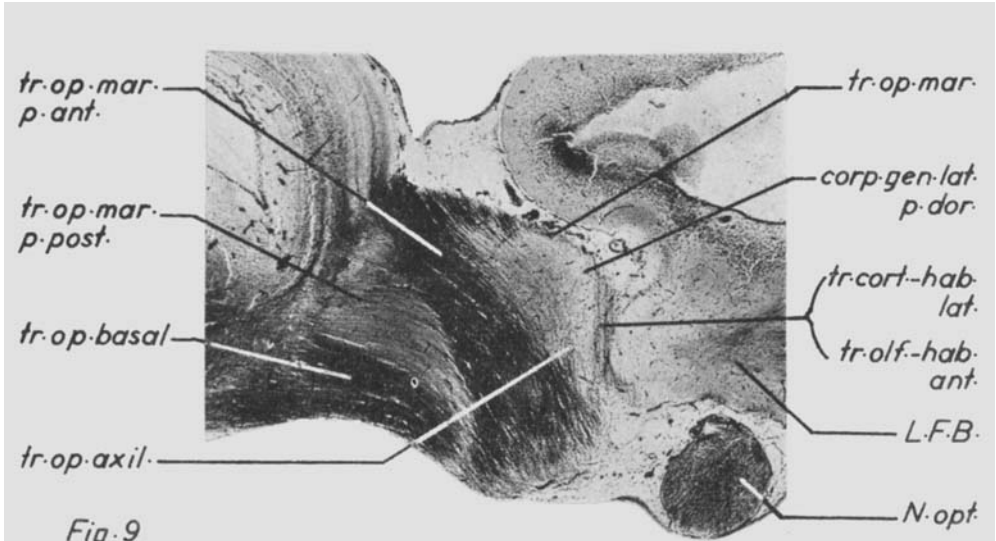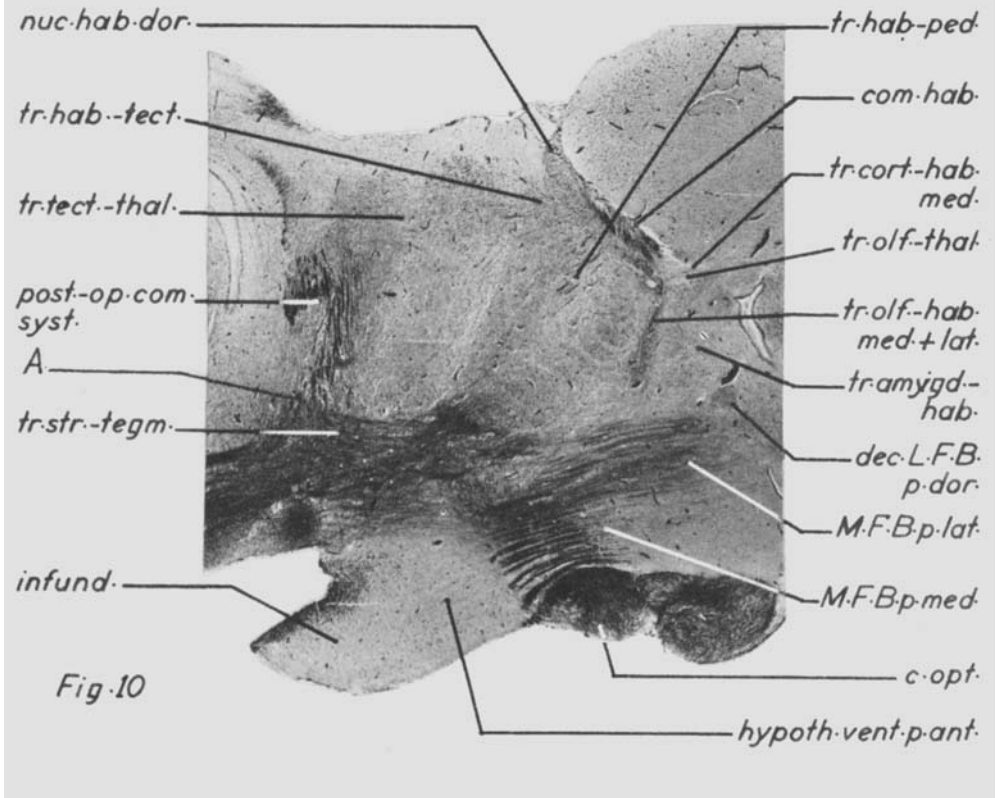
JOSE GUILLERMO FRONTERA

tr·op·mar·
p·ant·

tr·op·mar·
p·post·

tr·op·basal

tr·op·axil·

Fig·9

tr·op·mar·

corp·gen·lat·
p·dor·

tr·cort·-hab·
lat·

tr·olf·-hab·
ant·

L·F·B·

N·opt·

nuc·hab·dor·

tr·hab·-tect·

tr·tect·-thal·

post·-op·com·
syst·

A

tr·str·-tegm·

infund·

Fig·10

tr·hab·-ped·

com·hab·

tr·cort·-hab·
med·

tr·olf·-thal·

tr·olf·-hab·
med·+lat·

tr·amygd·-
hab·

dec·L·F·B·
p·dor·

M·F·B·p·lat·

M·F·B·p·med·

c·opt·

hypoth·vent·p·ant·

11 Horizontal section of the diencephalon, series H71. The figure shows the position of stria medullaris, some of its fibers entering the dorsal habenular nucleus. From the latter nucleus, tractus habenulo-tectalis is seen in part of its course. The anterior division of the marginal optic tract is on its way to distribute in the front part of the tectum. Weigert. × 20.

12 Section of the same specimen as the preceding figure taken ventral to the plane of figures 7 and 11 but dorsal to that of figure 8. Fibers from stria medullaris pass to the ventral habenular nucleus, from which the habenulo-peduncular tract is flowing out. A few fibers from the axial bundle of the optic tract are seen spreading among the cells of the dorsal nucleus of the lateral geniculate body. From the latter nucleus, fibers of the geniculo-tectal tract course caudalward. Weigert. × 20.
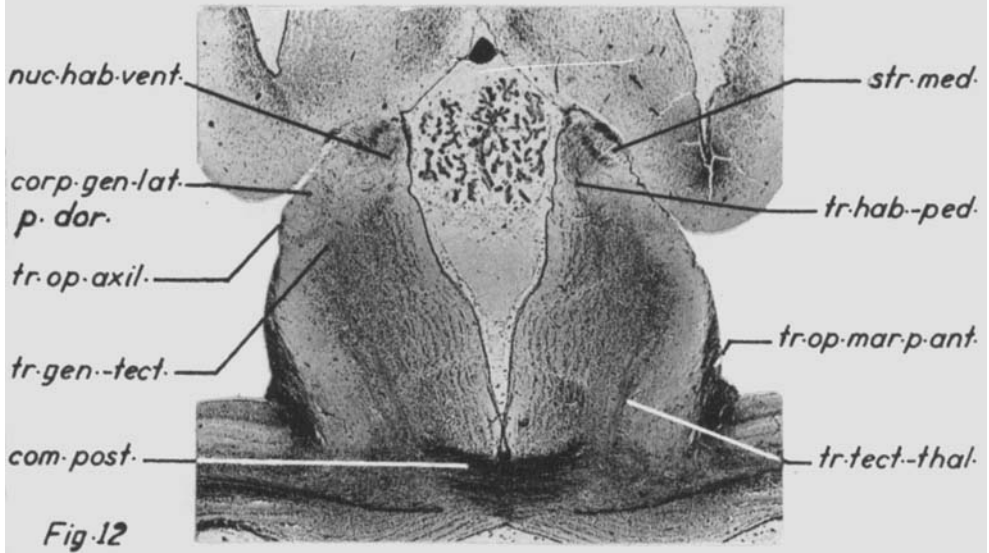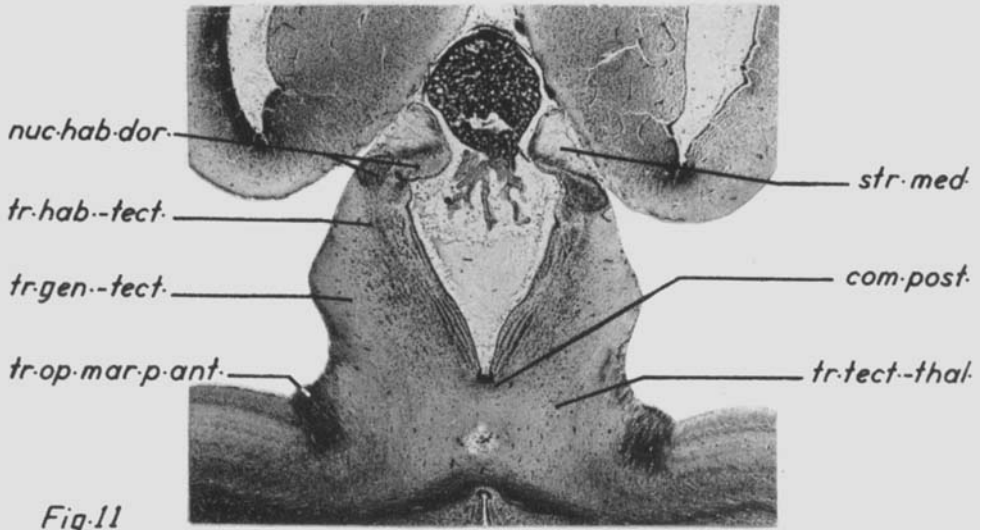
nuc·hab·dor·

tr·hab·-tect·

tr·gen·-tect·

tr·op·mar·p·ant·

Fig·11

str·med·

com·post·

tr·tect·-thal·

nuc·hab·vent·

corp·gen·lat·
p·dor·

tr·op·axil·

tr·gen·-tect·

com·post·

Fig·12

str·med·

tr·hab·-ped·

tr·op·mar·p·ant·

tr·tect·-thal·

PLATE 7

13 Transverse section of the commissural area, series H73. The plane of the section is such that the right and ventral portions of the figure are farther caudal than the left and dorsal. The hippocampal commissure, which is the dorsorostralmost of the commissural fields shown, appears as a thick bundle of fibers. The interamygdoloid fibers are few and scattered; the decussation of the dorsal peduncle of the lateral forebrain bundle is beginning to appear in the field below. Pyridine-silver. × 20.

14 Section of the same specimen as the preceding figure at the level of the habenular commissure. The position of the olfactory tracts in course is shown. Pyridine-silver. × 20.
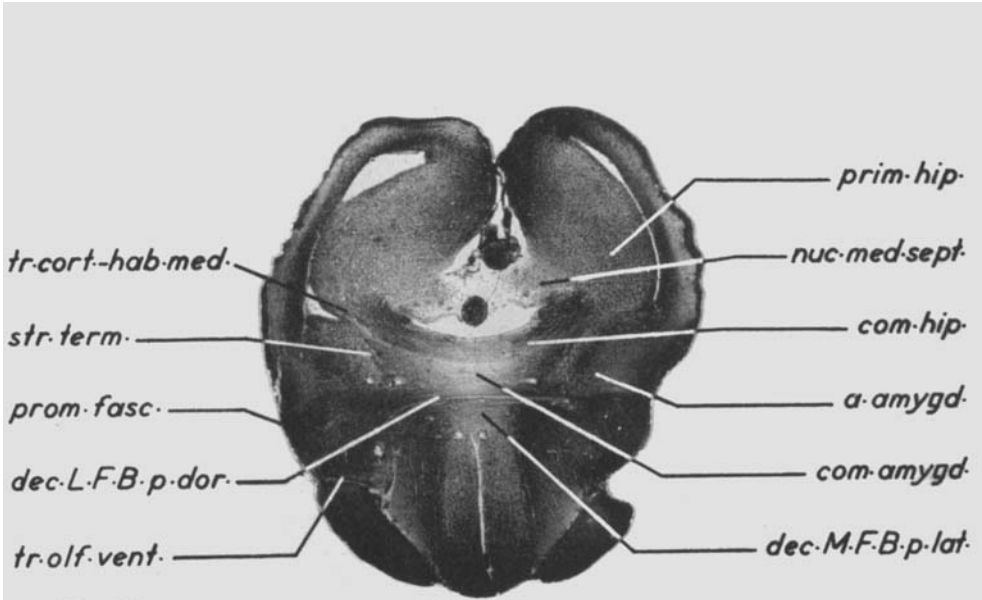
tr·cort·-hab·med·
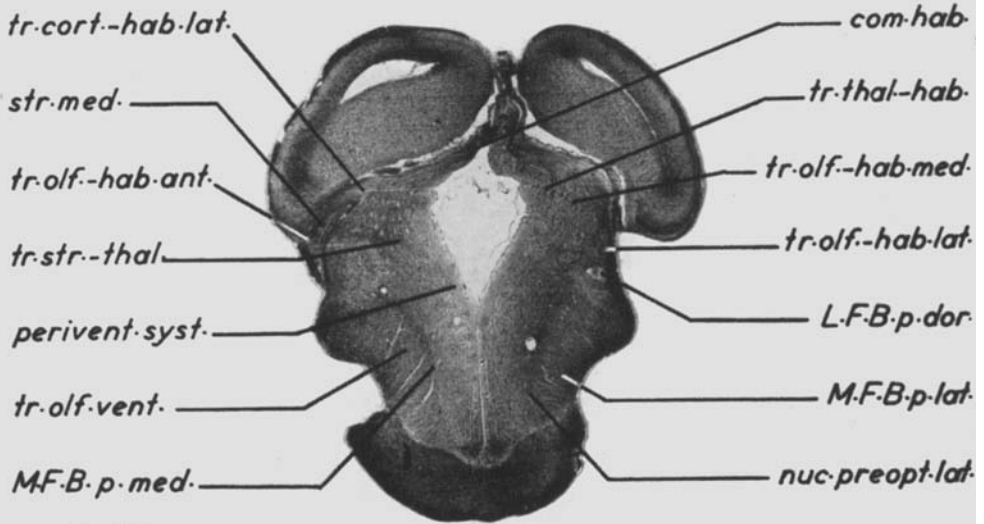str· term·
prom· fasc·
dec·L·F·B·p·dor·
tr·olf·vent·

prim·hip·
nuc·med·sept·
com·hip·
a·amygd·
com·amygd·
dec·M·F·B·p·lat·

Fig·13

tr·cort·-hab·lat·
str·med·
tr·olf·-hab·ant·
tr·str·-thal·
perivent·syst·
tr·olf·vent·
M·F·B·p·med·

com·hab·
tr·thal·-hab·
tr·olf·-hab·med·
tr·olf·-hab·lat·
L·F·B·p·dor·
M·F·B·p·lat·
nuc·preopt·lat·

Fig·14

15 Transverse section of the diencephalon, series H74, caudal to the habenular commissure. The right side of the figure lies in a plane rostral to that of the left. The position occupied by the two divisions of the lateral geniculate body and part of the fibers entering them are illustrated. A few of the fibers of stria terminalis are seen on the left side of the figure. Pyridine-silver. × 20.

16 Section of the same specimen as in the preceding figure at a more caudal level. The post-optic system of fibers as well as some strio-tectal and tegmental bundles can be seen in the upper portion of the figure. Tractus preoptico-hypothalamicus and part of the distribution of the medial division of the lateral forebrain bundle are shown in the walls of the infundibular recess. Pyridine-silver. × 20.
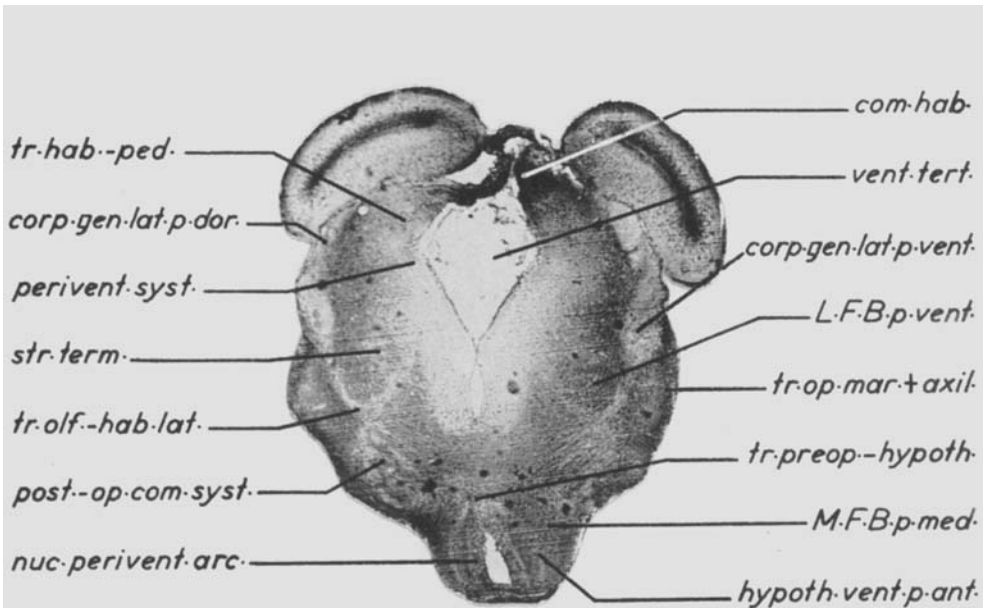
tr·hab·-ped·

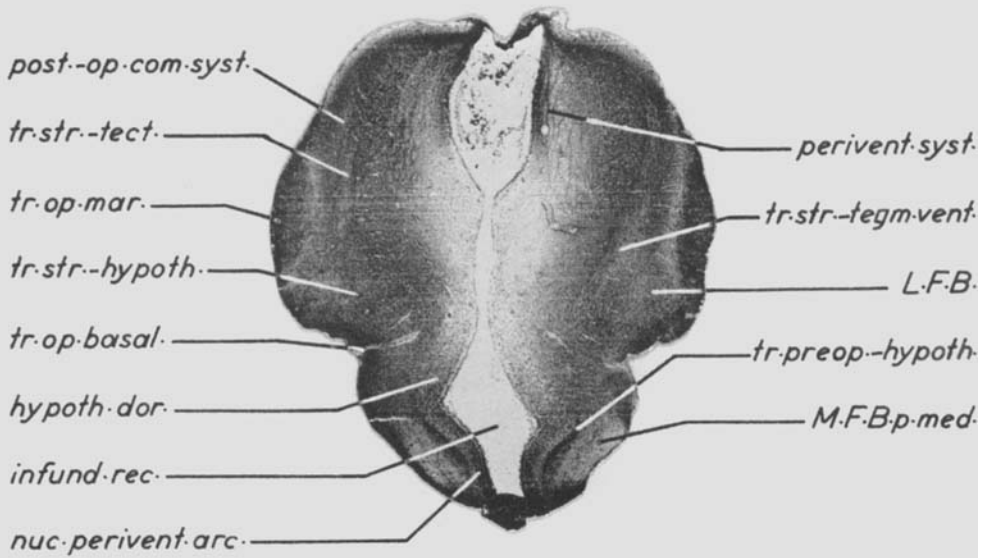corp·gen·lat·p·dor·

perivent·syst·

str·term·

tr·olf·-hab·lat·

post·-op·com·syst·

nuc·perivent·arc·

com·hab·

vent·tert·

corp·gen·lat·p·vent·

L·F·B·p·vent·

tr·op·mar·+axil·

tr·preop·-hypoth·

M·F·B·p·med·

hypoth·vent·p·ant·

Fig·15

post·-op·com·syst·

tr·str·-tect·

tr·op·mar·

tr·str·-hypoth·

tr·op·basal·

hypoth·dor·

infund·rec·

nuc·perivent·arc·

perivent·syst·

tr·str·-tegm·vent·

L·F·B·

tr·preop·-hypoth·

M·F·B·p·med·

Fig·16

17 Parasagittal section of the right side of the diencephalon passing through the lateral forebrain bundle. The plane of the section is oblique to the lateral axis so that rostral areas are slightly more superficial than the caudal part. Some of the tracts forming the medullary stria are shown. Pyridine-silver. × 20.

18 Horizontal section of the forebrain and diencephalon, series H79, taken at the level of the hippocampal commissure. This figure and the following two were selected primarily to illustrate the formation of the lateral and the medial forebrain bundles and some of their relationships to other tracts and nuclear masses. Pyridine-silver. × 20.
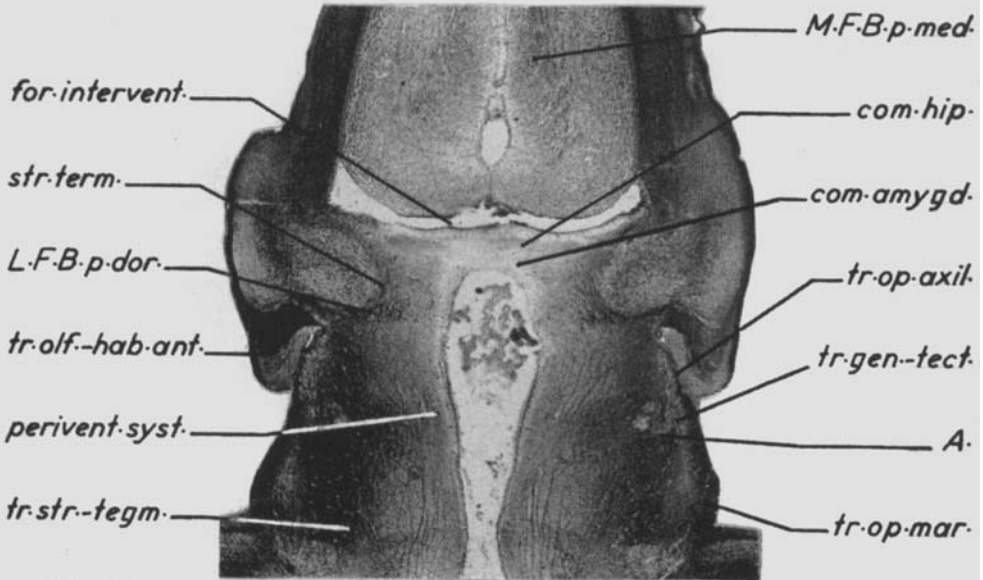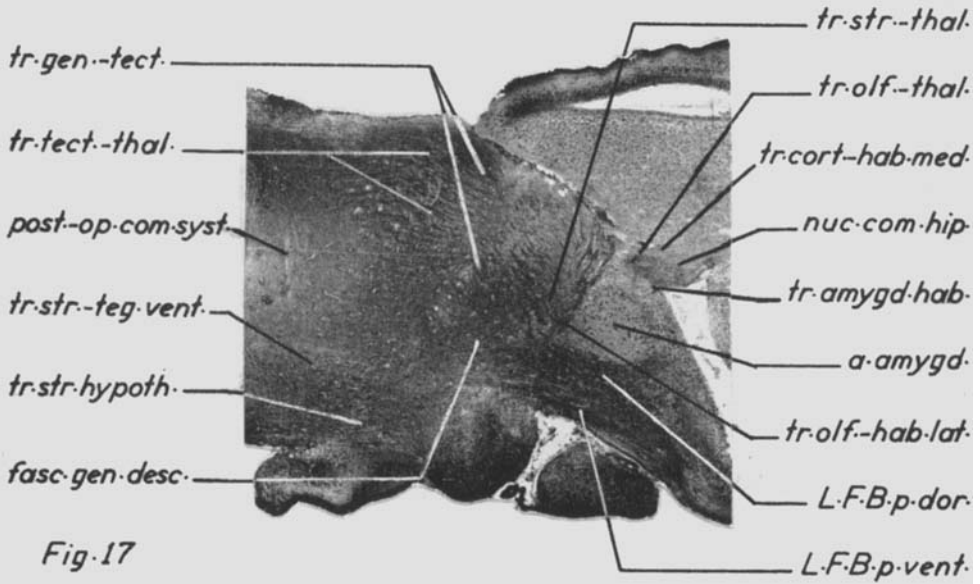
Fig. 17

Labels (left, top to bottom):
tr. gen.-tect.
tr. tect.-thal.
post.-op. com. syst.
tr. str.-teg. vent.
tr. str. hypoth.
fasc. gen. desc.

Labels (right, top to bottom):
tr. str.-thal.
tr. olf.-thal.
tr. cort.-hab. med.
nuc. com. hip.
tr. amygd. hab.
a. amygd.
tr. olf.-hab. lat.
L.F.B. p. dor.
L.F.B. p. vent.

Fig. 18

Labels (left, top to bottom):
for. intervent.
str. term.
L.F.B. p. dor.
tr. olf.-hab. ant.
perivent. syst.
tr. str.-tegm.

Labels (right, top to bottom):
M.F.B. p. med.
com. hip.
com. amygd.
tr. op. axil.
tr. gen.-tect.
A.
tr. op. mar.

19 Horizontal section of the forebrain and diencephalon, series H79, at a plane ventral to that of figure 18, showing the decussation of the dorsal peduncle of the lateral forebrain bundle and part of the course of the ventral peduncle. Pyridine-silver. × 20.

20 Section of the same specimen as in the preceding figure at a more ventral level. The decussation of both portions of the medial forebrain bundle is illustrated. Pyridine-silver. × 20.
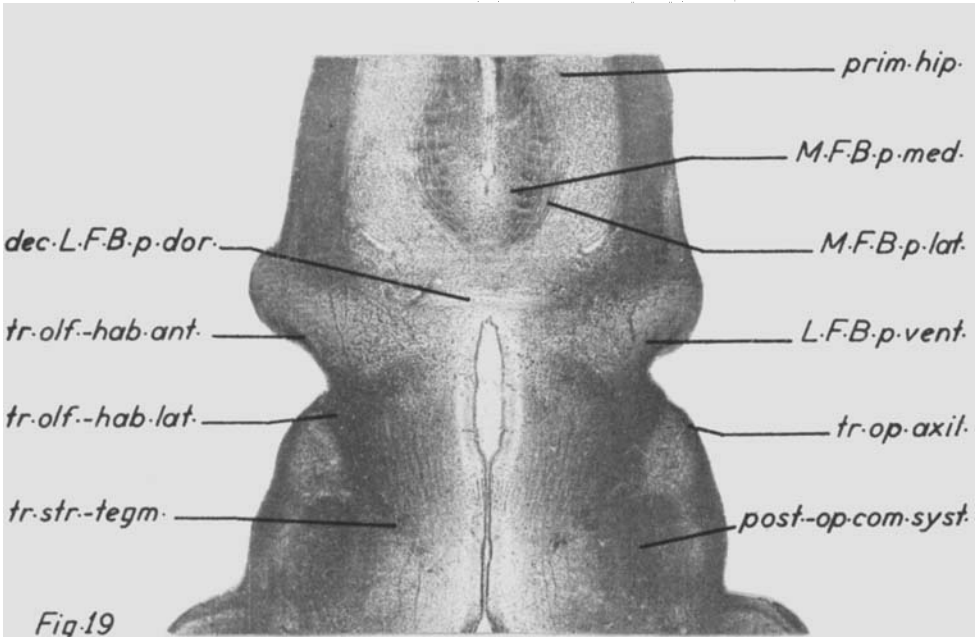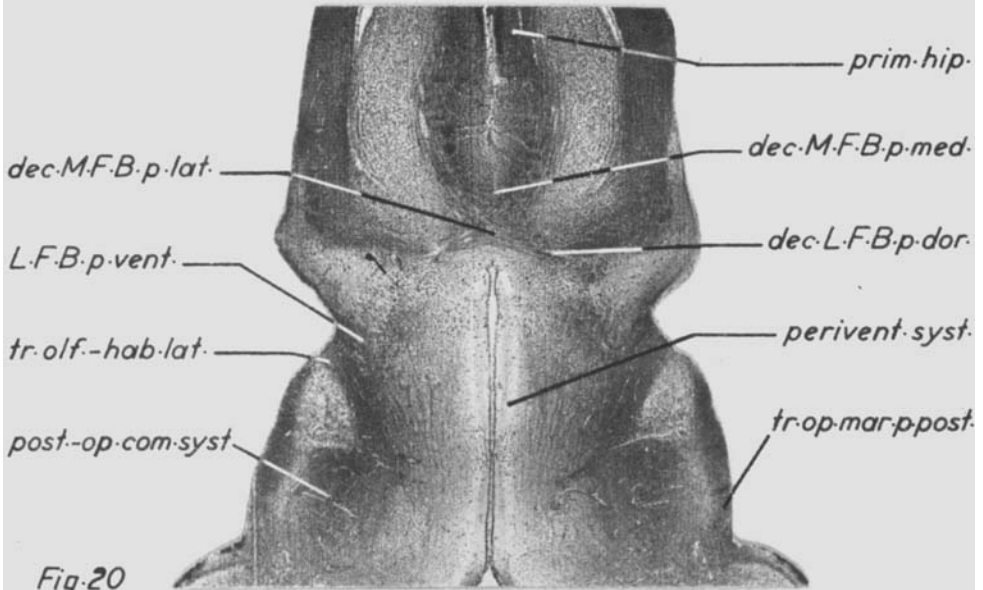
Fig. 19

prim. hip.
M.F.B. p. med.
dec. L.F.B. p. dor.
M.F.B. p. lat.
tr. olf.-hab. ant.
L.F.B. p. vent.
tr. olf.-hab. lat.
tr. op. axil.
tr. str.-tegm.
post.-op. com. syst.

Fig. 20

prim. hip.
dec. M.F.B. p. lat.
dec. M.F.B. p. med.
L.F.B. p. vent.
dec. L.F.B. p. dor.
tr. olf.-hab. lat.
perivent. syst.
post.-op. com. syst
tr. op. mar. p. post.