THE TELENCEPHALON OF THE BAT

I. THE NON-CORTICAL NUCLEAR MASSES AND CERTAIN PERTINENT FIBER CONNECTIONS

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SIXTEEN FIGURES

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INTRODUCTION

The present account of the telencephalon of the bat is preliminary in character and intended to give a survey of the entire field as well as to provide the basis for more comprehensive and detailed studies of the basal and cortical areas as revealed in specially prepared normal and experimental material. A consideration of this form is of especial interest since it is the only mammal which has true flight, since it has notably very poor eyesight, and since, as yet, it has been studied very little.

The material for study was provided by Prof. G. Carl Huber from the collection of the Laboratory of Comparative Neurology of the Department of Anatomy at the University of Michigan. For the use of this material, for the privilege of working in his laboratory, and for his constant interest in the work, I take this opportunity of expressing my sincere appreciation and thanks. I wish also to express my gratitude to Dr. Elizabeth Crosby for her unfailing assistance, encouragement, and suggestions in the preparation of this paper.

MATERIAL AND METHODS

Serial sections of the brain of the free-tailed bat, Tadarida mexicana, very kindly identified by Prof. Lee R. Dice of the University of Michigan Museums, were used in this study. Altogether nine series of cell preparations and five series of fiber preparations, all of which were prepared by Prof. G. Carl Huber, were studied. The cell material was stained by the special toluidin blue method devised by Professor Huber ('27), two of the series being sagittally sectioned, two horizontally, three transversely and two in oblique planes. Four of the fiber tract series were stained by the pyridine silver method, two being sectioned transversely and two sagittally. For the fifth fiber tract series the brain was cross-sectioned, the sections mordanted with iron alum, and stained with haematoxylin.

The outlines of the figures together with some of the major details were made by means of the projection apparatus and the figures then filled in by the use of the microscope. The outlines for the diagrams were also made with the projection apparatus and certain of the relations of the nuclear masses determined by the aid of camera lucida drawings and graphic reconstructions.

LITERATURE

Only a brief summary will be given here of the literature dealing with Chiroptera. Other references to the pertinent literature are made throughout the text and will not receive general consideration.

Very few studies have been made of the forebrain in Chiroptera and most of the references in the literature deal only briefly with some limited region. The earliest remarks found in the available literature on the bat forebrain are the casual references of Ganser (1879 and 1882) concerning the anterior commissure and the amygdala, those of Spitzka (1883) on the pyramidal paths and the fornix in Pteropus fuliginosus, and the comments of Zuckerkandl (1887) on the corpus callosum of Pteropus samoensis. Somewhat later, Turner (1891) and Ziehen (1896) commented briefly on the fissures in certain Macrochiroptera, and Turner figured the corpus callosum in two such forms. Short accounts of the hippocampal region, the fornix, and the origin of the corpus callosum were given by Elliot Smith (1897, 1897 a, 1897 b and 1897 c). Flatau and Jacobsohn (1899) mentioned various gross features in both Microchiroptera and Macrochiroptera and in 1900 Ärnbäck Christie Linde gave a brief account of the brain of Vesperugo pipistrellus. Kohlbrugge ('02) likewise contributed to the knowledge of the macroscopic structure of the brain of the

Macrochiroptera and Dräseke ('03) described many gross, and some microscopic, features of brains from both groups of Chiroptera. Haller ('07 and '07 a) also described representatives of both groups of Chiroptera, particularly with reference to their commissural systems, and Hirsch ('07) added to Haller's description of Pteropus edulis. In the same year Zuckerkandl described the indusium griseum for nine different species of Chiroptera, and in a later communication ('09) mentioned the commissura mollis in Vesperugo noctula. Beccari ('10), in his study of the tuberculum olfactorium of various forms, referred briefly to one specimen of Pteropus and Spiegel ('19) gave a brief description of the caudate-putamen, the claustrum and the amygdala in Pteropus edulis. The cortical areas of the bat were studied by Rose ('12). Among the most valuable accounts of the Chiroptera are those of Johnston, who in 1913 figured and compared briefly with other forms certain areas of the telencephalon of Myotis (the septal region, the pallial commissures and the hippocampus particularly) and in 1923 gave a brief description of the amygdaloid region. The development of the commissures of the hemispheres was described and figured by Werkman ('14) for Vesperugo.

DESCRIPTION OF MATERIAL

Certain general characteristics of the brain of Tadarida

The brain of the free-tailed bat (Tadarida mexicana) shows many evidences of compression. The ventricles are small, flattened into 'mere slits' as described by Johnston ('13) for Myotis, or obliterated completely or in part in many places (see p. 607 and figs. 1 to 3, 8 and 9). For the most part the fissures are shallow and difficult to distinguish. The brain is also crowded up dorsally so that it forms almost a right angle in the middorsal region, a fact that makes it impossible to obtain cross sections which are not actually at an unusual slant throughout some part of the series. Likewise, as a result of the compression, the cellular masses are unusually compact, and show somewhat more than the usual tendency to merge with each other.

The nuclear groups

THE OLFACTORY BULB. THE OLFACTORY VENTRICLE. The olfactory bulb in mammals has been described in detail by numerous observers and the literature reviewed. Among these observers are von Kölliker (1896), Barker (1899), Ramón y Cajal ('11), Winkler and Potter ('11 and '14), McCotter ('12), Gurdjian ('25), Obenchain ('25) and many others. For details concerned with the literature these authors should be consulted. The figures of Kohlbrugge ('02), Dräseke ('03) and others give the gross appearance of the olfactory bulb in Chiroptera.

The olfactory bulb in the free-tailed bat (figs. 1A and 10A) is relatively small for the size of the brain, but broad, flattened frontocaudalward, and slightly pointed at the tip. It is sessile in type, the stalk consisting only of a very short, constricted area formed by the fissura circularis rhinencephali.

The bulb is compact in structure and shows other evidences of compression, the olfactory ventricle either being absent, or, if present, wholly or partially occluded so that it may consist only of a thickened ependymal lining with no lumen. A connection with the lateral ventricle may be demonstrated in one series, while in certain others, although the ventricular ependyma may be seen in the bulb, its relation to the lateral ventricle is not evident. In still other series there is no evidence of any connection between the ventricular ependyma in the bulb and that of the lateral ventricle.

The layers of the bulb and their arrangement are typical of those in mammals. Both the layer of olfactory nerve fibers (fila olfactoria) and the glomerular layer are thicker on the ventral surface of the bulb, where, in certain parts of the bulb, two layers of glomeruli may be seen. On the dorsolateral surface, except at the tip of the bulb, the glomerular layer is not complete. Granule cells of the external granular layer are present both around and within the glomeruli (periglomerular and intraglomerular cells of Ramón y Cajal, '11). The molecular layer has many displaced mitral cells of

Ramón y Cajal scattered through it, especially in the ventrolateral portion of the bulb, where they are numerous enough to suggest an additional cell layer, about midway of the molecular layer. Such displaced mitral cells are described by Young ('36) for the rabbit. The internal granular layer is wide and extends inward to the ventricular ependyma. Its cells are arranged in small groups to form incomplete concentric laminae about the olfactory ventricle. These cell groups are smaller toward the center of the bulb, where they are interspersed with the fibers of the olfactory tract, which in the bat does not form a separate layer around the ventricle in this region.

Lack of an accessory olfactory bulb. The literature concerned with the early descriptions of the accessory olfactory bulb is reviewed in detail in the 1912 paper of McCotter, to which the reader is referred. Since then this structure has been noted or described for representatives of the majority of mammalian phyla, such as marsupials (Herrick, '24; Obenchain, '25), rodents (Gurdjian, '25; Young, '36), carnivores (Winkler and Potter, '14), and insectivores (Le Gros Clark, '33). In the bat, however, no accessory olfactory bulb is present. It is lacking also in birds and in some higher reptiles (Ariëns Kappers, Huber and Crosby, '36).

NUCLEUS OLFACTORIUS ANTERIOR (figs. 1 and 10A). The anterior olfactory nucleus of the bat shows the same general pattern as does that of Caenolestes and of the opossum, although it is more limited in its caudal extent and is less well differentiated. The intrabulbar portion of the nucleus consists, in cross sections through its cephalic end, of a small mass of cells situated dorsal and somewhat lateral to the olfactory ventricle, when the latter is present. Its cells are multipolar and larger than those in the granular layer of the bulb, approaching in type those of the pyriform lobe cortex. In the region of the short olfactory crus the number of cells has increased to form a thick band completely surrounding the ventricle, an arrangement described by Herrick ('24) for the opossum, Obenchain ('25) for Caenolestes, and

Young ('36) for the rabbit. In the bat, however, the layer of cells extends inward to the ependymal lining of the ventricle. Although on the basis of topographical relationship to the ventricle it is possible to designate a pars dorsalis, a pars lateralis, a pars ventralis and a pars medialis of the nucleus olfactorius anterior, no differences in cell type and arrangement or in fiber connections have been noted. Just caudal to the crus the medial portion of the nucleus passes toward the septal region, where it comes into close relation with the nucleus septalis lateralis lying dorsolateralward and the anterior hippocampal cortex lying dorsomedialward. At the same levels the lateral portion of the nucleus appears to pass over into both the deep and the cortical layers of the pyriform lobe lateral to it. Those cells lying dorsal to the ventricle become continuous with the cortex of the frontal lobe overlying the region, as does the pars dorsalis of Herrick ('24, p. 343). The ventral part of the nucleus extends farthest caudalward where it appears to be continuous with the pyramidal cell layer of the tuberculum olfactorium directly caudalward, although blending with both pyramidal and polymorphic cell layers at its lateral border. This relationship is clearly demonstrable only in sagittal sections, however. In some cross cut series the anterior olfactory nucleus appears to be continuous with the superficial, in others, with the deep layer of the tuberculum, depending possibly on the plane of the series in question. There is no indication of lamination or the formation of a cortical layer of the anterior olfactory nucleus such as Herrick described for the opossum, but one cannot help feeling that the connection with the superficial or pyramidal layer of the tuberculum is an indication of a tendency toward differentiation which lifts this nuclear mass above the level of undifferentiated gray.

The pars externa in the bat appears lateral to the main anterior olfactory nucleus in cross sections near the rostral end of the nucleus. In some series a few scattered cells are found ventral to the main nucleus also and in still others the cells to appear first lie dorsal to it, the differences apparently depending upon the plane of the series. The pars externa is a small cell mass consisting of multipolar cells which are not so large but are more deeply staining than those of the main cell mass. At its rostral end the more ventrally placed cells are intermingled with the cells of the granular layer of the bulb and the cells of the principal anterior olfactory nucleus itself but, due to the differences just mentioned, are easily distinguishable from them. Farther caudalward the pars externa passes lateralward as a curved band close to the deep surface of the lateral olfactory tract. It disappears abruptly without merging with any other cell group at its caudal end. In many of the series studied there is no evidence of a subdivision of the pars externa into dorsal and ventral limbs as described by Herrick ('24), Obenchain ('25) and Young ('36). This may be due either to the plane of the series or it may be related to the fact that the dorsal limb, according to Herrick, is associated with the accessory olfactory bulb, which is absent in the bat. In certain series, however, a very small cell mass appears to separate from the larger part of the pars externa at its dorsal surface. This small cell mass, located in the region where the accessory bulb is found in those forms in which it is present, is distinguishable only in a very few sections. Although extremely small and with its cells intermingled in part with those of the granular layer of the bulb, it is possible to distinguish the two on the basis of cell type. This small and inconstant cell mass probably represents the dorsal limb while the main mass represents the ventral limb of the pars externa.

Tuberculum olfactorium (figs. 2, 3 and 8). The tuberculum olfactorium (parolfactory lobe of Beccari, '10) of the bat shows an anterior, less differentiated region (fig. 2), and a posterior, more highly developed portion (figs. 3 and 8), corresponding in general to the anterior and intermediate regions described by Ramón y Cajal ('11). The anterior part (fig. 2) is very thin and atypical in appearance so that in cross section series it is practically impossible to distinguish it from the caudal end of the anterior olfactory nucleus.

In sagittal series, however, in this region it is possible to distinguish a shallow fissura circularis rhinencephali, which delimits the frontal end of the tuberculum. There is also some difference in the cell arrangement in the two regions, particularly in the lateral part of the tuberculum, where two cell layers become evident at the region of the fissure. Except in this lateral region it is not possible to distinguish separate pyramidal and polymorphic cell layers in the anterior portion of the tuberculum even in sagittal sections. The single cell layer present through the remainder of the anterior part of the tuberculum shows a tendency to be somewhat broken up into groups of cells, but there are no convoluted folds or typical islands of Calleja such as are characteristic of the tuberculum farther caudalward. The deep or polymorphic layer appears to be merged with the superficial one and the combined cell layer is so intimately in contact with the underlying head of the caudate that it is not possible to determine how much of the cell mass belongs to the tuberculum (see also fig. 3). Such areas, present also in the posterior part of the tuberculum, would correspond to the strio-tubercular fusion described by Obenchain ('25) for Caenolestes. It would appear, however, that the polymorphic layer is composed primarily of the more deeply situated, scattered cells intermingled with fibers. Haller ('07, p. 143) appears to have included much of the still deeper cell mass (n.caud. (caput), fig. 2) in his 'ganglia areae olfactoriae' (in Vespertilio and Vesperugo), which he considered large in all Chiroptera. The superficial plexiform or molecular layer of the tuberculum is very thin except in the lateral part of the anterior region.

The posterior region of the tuberculum olfactorium (fig. 3) is larger, more highly developed, and shows the usual lamination (Beccari, '10; Ramón y Cajal, '11)—a superficial fiber or plexiform layer, a pyramidal cell layer and a polymorphic cell layer. In following cross section series caudalward, the appearance of the polymorphic layer is first indicated by a very large medial island of Calleja (figs. 2, 3 and 6), while a typically convoluted pyramidal cell layer is soon noted lateralward. In this posterior part of the tuberculum, medial, intermediate and lateral portions may be distinguished topographically, following the terminology of Ramón y Cajal ('11), Loo ('31) and Young ('36). The plexiform layer, except in the lateral part where it is invaded by the convolutions of the pyramidal cell layer, is extremely thin throughout. The pyramidal cell layer appears as a folded band with islands of cells—such as those described by Ganser (1882) for the mole and by Calleja (1893; quoted from Beccari, '10)—only in the lateral part, being represented in the intermediate area by small clumps of granule cells and in the medial part by a thin cell band which extends into the septal region. The polymorphic cell layer is present in the lateral part of the tuberculum as a thin wedge-shaped cell mass with its base dorsolateralward and its tip extending into the intermediate part, where it is fused with the head of the caudate and with the pyramidal layer through scattered cells. In the medial part of the tuberculum this layer is represented by the large island of Calleja mentioned above and figured by Johnston ('13) for Myotis also; in the other portions of the polymorphic layer islands are not present, however. Since the caudal boundary of the tuberculum is indicated by the diagonal band of Broca with its nucleus, its lateral part is found to extend farthest caudalward (fig. 8).

The lack of differentiation evidenced in the anterior portion of the tuberculum may be due to the great compression of the brain, the pressure in this region being contributed to by the high degree of development of the head of the caudate nucleus. On the one hand, there may be a correlation between the relatively small size of the olfactory bulbs and the somewhat limited degree of development of the anterior part of the tuberculum olfactorium. On the other hand, the higher degree of differentiation caudalward may be related to the great development of the lateral amygdaloid nucleus, with which it is connected (see p. 655), or to ascending connections from lower centers, the details of which have yet to be studied.

THE BASAL NUCLEI OF THE MEDIAL HEMISPHERE WALL. In this grouping are included certain (the lateral and medial septal nuclei, the nucleus septalis fimbrialis and the bed nucleus of the anterior commissure), but not all, of the nuclei usually included in the septal region (corpus paraterminale of Elliot Smith or parolfactory nuclei of Johnston). This arrangement is used because of the relationship which has been found in the bat between the cell masses of the septal region and the dorsal commissural systems, these nuclei aiding in surrounding both the hippocampal commissure and the corpus callosum by hippocampal vestiges (see pp. 617–625). For a discussion of the varied terminologies used for the septal region, and the nuclear masses included in it, the reference book of Ariëns Kappers, Huber and Crosby ('36) should be consulted. In the available literature no actual description of the nuclear masses of the septal region in Chiroptera is to be found, although the region itself is figured and mentioned by Haller ('07) for Vespertilio and Vesperugo and by Johnston ('13, p. 390, figs. 41, 45 and 46) as the area parolfactoria in Myotis.

Nucleus septalis lateralis (figs. 1B, 2 and 3). The lateral septal nucleus is located farther frontalward than the other septal nuclei. At its rostral end it is lateral to the anterior hippocampal cortex, and its ventral part lies in relation with the medial portion of the anterior olfactory nucleus. In the bat there is no indication of a division into dorsal and ventral parts as described by Loo ('31) for the opossum. The most cephalic part of the nucleus is seen in sections passing through the corpus callosum; its most caudal portion is located in sections through the rostral boundary of the anterior commissure. The more scattered cells in the dorsolateral part of the nucleus in caudal regions appear to correspond to the nucleus septalis fimbrialis of Loo ('31). Unless further study indicates a difference in fiber relations, however, there is no basis for considering this region of the nucleus as a separate cell mass in the bat.

The nucleus septalis lateralis increases in size in its caudal portion, and, in sections passing through the caudal part of the hippocampal commissure, may be seen as a large, lightly staining cell mass just medial to the lateral ventricle, dorsomedial to the nucleus accumbens (from which it is distinctly separated), dorsal to the medial portion of the tuberculum olfactorium, lateral to the bed nucleus of the anterior commissure and to the medial septal nucleus, and ventral to the hippocampal commissure and its bed nucleus. In the region of the anterior commissure the lateral septal nucleus gradually decreases in size (its medial cells being replaced by the bed nucleus of the anterior commissure), and becomes more dorsal in position, its most caudal cells finally appearing to pass dorsal to the anterior commissure.

The cells of the lateral septal nucleus are of two types throughout, the larger and less numerous cells being three-cornered, while the smaller, spindle-shaped cells are greater in number. Both types have large, lightly staining nuclei and indistinct Nissl granules. This nucleus was figured by Johnston ('13, fig. 42, p.h.), but labeled as primordium hippocampi, of which he considered it a part.

Nucleus septalis medialis (figs. 2, 3 and 6). The rostral end of the medial septal nucleus may be located in cross sections through the hippocampal commissure, where it lies ventral to the precommissural portion of the bed nucleus of that commissure and medial to the lateral septal nucleus. From this point it extends caudalward as far as sections passing through the fornix columns and the more cephalic portion of the tuberculum olfactorium. The majority of its cells are deeply staining, dorsoventrally oriented, spindle-shaped cells, but a few multipolar neurons are present also. Anterior and posterior parts of the medial septal nucleus are not recognizable in the bat as they are in the opossum (Loo, '31).

In following cross sections caudalward, the nucleus of the diagonal band of Broca appears ventrolateral to, and near the rostral end of, the medial septal nucleus, which is separated from the bed nucleus of the hippocampal commissure by the columns of the fornix. The lateral relations of the nucleus remain the same. In sections just caudal to the hippocampal commissure, the medial septal nucleus has shifted slightly dorsolateralward so that the bed nucleus of the anterior commissure now lies ventral to it, separating it from the nucleus of the diagonal band of Broca, and the rostral end of the nucleus preopticus medianus separates the medial septal nuclei of the two sides. At such levels, the medial septal nucleus, the bed nucleus of the anterior commissure and the nucleus of the diagonal band of Broca are in such close contact that it is very difficult to distinguish them in cell material. Only one cell type, however, is found in this frontal portion of the bed nucleus of the anterior commissure as compared to two types of cells in the medial septal nucleus. In the bat these three nuclei are present in the same cross section for only a short distance near the caudal end of the medial septal nucleus, probably because of the tilt of the sections. The medial septal nucleus disappears in sections through the rostral border of the anterior commissure, after having shifted still more dorsolateralward, and while the lateral septal nucleus is still present. The medial septal nucleus is figured and briefly mentioned by Johnston ('13, figs. 41, 45 and 46) for Myotis, where its relations appear to be essentially similar to those in the free-tailed bat.

The bed nucleus of the anterior commissure (figs. 2 and 3). The relations of this nuclear mass, which lies along the rostral and rostroventral surfaces of the anterior commissure, are best seen in sagittal sections, where, near the midline, a semilunar mass of gray is found along the frontal and ventral surfaces of the commissure on either side of the midline. The cephalic part of each bed nucleus is near the midline only, and here the two nuclei are in contact with each other, but the ventrocaudal portions diverge so that the nucleus preopticus medianus lies between them. Although along the frontal surface of the commissure the cells of the nucleus are spindle-shaped, vertically-oriented cells with deeply staining Nissl substance, those of the ventrocaudal part appear larger, are nearly triangular in outline and show a slight tendency toward forming a separate cell mass. This ventrocaudal part is designated as the nucleus preopticus anterior by Loo ('31), but in the bat might equally well be included in the bed nucleus of the anterior commissure (see also p. 628). The cells embedded in the fibers of the commissure also form a part of its bed nucleus. A bed nucleus of the anterior commissure was described by Gurdjian ('25) for the rat and by Young ('36) for the rabbit, as well as by Loo for the opossum.

In the cross section series of bat material figured, the rostral end of the bed nucleus of the anterior commissure first appears near the midline of the septum in sections through the most frontal part of the fornix. Here it lies medial to the more ventral part of the lateral septal nucleus, between the medial septal nucleus dorsalward and the nucleus of the diagonal band ventralward, and is in close contact with these two nuclei, from which it is only indistinctly differentiable on the basis of cell type (see pp. 615 and 630). In cross sections through the rostral border of the anterior commissure the bed nucleus is more dorsally and more laterally situated so that it is separated from the bed nucleus of the opposite side by the nucleus preopticus medianus. Here the anterior commissure lies immediately dorsal to the bed nucleus, while the head of the caudate nucleus is lateral to it. For a short distance a few of the cells extend across the midline, between the nucleus preopticus medianus and the anterior commissure, to the bed nucleus of the opposite side. Farther spinalward the bed nucleus may be seen at the caudal border of the anterior commissure, where it has a more ventral position, dorsolateral to the nucleus preopticus principalis and dorsomedial to the nucleus of the diagonal band of Broca. Caudal to the anterior commissure the bed nucleus is still more ventrolateral in position, being represented here for a short distance by a somewhat denser region, which corresponds to the nucleus preopticus anterior of Loo.

THE HIPPOCAMPAL VESTIGES IN RELATION WITH THE DORSAL COMMISSURAL SYSTEMS. Many of the nuclei usually described with the septal region are grouped here under this heading because of the relationship of the hippocampal vestiges to the corpus callosum and the hippocampal commissure in the bat. A suggestion, at least, of this relationship to the corpus callosum is to be found in Johnston's ('13, p. 398) account of Myotis, although this observer included the lateral septal nucleus of the present description in the part of the primordium hippocampi ventral to the corpus callosum.

The bed nucleus of the hippocampal commissure (figs. 1B to 7). In the bat, the hippocampal commissure is almost completely surrounded on its frontal, ventral, caudal, and dorsal surfaces by the gray which forms its bed nucleus. These relations are most plainly seen in sagittal sections (figs. 4 and 6) and are illustrated further by a diagram (fig. 7). To designate its different parts the terms pre-, infra-, post-, and supracommissural portions of the bed nucleus are used. From the description of Elliot Smith (1897, fig. 23 and p. 51) the very small hippocampal commissure of the marmoset, Midas, is entirely surrounded by a 'matrix of grey matter,' corresponding to the bed nucleus in the bat.

The cells of the bed nucleus of the hippocampal commissure are of two types—spindle-shaped cells with lightly staining nuclei and fine Nissl granules, and small, triangular cells with more deeply staining nuclei. These latter cells are fewer in number and present only in the precommissural portion of the nucleus.

The precommissural portion (figs. 1, 2, 4, 6 and 7) of the bed nucleus, frontal to the commissure and extending between the fornix columns, is its largest part in the bat and is the portion described as the bed nucleus of the hippocampal commissure by Gurdjian ('25) for the rat. In cross sections through the hippocampal commissure and the fornix columns, this precommissural part appears as a triangular cell mass ventral to, and with some of its cells embedded in, the commissure, and has been designated the triangular nucleus by Ramón y Cajal ('11) for the mouse, and the nucleus septalis triangularis by Loo ('31) for the opossum. It is also the small celled portion of the primordium hippocampi of Johnston ('13, p. 398, fig. 46) for Myotis.

Cells of the bed nucleus which continue from the frontal along the ventral surface of the commissure, and are designated as the infracommissural part (figs. 3, 4, 6 and 7) in the bat, are present also in the opossum (Loo, '31, fig. 83), where they have been described as the bed nucleus of the tractus cortico-habenularis medialis. As seen in cross sections through this region (fig. 3) of the hippocampal commissure, the infracommissural portion of the nucleus extends lateralward and caudalward from the triangular precommissural part, the ventral angle of which, at such levels, has been replaced by the anterior columns of the fornix.

Along the posterior border of the commissure a single row of cells connects the supra- and infracommissural parts of the bed nucleus and forms its postcommissural portion (figs. 4B and 7). In some series (figs. 4B, 6 and 7) the supracommissural portion may be located farther ventralward where, however, it has a postcommissural, rather than a supracommissural, position.

In the bat, the region of junction of the hippocampal commissure with the corpus callosum is capped by a very compact cell mass of hemispherical shape, which was described by Werkman as the "couche supracommissurale du lit commissural" or supracommissural part (layer) of the commissural bed, the term employed here, and considered by him as a part of the commissural bed, being in continuity with it in a 15.5 mm. Vesperugo embryo (Werkman, '14; p. 57 and fig. 21, l.c.s.). In the bat material used for this study (Tadarida mexicana) this supracommissural portion (figs. 1B, 4, B and D, 5, 6, 7 and 16) varies somewhat in position in different series, and in one sagittal series (figs. 4B and 6) has a postcommissural location corresponding to its posterior position in Vesperugo pipestrellus and its ventral location in the shrew (Sorex vulgaris) as described by Ärnbäck

Christie Linde ('00, figs. 1 and 5, X). In either position, however, the tela chorioidea is attached to its more dorsal border, as indicated by Elliot Smith (1897 c) and Johnston ('13). In Tadarida, relations suggesting the embryonic connection with the precommissural portion are seen in sagittal series (fig. 4B), where a fine strand of cells connects the pre- and postcommissural regions, and the suggestion, at least, of a similar relationship is seen where the supracommissural cell mass caps the region of commissural junction (fig. 7). In cross sections through this region the supracommissural part of the bed nucleus appears as a semicircular, ependyma-covered, cell mass either dorsal (figs. 1B and 4D) or ventral (fig. 5B) to the dorsal commissure, depending on its location and the plane of the section, while the triangular precommissural portion lies ventral to it. In such sections many cells are also scattered among the commissural fibers between the two cell masses, and a few scattered cells may even join the gyrus dentatus and the supracommissural part of the bed nucleus (fig. 4D, y).

The supracommissural part of the commissural bed was noted and figures for Nyctophilus by Elliot Smith (1897 c, pp. 234 and 236) as "a small nodule of grey matter upon the caudal aspect of the hippocampal commissure." In 1900 Ärnbäck Christie Linde mentioned and figured the same mass of cells in another bat (Vesperugo pipestrellus) and in the shew (Sorex vulgaris). Zuckerkandl ('07) stated that in an 11.5 mm. embryo of Rhinolophus hipposideros the corpus callosum ends caudally in a cell mass (apparently such as described above), although no mention is made of a similar mass in the other Chiroptera which he studied. This author ('09, pp. 388–389, fig. 8) also described and figured such a cell mass in rat embryos, stating that, in the part nearest the corpus callosum, fibers of this commissure pass through it. In the free-tailed bat, however, a few corpus callosum fibers even pass through the supracommissural part at some distance from the commissure (see fig. 16A, e, and p. 658). In Johnston's 1913 paper this cell mass is figured for Myotis (figs. 44 to 46), and the name 'nodulus marginalis' suggested. This author (p. 399) interpreted it as "the primary upper border of the lamina supraneuroporica" and stated that its "cells belong to the indusium verum" of Elliot Smith (1897 b). Werkman ('14) found this cell mass in both bat (Vesperugo noctula) and hedgehog (Erinaceus europaeus) embryos in the same relative position and considered it a part of the commissural bed, which, becoming separated by the growth of the dorsal commissure, ceases to develop. It is figured, but not labeled, by Gurdjian ('25, fig. 10) for the albino rat, where its position appears to be postcommissural.

The gray in relation with the corpus callosum. Nuclear masses representing hippocampal vestiges are present on all surfaces of the corpus callosum. Dorsal to it is the indusium griseum with its subdivisions, ventral to it, the septo-hippocampal nucleus, and at its frontal end, the anterior hippocampal cortex, all of which are described below. In addition to these cell masses, the supracommissural part of the bed nucleus of the hippocampal commissure (described with the bed nucleus, p. 617) is usually situated dorsal to the caudal end of the corpus callosum, at the region where the two commissures join.

The anterior hippocampal cortex (figs. 4, A and C, and 7). In sagittal sections a club-shaped mass of cells, the anterior hippocampal cortex, is present at the cephalic tip of the corpus callosum, where it continues frontoventralward from the indusium griseum to about the region of the olfactory crus. Along its medial side the anterior hippocampal cortex is distinct from the neocortical areas, but laterodorsalward it is directly continuous with the adjacent frontal neocortex. Not only is the anterior hippocampal cortex continuous with the indusium griseum, dorsal to the corpus callosum, but it is continuous also with a second hippocampal vestige, the septo-hippocampal nucleus, ventral to this commissure. In horizontal and in cross sections the relation of the anterior hippocampal cortex to the indusium griseum is also clear. In cross sections, the medial part of the anterior olfactory nucleus lies just ventrolateral and the frontal end of the lateral septal nucleus dorsolateral to the anterior hippocampal cortex.

Elliot Smith referred to the region of the anterior hippocampal cortex in the Australian bat, Nyctophilus timorensis, as the precommissural portion of the vestigial hippocampus, stating that its pyramidal cells are characteristic of those of the hippocampus. This region was figured by Ärnbäck Christie Linde ('00) for Vesperugo pipestrellus along with the indusium griseum, the entire formation being labeled Ammon's horn, but no reference was made to it by Zuckerkandl ('07). The anterior hippocampal cortex was included in the primordium hippocampi of Myotis by Johnston ('13), who stated that in this bat the primordium reached the region of the olfactory peduncle.

The septo-hippocampal nucleus (figs. 4, B and C, 5A, 6 and 7). Certain of the sagittal sections which pass through the anterior hippocampal cortex show that it is continuous with a narrow cell band which passes, close to the ventral surface of the corpus callosum, as far caudalward as the precommissural part of the bed nucleus of the hippocampal commissure (figs. 4B and 7). This cell mass, the primordium hippocampi of Crosby ('17) and the septo-hippocampal nucleus of Young ('36) and of Ariëns Kappers, Huber and Crosby ('36), is traversed by a few fibers parallel with the ventral surface of the corpus callosum (fig. 16, C and D), and in the bat is distinguishable from the lateral septal nucleus, just ventralward, largely by the striated appearance produced by these fibers, since the cells of the two nuclear masses are very similar. A few cells of the septo-hippocampal nucleus extend dorsalward into the corpus callosum for varying distances and a still smaller number of them pass between the corpus callosum and the hippocampal commissure (fig. 4C). In cross sections the septo-hippocampal nucleus is less plain, but it can be located at the frontal end of the lateral septal nucleus, along the dorsomedial surface of which it is situated (fig. 5A). In midsagittal sections of the bat brain, a few cells, apparently belonging to this nucleus, may be seen near the caudal end of the corpus callosum (fig. 6).

The septo-hippocampal nucleus forms a minor part of the large celled portion of the primordium hippocampi which Johnston ('13, fig. 41) described in Myotis ventral to the corpus callosum. The greater part of Johnston's large celled portion of the primordium hippocampi located in this region is the lateral septal nucleus of this account, however.

The indusium griseum (figs. 1A, 4, A and C, 5 and 7). As used in this account the indusium griseum refers to the band of gray matter passing over the dorsal surface of the corpus callosum on either side of the midline. Before giving a detailed description of the indusium in the free-tailed bat, however, it seems advisable to present a brief summary of the pertinent literature.

The indusium griseum has been called by some writers the lateral stria of Lancisius, who, according to Fish (1893), described the band of gray, as well as the white stria more commonly known as the stria of Lancisius. For the numerous references dealing with early accounts of the indusium griseum the review of Fish should be consulted; the somewhat more recent work has been reviewed by Johnston ('13). It is possible to discuss here only those papers dealing with the indusium in Chiroptera.

The indusium griseum of two Australian bats, Nyctophilus timorensis and Miniopterus schreibersii, was described by Elliot Smith (1897 a, quoted from his 1897 c paper, p. 232) as a hippocampal vestige extending over the dorsal surface of the corpus callosum, and Ärnbäck Christie Linde ('00, figs. 1 and 2) figured and described this same cell band, along with the anterior hippocampal cortex, as the dorsal part of Ammon's horn, showing its main relations essentially as seen in figure 4A. In his 1907 paper Zuckerkandl described the indusium griseum for nine species of Chiroptera under the name of gyrus supracallosus, stating that it was continuous with Ammon's horn, but not mentioning its relation to the anterior hippocampal cortex. Haller ('07) also spoke of the lateral stria as a rudimentary Ammon's horn on the dorsal surface of the corpus callosum.

In the free-tailed bat the indusium griseum appears, in some series, as an undifferentiated, ribbon-like band of gray over the dorsal surface of the corpus callosum, connecting the anterior hippocampal cortex frontalward with the hippocampal formation caudalward. In other series, however, there is a tendency toward a differentiation of the indusium, especially near its caudal end, into a medial part, which, when followed caudalward, becomes differentiated into Ammon's horn, and is designated, therefore, as the pars ammonis, and a more lateral portion, representative of and continuous with the subiculum, and called the pars subicularis. In two of the series studied, these two subdivisions are distinguishable even as far frontalward as the cephalic tip of the corpus callosum, while in other series the distinction can be made only far caudalward. In some series, the medial subdivision shows a still further tendency toward differentiation. Sometimes, at the very caudal end of the corpus callosum (although usually posterior to the hippocampal commissure), its cells split into two layers, the more dorsal of which, when followed caudalward, becomes differentiated into the gyrus dentatus, while the ventral layer becomes the cornu ammonis. In such instances, the more dorsomedial portion would represent a pars dentata (figs. 4 and 5; see also p. 625).

From these relations, then, it appears that not only the cornu ammonis may be represented over the dorsum of the corpus callosum, as stated by Ärnbäck Christie Linde, Zuckerkandl, and others, but also the subiculum, and even the gyrus dentatus may have such representation. For the most part, however, this representation is in the form of undifferentiated hippocampal gray, although in some instances there may be enough differentiation to indicate the presence of all portions of the hippocampal formation throughout a small part, at least, of the extent of the indusium. No doubt the amount of differentiation would have a reverse relation with the actual degree of development of the corpus callosum in the series in question. Therefore, in mammals having a well-developed corpus callosum, only the undifferentiated hippocampal gray might be found in the indusium griseum. However, such gray undoubtedly has potentialities for the development of all portions of the hippocampus, potentialities which are inherent, likewise, in the anterior continuation of the hippocampus.

Elliot Smith (1897, 1897 b and 1897 c) used the term 'indusium verum' for the "mesial film of grey matter" (1897 c, p. 238) upon the dorsal surface of the corpus callosum—gray, which, according to a previous account (1897 b, p. 24), connects "the fasciae dentatae of the two sides." To distinguish this gray from the more laterally situated cell bands, this author (1897, p. 46) suggested for the latter, the name 'false indusium.' In the account of Zuckerkandl ('07) the term 'das intermediäre Indusium' was employed to designate both this medially situated scattered gray and the fibers with it, the striae of Lancisius. In eight of the nine species of Chiroptera studied by him the 'intermediäre Indusium' was fine for the most part, being affected, according to this author, by the position of the large blood vessels above the commissure.

In the free-tailed bat, only an occasional cell is found scattered along the course of the fibers forming the striae of Lancisius, such cells passing over, at the frontal tip of the corpus callosum, into an inconstant cell mass (figs. 6 and 7, x) located in the midline in some of the series (two transverse, one horizontal, and two sagittal). Those fibers of the striae of Lancisius which turn caudalward to join the postcommissural fornix pass through this cell mass, giving it the appearance of a cell group carried along the course of these fibers. In that event, the apparent absence of this nucleus is probably due to the presence of fewer and more scattered cells along the fiber bundle. The crowding due to the numerous blood vessels of the region might also account for the inconstancy.

Apparently the supracommissural part of the bed nucleus of the hippocampal commissure also represents a part of the indusium verum, as is implied in the papers of Elliot Smith and as stated by Johnston ('13, p. 399) and Werkman ('14, p. 59), although it is not possible to say with certainty. If such be the case, then both the medial position of the indusium verum and the relation of the gyrus dentatus to the cells of the supracommissural part of the bed nucleus of the hippocampal commissure (p. 619 and fig. 4D) suggest that this part of the bed nucleus may also represent a pars dentata of the indusium griseum, a possibility also suggested by the relation of its fibers to those from gyrus dentatus (p. 686).

THE PREOPTIC AREA. Since no description of this region in Chiroptera is to be found in the available literature, the terminology and grouping of Loo ('31) for the opossum are followed here as far as possible. For a description of the boundaries and general relations of the area the papers of this observer and of Young ('36, rabbit) should be consulted. In the bat, differentiation of the nuclear masses described by Loo is difficult, because of the compactness of the area and the crowding of its cells, so that without a detailed study of the fiber connections of the region, any subdivisions can be made only on a purely arbitrary basis.

Nucleus preopticus medianus (figs. 3 and 6). The nucleus preopticus medianus is a cell mass which curves along the dorsal, rostral, and ventral surfaces of the anterior commissure at the midline (fig. 6). In cross sections through the tuberculum olfactorium (fig. 3) the main portion of this nucleus is located between the anterior pillars of the fornix, ventral to the precommissural part of the bed nucleus of the hippocampal commissure (nucleus septalis triangularis of Loo), and immediately frontal to the anterior commissure. Its cells are small, spindle-shaped cells with large nuclei and deeply staining cytoplasm; they show a marked dorsoventral orientation. Since the dorsal portion of the nucleus curves above the anterior commissure slightly, in cross sections just caudal to its cephalic tip the nucleus is divided, for a short distance, into a smaller part, dorsal to the most rostral fibers of the commissure, and a larger part ventral to it. More caudally situated cross sections show the nucleus ventral to the commissure, where it lies in front of the preoptic recess. As it becomes continuous ventrally and caudally with the preoptic periventricular nuclei, its cells stain less deeply, appearing, then, so similar to those of the latter nuclei as to be indistinguishable from them. The relation of these nuclear masses is distinctly evident in sagittal sections (fig. 6), but easily determined from transverse series also, the portion of the nucleus preopticus medianus situated ventral to the commissure (actually rostral to it as shown in sagittal sections) appearing between the two bed nuclei of the anterior commissure, which are replaced caudalward by the two principal preoptic nuclei at about the same level that the nucleus preopticus medianus becomes continuous with the broader nucleus preopticus periventricularis.

Nucleus preopticus periventricularis (figs. 6, 8 and 9, A, B and C). The nucleus preopticus periventricularis is situated in the region of the preoptic recess, where it borders the rostral and lateral walls of the third ventricle. It is continuous dorsally and rostrally with the nucleus preopticus medianus, and caudally, without any evidence of demarcation, with the nucleus periventricularis hypothalami, and is in contact ventrally with the nucleus suprachiasmaticus anterior.

The cephalic part of the nucleus preopticus periventricularis is present in cross sections through the most caudal portion of the anterior commissure (fig. 8), where it lies along the rostral wall of the ventricle, ventral to the commissure and between the two principal preoptic nuclei. More caudalward the nucleus lies along the ventral two-thirds of the lateral wall of the ventricle (fig. 9). As the preoptic recess widens out lateralward, it extends out along the dorsal wall of this recess to become continuous with the nucleus suprachiasmaticus anterior, where the latter lies in the ventral wall of the recess. The more dorsal cells of the nucleus tend to be irregularly arranged in four or five concentric layers. The inner of these layers, which is in contact with the ependyma of the ventricle, is quite distinctly separated from the other laminae; its scattered cells are oriented transversely. The cells of the other layers, as also those lying along the rostral wall of the preoptic recess, are oriented vertically. They are spindle-shaped, with large, lightly staining nuclei, and resemble very closely those of the nucleus preopticus principalis with which they are in contact lateralward. The more dorsal portion of the nucleus preopticus periventricularis has been designated pars medialis and the ventral part, pars suprachiasmatica, by Loo ('31) for the opossum. The cells of the latter portion are not arranged in layers, but form a dense cell mass along the dorsal and lateral walls of the preoptic recess. The cells are of the same type as in the remainder of the nucleus, but show no orientation, so that they are distinguishable with difficulty, if at all, from those of the nucleus preopticus principalis lateralward.

Nucleus suprachiasmaticus anterior (figs. 9, A, B and C). Nucleus suprachiasmaticus anterior is located along the ventral wall of the preoptic recess, rostral to the optic chiasm, with its frontal, dorsal, and lateral borders in contact with the ventral part (pars suprachiasmatica) of the nucleus preopticus periventricularis. The cells differ from those of this latter nucleus, however, being of the small granule type with large, lightly staining nuclei, and are even more closely packed together. The anterior suprachiasmatic nucleus extends from the frontal end of the preoptic recess, where only a few cells are present, to the frontal border of the optic chiasm, forming quite a prominent cell mass toward its more caudal end. In the bat, the nucleus is proportionately much larger, and its longitudinal extent appears relatively greater, than in the opossum as described by Loo ('31).

Nucleus suprachiasmaticus diffusus (fig. 9D). A few small cells, arranged as two concentric laminae, lie along the ventral surface of the third ventricle just caudal to the preoptic recess and dorsal to the most cephalic fibers of the chiasmal ridge. They are in contact dorsalward with the periventricular gray, and appear to be intercalated in the course of a fiber tract, which, according to Gurdjian ('27) and Loo ('31), is Ganser's commissure, for which the former author suggests that they act as a bed nucleus.

Nucleus preopticus anterior (fig. 8, see also p. 616). In the present description Loo's ('31) nucleus of this name is included with the bed nucleus of the anterior commissure, since it forms the ventrocaudal part of that cell mass with only slight evidence of differentiation either on the basis of cell type or of massing of cells. In this respect it appears to be more nearly comparable to the condition in birds, where, according to Huber and Crosby ('29, p. 66), it is not possible "to differentiate a clear nucleus preopticus anterior as distinct from the bed nuclei of the commissures in dove, although a slight massing of the cells in the appropriate region can be seen."

Nucleus preopticus principalis (figs. 8 and 9, A, B and C). Nucleus preopticus principalis is a large nuclear mass occupying the major portion of the medial preoptic area, lateral to the nucleus preopticus periventricularis. The nucleus is indistinctly separable into dorsal and ventral parts as described by Loo, but the whole cell mass is distinguishable from surrounding nuclei only indistinctly, and does not extend so far caudalward as in the opossum. Its cells are spindle-shaped with large nuclei and abundant Nissl substance, closely resembling those of the bed nucleus of the anterior commissure.

The frontal part of the nucleus preopticus principalis is present in cross sections which pass through the caudal part of the tuberculum olfactorium and the middle of the anterior commissure, where the medial portion of the cell mass, ventral to the commissure, becomes somewhat separated from the remaining cells of the region to form this nucleus. At its rostral end it lies ventrolateral to the caudal end of the bed nucleus of the anterior commissure (nucleus preopticus anterior, see p. 616 and above), ventral to the head of the caudate, dorsal to the nucleus of the diagonal band of Broca, and medial to the nucleus preopticus magnocellularis. In sections caudal to the anterior commissure, the nucleus preopticus principalis is larger and indistinctly separated into dorsal and ventral branches, both of which extend more medialward. As the caudal end of the bed nucleus of the anterior commissure disappears the dorsal branch replaces it, and becomes continuous medially with the ventral branch, to form an indistinct, C-shaped mass with its open side lateralward. Here it lies just lateral to the nucleus preopticus periventricularis and partially surrounds the nucleus preopticus interstitialis for a short distance. Still more caudalward the dorsal and medial portions of this nucleus are slightly separated from the ventral part, which soon disappears. The remainder of the nucleus remains in contact, on it ventromedial aspect, with the periventricular preoptic nucleus, continuing caudalward to disappear rostral to the optic chiasm and to the most cephalic part of the nucleus supraopticus.

Nucleus epichiasmaticus (no figure). The nucleus described under this name by Loo ('31) for the opossum, in the bat material studied, either appears to be absent (in most series) or represented (in some series) by a few small, deeply staining cells scattered throughout the other nuclei just dorsal to the chiasmal ridges. When present, these cells appear to be in the course of the supraoptic decussations, however, rather than to form a separate nuclear mass.

Nucleus supraopticus (figs. 6 and 9, C and D). The nucleus of this name described by Loo ('31) for the preoptic area of the opossum is the nucleus perichiasmaticus or tangentialis of Ramón y Cajal ('11), the tangential nucleus of Gurdjian ('27) for the rat, and the ganglion opticum basale of Malone ('16) and others. A discussion of other references in the literature is given by Loo.

In the bat, the nucleus supraopticus is a large, somewhat H-shaped cell mass situated along the optic chiasm and optic tracts with the cross-bar portions of the H situated just caudal to the chiasm. The nuclear mass as a whole is well developed and consists of very large, multipolar neurons with abundant, deeply staining, coarse Nissl granules and large, lightly staining nuclei. The broad cephalic extensions of the nucleus are located frontal to the optic chiasm in the region of the ventral rhinal fissure (fig. 9D), from which they extend medialward, at and near the surface of the brain, toward the preoptic recess. In the region of the optic chiasm all the cells have collected into a thinner cell layer on either side, at the very surface, and just caudal to the chiasm these cell layers of the two sides are connected across the midline, at first only by a few scattered, more deeply situated cells, then by a narrow cell band at the surface. The caudal extensions of the H-shaped nuclear mass are shorter and narrower than the frontal extensions, but extend spinalward along the surface of the brain to the region of the infundibular portion of the hypophysis.

Nucleus of the diagonal band of Broca (figs. 2, 3, 6, 8 and 9A). In the bat the nucleus of the diagonal band of Broca extends from the medial portion of the septal region, slightly ventralward, then caudolateralward to the region of the fissura endorhinalis (fig. 9A), where it is no longer distinguishable from the cortico-medial amygdaloid complex. Its cells are large, spindle-shaped and multipolar cells, with lightly staining nuclei and deeply staining Nissl granules, but without such marked vertical orientation as the cells of the medial septal nucleus.

At its rostral end the nucleus of the diagonal band of Broca lies ventral and slightly ventrolateral to the medial septal nucleus and in close contact with it. This portion of the nucleus may be seen in sections passing through the middle of the precommissural part of the bed nucleus of the hippocampal commissure and rostral to the region where the tuberculum olfactorium has assumed its characteristic cellular structure. In more caudal sections, the nucleus of the diagonal band is larger and slightly more ventral in position, with the bed nucleus of the anterior commissure dorsal to it, thus separating the nucleus of the diagonal band from the caudal end of the medial septal nucleus. Still farther caudalward the nucleus of the diagonal band extends lateralward to cross the ventral surface of the brain just caudal to the tuberculum olfactorium. As it becomes indistinguishable from the cortico-medial amygdaloid complex, it extends deep in toward the anterior commissure. Among the descriptions of this nucleus in mammals are those of Johnston ('23) for the opossum, the rabbit, and man, of Loo ('31) for the opossum, and of Young ('36) for the rabbit.

Nucleus preopticus interstitialis (figs. 8 and 9A). From the account of Gurdjian ('27) the cells intermingled with the medial forebrain bundle in the preoptic area constitute the lateral preoptic area or nucleus in the rat. According to Loo ('31), in the opossum, the cells among the 'deeper less myelinated fascicles' of the medial forebrain bundle are described as the nucleus preopticus interstitialis, while those of the 'outer more myelinated fascicles' form a nucleus preopticus magnocellularis. In the bat a subdivision of the lateral preoptic area, as this entire region is described by Gurdjian ('27) for the rat, into two such nuclei is very indistinct but since there is some evidence of differentiation Loo's terminology is followed.

In sections passing through the most caudal part of the anterior commissure the rostral end of the nucleus preopticus interstitialis is situated medial to the nucleus preopticus magnocellularis, dorsolateral to the nucleus preopticus principalis, lateral to the ventrocaudal portion of the bed nucleus of the anterior commissure (nucleus preopticus anterior), and ventral to the head of the caudate nucleus. Its cells are similar in type to those of the nucleus preopticus principalis, and throughout its extent the two nuclei are scarcely distinguishable from each other. Caudally (fig. 8, left) the nucleus preopticus interstitialis is in the hollow of the C-shaped mass of the nucleus preopticus principalis, later shifting ventralward to replace the ventral portion of this latter nucleus. Then it is located dorsomedial to the nucleus of the diagonal band of Broca, dorsolateral to the nucleus preopticus periventricularis, ventral to the dorsal part of the nucleus preopticus principalis and medial and ventro-medial to the nucleus preopticus magnocellularis. It extends caudalward as far as sections through the caudal end of the nucleus of the diagonal band, where it lies dorsal to this latter nucleus.

Nucleus preopticus magnocellularis (figs. 8 and 9, A and B). The nucleus preopticus magnocellularis consists of cells scattered along the course of the lateral part of the medial forebrain bundle. It extends from the caudal border of the anterior commissure as far spinalward as the caudal end of the nucleus of the diagonal band of Broca, where it merges laterally with the cortico-medial amygdaloid complex (see p. 645) and is replaced ventromedially by the nucleus preopticus interstitialis. In transverse sections through its cephalic end, the nucleus preopticus magnocellularis is a scattered band of fairly large, triangular cells, located dorsomedial to, and parallel with, the polymorphic layer of the lateral part of the tuberculum olfactorium, and dorsolateral to the nucleus of the diagonal band. At its caudal end, the nucleus preopticus magnocellularis replaces the polymorphic layer of the tuberculum olfactorium, thus lying lateral to the nucleus of Broca's diagonal band, ventromedial to the cortico-medial amygdaloid complex, and lateral to the nucleus preopticus principalis and the nucleus preopticus interstitialis.

THE CAUDATE-PUTAMEN COMPLEX AND THE GLOBUS PALLIDUS. In general the corpus striatum of the bat is relatively small and undifferentiated. The caudate nucleus and the putamen are fused into a common mass at their frontal end and again caudalward, and, at their lateral surface, are separated elsewhere only by scattered bundles of internal capsule fibers. As in other mammals, the lentiform nucleus is made up of the putamen and the globus pallidus. It is relatively small in the bat, however, and in cross sections resembles a concavo-convex, rather than a biconvex, lens in shape, its concave surface facing the basolateral amygdaloid complex lateralward (see p. 634).

The caudate-putamen complex (figs. 1 to 3, 8 and 9A). Since the putamen and the caudate nucleus are represented by an undifferentiated cell mass both at the caudal end and at the cephalic end of the corpus striatum, and are only partially separated from each other by the fascicles of the internal capsule elsewhere, they are described together as the caudate-putamen complex. The caudate portion of the nucleus, as in higher mammals, consists of a head (including the nucleus accumbens) and a tail, the head being large as compared with the remainder of the complex. The tail of the caudate is relatively short and only slightly curved.

The cells of the caudate-putamen are similar in type throughout—largely fusiform cells of varying size, with large, lightly staining nuclei and fine Nissl granules, but with a few large, multipolar cells having coarse Nissl granules. At the rostral end of the common cell mass, and again at its caudal end, the small fusiform cells predominate, there are a very few large, multipolar cells and small, deeply staining, triangular cells, with coarse Nissl substance, are also present and become increasingly numerous.

In following a series of cross sections caudalward the entirely undifferentiated caudate-putamen extends as far as sections through the rostral end of the corpus callosum. Here small, scattered bundles of fibers of the internal capsule begin to penetrate the caudate-putamen on its dorsolateral surface. Both the number and the size of these fiber bundles increase farther caudalward and are scattered throughout the dorsolateral portion of the cell mass for a considerable distance. This dorsolateral area of intermingled fiber bundles and neurons now represents the putamen, while the remainder of the cell mass medialward is the caudate nucleus (figs. 1B, 2 and 3, right). These two nuclear masses remain completely undifferentiated ventralward, where the distinctly rounded mass formed in this region and apparently representing largely the head of the caudate nucleus, tends to be fused with the frontal, less differentiated portion of the tuberculum olfactorium (see p. 610). Dorsomedialward, the head of the caudate becomes continuous under the ventricle with the nucleus accumbens. The head region of the caudate-putamen complex contains small islands of cells, somewhat similar to the islands of Calleja (figs. 2 and 3, on right but unlabeled), which often lie at the lateral border of the region representing the nucleus accumbens.

Farther caudalward (fig. 2), in sections through the rostral end of the baso-lateral amygdaloid complex, the putamen shows a differentiation into two zones—a lateral area free from fiber bundles, and a medial one consisting of intermingled strands of cells and small fascicles of the internal capsule. Both on the ventrolateral and the ventromedial surfaces of the complex, the head of the caudate and the putamen remain continuous with each other, at least in part, while the compact portion of the internal capsule separates them through the central region. Dorsolaterally, along the border of the complex, small fiber bundles are intermingled with strands of cells connecting the two nuclei, but the strands of cells always predominate over the fiber bundles.

The anterior commissure passes through the ventral part of the putamen and through the head of the caudate, which at this level has decreased in size (fig. 3, left). In sections just rostral and just caudal to the anterior commissure, then, small parts of each of these nuclei (the putamen and the head of the caudate), lying ventral to the commissure, become continuous with their corresponding main nuclear masses dorsalward. The ventral portion of the putamen, cut off by the external capsule component of the anterior commissure, is described by Loo ('31) for the opossum as a part of his nucleus intermedius striati. The portion of the head of the caudate ventral to the anterior commissure, after uniting with the dorsal part caudal to the commissure, extends caudalward to the region of the nucleus preopticus principalis, from which it cannot be distinguished with certainty in cell material.

In the region of the cephalic border of the anterior commissure (fig. 3, left) the baso-lateral amygdaloid complex is separated from the concave lateral border of the putamen by fibers of the external capsule, while medial to the putamen lie the cephalic tip of the globus pallidus ventrally and the internal capsule at the middle of the region; dorsally is the tail of the caudate, more or less intimately united to the putamen by strands of cells intermingled with fiber bundles. At these levels, also, the ventral part of the head of the caudate is partially separated from the polymorphic layer of the tuberculum olfactorium by intervening small fiber bundles joining the anterior commissure. That part of the head of the caudate dorsal to the anterior commissure forms a small triangular cell mass the base of which rests on the commissural fibers. Near the rostral border of the commissure, as seen in cross sections, the apex of this triangular mass is joined to the tail of the caudate by fibers of the stria terminalis and its bed nucleus, while near the caudal border it appears to be completely separated from the tail of the caudate by the internal capsule (fig. 8, right). Otherwise, the tail of the caudate nucleus is continuous with the head.

Likewise in the region of the anterior commissure, the putamen is completely continuous with the tail of the caudate nucleus to form a comma-shaped nuclear mass in which the head of the comma is formed by the tail of the caudate, the tail of the comma by the putamen, and the ventromedial indentation between the caudate and the putamen by the internal capsule. At the rostral border of the anterior commissure, however, the putamen is partially separated from the tail of the caudate by a region of intermingled cells and bundles of fibers of the internal capsule, while, at the caudal border of the commissure, the comma-shaped caudate-putamen decreases in size and there are no longer any fiber bundles partially separating its two parts dorsolateralward. Ventrally the complex is now in contact with the lateral portion of the tuberculum olfactorium, and medially it is bordered by the globus pallidus. Immediately caudal to the anterior commissure the tail of the caudate and the putamen become so completely merged as to form a common rectangular nuclear mass medial to the baso-lateral amygdaloid complex, ventral to the lateral ventricle, lateral to the internal capsule and the stria terminalis and dorsal to the cephalic end of the nucleus centralis amygdalae.

Caudal to this region (fig. 8), the caudate-putamen complex decreases rapidly in size, as the baso-lateral amygdaloid complex and the central amygdaloid nucleus become larger, and comes to have a more oval shape. Its dorsal and lateral relations remain the same, while medially the stria terminalis and its bed nucleus lie in contact with it, and ventrally it rests in the concavity of the semilunar central amygdaloid nucleus. At its caudal end (fig. 9A) the caudate-putamen becomes increasingly difficult to distinguish from the central amygdaloid nucleus, which later occupies the dorsomedial angle of the temporal lobe (fig. 9B).

That portion of the head of the caudate nucleus which lies medial to the lateral ventricle is known as the nucleus accumbens (figs. 1B and 2). In the bat this relation to the medial wall of the ventricle is inconstant and can be demonstrated only in certain series of the material. In other series the nucleus is found only in relation with the ventral surface of the ventricle, although extending on into the medial wall of the hemisphere. Because of the density of its cells, however, the nucleus accumbens appears more deeply staining than the remainder of the caudate nucleus, and an area corresponding to it can be identified in all series. The nucleus accumbens is distinctly separated from the septal nuclei dorsal and medial to it by a small fiber band; ventrolaterally small clusters of cells, resembling the islands of Calleja, are found in the region where the densely packed cells of the nucleus accumbens pass over into the less dense head of the caudate lateralward (see p. 634).

The caudate-putamen complex as briefly described by Spiegel ('19) for Pteropus edulis resembles that of the free-tailed bat, although in the former animal there appears to be more massing together of the bundles of the internal capsule. Other available accounts of the Chiroptera, such as those of Hirsch ('07), and Johnston ('13 and '23, figs. 40 and 79 respectively, although not labeled in the former figure) give some figures of this complex, and Haller ('07) figured and briefly mentioned the caudate and lentiform nuclei. This latter observer, however, included in his 'ganglia areae olfactoriae' (tuberculum olfactorium) a part, at least, of the nuclear mass described in this account with the head of the caudate nucleus. A definite nucleus accumbens was figured, although not labeled, by Ganser (1882, fig. 9) for the mole.

The globus pallidus (figs. 3 and 8). In the bat, the globus pallidus is relatively small, extending from the rostral border of the anterior commissure to a region slightly frontal to the preoptic recess, or an actual distance of about 0.75 mm., and shows no subdivision into lateral and medial parts by medullary laminae. It is triangular in shape in cross sections, and consists of intermingled neurons and fibers situated medial to the putamen and lateral to the internal capsule. Its cells are large, multipolar and spindle-shaped neurons with coarse, deeply staining Nissl substance.

In cross sections through the rostral border of the anterior commissure, a few scattered cells of the globus pallidus lie dorsal to the commissure, medial to the ventral portion of the putamen and lateral to the internal capsule. Farther caudalward these neurons increase in number to form a roughly triangular area dorsal to the commissure, while a very few cells lie ventral to the commissural fibers, forming there a part of the nucleus intermedius striati of Loo ('31). At the caudal border of the commissure the two parts of the nucleus are united again. Toward the caudal end of the globus pallidus, and the head of the caudate nucleus, the ventral border of the globus pallidus is continuous with the large celled, lateral portion of the preoptic area, nucleus preopticus magnocellularis. Here also its most ventromedial cells lie in contact with the caudal end of the head of the caudate nucleus rather than with fibers of the internal capsule. Where it decreases rapidly in size at its caudal end, the globus pallidus is continuous medially with the scattered cells of similar type in the cerebral peduncle.

According to Spiegel ('19) the globus pallidus is also decidedly limited in development in Pteropus edulis (one of the Macrochiroptera), and shows no evidence of medullary lamination, either in this form or in the Insectivora. Although figured by Haller ('07) for Vesperugo, the region is not described.

THE CLAUSTRUM (figs. 8 and 9, A and B). Deep to the rhinal fissure (fig. 8) and the insular cortex the claustrum is present as a thin plate of cells located superficial to the external capsule and the baso-lateral amygdaloid complex and imperfectly separated from the overlying cortex. It extends from the region of the caudal part of the caudate-putamen to about the middle of the cortico-medial amygdaloid complex. Ventrorostrally the claustrum is continuous with the deeper portion of the pyriform lobe and dorsalward with the deeper portion of the neopallial cortex (fig. 8). In sections through the more caudal portion of the claustrum, where it is thinner than farther frontalward, the dorsoventral extent of this plate of cells decreases and soon it becomes indistinguishable from the overlying deep cortex.

Haller ('07) described and figured as the claustrum in Vesperugo the baso-lateral amygdaloid complex of this account and stated that it was extremely well developed. From the figure and description of Pteropus edulis given by Spiegel ('19), the claustrum of this species of Macrochiroptera resembles that of the free-tailed bat. Some indication of a separation of cortical layers, such as is seen at the most caudal end of the claustrum in the present account, was figured by Johnston ('23, fig. 77) for Myotis but not labeled or described. In insectivores (mole and hedgehog) Spiegel found this cell layer difficult to distinguish.

THE AMYGDALOID COMPLEX. In the free-tailed bat, the amygdaloid complex as a whole is relatively very large, extending from regions as far frontalward as the anterior commissure to the caudal pole of the hemisphere. In the species under consideration it is similar in size and extent to the amygdaloid complex seen by Spiegel ('19) in Pteropus edulis and by Johnston ('23) in Myotis. According to both Ganser (1882) and Spiegel ('19), the degree of development of the amygdala of the mole is also surprising. Spiegel stated that Ganser's amygdala corresponds largely to his basal ('Hauptkern') and lateral amygdaloid nuclei, and described an additional cell group, the medial amygdaloid nucleus. The amygdaloid nuclei of Erinaceus were described by Völsch ('06 and '11) as B, D, E, M and T, and the nuclei corresponding to these cell masses of Völsch are discussed by Johnston ('23).

The amygdaloid complex of the free-tailed bat may be considered as composed of two primary nuclear masses, a baso-lateral (or ventrolateral) nuclear complex and a cortico-medial (or ventromedial) complex. These subdivisions correspond, in general, to the nuclear groupings made by Johnston ('23, p. 474) and to Berkelbach van der Sprenkel's ('26) subdivisions of the amygdaloid complex. In the present account, however, the cortical amygdaloid nucleus is included within the cortico-medial rather than within the baso-lateral complex, because of its fiber connections (the anterior and medial part rather than the posterior and lateral part of Berkelbach van der Sprenkel in the opossum). In the free-tailed bat, throughout the caudal extent of each of these primary nuclear masses there is a differentiation into those amygdaloid nuclei which have been recognized for other mammals in the general region in question, although each complex is represented at its frontal end, in cell material at least, by an undifferentiated cell mass.

The baso-lateral amygdaloid complex is probably homologous with the cells intercalated in the course of the occipito-mesencephalic tract (archistriatum) of birds (Huber and Crosby, '29, p. 49) and with the ventrolateral part of the dorsolateral area in the alligator (Crosby, '17). Likewise, the cortico-medial complex is probably homologous with the nucleus taeniae of birds and with the ventromedial nucleus of the alligator (Huber and Crosby, '29, p. 55). The possible homologies with similar regions in the turtle are discussed in relation with the connections of the amygdaloid complex (p. 673).

The baso-lateral amygdaloid complex (figs. 2, 3, 8 and 9). The baso-lateral nuclear mass is relatively very much larger than the cortico-medial complex in the bat, the marked increase in size of the entire amygdala being due mainly to this complex. The baso-lateral nuclear complex extends from the rostral border of the anterior commissure caudalward to the tip of the temporal lobe, its cephalic end consisting, in cell material, of an undifferentiated cell mass, which, as it continues caudalward, is indistinctly divisible into the three nuclei described by Johnston ('23) for the ventrolateral amygdaloid region of Myotis and other mammals—the nucleus amygdalae lateralis, the nucleus amygdalae basalis, the nucleus amygdalae basalis accessorius, and, in addition, the massa intercalata. In pyridine silver preparations, a large part of this apparently undifferentiated portion is shown to be composed of both the basal and the lateral nuclei, while the very frontal end of the mass actually represents only the lateral amygdaloid nucleus (figs. 11B, 13 and 14). Throughout its extent, the cells of the baso-lateral complex closely resemble those of the caudate-putamen, being multipolar cells with large, faintly staining nuclei and distinct Nissl granules.

In following a cross section series of toluidin blue material caudalward, the cephalic undifferentiated end of the baso-lateral complex is first seen at the rostral border of the anterior commissure as an elongated mass of cells in the course of the fibers of the external capsule (figs. 2 and 3). On both its medial and lateral surfaces the baso-lateral complex is bordered by the fibers of the external capsule, which splits into two portions, as described by Haller ('07), the larger part passing dorsomedial to the baso-lateral complex to reach the anterior commissure (its external capsule component, see p. 666), while a few fibers pass lateral to it. Ventrally this nuclear mass is bordered by the interpyriform component of the anterior commissure. A few cells are partially separated from the baso-lateral complex on its ventral border by commissural fibers passing through it from the pyriform lobe, and probably represent a part of the nucleus intermedius striati described by Loo ('31) in the opossum. At its cephalic end, then, the baso-lateral amygdaloid complex is very distinctly separated from the putamen medial to it, but less plainly distinguished from the deep layers of the cortex lateral to it.

In sections farther caudalward, through the caudal border of the anterior commissure (fig. 8, right), the baso-lateral complex increases in size so that it at first equals, then soon exceeds, the putamen in every dimension. It now appears roughly lens-shaped in outline with its external or lateral surface distinctly convex and its internal surface only slightly so. At such levels it is just as distinctly separated from the overlying cortical area as from the putamen deep to it. Here the lateral portion of the nuclear complex shows a more scattered arrangement of its cells, which, however, are similar in type to those of the medial compact portion although slightly larger. These differences in the arrangement and size of its cells are continued almost as far frontalward as the tip of the baso-lateral complex, although less clearly distinguishable farther forward. In sections still more caudally situated, it is possible, in toluidin blue material, to distinguish the different nuclei which constitute the baso-lateral amygdaloid complex. A description of each of these nuclei follows.

Nucleus amygdalae lateralis (fig. 9, A, B and C). In toluidin blue material, the frontal end of the lateral amygdaloid nucleus is first differentiable from the remainder of the baso-lateral amygdaloid complex in regions where cross sections pass through the cephalic part of the preoptic recess. Here the differentiation is largely on the basis of a slight indentation along the lateral border of the complex (fig. 9A) dorsal to which is the lateral amygdaloid nucleus, the cells of which are slightly more closely packed together and all of the smaller type. In this region the nucleus lies ventral to the line of the obliterated lateral ventricle, lateral to the caudal end of the caudate-putamen and the massa intercalata, dorsal to the basal amygdaloid nucleus and medial to the claustrum. In sections farther caudalward the lateral amygdaloid nucleus is smaller and more triangular in outline; its dorsal, lateral and ventral relations remain the same, while medialward it borders on the dorsocaudal part of the medial amygdaloid nucleus. The lateral nucleus decreases rapidly in size at its caudal end, where its ventromedial angle comes in contact with the accessory basal nucleus. There is no further change in its relations dorsally, laterally or ventrally. Throughout their caudal extent the separation of basal and lateral nuclei is indicated by the lateral indentation mentioned above, this indentation becoming increasingly marked farther caudalward.

As seen in pyridine silver series (figs. 11B, 13 and 14), where both basal and lateral amygdaloid nuclei can be distinguished throughout their entire extent, the lateral nucleus extends farther frontalward, while the basal continues farther caudalward (figs. 9D and 15). According to the figures and descriptions of Spiegel ('19), however, the lateral and basal amygdaloid nuclei are differentiable in cell preparations at their frontal end in Pteropus and Talpa, both of which have a larger basal nucleus. In Pteropus, according to this author, the lateral nucleus extends farther caudalward, however.

Nucleus amygdalae basalis (fig. 9). The basal amygdaloid nucleus, located ventral to the indentation along the surface of the baso-lateral amygdaloid complex, shows, even as far frontalward as it can be distinguished from the lateral nucleus, a lateral area, with large, scattered cells, and a more narrow, medioventral portion with smaller, more closely arranged neurons. At such cross section levels (fig. 9A) the massa intercalata is situated medial to the basal amygdaloid nucleus, the medial and cortical amygdaloid nuclei lie along its ventromedial surface, and the pyriform lobe cortex along its lateral and ventrolateral surfaces. Farther caudalward, due to the shift of the cortical and medial amygdaloid nuclei medialward, only the cortical nucleus remains in contact with the ventral surface of the basal amygdaloid nucleus medialward (fig. 9B). Between the pyriform cortex and the cortical amygdaloid nucleus, and ventral to the basal nucleus, is an area from which cells extend to the basal amygdaloid nucleus above it (fig. 9C). This is the region referred to by Johnston ('23) in Myotis as "an infolding from which cells appear to be migrating into the basal nucleus." At its most caudal end (fig. 9D) the basal amygdaloid nucleus appears as a double fold of cells, difficult to distinguish either from the pyriform cortex or from the accessory basal nucleus, and described by Johnston as "a simple fold of the ventral wall." Since Johnston has not identified an accessory basal amygdaloid nucleus in Myotis, it is possible that only his 'ventral small-celled part' represents the basal, while the "internal large-celled part of irregular form" may be the accessory basal nucleus of the present account. Spiegel's ('19) 'Hauptkern' in Pteropus edulis corresponds to the basal amygdaloid nucleus, which, in this form, apparently is larger than the lateral nucleus (see also p. 642).

Nucleus amygdalae basalis accessorius (fig. 9, B, C and D). In the bat the accessory basal amygdaloid nucleus occupies a position medial to the basal nucleus rather than lateral to it, as in the opossum (Johnston, '23 and Berkelbach van der Sprenkel, '26), and is relatively much larger and more extensive. A medial position for the accessory basal nucleus was also noted by Young ('36) in the rabbit. This change in the relative positions of the two nuclei might be the result either of the great development of the baso-lateral as compared with the cortico-medial complex, or of the general compression of the brain in the bat.

In cell material the accessory basal amygdaloid nucleus appears just caudal to the caudate-putamen complex, in a position medial to the basal nucleus, ventral to the massa intercalata, and dorsal to the cortical amygdaloid nucleus. As it becomes larger the accessory basal nucleus equals, and at its caudal end even exceeds, the basal nucleus in size. The accessory basal nucleus lies ventromedial to the lateral nucleus, medial to the basal nucleus, dorsal to the cortical nucleus and the nucleus of the lateral olfactory tract, and lateral to the medial amygdaloid nucleus. The accessory basal, as well as the basal amygdaloid nucleus, reaches the caudal pole of the hemisphere, where it gradually extends farther medialward and replaces the cortico-medial amygdaloid complex. At its caudal end the most medial cells of the accessory basal nucleus become continuous with cells of the hippocampal formation dorsalward (fig. 9D). In this region it is difficult to differentiate the accessory basal nucleus either from the cortical areas of the region or from the basal amygdaloid nucleus. Pyridine silver material shows no differences in appearance between basal and accessory basal amygdaloid nuclei (figs. 13 and 14).

Neither Spiegel ('19) nor Johnston ('23) described an accessory basal nucleus, although both Spiegel's figure of Talpa and Johnston's figure of Myotis are suggestive of its presence, and Johnston described "an internal large-celled part (of the basal nucleus) of irregular form," which may represent the accessory basal nucleus of this account.

Massa intercalata (figs. 8 and 9, A and B). Between the basal and central amygdaloid nuclei, and dorsal to the frontal end of the medial amygdaloid nucleus, is a small, compact mass of cells corresponding to those described by Johnston ('23) for the rabbit as intercalated masses, and to that described by Berkelbach van der Sprenkel ('26) for the opossum as the massa intercalata (or intermedia) amygdalae. In the bat, this cell mass increases in size farther caudalward and occupies a more dorsal position, although its relations with surrounding nuclear masses remain the same. As the accessory basal amygdaloid nucleus appears, the intercalated cell mass, which is at first dorsal to its frontal tip, is replaced by the accessory basal nucleus slightly more caudalward.

The topographical relations of the massa intercalata and the accessory basal amygdaloid nucleus, the position of the former in the course of the fiber lamina medial to the lateral and basal amygdaloid nuclei, and the gradation of these two nuclear masses into each other suggest that the massa intercalata may represent a cell group migrating dorsofrontalward along the course of these fibers and actually forming a closely related part of the accessory basal amygdaloid nucleus. In his accounts of Pteropus and Talpa, however, Spiegel ('19) mentioned the small groups of cells in this location as possibly bands of glia cells.

The cortico-medial amygdaloid complex (figs. 8 and 9). The cortico-medial nuclear mass, although relatively small in the bat, especially as compared to the large baso-lateral complex, extends from the level of the caudal border of the anterior commissure almost to the caudal end of the lateral amygdaloid nucleus. This nuclear complex consists of the nucleus amygdalae corticalis, the nucleus amygdalae medialis, the nucleus amygdalae centralis, and the nucleus of the lateral olfactory tract. Like the baso-lateral nuclear mass, the cortico-medial complex is represented by an undifferentiated region frontalward, although composed of these various nuclei caudalward.

In cross sections through the main part of the anterior commissure and the most caudal portion of the tuberculum olfactorium, an inconspicuous mass of small cells may be located deep to the endorhinal fissure and between the pyriform lobe lateralward and the polymorphic layer of the tuberculum olfactorium medialward, with both of which it is continuous (fig. 8, right). This cell mass corresponds to the 'small-celled cortical area' described for Myotis by Johnston ('23), and is considered in the present account to represent the cephalic, undifferentiated end of the cortico-medial amygdaloid complex. According to Johnston the cortical amygdaloid nucleus in Myotis is continued frontalward to the region of the anterior commissure as this 'small-celled cortical area,' which this author considered comparable to the lateral olfactory area of lower vertebrates in its form and relations. In sections through the caudal border of the anterior commissure, both the cells of the nucleus of the diagonal band of

Broca and the cells of this cortico-medial amygdaloid area extend in toward the commissural fibers. On following this undifferentiated cortico-medial cell mass caudalward it increases in size, is more distinct from the pyriform cortex, and shifts lateralward to lie ventromedial to the basal amygdaloid nucleus, entirely lateral to the endorhinal fissure and medial to the amygdaloid fissure. In sections still farther caudalward (fig. 8, left), this area begins to take on the characteristics of the medial amygdaloid nucleus on its medial side, while at levels caudal to this (fig. 9) the cortical amygdaloid nucleus and the nucleus of the lateral olfactory tract replace its lateral side. A description of these nuclei and of the central amygdaloid nucleus, which also constitutes a part of the cortico-medial complex, follows.

Nucleus amygdalae medialis (figs. 8 and 9, A, B and C). The medial amygdaloid nucleus is the largest of the nuclei forming the cortico-medial amygdaloid complex, and extends farther frontalward than the other nuclei, but not so far caudalward as the cortical nucleus. The majority of the cells of this nucleus are small, spindle-shaped neurons with large, lightly staining nuclei and fine, lightly staining Nissl granules. A lesser number of small, triangular cells, with more deeply staining Nissl substance, and occasional larger, multipolar cells, with heavier and deeply staining Nissl granules, are also present.

At its frontal end the medial amygdaloid nucleus occupies a position between the endorhinal fissure medialward and the amygdaloid fissure lateralward (fig. 9A), that is, between the pyriform cortex and the nucleus of the diagonal band of Broca and ventral to the baso-lateral amygdaloid complex. Soon after it is differentiable as a nuclear entity, the medial amygdaloid nucleus begins to show lamination, at first two, then, farther caudalward, three layers appearing. At the same time this nucleus moves medialward and somewhat dorsalward, so that, at the region where it is most highly developed, the medial nucleus occupies the ventromedial angle of the hemisphere. Since the inner of its three laminae is the smallest, while the outer is the largest, the nucleus acquires a somewhat pyramidal appearance in cross sections, with the rounded base of the pyramid facing ventromedialward, the central amygdaloid nucleus lying along its dorsolateral border, and the massa intercalata, the accessory basal nucleus and the cortical amygdaloid nucleus along its ventrolateral side. Near the caudal end of the medial nucleus, it shifts still farther dorsalward to surround the central nucleus caudalward, the nucleus of the lateral olfactory tract appears at its most lateral tip (or within the medial nucleus itself, see p. 649), and its inner two layers disappear. Caudal to the central nucleus, the medial nucleus is represented only by more or less isolated patches of cells, the most caudal of which become continuous with the hippocampal formation dorsomedialward (fig. 13, A and B). The medial nucleus thus makes a shallow, basket-like formation of varying thickness around the central nucleus, with the open side of the basket facing laterodorsalward.

In Pteropus edulis, Spiegel ('19) described a medial amygdaloid nucleus, which, in position and general relations, corresponds to the medial nucleus of Johnston ('23) in Myotis and to the medial amygdaloid nucleus of the present account. According to Spiegel, toward its caudal end the medial nucleus of Pteropus is fused with the cortical gray of the hippocampus, as seen in the species under consideration. The very brief descriptions of these authors do not permit of further comparisons. Spiegel also described the medial nucleus in Talpa, in which, as in Pteropus, he found it to be continuous with the hippocampal cortex.

Nucleus amygdalae corticalis (figs. 9, 13 and 14). The cortical amygdaloid nucleus is a flattened lamina of cells resembling an equilateral triangle in shape, and having about the same frontocaudal extent as the accessory basal amygdaloid nucleus, ventral to which it is located. The apex of the triangular cortical nucleus is located frontalward, while its base extends to the caudal end of the amygdaloid complex, where it can no longer be distinguished either from the cortex or from the accessory basal amygdaloid nucleus. Lateralward the cortical nucleus is bordered throughout its extent by the amygdaloid fissure and the pyriform lobe cortex; medialward it is adjacent to the medial amygdaloid nucleus, except for the small region where the nucleus of the lateral olfactory tract may lie between the cortical and medial nuclei (see p. 649). The cells of the cortical amygdaloid nucleus are larger, more loosely arranged, and more deeply stained than those of the medial nucleus, and resemble the cells of the pyriform cortex, although they are not so closely packed together. A few smaller triangular or multipolar cells, with more deeply staining, fine Nissl substance, are also present.

In following a cross section series caudalward (fig. 9), the frontal end of the cortical amygdaloid nucleus appears between the pyriform cortex and the medial nucleus at about the same time as the accessory basal nucleus can be distinguished. At first the cortical nucleus appears as a small, oval, transversely oriented mass of cells, but as it increases in size caudalward it takes the form of a cell layer, which shifts farther medialward at the same time, although always retaining a ventral position. Toward the caudal end of the amygdaloid complex the region of demarcation between the cortical nucleus and the pyriform cortex becomes more marked, due to the increase in the appearance of 'infolding' (Johnston, '23) of the pyriform cortex dorsal to the amygdaloid fissure (see p. 643; also fig. 9C).

The cortical amygdaloid nucleus is described briefly by Johnston ('23) for Myotis, in which the position and general relations are essentially the same as in the free-tailed bat. This nucleus is not described by Spiegel ('19) either for Pteropus or Talpa, however.

The nucleus of the lateral olfactory tract (fig. 9C). Although the smallest of all the amygdaloid nuclei in the bat, the nucleus of the lateral olfactory tract is the most distinctly circumscribed. In cross sections it appears as a distinct, round or ovoid mass of small granule cells, usually located between the medial and the cortical amygdaloid nuclei (although sometimes within the medial) and in most series near the frontal end of the cortical nucleus. Its cells are very closely packed together, small, granule cells with large nuclei surrounded by a rim of deeply staining, finely granular Nissl substance, thus making the whole nuclear mass appear much like one of the islands of Calleja in the tuberculum olfactorium. The entire frontocaudal extent of the nucleus averages only about 125 μ; its mediolateral extent appears to be somewhat greater.

In the majority of series (eight out of thirteen), the nucleus of the lateral olfactory tract appears as two separate cell masses. Sometimes the more frontal of the two is the larger and sometimes the more caudal one. Either one of the two nuclei may be located between the medial and the cortical amygdaloid nuclei, while the other is situated within the more lateral part of the medial nucleus. When only one nucleus is present it may be found in either position. In all series, however, whether one nucleus or two nuclei are present, there is a tendency for the nucleus to assume a more dorsal position in relation with the stria terminalis fibers, rather than one close to the lateral olfactory tract. From relations in reptiles and birds, as well as in mammals, it is probable that during the course of its development this nucleus formed a continuous mass along the course of the lateral olfactory tract, and in some of the series studied the continuity of the two cell masses is interrupted only by a single section (25 μ thick).

The nucleus of the lateral olfactory tract has been described for various mammals, among which are Caenolestes (Obenchain, '25), the opossum (Johnston, '23 and Berkelbach van der Sprenkel, '26), the rat (Gurdjian, '28), and the rabbit (Johnston, '23 and Young, '36). The accounts of these observers contain further references. In the available literature dealing with the Chiroptera no reference is made to this nucleus. In Insectivora, however, it was described and figured as early as 1882 by Ganser for the mole, and was described again for this form by Spiegel ('19). According to these authors the nucleus of the lateral olfactory tract in the mole is also sharply circumscribed, and similar in shape to that in the bat, but larger and located at the level of the optic chiasm, a position which appears to be more nearly comparable to that of the more caudal of the two nuclei in the bat.

Nucleus amygdalae centralis (figs. 8 and 9, A and B). The central amygdaloid nucleus appears at the caudal end of the bed nucleus of the stria terminalis, where it is continuous with that nucleus somewhat in the manner of a caudal, much-enlarged end, as described by Johnston ('23). The central nucleus extends from the region of the caudal border of the anterior commissure to levels slightly caudal to the putamen-caudate, being small at both its cephalic and caudal ends, although large through the main portion, where its dorsoventral is greater than its lateral extent. The cells of the central nucleus resemble those of the caudate-putamen very closely, so that the line of demarcation between the two nuclear groups is decidedly indefinite, and actually determinable at all, only by the faintly striated or laminated arrangement of the central nucleus, due to the passage of stria terminalis fibers across it to more lateral and ventral regions of the amygdaloid complex.

In cross section series, sections just caudal to the anterior commissure pass through the cephalic end of the central amygdaloid nucleus, which appears as a small, faintly striated, semilunar cell mass, with its concave surface ventral to the caudate-putamen, and its convex surface dorsal to the medial amygdaloid nucleus. Lateralward it borders the massa intercalata. In sections farther caudalward the central nucleus is larger, and lies slightly more dorsalward, due to the decrease in size of the caudate-putamen, and the dorsolateral shifting of the medial amygdaloid nucleus. In sections through its caudal end, which is located just caudal to the caudate-putamen, the central amygdaloid nucleus, now small again, occupies the dorsomedial part of the amygdaloid complex, while small groups of cells belonging to the medial nucleus appear dorsal to it, and finally replace the central nucleus still more caudalward. It becomes apparent, then, that the central nucleus is surrounded by the medial amygdaloid nucleus along the caudal portions of its ventral, medial, and even dorsal surfaces (see also p. 647).

The central amygdaloid nucleus of Myotis was located and figured by Johnston ('23), who apparently found its relations quite similar to those in the free-tailed bat. No other accounts of the central nucleus are given in the available literature dealing with Chiroptera or Insectivora.

General discussion of the amygdaloid complex. On the basis of its connections with the stria terminalis (p. 667) and the anterior commissure (p. 659) the amygdaloid nuclei of the bat may be grouped into three phylogenetically different regions. One of these, the cortico-medial complex, is connected with preoptic and hypothalamic areas by way of the stria terminalis, but not by way of the anterior commissure. A second region, consisting of the large lateral amygdaloid nucleus, has no relation with the stria terminalis (see p. 668), but is connected with preoptic and hypothalamic areas by way of the anterior commissure. The third region, which includes the basal and accessory basal amygdaloid nuclei, and is located between the other two areas, is intermediate in its type of connections, since the cephalic tip of the basal nucleus is connected with preoptic and hypothalamic areas by way of the anterior commissure, while both its caudal more clearly differentiated portion and the accessory basal nucleus send their fibers by way of the stria terminalis. Whether or not, on the basis of the type of fiber connections, at least, any one of these three amygdaloid regions may be considered phylogenetically older than the other two, as has been stated by Johnston and van der Sprenkel for the anteromedial nuclear group in the opossum, it is difficult to say, since even in anural amphibians, where a true amygdala is clearly recognizable (Herrick, '21, p. 256), it has connections both by way of the anterior commissure (commissura amygdalarum, Herrick, p. 227) and the stria terminalis (Herrick, p. 231). In the course of development of this simple amygdala of amphibians into the various nuclei of the present mammalian form, however, only the intermediate nuclear region retains both types of connection, the ventromedial region (cortico-medial amygdaloid complex) differentiating entirely in relation with one system of fiber connections (stria terminalis), while the lateral amygdaloid nucleus develops only in relation with the other fiber system (anterior commissure).

THE BED NUCLEUS OF THE STRIA TERMINALIS (figs. 3, 8 and 9, A and B). Dorsal to the cephalic end of the central amygdaloid nucleus, medial to the caudate-putamen, and ventral to the lateral ventricle, are a few small cells intercalated along the stria terminalis fibers (see fig. 9A) and constituting, at this region, the bed nucleus of the stria terminalis. Slightly farther frontalward these cells are fewer in number and more scattered, and in the region where the tail portion of the caudate-putamen can be identified, only an occasional cell is present. Dorsal to the caudal part of the anterior commissure and medial to the head of the caudate nucleus, however, the bed nucleus of the stria terminalis forms a quite dense, ovoid cell mass, resembling the caudate nucleus in appearance (fig. 8). Still farther frontalward, but while still dorsal to the anterior commissure, the density of the bed nucleus of the stria decreases, and small fiber fascicles can be seen passing ventromedialward through it. Near the frontal border of the anterior commissure the nucleus is elongated into a spindle-shaped mass with its dorsal end directed dorsolateralward and its ventral end directed ventromedialward. At the frontal border of the anterior commissure the ventromedial end of the bed nucleus becomes continuous with the medial septal nucleus, while its dorsal end appears as small clumps of cells lying ventral (and somewhat ventrolateral) to the lateral ventricle and dorsomedial to that portion of the head of the caudate which is located dorsal to the anterior commissure (fig. 3). At its most frontal end, the bed nucleus of the stria terminalis remains only as the scattered cells along the fiber band connecting the head and the tail of the caudate, where it is located medial to the internal capsule.

The bed nucleus of the stria terminalis was described by Johnston ('23) for Myotis, a form in which it also forms an unusually large cell mass dorsal to the anterior commissure. Other references to this nucleus have not been found in the literature on Chiroptera and Insectivora. For its relations in other mammalian forms the papers of Johnston ('23), Gurdjian ('28), Loo ('31) and Young ('36) should be consulted.

Certain fiber connections of the telencephalon

THE OLFACTORY TRACTS (figs. 10A, 11 and 14). Fibers which form the olfactory tracts accumulate in the region of, and internal to, the mitral cell layer, and form a fiber band completely encircling the olfactory bulb. As the fibers increase in number within the bulb they form a whorl, thicker on the lateral and ventral sides, similar to that described by Obenchain ('25) for Caenolestes. Farther caudalward a second whorl of fibers, incomplete dorsomedially, forms within the first in such a way as to lie external to the nucleus olfactorius anterior and largely dorsolateral to the ventricle. This latter bundle is contributed to largely, although not entirely, by the anterior olfactory nucleus. Caudal to the olfactory crus, the inner bundle, designated by some observers (Obenchain, '25, and others) as the intermediate olfactory tract, passes gradually lateralward and dorsalward, then swings medialward as the anterior limb or interbulbar portion of the anterior commissure (figs. 10, 11, 12 and 15; see also p. 660).

The lateral olfactory tract (figs. 10A, 11 and 14). The lateral olfactory tract, formed by the outer whorl of fibers and arising from all parts of the bulb, may be subdivided into a small pars dorsalis, a large pars intermedia, and a small pars ventralis, on the basis of the region of origin of the fibers in the bulb, as was done by Herrick ('24) and Loo ('31) for the opossum. As the lateral olfactory tract extends caudal to the olfactory crus and spreads out along the lateral wall of the hemisphere, the pars dorsalis, located dorsal to the endorhinal fissure and consisting of unmedullated or very thinly medullated fibers, distributes to the pyriform lobe cortex. The pars intermedia (or pars lateralis, Herrick), which is the largest and a heavily myelinated portion of the tract, distributes largely to the pyriform lobe cortex, the nucleus of the lateral olfactory tract, the medial amygdaloid nucleus, and apparently to the cortical amygdaloid nucleus as well, although the material available is not adapted to determining this last connection so definitely. A few fibers from the region just lateral to the fissura rhinalis arcuata (not illustrated) may pass to the laterocaudal part of the tuberculum olfactorium also. In sagittal series a very few fibers can be traced as far caudalward as the hippocampus, as has been described for some mammals (Ariëns Kappers, Huber and Crosby, '36). The unmedullated or thinly medullated fibers of the pars ventralis cover the ventral surface of the tuberculum olfactorium in its plexiform layer and certain of them contribute to the formation of small fascicles which pass through the deeper part of the tuberculum in the region of the strio-tubercular fusion (see p. 611) to join the medial forebrain bundle and continue caudalward as far as the hypothalamus. These small fascicles, which appear to be homologous to the tractus olfacto-hypothalamicus ventralis as described by Loo ('31) for the opossum, probably contain, in addition to a few fibers arising in the bulbar formation, many others which originate in the olfactory areas caudal to the bulb—the anterior olfactory nucleus and the tuberculum olfactorium.

The medial olfactory tract (fig. 10A). The medial olfactory tract is very much reduced in size, consisting only of a few scattered, unmedullated fibers near the medial wall of the bulb, most of which probably arise from the anterior olfactory nucleus rather than from the mitral cells. In more caudal regions these fibers collect into small fascicles along the medial wall of the hemisphere where they extend as far as the lower tip of the anterior continuation of the hippocampus and perhaps to other regions of the septum as well, although the number distributing in this manner is minimal.

This reduced condition of the medial olfactory tract is somewhat similar to that found in birds, where the olfactory bulbs are very small, the accessory bulbs absent and the medial olfactory tract much decreased in size (Huber and Crosby, '29).

Tractus olfactorius dorsomedialis (not illustrated). At the dorsomedial angle of the olfactory crus, Herrick ('24) described two small fascicles of the medial olfactory tract in the opossum under the name of tractus olfactorius dorsomedialis. If present in the bat, this tract is represented by a small group of scattered, unmedullated fibers. Since there is no accessory bulb in the bat, the superficial layer of this tract, considered by Herrick as arising entirely from the accessory bulb, is probably absent. The deeper fascicle, which according to this author is contributed to also by the accessory bulb in small part, may be represented in the few fibers present in this region in the bat. In this form these fibers appear to distribute entirely to the anterior olfactory nucleus, although a few may end in the adjacent cortical areas—the frontal cortex and the anterior hippocampal cortex. Neither this tract, nor the pars dorsalis of the lateral olfactory tract, both of which receive fibers from the accessory bulb in the opossum, contribute fibers to the amygdala in the bat, the region which, in Amphibia (Herrick, '21, pp. 220 and 226), receives the fibers from the accessory bulb (the ventrolateral olfactory tract), and which, according to Herrick ('21, although not later, '27), develops in close relationship with the vomeronasal organ.

TRACTUS TUBERCULO-AMYGDALOIDEUS (figs. 11A and 15). Although fibers from the lateral olfactory tract pass directly to the cortico-medial amygdaloid complex (see p. 654) in the bat, such fibers do not reach the baso-lateral amygdaloid complex. However, fibers from an intermediary olfactory area, the tuberculum olfactorium, do reach the lateral amygdaloid nucleus. In transverse sections passing through the caudolateral portion of the tuberculum a few fine, scattered, unmedullated fibers may be seen passing dorsolateralward into the cephalic end of the lateral amygdaloid nucleus. Johnston ('23, p. 448 and figs. 85 to 88) described a small but distinct fiber bundle from the amygdaloid complex to the tuberculum in the human foetus. Whether or not this bundle corresponds to the fibers present in the bat it is not possible to say from the description given by this author.

THE COMMISSURES OF THE HEMISPHERES. The commissures of the hemispheres include the hippocampal commissure, the corpus callosum, and the anterior commissure. In the bat, these commissures show a transition from conditions in lower mammals such as the opossum, where there is no corpus callosum and all the neopallial fibers pass through the anterior commissure, to those in higher mammals, where all, or almost all, of the neopallial fibers cross through the corpus callosum.

The hippocampal commissure (figs. 4 to 7, 11A, 12 and 16, A, C and D). The hippocampal commissure interconnects the two hippocampi and sends both homolateral and contralateral fibers into the columns of the fornix, although the number of decussating fornix fibers (ventral psalterium) is minimal. Fibers of the commissure also end in the precommissural part of the bed nucleus of the hippocampal commissure. Its dorsal end is continuous with the caudal end of the corpus callosum, the two structures together having the shape of an inverted letter V. The fibers adjacent to the corpus callosum actually cannot be distinguished from the fiber bundles of the latter commissure and probably are intermingled, at least in the region of the point of the V formed by the two commissures (see p. 657 and fig. 16).

The hippocampal commissure is present not only in mammals but also in various submammalian forms. In all the mammalian forms it maintains essentially similar relationships. Descriptions and figures of this commissure in various mammals are to be found in the contributions of Elliot Smith (1894, 1897 b, 1897 c, and elsewhere), Winkler and Potter ('11 and '14), Obenchain ('25), Loo ('31), and Young ('36), and in the recent Ariëns Kappers, Huber and Crosby reference book ('36).

The corpus callosum (figs. 4 to 7, 11A, 12 and 16). Under normal conditions the corpus callosum is present in all mammals, with the exception of monotremes and most marsupials, although smaller and less well differentiated in the lower forms. According to Johnston ('13) neopallial fibers cross in the dorsal pallial commissure of the opossum. In another marsupial, Macropus, Ariëns Kappers ('21) described some bundles of neopallial fibers dorsally in relation with the hippocampal commissure and so constituting a primordial corpus callosum. Neopallial fibers in relation with the hippocampal commissure have been described also in submammalian forms (reptiles and birds, Ariëns Kappers, Huber and Crosby, '36, p. 1484). Although normally highly developed in higher mammalian brains, including that of man, a considerable number of human brains without a corpus callosum have been described (Mingazzini, '22; de Lange, '25). The literature dealing with this commissure is enormous and, except that involving the Chiroptera, cannot be included here. A comprehensive review may be found in the Ariëns Kappers, Huber and Crosby text recently published.

In the free-tailed bat the corpus callosum is present, but small, receives fibers from only a small part of the neopallial cortex, and is located entirely frontalward. As seen in sagittal sections it lacks the caudal and frontal thickenings of higher forms, designated as the splenium and genu respectively. Instead, as described by Johnston ('13) for Myotis, it is slightly crescent-shaped, tapering to a point at its frontal end. Sometimes a few cells of the nucleus septo-hippocampalis, ventral to the corpus callosum, form fine strands across the commissure, or isolated cells may be seen intermingled with its fibers (figs. 6 and 7). Such cell strands are more numerous at the cephalic end of the commissure. Similar relations were described and figured by Johnston ('13) for Myotis, although in this species the number of such cells is greater.

At the caudal end of the corpus callosum, the hippocampal commissure is in direct contact with it so that any line of demarcation between the two is an arbitrary one. Although actual proof of the nature of this region is dependent on experimental methods, the variability in position of the supracommissural part of the bed nucleus of the hippocampal commissure, through which pass a few fibers of the corpus callosum (fig. 16A, e), along with the minute differences in staining reaction between the fiber bundles of that area, suggests that the fibers of the two commissural systems may be intermixed to a varying degree in the different series. An admixture of hippocampal and corpus callosum fibers is also described by Young ('36) for the rabbit.

In Vesperugo pipistrellus Ärnbäck Christie Linde ('00) described a V-shaped dorsal commissural system, like that found in the free-tailed bat, and stated that its caudal part contained only hippocampal fibers, while its frontal portion has (neo-) pallial fibers, as well as fibers interconnecting the Ammon's horns. Essentially similar relations had been described previously by Elliot Smith (1897 a and 1897 c) for two small Australian bats. According to Haller ('07), the dorsal commissural system in Vesperugo pipistrellus and Vespertilio murinus has a purely (neo-) pallial portion as well as a part containing only hippocampal fibers and a region where both types of fibers are intermingled. In Myotis (Johnston, '13, p. 452), the rostral limb of this commissural complex, or the corpus callosum, contains many hippocampal fibers and probably "differs from the corresponding part of the anterior pallial commissure in the opossum only in having a somewhat larger number of callosal fibers." From his study of the development of the commissures in Vesperugo, however, Werkman ('14) concluded that the caudal part of the dorsal commissure carries only hippocampal fibers, and the most cephalic part only neopallial fibers, while the intermediate region consists of both hippocampal and neocortical fibers intermingled.

In the bat material used in this study, fibers entering the corpus callosum arise only from the dorsomedial portions of the neopallium, very largely from the frontal areas, but some fibers also enter it from the parietal regions, and, to a lesser extent, from the occipital areas, swinging forward to do so (fig. 12, a). According to Haller ('07) the few fibers crossing in the (neo-) pallial portion of the dorsal commissure are from the anterior poles of the hemispheres exclusively.

In contrast with the more primitive corpus callosum found in the Microchiroptera is the well-developed one of the Macrochiroptera. For these forms it was described first by Zuckerkandl (1887) for Pteropus samoensis as completely developed. In 1891 Turner figured (but did not describe) the corpus callosum in two other Macrochiroptera (Cynonycteris collaris and Pteropus medius) in one of which (Pteropus) the corpus callosum is quite like that of higher forms, and a similar figure was shown by Kohlbrugge ('02) for Pteropus edulis, a form for which the corpus callosum has been described by Haller ('07 a). The general shape of the corpus callosum in these Macrochiroptera is similar to that of many of the Insectivora figured by Le Gros Clark ('33).

The anterior commissure (figs. 2, 3, 4, 6 to 8, 10B to 12, 14A, 15 and 16). The anterior commissure of the free-tailed bat is large and oval in outline in sagittal sections (figs. 10B and 16), with the longer diameter directed almost vertically, as figured by Elliot Smith (1897 c) for the Australian bat, Nyctophilus, while in the opossum, the longer diameter of the oval commissure is horizontally directed (Loo, '31). In the bat eight components can be distinguished in the commissure (figs. 10B, 11, 12, 14A, 15 and 16): a large interbulbar component; smaller components from the pyriform lobe, the basal amygdaloid nucleus and the lateral amygdaloid nucleus; a still smaller fiber bundle from the tuberculum olfactorium; a very tiny component from the stria terminalis; and, from the neopallial cortex, the largest fiber bundle, consisting of a large external capsule component and a small internal capsule component.

In the anterior commissure of Nyctophilus, Elliot Smith (1897 c) recognized two distinctly separated fiber bundles (apparently the interbulbar, lateral interamygdaloid, and neopallial components of the above description), between which he thought that fibers not taking the medullary stain were to be found. It is in the region corresponding to this space that the interpyriform, intertubercular, and basal interamygdaloid components of the free-tailed bat are located. In the edentate, Orycteropus, four components of the anterior commissure were recognized by Sonntag and Woollard ('25), and Gurdjian ('25) described four in the albino rat, two of which, however, contained fibers from more than one of the regions represented in the bat. Loo ('31) recognized five components in the anterior commissure of the opossum. It has not been possible to homologize precisely the components described by these observers with those found in the bat, possibly because of differences in development of the pyriform lobe cortex and the amygdaloid complex of rodents and marsupials as compared with these regions in Chiroptera. Wherever such homologies have been possible, reference is made to them in the following descriptions. A detailed review of the early literature concerning the anterior commissure may be found in the account of Ramón y Cajal ('11).

Brief descriptions of the anterior commissure in different Chiroptera have been made by various observers. Among these authors are Ganser (1879 and 1882), Elliot Smith (1897 c), Ärnbäck Christie Linde ('00), Haller ('07), Hirsch ('07), and Johnston ('23). The findings of these observers will be referred to in relation with the descriptions of the different components of the anterior commissure in the free-tailed bat.

The interbulbar component (figs. 10 to 12 and 15). The large, heavily medullated interbulbar component (the intermediate olfactory tract of some observers) is located anteroventrally and consists of fibers from the bulbar formation and from the anterior olfactory nucleus which probably pass to the corresponding contralateral regions. A few fibers turn into the gray just anterior to the commissure near the midline, probably into its bed nucleus. This interbulbar bundle corresponds to the pars olfactoria of Ganser (1879 and 1882), and of Elliot Smith (1897 c) in Nyctophilus. It is figured by Ärnbäck Christie Linde ('00) for Vesperugo pipistrellus but not described, and is both figured and described briefly by Haller ('07) for Vesperugo pipistrellus and Vespertilio murinus, as well as by Hirsch ('07) for Pteropus edulis. The interbulbar component is comparable also with the pars anterior of Loo ('31) in the opossum and the interbulbar component of Gurdjian ('25) in the albino rat, but in the free-tailed bat includes as well fibers from the nucleus olfactorius anterior, as was suggested by Herrick ('24) for the opossum and described by Young ('36) for the rabbit.

The interpyriform component (figs. 10B, 11 and 12). Dorsal to the interbulbar component and in the frontal part of the commissure lies the interpyriform component, while dorsocaudalward is the basal interamygdaloid component; both of these are lightly myelinated, the former even more so than the latter. The interpyriform fibers collect from the pyriform lobe, and especially from its deeper portion (nucleus endopiriformis of Loo, '31, for the opossum). All the fibers swing ventralward below the lateral amygdaloid nucleus, and largely in front of the cephalic tip of the basal amygdaloid nucleus, although some may pass across it, to reach the commissure. No evidence has been found to indicate that any of these fibers end in the gray around the commissure—probably they are entirely commissural in character.

Fibers from the pyriform lobe to the anterior commissure were described by Ganser (1879 and 1882) for various mammals, including the mole and the bat (1879, p. 289). Fibers from this region are shown in the figures of Haller ('07) for Vesperugo and are evidently included either in his fibers "von der basalen Stirnpolhäfte der Hemisphäre," (p. 132 and fig. 3) or those 'aus dem Schläfenteile.' The interpyriform bundle of the bat, as described here, forms part of the intertemporal component of Gurdjian ('25, for the rat) and of other observers. In part, at least, it corresponds to the pars piriformis of Loo ('31) for the opossum, although fibers from the nucleus endopiriformis of this observer are included in his pars lateralis of the anterior commissure. Fibers from the pyriform lobe are described by Young ('36) in relation with the anterior, the transverse, and the posterior limbs of the commissure in the rabbit.

The basal interamygdaloid component (figs. 10B, 11B, 12, 14A and 15). This lightly medullated fiber bundle lies dorsal to the more caudal portion of the interbulbar component. The fibers of this component are not numerous and arise only from the anterior end of the nucleus, so that the more frontal of them sweep almost directly dorsomedialward across the field to reach the commissure. A few of them turn into the homolateral gray of the lateral preoptic area and the bed nucleus of the commissure (figs. 10B and 15), while a greater number enter the medial preoptic area, including the nucleus preopticus medianus. Other fibers no doubt reach the opposite basal amygdaloid nucleus as well.

The lateral interamygdaloid component (figs. 10B, 11B, 12, 14A and 15). At the caudal border of the anterior commissure, dorsal to the basal interamygdaloid component and ventral to the external capsule component, is the large lateral interamygdaloid fiber bundle, which resembles the interbulbar component in being heavily medullated. Just as with the basal interamygdaloid component, in addition to fibers which probably reach the contralateral amygdaloid nucleus, other fibers turn into the homolateral gray ventral to the commissure, although in this instance only into the medial preoptic area and the nucleus preopticus medianus (figs. 10B and 15). Within the lateral amygdaloid nucleus, the fibers of this component do not appear as a separate fiber bundle, although apparently arising from, and traversing, its entire extent. Instead, a network of fibers is formed within the nucleus and the number of these increases toward its frontal end so that this meshwork gradually becomes more dense in the frontal portion of the nucleus. At the cephalic end, where this network of fibers is most dense, small bundles, sweeping medialward from its surface, join into a large, compact bundle as they enter the commissure. Between the dorsofrontal border of this bundle and the external capsule component, as seen in a cross section of the commissure (fig. 10B), are a few scattered fascicles which have the same staining reaction as does the lateral amygdaloid component and actually represent bundles of this component which have been separated from the main fiber mass by fibers of the external capsule component.

As early as 1882 Ganser described and figured (Ganser, 1882, fig. 30) fibers from the amygdala to the anterior commissure in the mole and stated that this relationship was still clearer in the bat, where he found two branches of this bundle, which, from his description, appear to correspond to the two amygdaloid components described above. Hirsch ('07) stated that a bundle from the anterior commissure could be followed to the amygdala in Pteropus edulis. In the intertemporal component in the rat Gurdjian ('25) included fibers which he believed reached the amygdaloid complex and which may represent one or both of these bundles in the bat. Sonntag and Woollard ('25) stated that in Orycteropus, an edentate, "the contribution from the amygdaloid is considerable." Young ('36) included with the posterior limb of the anterior commissure in the rabbit fibers from the lateral amygdaloid nucleus which are undoubtedly homologous with the lateral amygdaloid component of the bat.

The intertubercular component (figs. 10B, 12 and 15). Between the interpyriform and the basal interamygdaloid components lies a third, and smaller, bundle—the intertubercular component—the fibers of which show about the same degree of myelination as do those of the interpyriform component. These fibers collect from both the polymorphic and pyramidal cell layers of the lateral portion of the tuberculum and pass caudodorsalward, first lateral to, and, after joining the commissure, dorsal to the interbulbar component. In iron hematoxylin material, where this bundle is readily distinguished by its thinly myelinated fibers, two of these small fiber groups may be seen entering the commissure, but in the pyridine silver material the fibers are less definitely delimited. They appear to be purely commissural in nature. Although referred to definitely in the literature dealing with the mammalian anterior commissure only in the rabbit, fibers from the tuberculum to the anterior commissure are described by Crosby ('17) for the alligator. However, in the rat, Gurdjian ('25) called attention to "a narrow band of fibers" on the lateral aspect of the interbulbar component, stating that this band of fibers "interconnects the lateral olfactory areas of the hemisphere just lateral to the bulb." As figured by Gurdjian (Gurdjian, '25, fig. 14, comp.ant.com.) this bundle corresponds in position, at least, with the intertubercular component of the bat and probably is homologous with it. In the rabbit Young ('36) included fibers from the tuberculum olfactorium in the anterior limb of the anterior commissure, although these fibers did not appear as a separate bundle such as is seen in the bat.

The stria terminalis component (figs. 10B, 11B, 13, B, C and D, 14 and 15). The fibers from the stria terminalis constitute the smallest, and an unmedullated, component of the anterior commissure. They appear to arise entirely from the nucleus of the lateral olfactory tract, or, when two nuclei are present (see p. 649), from both of them, uniting to form a single bundle, the fibers of which form a very small, but distinct and deeply staining fascicle in pyridine silver material. The fibers of this bundle pass dorsocaudalward and slightly medialward as a compact bundle, lying between the two parts of the preoptic component of the stria terminalis (see p. 669 and fig. 13, B to D), to swing forward over the internal capsule. This component then passes through that part of the head of the caudate nucleus lying dorsal to the anterior commissure, coming into relation with the commissure on its ventrocaudal surface (fig. 14A). Except near the midline region this tiny bundle remains distinct and slightly separated from the commissure. Where some of its fibers enter the bed nucleus of the anterior commissure, and the medial preoptic area (including the nucleus preopticus medianus), however, the bundle is diffuse in nature and no longer distinct from the commissure. Whether or not fibers enter the contralateral nucleus of the lateral olfactory tract cannot be determined definitely with the material at hand, although a few appear to cross the midline before entering the nucleus preopticus medianus. However, the nuclei of the lateral olfactory tracts are probably interconnected by this stria terminalis component of the commissure, which evidently is homologous with the first component of Johnston ('23) in the opossum, with the stria terminalis component of Gurdjian ('25) in the rat, with the bundle 1a of Berkelbach van der Sprenkel ('26), with the pars amygdaloidea of Loo ('31) in the opossum, and with the stria terminalis fibers in the posterior limb of the anterior commissure of Young ('36) in the rabbit.

The internal capsule component (figs. 10B, 11 at g and z, and 12). The neopallial bundle, which occupies about the dorsal half of the anterior commissure and consists of a large component entering the commissure by way of the external capsule, and, apparently, a small group of fibers entering by way of the internal capsule, is the largest group of fibers in the anterior commissure of the bat. The smaller bundle, or the internal capsule component as it is designated in this account, arises from the most dorsomedial portion of the cortex in the frontal region and enters the deepest layer of the external capsule. Farther caudalward fibers from this deep layer of the external capsule turn into the internal capsule on its medial surface (fig. 11A, g). Still more caudalward fibers from the medial border of the internal capsule enter the anterior commissure (fig. 11B, z), where they are distinguishable from the external capsule component only with difficulty as the dorsofrontal portion of the neopallial component (fig. 10B). These fibers are diagrammed in figure 12, as an internal capsule component of the anterior commissure, although proof of their nature must depend on degeneration methods.

In addition to fibers from the medial aspect of the internal capsule, a varying number of fibers appears to turn into the anterior commissure from any of the more lateral portions of the internal capsule, in some sagittal series the most lateral fascicles being largest. It seems probable that the pattern for the entrance of neopallial fibers into the anterior commissure consists of a continuous sweep of fibers passing from the external capsule ventromedialward, the more medial of these fibers passing by way of the internal capsule, while the more lateral and greater number of them traverse only the external capsule. The intermediate fibers probably tend to disappear, apparently leaving only the lateral group as the external capsule component of the anterior commissure, in most instances, although the most medial fibers may appear to persist as with the aberrant bundle of Elliot Smith ('02 a) in diprodont brains. All stages may be represented, as in the bat. If the above pattern represents the manner in which neopallial fibers reach the anterior commissure, it seems likely that any of the fibers representing the internal capsule component in the bat may be present in many other mammals as well.

The external capsule component (figs. 10B to 12). The great majority of neopallial fibers crossing in the anterior commissure enters it by way of the external capsule. They arise in frontal, parietal, and occipital regions of the cortex on the dorsolateral surface of the hemisphere, and form a continuous sweep of fibers from the dorsofrontal cortex caudalward to the dorsooccipital cortex and ventralward to the pyriform lobe, as they enter the anterior commissure. These fibers constitute the external capsule component, which, in the bat, as in the opossum (pars neopallialis, Loo, '31), is the largest bundle in the anterior commissure.

The decussation of neopallial fibers in the anterior commissure in monotremes and certain marsupials has been described by various observers (Elliot Smith, 1894; Obenchain, '25; Loo, '31, and others). The figures of Ärnbäck Christie Linde ('00) show such fibers in Vesperugo pipistrellus, although she did not describe them. Hirsch ('07) described and figured a large bundle of fibers entering the anterior commissure from the external capsule in Pteropus edulis. A large bundle of these fibers is present also in Vesperugo pipistrellus and Vespertilio murinus, according to Haller ('07), who stated that in the latter form, where the corpus callosum is less primitive, fewer fibers pass through the anterior commissure. This observer also stated that in these Chiroptera only the cortex of the frontal pole of the hemisphere fails to send fibers through the anterior commissure. In the edentate, Orycteropus, however, the neopallial fibers which enter the anterior commissure form its smallest fiber bundle, according to Sonntag and Woollard ('25). In at least one of the higher mammals, the rabbit, Winkler and Potter ('11) found a few, and Young ('36) a considerable number, of neopallial fibers crossing in the anterior commissure in addition to a dorsal corpus callosum. Probably in most mammals neopallial fibers enter the anterior commissure by way of the external capsule, although the proportional number will vary with the form under consideration; in higher forms the number of such fibers tends to be minimal.

THE STRIA TERMINALIS (figs. 10B, 11 and 13 to 15). Detailed descriptions of the stria terminalis in mammals have been given by Johnston ('23) and Berkelbach van der Sprenkel ('26) for the opossum. These authors included five components in the stria: a commissural, a hypothalamic, an infracommissural, a supracommissural, and a stria medullaris component. These bundles have been identified and figured by Obenchain ('25) for Caenolestes and, with the exception of the infracommissural portion, they have been described for the rat by Gurdjian ('25 and '28), and for the rabbit by Young ('36). The stria terminalis in Chiroptera has been briefly mentioned and figured by Haller ('07, funiculus striati).

In the free-tailed bat, as in the opossum, five components can be identified, but the relations of the various bundles as they pass over the internal capsule, where they are very much compressed in the bat, are less clear. A brief description of each of these bundles in the bat follows.

The supracommissural component (figs. 11 and 13 to 15). The fibers described by Johnston and Berkelbach van der Sprenkel as the infracommissural bundle are included in the following account of the supracommissural component in the bat. This largest and most heavily myelinated portion of the stria is connected caudalward with almost the entire extent of the basal and accessory basal amygdaloid nuclei and is added to also by a few fibers from the cortical nucleus and the caudal tip of the medial amygdaloid nucleus. Fibers from the intercalated cell mass also enter into the component. However, no fibers have been seen to enter it from the lateral amygdaloid nucleus as in the opossum (infracommissural bundle, Berkelbach van der Sprenkel), although some small fiber bundles from the dorsolateral region of the basal nucleus cross the ventral portion of the lateral nucleus and, farther frontalward, the putamen, to join the supracommissural component. In the bat the greater part of the supracommissural component, consisting of those fibers which are located most lateralward in the bundle as its leaves the amygdaloid complex, are heavily myelinated. A smaller, somewhat more lightly medullated portion of the bundle, lying more medialward and just lateral to the preoptic bundle (fig. 13), appears to arise largely in relation with the accessory basal nucleus and corresponds to the fibers designated by Johnston and Berkelbach van der Sprenkel as the infracommissural bundle in the opossum. As the supracommissural bundle passes dorsalward through the central amygdaloid nucleus it probably receives additional fibers from this cell mass. In company with the other stria components it crosses over the internal capsule, where it lies most dorsalward (the order of the stria components being the same as that of the labels in figs. 13D and 14B), and passes toward the midline to lie dorsal to the anterior commissure and lateral to the medial cortico-habenular and cortico-mammillary fibers (figs. 11B and 14A). In this region the supracommissural bundle flattens out into a sheet of fibers lying between the medial border of the internal capsule and the fibers of the postcommissural fornix system. A few of its less heavily myelinated fibers pass ventralward, close to the medial border of the internal capsule, and extend frontalward and medialward ventral to the anterior commissure, to both medial and lateral preoptic areas. This portion of the bundle (fig. 14A) corresponds to the infracommissural bundle of the opossum. The greater part of the supracommissural bundle, its more medially situated and more heavily medullated portion, curves around the anterior commissure, close to its frontal border, and then passes caudalward ventral to it. Small fascicles can be followed caudalward to the medial preoptic and hypothalamic regions, while farther lateralward similar fibers pass to the lateral preoptic region and probably continue to the lateral hypothalamic region as well, although as they cross and intermingle with the fascicles of the medial forebrain bundle the more caudal part of their course is not definite. In the bat, as in the opossum (Johnston, 23; Loo, '31), although not in the rat (Gurdjian, '25) or the rabbit (Young, '36), some of the most cephalic of the fibers pass frontalward instead of caudalward to reach the septal area (parolfactory area of Johnston), while other fibers extend into the head of the caudate nucleus (fig. 11A) as indicated by Loo (p. 79).

The infracommissural component (figs. 13 and 14A). Since in the bat the fibers corresponding to the infracommissural bundle in the opossum are very closely related to the supracommissural fibers and distinguishable from them only in certain regions, they are considered here as forming a part of the supracommissural bundle and are described with it (see p. 668).

The preoptic component (figs. 13 to 15). This bundle of the stria terminalis arises entirely in the cortico-medial amygdaloid complex—the cortical, the medial, and the central amygdaloid nuclei. Its rather lightly medullated fibers swing dorsofrontalward through the central nucleus and converge on either side of the unmedullated commissural bundle (fig. 13, B to D), where they lie medial to the supracommissural component and lateral to the stria medullaris component. After going over the internal capsule, where they form the most ventral part of the stria (figs. 13D and 14B), these fibers spread out and pass ventralward, caudal to the anterior commissure. Here again the preoptic component is split into two parts (fig. 14A), an anterior and a posterior, by the commissural component. The anterior bundle passes directly ventralward into the lateral preoptic region, while part, at least, of the fibers of the posterior portion turn caudalward with the medial forebrain fascicles and probably reach the hypothalamus. This component is homologous with the preoptic component of Gurdjian ('25) and Young ('36), the hypothalamic bundle of Johnston ('23), and bundle two of Berkelbach van der Sprenkel ('26), although varying in certain details. Closely related to it, since they arise in the cortico-medial amygdaloid complex, are the fibers of the commissural and the stria medullaris components.

The commissural component (figs. 10B, 11B, 13, B to D, and 15). The commissural component of the stria terminalis consists of a small but very distinct bundle of rather coarse, unmyelinated fibers which arise entirely in the nucleus of the lateral olfactory tract. When two nuclei of the lateral olfactory tract are present, fibers arising in the more frontally situated one pass caudalward to be joined by the fibers arising in the second nucleus (see p. 649). In one such instance, where the more cephalic nucleus is far frontalward, the fibers from it are joined by a few unmedullated fibers from the caudolateral portion of the tuberculum olfactorium. In the sagittal series in which fibers from the tuberculum are noted, they appear as a distinctly fan-shaped fascicle which joins the commissural component just dorsofrontal to the nucleus of the lateral olfactory tract. Although no reference to such a relationship between the tuberculum and the commissural bundle has been found in the literature, according to Crosby ('17), in the alligator the ventral portion of the nucleus of the lateral olfactory tract is in close relation, frontally, with the cortex of the tuberculum olfactorium, as is more nearly the case in those bat series in which both cephalic and caudal parts of this nucleus are present.

After its formation, the small, deeply staining commissural bundle swings dorsalward through the central amygdaloid nucleus (fig. 13D), between the two portions of the preoptic component of the stria. It is not possible to determine whether or not fibers join the bundle from the central amygdaloid nucleus. Upon reaching the medial side of the internal capsule the fibers spread out slightly as they pass through the bed nucleus of the stria to come into relation with the anterior commissure (fig. 14A). The termination of these fibers as well as their relation to the anterior commissure is described on page 664. In the bat there is no indication of any relation with the claustrum, such as described by Berkelbach van der Sprenkel for the opossum. It is possible that this fiber bundle not only provides a commissural connection between the nuclei of the lateral olfactory tracts, but may perform a similar function for the tuberculum olfactorium, which also has a direct commissural connection through the anterior commissure (see p. 663).

The commissural component in the bat corresponds to that of Johnston, or bundle 1 of Berkelbach van der Sprenkel, and to the pars amygdaloidea of the anterior commissure of Loo for the opossum. It is also the commissural component of Gurdjian ('25) for the rat and of Young ('36) for the rabbit.

The stria medullaris component (figs. 13B and 14A and str.med. of fig. 15). In the bat it is possible to follow the stria medullaris component in its caudal as well as its frontal extent, although only part of the extensive caudal distribution noted by Johnston and Berkelbach van der Sprenkel for the opossum is evidenced in the bat. In this latter mammal the fibers of the stria medullaris component are few in number and coarse, although unmedullated. They arise far caudalward just frontal to the region of transition from the amygdaloid complex to the hippocampus (see pp. 644 and

647), appearing to come largely from the medial, but to a lesser extent from the cortical, amygdaloid nucleus, as well as from the adjacent region of the hippocampus. The tiny fascicle formed by these fibers ascends just lateral to the optic tract to come into relation with the other components of the stria, at first lying medial to the preoptic component, but apparently swinging caudal, then dorsal, to the other bundles as the stria crosses the internal capsule, so that the stria medullaris fibers lie dorsomedial to the supracommissural component frontalward. Thus the fibers to the stria medullaris appear to leave the medial border of the supracommissural bundle as they turn dorsalward into the stria medullaris to go to the habenula. In the bat no evidence has been found as yet indicating that any of the fibers of this fascicle originate in the tuberculum olfactorium as in the opossum (Johnston, Berkelbach van der Sprenkel, Loo), where this bundle is evidently much larger, although fibers from the tuberculum do join the commissural bundle (see p. 670). Because of their relation with the cortico-medial amygdaloid complex and their close association with the preoptic component, the fibers passing to the stria medullaris are considered as a differentiation of the preoptic bundle (see p. 674).

General discussion of the stria terminalis. As usually described, the stria terminalis includes fibers which relate the lateral olfactory areas, as represented by the amygdaloid complex, with the medial, basal regions of the forebrain—the preoptic regions, the hypothalamic areas, and probably also the septal (parolfactory) areas. Along with these fibers are included others which leave the amygdaloid complex with the stria terminalis, but join the stria medullaris to pass to the habenula. Only fibers of the nature indicated above are included in the description of the stria terminalis in the bat. However, certain observers have included with the stria other fibers of adjacent regions, among which are fibers arising from "the gray intermingled with the fasciculi of the medial forebrain bundle" (Berkelbach van der Sprenkel, '26), fibers which, as represented in the bat, at least, are generally considered to form the lateral cortico-habenular tract, and in this account are described with the stria medullaris (see p. 676). Likewise it is suggested that possibly those fibers relating the supraoptic nucleus with the habenula, and described by this author as part of the stria terminalis (his bundle 5a), also may be a part of the stria medullaris of other authors (the lateral olfacto-habenular tract).

Although five bundles of the stria terminalis can be identified in the bat, as in certain other mammals, on the basis of their relations with the subdivisions of the amygdaloid complex these fascicles consist of two fiber systems, the supracommissural bundle with the closely related infracommissural fibers comprising a fiber system in association with the baso-lateral amygdaloid complex, while the preoptic component and the closely related commissural and stria medullaris fibers make up a second system related with the cortico-medial complex. Although it forms a part of the system related with the cortico-medial amygdaloid complex, the constant presence of the commissural bundle, its relation to a single nucleus and its unusual distinctness seem to warrant its consideration as a third fundamental part of the stria terminalis. These three fundamental portions of the stria are represented in reptiles such as the alligator (Crosby, '17) in the distribution of fibers to the nucleus of the lateral olfactory tract, to the ventromedial nucleus (homologous with the cortico-medial amygdaloid complex), and to the ventrolateral part of the dorsolateral area (homologous with the baso-lateral amygdaloid complex). For the turtle, also, Johnston ('15 and '23, p. 397) noted the distribution of stria fibers to three amygdaloid areas, the 'chief amygdaloid nucleus' and the 'large-celled medial nucleus' as well as the nucleus of the lateral olfactory tract. Homologies of the first two areas with the amygdaloid complex of the bat are less certain than in the alligator, although from Johnston's description it appears that the chief or small-celled amygdaloid nucleus corresponds with the baso-lateral amygdaloid complex, while the large-celled medial nucleus is homologous with the cortico-medial complex. In birds, as well as in reptiles, these three portions of the stria terminalis appear to be represented in the distribution of fibers of the stria (tractus occipito-mesencephalicus, Huber and Crosby, '29, p. 134) to nucleus taeniae, homologous with the ventromedial nucleus of the alligator (Huber and Crosby, '29, p. 55) and probably also with the cortico-medial complex of mammals, in the passage of fibers to the cells intercalated in the course of the occipito-mesencephalic tract and probably homologous with the mammalian baso-lateral amygdaloid complex, and in the commissura interstriatica which represents the commissural component of the mammalian stria. Possibly these three portions of the stria may be represented also in amphibians, by the olfactory projection tract and the stria terminalis with its commissural fibers as described by Herrick for Amblystoma and Necturus ('27, p. 305 and '33, pp. 158–160), although in the latter form, according to this observer, the nucleus amygdalae is unspecialized as yet ('33, p. 153).

In all mammals for which the stria terminalis has been studied in any detail, with the exception of Ornithorhynchus (Hines, '29), these three major divisions of the stria are clearly evident. In all of them, also, the fibers to the stria medullaris, which are considered here as a clearly developed subdivision of the preoptic bundle, are identifiable as they join the stria medullaris, although not always (rat and rabbit) discernible in relation with the amygdaloid complex. The infracommissural bundle of Johnston, however, was not identified by Gurdjian for the rat and was considered by Young to be represented by a part of the preoptic component in the rabbit. From a review of these relations it is suggested that, in mammals as well as in reptiles and birds, in its relation to the amygdaloid complex three fundamental portions of the stria are always present, and that the other bundles described for some mammals represent a further differentiation of these components, which are more or less clearly evidenced, depending, to a certain extent at least, on the degree of development of the amygdaloid complex in the mammal under consideration. In certain mammals the degree of differentiation may be still greater (Gurdjian, '28, rat) although these fundamental fiber groups remain evident.

THE STRIA MEDULLARIS (figs. 11B, 14 and 15). The complex fiber bundle known as the stria medullaris consists of tracts which connect the olfactory areas of the forebrain with the habenula. It is composed of two groups of related fiber systems: 1) fibers from the olfactory areas of the hemispheres —both cortical olfactory regions (the hippocampus and the pyriform cortex) and non-cortical olfactory areas (the amygdaloid complex)—passing directly to the habenula by way of the medial and lateral cortico-habenular tracts, and 2) fibers from basal forebrain areas (the tuberculum olfactorium and the septal, preoptic and hypothalamic regions), which also reach the habenula directly through the medial and lateral olfacto-habenular tracts and the septo-habenular tract. Associated with the first of these two systems are other fibers which join the system from the bed nuclei of the stria terminalis and of the anterior commissure, and in this way indirectly relate the olfactory areas of the hemispheres with the habenula, after passing through a region of synapse. The mechanism for a similar indirect connection of the hippocampus with the habenula may be seen in the fibers which join the septo-habenular tract from the bed nucleus of the hippocampal commissure.

An excellent review of the earlier literature dealing with the stria medullaris, as well as the many names which have been applied to it, may be obtained from the account of Gurdjian ('25), and certain additional references are to be found in the discussion of Loo ('31). Recent descriptions of the stria medullaris in submammalian forms are given by Herrick ('33) for Necturus, and by Huber and Crosby ('26) for reptiles and ('29) for birds. Since no description of the stria medullaris in Chiroptera is available, aside from certain additional references to the more pertinent descriptions of the various fiber tracts, no further discussion of the literature will be included.

Tractus cortico-habenularis lateralis (figs. 13D and 14B). In the bat, this tract consists mainly of fine unmedullated fibers which arise in the more cephalic part of the medial amygdaloid nucleus and extend dorsomedialward, passing between the fascicles of the medial forebrain bundle to join the lateral olfacto-habenular fibers, just medial to them, in the manner described by Gurdjian ('25) for the rat. Whether or not fibers from the pyriform lobe and from other nuclei of the cortico-medial amygdaloid complex pass along with those from the medial amygdaloid nucleus is less certain from the material at hand at the present time. However, as the fibers from the medial amygdaloid nucleus cross through the medial forebrain bundle they are joined ventromedially by a few additional fibers, similar in type, which have collected as a little cross-cut fascicle located at the ventromedial angle of the hemisphere. This latter fiber bundle accumulates, farther caudalward, from the region of the cortical amygdaloid nucleus and possibly from the pyriform lobe and passes medialward just dorsal to the lateral olfactory tract and in intimate contact with it. It is not possible to say whether or not fibers from the nucleus of the lateral olfactory tract join it, although in certain other forms (alligator, Crosby; rat, Gurdjian), fibers from this nucleus do join the lateral cortico-habenular tract. These unmedullated fibers which join the lateral cortico-habenular tract are distinguishable from the lateral olfactory tract since they pass medialward, while the medullated lateral olfactory tract fibers pass caudolateralward. This portion of the lateral cortico-habenular tract, which arises from the pyriform lobe and cortical amygdaloid nucleus, appears to correspond to certain of the fibers designated as a part of the stria terminalis five of Johnston ('23, fig. 35) and Berkelbach van der Sprenkel ('26).

The fibers included in the lateral cortico-habenular tract as described above correspond to the pars anterior of that tract in reptiles (Crosby, '17; Huber and Crosby, '26) and to the taenio-habenular tract in birds (Huber and Crosby, '29). Whether or not any fibers corresponding to the pars posterior of reptiles are present in the bat it is not possible to say with certainty from the material at hand. If present, they are represented by a few lightly medullated fine fibers passing across from the region of the basal amygdaloid nucleus to that of the central amygdaloid nucleus, where their course is interrupted by the fibers of the region, so that they cannot be followed farther.

As the lateral cortico-habenular tract fibers ascend to the region of the habenula they appear to occupy first the more lateral, then the more dorsocaudal, portions of the stria medullaris in the series studied. Part of them, at least, cross in the caudal portion of the habenular commissure. Such decussating fibers are present also in reptiles (Huber and Crosby, '26, p. 146), and correspond to the commissura posterior telencephali of certain lower forms. The present material is not adequate to determine whether or not fibers of this bundle terminate in the habenular nuclei.

Tractus cortico-habenularis medialis (figs. 11B and 14). The fibers constituting this tract accompany the fornix fibers from the hippocampus; in the bat, it has not been possible to determine their relation with the hippocampus, however. The large, and dorsolaterally located, part of the anterior pillars of the fornix is made up of the medial cortico-habenular fibers, although they can be distinguished from the lighter staining fornix fibers only with difficulty in cross sections. At the caudal border of the anterior commissure, where the fornix lies just dorsocaudal to it, the large medial cortico-habenular tract separates and passes slightly lateralward, then dorsalward (frontal and lateral to the habenula), passing largely to the medial habenular nucleus, although fibers turn into the lateral nucleus of the habenula, also, as they pass lateral to it. A considerable number of the fibers of this tract cross in the more frontal part of the large habenular commissure (fig. 14B), but their termination has not been determined.

Discussion of the cortico-habenular tracts. The cortico-habenular tracts and the fibers associated with them relate the habenula with the hippocampus and with the amygdaloid complex in three different ways. From the more frontal portion of the cortico-medial amygdaloid complex, fibers reach the stria medullaris by the lateral cortico-habenular tract, while from the caudal end of this complex, fibers pass to the stria medullaris in a less direct route, by way of its connection with the stria terminalis. In addition to these fibers, the entire extent of the amygdaloid complex may be related with the habenula by means of the fibers which join the stria medullaris from the bed nuclei of the stria terminalis and of the anterior commissure. Likewise, the hippocampus is related with the habenula in a comparable fashion. The large medial cortico-habenular tract relates the hippocampus (and in reptiles, at least, its more frontal portion, Huber and Crosby, '26, p. 145) with the habenula, while a few fibers from the caudal end of the hippocampus may also reach the habenula through the stria terminalis fibers to the stria medullaris (see p. 671). By means of fibers which pass from the bed nucleus of the hippocampal commissure to the septo-habenular tract, any portion of the hippocampus also may be related, indirectly, with the habenula.

In contrast with these complex relations with the hippocampus as found in mammals is the connection of the entire primordium hippocampi with the habenula by the medial cortico-habenular tract in Necturus (Herrick, '33, p. 210). If the connections of the habenula with the amygdaloid complex and the pyriform lobe, as present in reptiles and mammals, are compared with those in amphibians, it will be seen that while in amphibians (Herrick, '33, p. 209) each of these areas (amygdala and primordium piriforme) is connected with the habenula by a separate fiber bundle (tractus amygdalo-habenularis and tractus cortico-habenularis lateralis respectively) in reptiles and mammals the fibers from the two regions have become intermingled. Therefore, although two tracts from these regions are recognized also in reptiles and in some mammals (Ornithorhynchus, Hines, '29, and possibly bat, see p. 677; tractus cortico-habenularis lateralis anterior and posterior), each contains fibers from both the amygdaloid complex and the pyriform lobe, that is, each contains fibers corresponding to both amphibian tracts. This intermingling of fibers from the two areas may be the result, in part at least, of the change in position of the primordium piriforme in relation to the amygdaloid complex in reptiles, as compared with amphibians, as well as to the further development and differentiation of the pyriform region. In the majority of mammals (rat, Gurdjian; rabbit, Young; opossum, Loo), perhaps as a result of the changes incident to the greater development and differentiation of the amygdaloid complex, only that portion of the fiber system corresponding to the tractus cortico-habenularis anterior remains. In birds, where the pyriform lobe is relatively reduced while the basal nuclei of the hemispheres are exceptionally large, although both the anterior and posterior parts of the lateral cortico-habenular tract of the alligator are represented (tractus taenio-habenularis and tractus archistriato-habenularis et precommissuralis respectively), no fibers from the pyriform lobe could be traced to either tract (Huber and Crosby, '29, pp. 139 and 140).

Tractus olfacto-habenularis lateralis (fig. 14B). In the bat, the few rather fine, unmedullated fibers making up this tract pass dorsolateralward and join the fibers of the lateral cortico-habenular tract in a manner essentially the same as that described by Gurdjian ('25) for the rat, the two tracts intermingling with each other, and with the most caudal fibers of the preoptic component of the stria terminalis, as they join the stria medullaris. Whether or not any of these fibers arise in the tuberculum olfactorium cannot be determined in the bat material available; the majority of them, at least, extend more directly ventromedialward and caudalward from the stria medullaris, having a course lateral to the cortico-mammillary fibers and between this bundle and the medial forebrain bundle, into which they turn caudalward for a short distance. During this portion of their course the fibers pass through the more caudal and lateral part of the preoptic region, in which some of them appear to terminate. Other fibers can be followed beyond the supraoptic commissures, which they cross, into the anterior hypothalamic region. A few of these fibers end in relation with the large cells of the nucleus supraopticus just frontal and dorsal to the optic chiasm.

Tractus olfacto-habenularis medialis (figs. 11B and 14). This tract, as described by Gurdjian ('25) for the rat, consists of two portions, one containing fibers from the preoptic region and the other consisting of fibers from the medial hypothalamic area. In the bat the fibers from the hypothalamic region, as seen in relation with the dorsomedial part of the anterior hypothalamic area, are deeply staining, rather coarse, but unmedullated fibers, a few of which, at least, can be seen in synapse with cells of this nucleus. These fibers form a rather large, but loose, bundle, passing dorsolateralward and frontalward to join the caudoventral surface of the medial cortico-habenular tract, just caudal to the anterior commissure. The portion from the preoptic region is represented by fine, scattered fibers, near the midline, which pass from the caudal preoptic region dorsalward, behind the anterior commissure. In the region of the sulcus limitans, where the various fiber bundles are joining to form the stria medullaris, these fibers are just medial to the stria bundle (fig. 14A). As the fibers from the preoptic region pass dorsalward, however, they lie near the wall of the third ventricle and separated from the other tracts of the stria medullaris, while on reaching the frontal end of the habenula these fibers are again just medial to the other bundles of the stria (fig. 14B). They appear to enter the more frontal part of the habenula, the medial habenular nucleus.

Discussion of the olfacto-habenular tracts. Both medial and lateral olfacto-habenular tracts have been described by Gurdjian ('25) for the rat, Hines ('29) for Ornithorhynchus, and Young ('36) for the rabbit. The lateral olfacto-habenular tract of these authors and of this account is the tractus olfacto-habenularis principalis of Loo ('31) for the opossum, although, as stated by Young and as described for the bat, the lateral olfacto-habenular tract includes also the tractus olfacto-habenularis supraopticus of Loo. The tractus olfacto-habenularis periventricularis of this latter author is the medial olfacto-habenular tract of the other accounts. In amphibians (Herrick, '27 and '33) and reptiles (Crosby, '17) both medial and lateral olfacto-habenular tracts are present. In birds, however, only the medial tract was identified by Huber and Crosby ('29).

Tractus septo-habenularis (not illustrated). The septo-habenular tract consists of fibers which join the lateral border of the medial cortico-habenular tract, while this bundle is still part of the anterior pillar of the fornix. Its fibers arise in relation with cells forming the bed nucleus of the hippocampal commissure (see p. 617), and, a little farther forward, in relation with cells just ventrolateral to the bed nucleus, and probably forming the medial septal nucleus, although their exact relationship is not clear. As they originate, the septo-habenular fibers form a little fringe of scattered, unmedullated fibers ventrolateral to the medial cortico-habenular tract, while farther caudalward they become incorporated in this cortico-habenular tract and are no longer distinguishable from the other stria bundles. A tract of the same name is described for other mammalian forms, in some of which the fibers from the bed nucleus of the anterior commissure are included also (opossum, Loo, '31). As described for amphibians (Herrick, '33) and birds (Huber and Crosby, '29) the septo-habenular tract is composed of fibers from the bed nucleus of the anterior commissure as well as from the septum, and, in birds, from the bed nucleus of the hippocampal commissure also.

Connections with the bed nuclei of the stria terminalis and of the anterior commissure (not illustrated). In the region where the medial cortico-habenular tract forms a part of the fornix columns, fine fibers from these two nuclei join the fibers of the medial cortico-habenular tract, those from the bed nucleus of the stria terminalis joining it laterally, those from the bed nucleus of the anterior commissure entering it ventrally. Connections of these bed nuclei with the medial cortico-habenular tract are also described by Gurdjian ('25) for the rat, and of the bed nucleus of the stria terminalis with this tract, by Young ('36) for the rabbit.

Fibers from the stria terminalis (fig. 14A and str.med. in fig. 15). A few unmedullated fibers from the stria terminalis join the lateral part of the medial cortico-habenular bundle and pass with it to the habenula as described by Gurdjian ('25) for the rat and Young ('36) for the rabbit. For the complete description of these fibers the description of the stria medullaris component of the stria terminalis should be consulted (p. 671). According to the later paper of Gurdjian ('27, pp. 9 and 103) a part of these fibers continue ventral to the stria medullaris, between it and the fornix, and pass along with the medial cortico-hypothalamic tract (p. 684) to medial preoptic and hypothalamic areas. Probably similar relations are present in the bat, although in this form many of the stria terminalis fibers extending nearest the medial cortico-hypothalamic tract can be seen to turn dorsalward into the stria medullaris, and their presence in the medial cortico-hypothalamic path cannot be determined definitely.

THE FORNIX SYSTEM (figs. 11, 12, 13, C and D, 14 and 16). It is not possible to include here a review of the literature concerned with the fornix or a discussion of the numerous terminologies which have been applied in describing it. Such accounts may be obtained from the paper of Loo ('31) and the recent reference work on comparative neurology by Ariëns Kappers, Huber and Crosby ('36). In the following description the terminology of Elliot Smith (1897 and 1897 c), of Loo ('31), and of Young ('36) is used, the fornix fibers being grouped into precommissural and postcommissural portions on the basis of their relation to the anterior commissure. The brief description and the figure of the fornix in Nyctophilus, given by Elliot Smith, show that its relations are essentially the same as those in the free-tailed bat.

The postcommissural fornix (figs. 11, 12, 13D, 14 and 16, C and D). This portion of the fornix is composed of those fibers from the hippocampus which pass caudal to the anterior commissure. It consists of the medial cortico-habenular tract, of cortico-hypothalamic (including cortico-mammillary) fibers, and probably of others also. In addition to those fibers from the hippocampus which cross in the hippocampal commissure, take part in the fornix decussation or pass to the homolateral anterior column of the fornix, the postcommissural system is joined by a few, at least, of the fibers from the medial stria of Lancisius, and by a somewhat larger number of the fibrae perforantes corporis callosi, particularly those more caudally situated (see also the precommissural fornix, p. 686). The fiber system formed in this manner distributes to the habenula, to anterior hypothalamic areas, to the mammillary bodies, and probably still farther caudalward, although the more caudal course of the bundle has not been followed. Just behind the anterior commissure the fibers of the fornix separate into certain bundles which continue to their several destinations in the fiber tracts described below. Other fibers originating with the postcommissural fornix system and traversing the hippocampal commissure pass frontal to the anterior commissure as part of the precommissural fornix (fig. 16 C and D, b).

The medial cortico-habenular tract (figs. 11B and 14). This tract has been described in connection with the stria medullaris (p. 677), which it joins almost immediately upon leaving the fornix. It is the largest of the bundles which leave the fornix just caudal to the anterior commissure.

Cortico-mammillary (and lateral cortico-hypothalamic) fibers (figs. 11B, 13, C and D, and 14). The cortico-mammillary fibers stain a dull brown in pyridine silver material, as compared to the golden brown color of the medial cortico-habenular fibers, so that, although they are intermingled with this latter bundle while forming a part of the fornix column, they may be seen to occupy the ventromedial portion of the fornix as it lies dorsal to the anterior commissure. Just caudal to this commissure, the cortico-mammillary fibers separate from the fornix and continue ventrolateralward and slightly caudalward, then more directly ventrocaudalward, and finally ventromedialward through the hypothalamus as far as the lateral aspect of the mammillary body. In this part of their course the fascicles decrease in size and number, evidently giving off fibers throughout the more lateral portion of the hypothalamus which they traverse. Such fibers might be said to constitute a lateral cortico-hypothalamic tract as compared with the medial cortico-hypothalamic tract described below. The more caudal course of these fibers has not been studied in the bat.

Medial cortico-hypothalamic (and cortico-preoptic) fibers (figs. 11B and 14B). In the region where the fibers of the medial cortico-habenular tract separate from the fornix column, a considerable number of deeply staining, loosely arranged, coarse, unmedullated fibers also separate from the fornix just caudal to the cortico-mammillary fascicles and pass ventralward and slightly medialward for a very short distance. Part of them enter the caudodorsal part of the medial preoptic region and others the large-celled portion of the anterior hypothalamic region, so constituting in the bat the medial cortico-hypothalamic tract described by Gurdjian ('27) for the rat. In the bat, however, the medial cortico-hypothalamic tract fibers are quite intimately in contact with the fibers of the medial olfacto-habenular tract, some of the more caudal of which they cross (intermingled slightly in fig. 14, where the tracts are labeled according to the greater number of fibers present). Since the fibers of these two bundles are of similar size and appearance, it is not possible to distinguish them except by the direction in which they pass, the fibers of the medial cortico-hypothalamic tract extending almost directly ventralward (although slightly medialward) from the fornix while those of the medial olfacto-habenular tract pass dorsolateralward from the region of termination of the cortico-hypothalamic fibers to join the stria medullaris.

The precommissural fornix (figs. 11A and 16, B to D). The fibers from the hippocampus which pass frontal to the anterior commissure constitute the precommissural fornix. On the basis of the way in which they reach the precommissural region, at least three groups of such fibers may be listed: 1) fibers from the hippocampal commissure, 2) fibers passing dorsal to the corpus callosum or the stria of Lancisius, and 3) fibers perforating the corpus callosum, or the fibrae perforantes corporis callosi.

Fibers from the hippocampal commissure (fig. 16, C and D, b). Part of the fibers of the precommissural fornix system traverse the posterior pillars of the fornix and the hippocampal commissure, but do not continue into the anterior columns of the fornix to form a part of the postcommissural fornix system. Instead, they leave the hippocampal commissure to pass frontoventralward into the medial septal areas (medial septal nucleus and the nucleus of the diagonal band of Broca) and the medial preoptic areas (nucleus preopticus periventricularis), as stated by Loo ('31), spreading out from the hippocampal commissure in the form of a frontocaudally directed, fan-shaped fiber mass. In the bat, it has not been possible with the material at hand to say whether or not part of these fibers continue still farther caudalward with the medial forebrain bundle as in the opossum (Loo, '31), nor has it been possible to determine from what portions of the hippocampus they arise. A few of the fibers located nearest to the anterior commissure extend well caudalward in the preoptic region and even into the anterior part of the medial hypothalamic region.

Fibers passing dorsal to the corpus callosum (see str.Lan., figs. 11A and 16). A small number of fibers from the hippocampus pass dorsal to the corpus callosum almost as far as the medial side of the olfactory stalk and form the white stria of Lancisius. Some of them may join the stria from the cingulum ammonale (figs. 11, 14 and 16, A and B) just lateral to and in contact with it, but the majority of them originate in the gyrus dentatus, and a few join the stria from the supracommissural part of the bed nucleus of the hippocampal commissure (see next paragraph). No indication of the addition of fibers from the cingulum limitans, as mentioned by Ariëns Kappers, Huber and Crosby ('36), has been noted in the bat, as yet. The great majority of the stria fibers pass ventralward, frontal to the anterior commissure, some of them to the region of the anterior hippocampal cortex (and possibly even to the caudal end of the medial part of the anterior olfactory nucleus), others, more caudally situated, to the most frontal septal areas—the region of the medial septal nucleus and the nucleus of the diagonal band of Broca. Still others extend farther caudalward, in the ventral part of the medial forebrain bundle, to medial preoptic regions, just frontal to the optic chiasm. Although the majority of the precommissural fibers pass frontal to the anterior commissure to distribute, a lesser number turn ventrocaudalward at the tip of the corpus callosum and join the postcommissural fornix (see w, fig. 16C).

In the bat material studied, unmedullated fibers may be seen to join the medial part of the stria of Lancisius from both lateral and frontal surfaces of the supracommissural part of the bed nucleus of the hippocampal commissure (fig. 16, B, C and D) as described by Werkman ('14, p. 60) for the 22.5 mm. embryo of Vesperugo. The fibers originating in the gyrus dentatus occupy a position in the stria lateral to those from the supracommissural part of the bed nucleus, while fibers from the cingulum ammonale may join the stria of Lancisius still more laterally, where these two fiber bundles lie in contact.

The fibrae perforantes corporis callosi (fig. 16, C and D). A few of the dark-staining fibers of the stria of Lancisius pass between the fasciculi of the corpus callosum to distribute as do the fibers passing dorsal to it, the more frontal ones continuing forward toward the anterior hippocampal cortex, the medial ones extending ventralward to the medial septal nucleus, and a few of the more caudal ones passing to join the frontal part of the postcommissural fornix. The number of such perforating fibers is greater toward the frontal tip of the corpus callosum, although a few cross between the commissural bundles as far caudalward as the junction of the corpus callosum and the hippocampal commissure. A few of the perforating fibers have been followed frontalward ventral to the corpus callosum (in the region of the nucleus septo-hippocampalis) for a varying distance, some of them even crossing again to the dorsal surface of the corpus callosum to continue frontalward, while others continue toward the anterior hippocampal cortex (fig. 16, C and D, unlabeled). Many of the perforating fibers pass ventralward from the corpus callosum into the medial septal regions. At the apex of the V-shaped dorsal commissural system a very few unmedullated fibers from the supracommissural part of the bed nucleus of the hippocampal commissure cross the dorsal commissure (as do some few cells in this region, see p. 621) to the ventral surface of the corpus callosum to join the other fibers passing through the septo-hippocampal nucleus (fig. 16, C and D, unlabeled).

In the bat, not all of the fibers which perforate the corpus callosum arise in relation with the hippocampal formation. In sagittal series, many such fibers appear to turn out of the ventral part of the corpus callosum, rather than to perforate it. In a cross section series stained with iron haematoxylin some of the fibers which reach the corpus callosum from the dorsomedial areas of the cortex pass to the ventral surface of the commissure almost immediately; other fascicles cross toward the ventral surface of the commissure after traversing it for a varying distance, some of them after crossing the midline. Such small, more heavily medullated fascicles pass from the ventral part of the corpus callosum into the region of the medial septal nucleus, the nucleus of the diagonal band of Broca, and, to a lesser extent, into the more medial portion of the lateral septal nucleus. It is not possible to determine whether the perforating fibers of this nature join the postcommissural fornix system or whether they pass only to septal regions. A further description of these fibers with due consideration of the literature is reserved for a projected paper on the cortex of the bat.

In addition to the fibers from the supracommissural part of the bed nucleus of the hippocampal commissure which pass dorsal and ventral to the corpus callosum, there is also some very slight evidence to indicate that an occasional fiber may pass ventralward from the caudolateral aspect of this cell mass along the caudal border of the hippocampal commissure (fig. 16, C and D, c). Such fibers probably end in synapse with other cells of the bed nucleus of the hippocampal commissure, such as its post- and infracommissural parts. Although a few unmedullated fibers can be seen to pass from the supracommissural part of the commissural bed in this manner, it is possible to follow them along the caudal border of the hippocampal commissure for only a part of its ventral extent. From the material at hand, however, it appears that not all the fibers of this region are impregnated, so that possibly some of them may continue into the postcommissural fornix. Occasionally a dorsoventrally directed, spindle-shaped cell in the postcommissural portion of the bed nucleus may be seen to have processes directed both dorsalward and ventralward along the course of these fibers.

DISCUSSION AND CONCLUSIONS

As was emphasized at the beginning of this account, the bat brain provides peculiarly interesting material for study since this form is a flying mammal with nocturnal habits and very poor eyesight. In addition it has received only cursory attention from neurologists in general.

The olfactory system and the primary and secondary olfactory centers exhibit an unusual type of development, since in some respects they show the usual differentiation while in other respects they are relatively poorly differentiated. The olfactory bulb, although small, has the typical mammalian structure. An accessory olfactory bulb is lacking, as in birds. In the nucleus olfactorius anterior all the major subdivisions described for the opossum can be recognized, although there are differences in the degree of development. The tuberculum olfactorium shows a better differentiation caudalward, and particularly caudolateralward, than frontalward, where its structure is distinctly atypical. Connections other than those invariably described for the tuberculum are fibers from the lateral olfactory tract, an intertubercular component of the anterior commissure, and connections with the lateral amygdaloid nucleus.

In the ventromedial quadrant of the hemisphere there are two major types of nuclear masses—one essentially cortical and the other primarily basal in nature. The basal portion is represented in the various nuclei of the septum, which have developed here along the lines characteristic of mammalian forms but show relatively somewhat less sharp differentiation than in certain other mammals such as marsupials. Their connections are those characteristic of the region and they appear to illustrate the fact pointed out in various other vertebrates, that the medial group is afferent and the lateral group efferent with respect to the hippocampus. The cortical portion of the ventromedial quadrant of the hemisphere finds representation in the anterior continuation of the hippocampus, in the septo-hippocampal nucleus, which connects this anterior continuation with the hippocampal formation behind the corpus callosum, and in the various subdivisions of the bed nucleus of the hippocampal commissure, which represent primordial hippocampal cortex and become continuous with the gyrus dentatus as well as with the indusium griseum which lies in the dorsomedial quadrant of the hemisphere, over the corpus callosum.

The indusium griseum, the thinned out portion of the hippocampus which passes around the cephalic end of the corpus callosum and extends over its dorsal surface to become continuous with the hippocampus, has, in the bat, representatives of all three portions of the hippocampus—the gyrus dentatus, the cornu ammonis, and the subiculum. The amount of such differentiation within the indusium griseum varies with the series under consideration, indicating that here there is an individual factor involved, but it seems probable that all three portions are always inherently present, both in the indusium griseum and in the anterior continuation of the hippocampus.

The relations of the vestigial hippocampal gray with the dorsal commissural systems suggest that the corpus callosum develops by an accumulation of its fibers frontal to the dorsal end of the hippocampal commissure in the region where the primordium hippocampi passes over into the differentiated hippocampal formation, and so thins out the hippocampal gray, the main mass of which is rolled caudalward in the hemisphere.

The preoptic area follows the common mammalian pattern, but on the whole shows slightly less differentiation than in some other forms such as the opossum. So far as they have been studied, the connections of the area appear to be typical.

The connections of the olfactory centers of the hemispheres with epithalamic and hypothalamic regions caudal to them have been discussed under the stria medullaris and the fornix. The relations of the stria medullaris are essentially the same as those described for the rat by Gurdjian ('25), while those of the fornix conform in all essentials to the description of the Australian bat by Elliot Smith (1897 c).

Particularly to be emphasized with regard to the caudate-putamen complex is the relatively enormous size of the head of the caudate nucleus and the fact that the caudate and putamen are separated from each other only through the middle part of their extent, being continuous with each other both frontalward and caudalward. The putamen is relatively small. So also is the claustrum, which is continuous with the deeper layers of the temporal cortex.

The amygdaloid complex may be subdivided into two major nuclear groups, designated as the baso-lateral complex and the cortico-medial complex. Of these the cortico-medial complex (which, according to Johnston, '23, is particularly concerned with olfacto-visceral correlations) is small, while the baso-lateral complex (said to be related to olfacto-somatic correlations) is unusually well developed. Both of these nuclear groups show a tendency to be much more highly differentiated in caudal as compared to frontal levels. Of special interest is the nucleus of the lateral olfactory tract, which, although the smallest nucleus of the entire complex, is almost startlingly distinct and may be represented by two cell masses on each side.

The connections of the amygdaloid complex are summarized in figure 15, to which the reader is referred. It should be emphasized here, however, that the connections, which are particularly clear in the bat and which afford the basis for the subdivision of this nuclear complex into the two subdivisions mentioned above, are those by way of the anterior commissure and the stria terminalis. These connections might equally well provide a basis for the subdivision of the complex into three major groups, one of which has connections only by way of the anterior commissure, another only by way of the stria terminalis, while a third has connections through both of these fiber systems. It is of interest that the commissural component of the stria is as distinct as are the nuclei of the lateral olfactory tracts which it interconnects. A discussion of the major connections of the amygdaloid complex is given on pages 672–675 and does not require repetition here.

Of particular interest are the relations of the commissures of the hemispheres in the bat. Neopallial fibers in part cross in the dorsal corpus callosum which lies in close proximity to, and probably to some extent intermingled with, the hippocampal commissure. The greater number of neopallial fibers cross through the anterior commissure, most of them reaching this commissure by way of the external capsule but a few passing to it through the internal capsule. In addition to these two groups of neopallial fibers, six other components of the anterior commissure have been identified in the bat, where the differentiation of the commissural components is unusually distinct.

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ABBREVIATIONS

a, fibers which enter the corpus callosum from the caudal part of the hemisphere

a.baso-lat.amyg., area baso-lateralis amygdalae

a.cort.-med.amyg., area cortico-medialis amygdalae

a.hypothal.lat., area hypothalamica lateralis

a.hypothal.med., area hypothalamica medialis

a.preopt.lat., area preoptica lateralis

a.preopt.med., area preoptica medialis

b, fibers from the hippocampal commissure which pass frontal to the anterior commissure, i.e., join the precommissural fornix system

b.v., blood vessel

bas.interamyg.comp., basal interamygdaloid component of the anterior commissure

bed n.com.ant., bed nucleus of the anterior commissure

bed n.hip.com., p.infracom., bed nucleus of the hippocampal commissure, infracommissural portion

bed n.hip.com., p.postcom., bed nucleus of the hippocampal commissure, postcommissural portion

bed n.hip.com., p.precom., bed nucleus of the hippocampal commissure, precommissural portion

bed n.hip.com., p.supracom., bed nucleus of the hippocampal commissure, supracommissural portion (usual position in the bat)

bed n.hip.com., p.supracom.′, bed nucleus of the hippocampal commissure supracommissural portion (occasional position in the bat)

bed n.str.term., bed nucleus of the stria terminalis

bulb.olf., bulbus olfactorius

c, a fiber passing ventralward from the supracommissural part of the bed nucleus of the hippocampal commissure (such fibers may be seen dorsal to this one in fig. 16, D and C, where they are unlabeled)

cap.ext., capsula externa

cap.extr., capsula extrema

cap.int., capsula interna

(caput), head of the caudate nucleus

(cauda), tail of the caudate nucleus

caud.-put., caudate-putamen complex

ch.op., chiasma opticum

cing.am., cingulum ammonale

cl., claustrum

com.ant., commissura anterior

com.ant.(bas.interamyg.comp.), commissura anterior (basal interamygdaloid component)

com.ant.(ext.cap.comp.), commissura anterior (external capsule component)

com.ant.(int.cap.comp.), commissura anterior (internal capsule component)

com.ant.(interbulb.comp.), commissura anterior (interbulbar component)

com.ant.(interpyr.comp.), commissura anterior (interpyriform component)

com.ant.(intertub.comp.), commissura anterior (intertubercular component)

com.ant.(lat.interamyg.comp.), commissura anterior (lateral interamygdaloid component)

com.hab., commissura habenularum

com.hip., commissura hippocampi

cor.am., cornu ammonis

cor.hip.ant., cortex hippocampi anterior (anterior continuation of the hippocampus)

cor.neopal., cortex neopallii

corp.cal., corpus callosum

d, dorsal portion of the hemisphere

e, fibers of the corpus callosum which pass through the supracommissural part of the bed nucleus of the hippocampal commissure

ep., epiphysis

ext.cap.comp., external capsule component of the anterior commissure

f., fornix

f.postcom., fornix postcommissuralis

f.precom., fornix precommissuralis

fib.perf.corp.cal., fibrae perforantes corporis callosi

fim., fimbria

fis.amyg., fissura amygdalae
fis.circ.rhin., fissura circularis rhinencephali
fis.endorh., fissura endorhinalis
fis.rhin., fissura rhinalis
fis.rhin.vent., fissura rhinalis ventralis
g, fibers from the neopallium joining the internal capsule; these are believed to enter the anterior commissure at more caudal levels (z, fig. 11B)
glob.pal., globus pallidus
gy.dent., gyrus dentatus
hab., habenula
hip., hippocampus
hyp., hypophysis
hypothal., hypothalamus
ind.gr., indusium griseum
ind.gr., p.am., indusium griseum, pars ammonis
ind.gr., p.dent., indusium griseum, pars dentata
ind.gr., p.sub., indusium griseum, pars subicularis
int.cap.comp., internal capsule component of the anterior commissure
interbulb.comp., interbulbar component of the anterior commissure
interpyr.comp., interpyriform component of the anterior commissure
intertub.comp., intertubercular component of the anterior commissure
isl.Cal., island of Calleja
l, lateral portion of the hemisphere
l.glom., lamina glomerularis
l.gran.ext., lamina granularis externa
l.gran.int., lamina granularis interna
l., mit.c., layer of mitral cells
l.molec., lamina molecularis
l.obl.lat.v., line of obliterated lateral ventricle
lat.interamyg.comp., lateral interamygdaloid component of the anterior commissure
lob.fr., lobus frontalis
lob.par., lobus parietalis
lob.pyr., lobus pyriformis
lob.temp., lobus temporalis
m.f.b., medial forebrain bundle
mas.interc., massa intercalata
n.acc., nucleus accumbens
n.amyg.bas., nucleus amygdalae basalis
n.amyg.bas.acces., nucleus amygdalae basalis accessorius
n.amyg.cent., nucleus amygdalae centralis
n.amyg.cort., nucleus amygdalae corticalis
n.amyg.lat., nucleus amygdalae lateralis
n.amyg.med., nucleus amygdalae medialis
n.caud., nucleus caudatus
n.caud.(caput), head of nucleus caudatus
n.diag.b.Broca, nucleus of the diagonal band of Broca
n.lent., nucleus lentiformis
n.olf.ant., nucleus olfactorius anterior
n.olf.ant., p.bulb., nucleus olfactorius anterior, pars bulbaris
n.olf.ant., p.ext., nucleus olfactorius anterior, pars externa
n.olf.ant., p.vent., nucleus olfactorius anterior, pars ventralis
n.op., nervus opticus
n.preop.ant., nucleus preopticus anterior
n.preop.int., nucleus preopticus interstitialis
n.preop.mag., nucleus preopticus magnocellularis
n.preop.med., nucleus preopticus medianus
n.preop.perivent., nucleus preopticus periventricularis
n.preop.prin., nucleus preopticus principalis
n.sept.-hip., nucleus septo-hippocampalis
n.sept.lat., nucleus septalis lateralis
n.sept.med., nucleus septalis medialis
n.suprachi.ant., nucleus suprachiasmaticus anterior
n.suprachi.dif., nucleus suprachiasmaticus diffusus
n.supraop., nucleus supraopticus
n.tr.olf.lat., nucleus tractus olfactorii lateralis

p, pyriform region of the hemisphere
pl.ch., plexus chorioideus
pl.ch.v.III, plexus chorioideus ventriculi tertii
pl.ch.v.lat., plexus chorioideus ventriculi lateralis
put., putamen
p.v.s., periventricular system
rec.preopt., recessus preopticus
str.Lan., stria of Lancisius
str.med., stria medullaris; fibers from the stria terminalis, the stria medullaris component of the stria terminalis, are shown entering the stria medullaris
str.term., com.comp., stria terminalis, commissural component
str.term.comp., stria terminalis component of the anterior commissure
str.term., infracom.comp., stria terminalis, infracommissural component
str.term., preopt.comp., stria terminalis, preoptic component
str.term., str.med.comp., stria terminalis, stria medullaris component
str.term., supracom.comp., stria terminalis, supracommissural component
sub., subiculum
supraop.s., supraoptic system
tect.opt., tectum opticum
thal., thalamus
tr.cort.-hypothal.med., tractus cortico-hypothalamicus medialis
tr.cort.-hab.lat., tractus cortico-habenularis lateralis
tr.cort.-hab.med., tractus cortico-habenularis medialis
tr.cort.-mam., tractus cortico-mamillaris
tr.olf.-hab.lat., tractus olfacto-habenularis lateralis
tr.olf.-hab.med., tractus olfacto-habenularis medialis
tr.olf.lat., tractus olfactorius lateralis
tr.olf.lat., p.dors., tractus olfactorius lateralis, pars dorsalis
tr.olf.lat., p.intermed., tractus olfactorius lateralis, pars intermedia
tr.olf.lat., p.vent., tractus olfactorius lateralis, pars ventralis
tr.olf.med., tractus olfactorius medialis
tr.op., tractus opticus
tr.tub.-amyg., tractus tuberculo-amygdaloideus
tub.olf., tuberculum olfactorium
tub.olf.plex.l., tuberculum olfactorium, plexiform layer
tub.olf.polym.l., tuberculum olfactorium, polymorphic layer
tub.olf.pyram.l., tuberculum olfactorium, pyramidal cell layer
v.lat., ventriculus lateralis
v.olf., ventriculus olfactorius
v.III, ventriculus tertius
w, fibers from the stria of Lancisius which join the postcommissural fornix
wall v.III, wall of ventriculus tertius
x, cells along the course of precommissural fornix fibers which, after passing frontal to the corpus callosum, join the postcommissural fornix system
y, cells connecting the gyrus dentatus with the supracommissural portion of the bed nucleus of the hippocampal commissure
z, fibers entering the anterior commissure from the internal capsule (see g, fig. 11A)

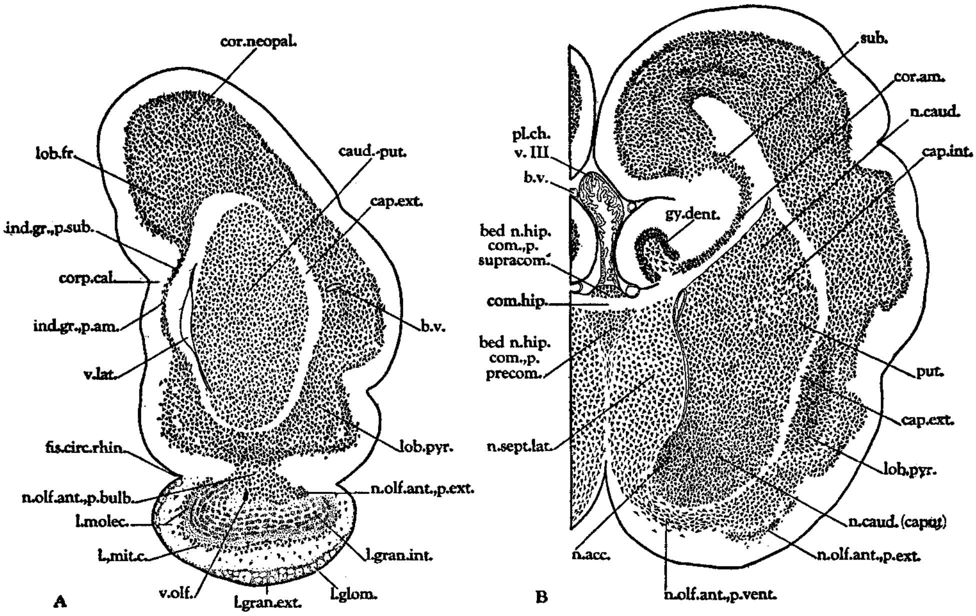
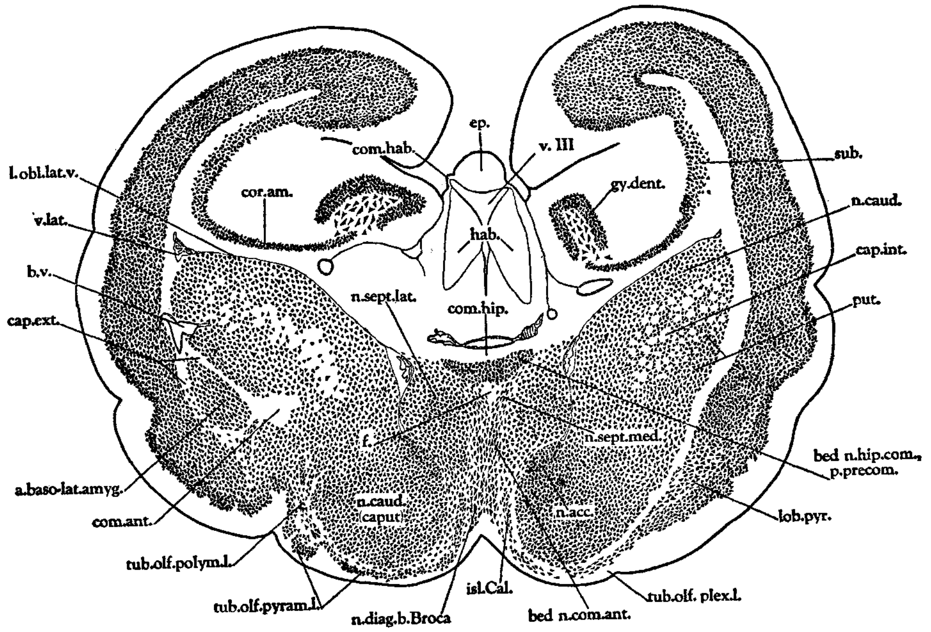


Fig. 1 Transverse sections through the frontal end of the telencephalon of the bat. Toluidin blue preparations. × 17.5. A, a section passing through the olfactory bulb and the frontal end of the corpus callosum. B, a section passing through the hippocampal commissure and its bed nucleus.

Fig. 2 A transverse section of the telencephalon of the bat just frontal to the globus pallidus to show the relations of the caudate-putamen complex, the septal nuclei and the tuberculum olfactorium. Toluidin blue preparation. × 17.5.

Fig. 3 A transverse section through the telencephalon of the bat about 225 μ caudal to that of the preceding figure and passing just frontal to the decussation of the anterior commissure. Toluidin blue preparation. × 17.5.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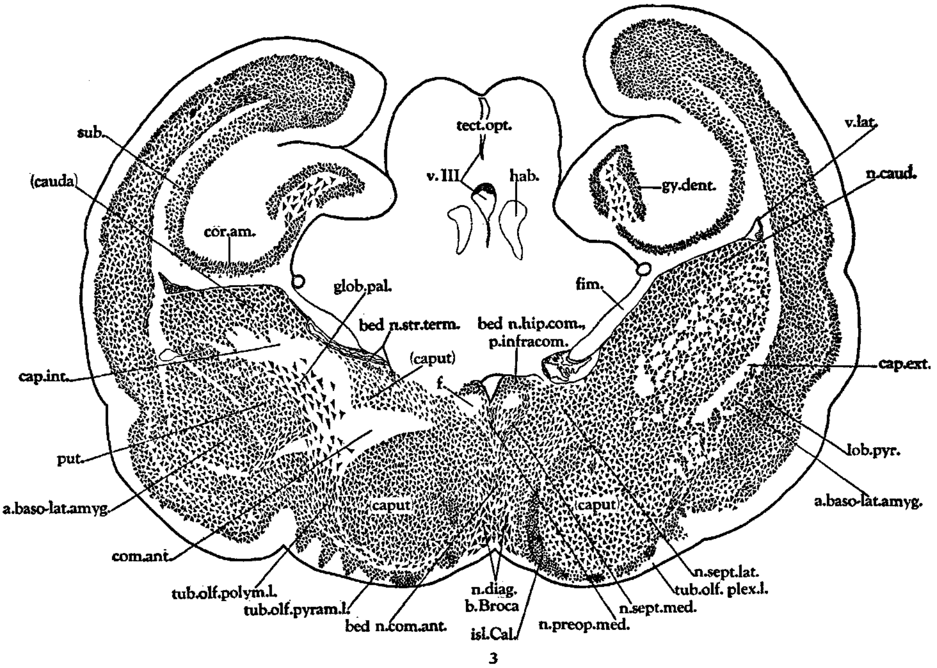
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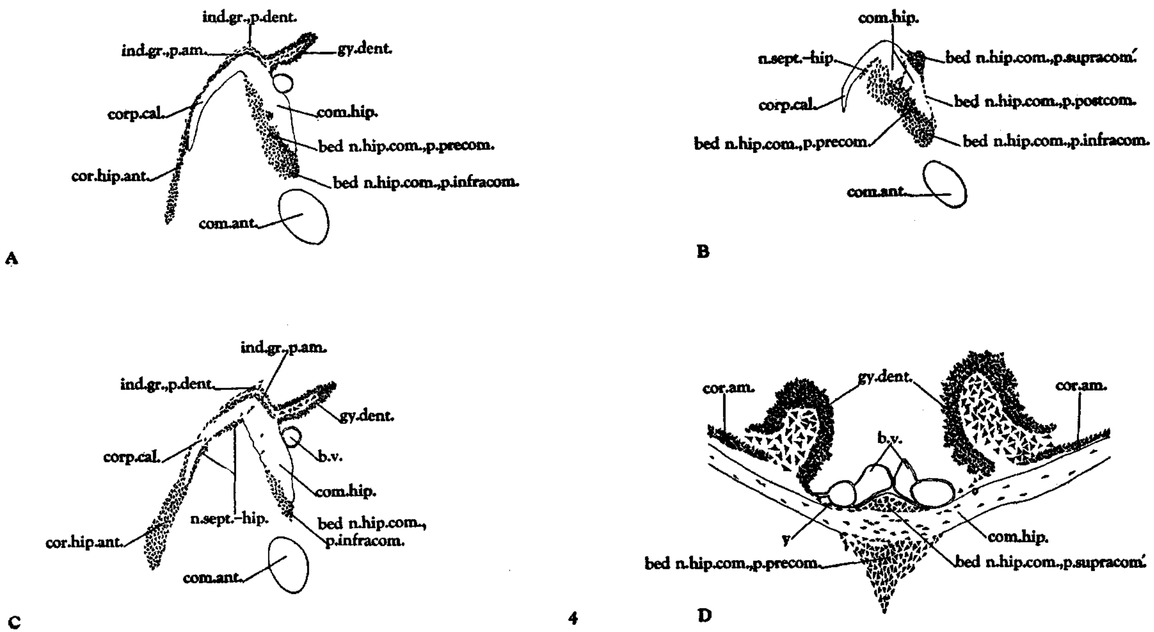

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Fig. 4 A series of drawings to illustrate the relations of the hippocampal vestiges to the dorsal commissural systems. Toluidin blue preparations. A, sagittal section through the dorsal commissural systems about 200 μ lateral to the midline. × 17.5. B, midsagittal section of the same series as A. × 17.5. C, sagittal section 50 μ lateral to figure A. × 17.5. D, transverse section showing the relation of the gyrus dentatus to the supracommissural portion of the bed nucleus of the hippocampal commissure. × 37.5.

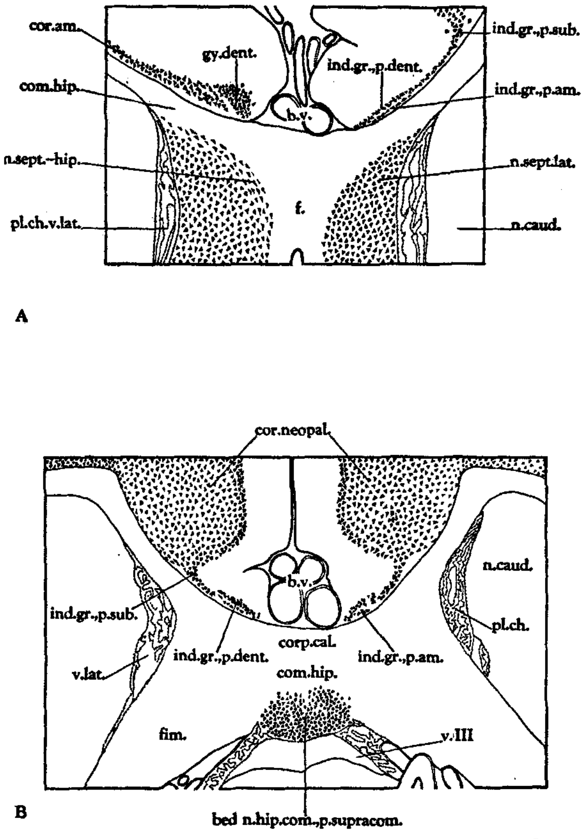
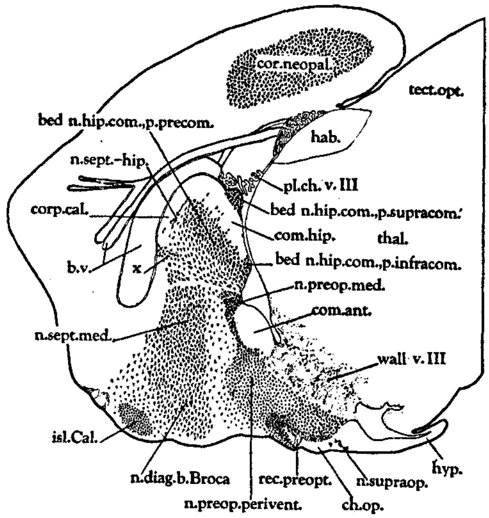


Fig. 5 Drawings to show the relations of the hippocampal vestiges to the dorsal commissural systems. Toluidin blue preparations. × 37.5. A, a section through the hippocampal commissure just frontal to the supracommissural portion of its bed nucleus. B, a section, frontal to A, through the dorsal commissural systems to show the relations of the subdivisions of the indusium griseum to the corpus callosum.



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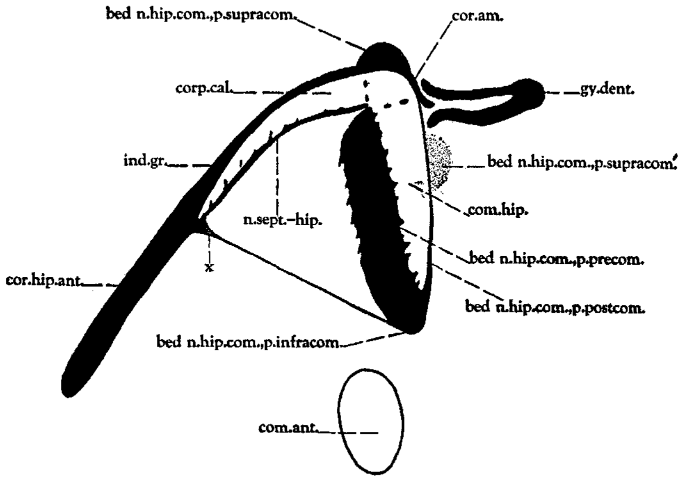

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Fig. 6 A midsagittal section through the brain of the free-tailed bat, illustrating particularly the medial septal and medial preoptic nuclear patterns. Toluidin blue preparation. × 17.5.

Fig. 7 A diagrammatic representation of the relations of the hippocampal vestiges to the dorsal commissural systems in the bat. Drawn to scale, at a magnification of 37.5.

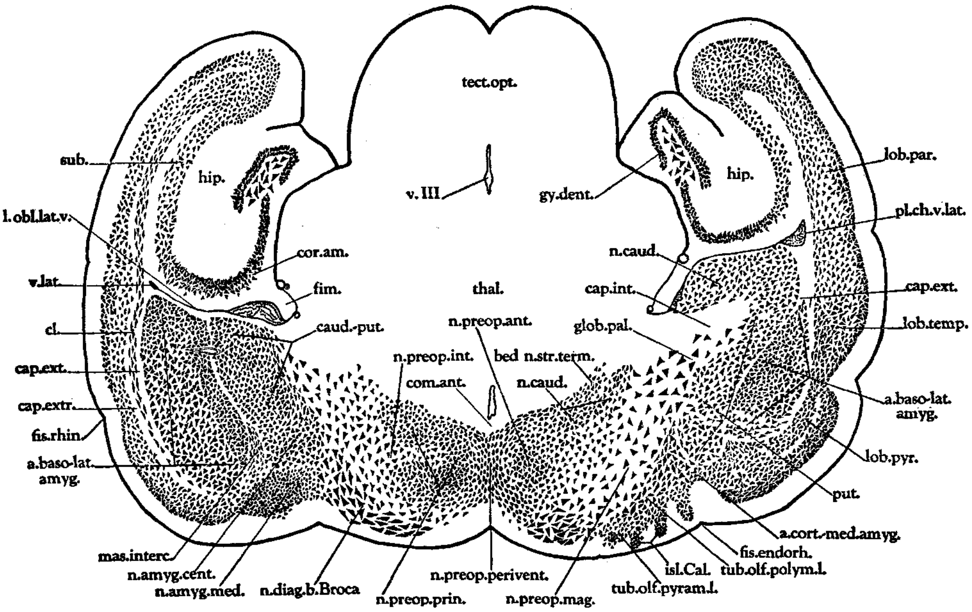

Fig. 8 A cross section of the brain passing through the caudal border of the anterior commissure. Centrally this level passes through the preoptic region, on the right through the middle of the caudate-putamen complex, and, on the left, nearer the caudal border of this complex. Toluidin blue preparation. × 17.5.

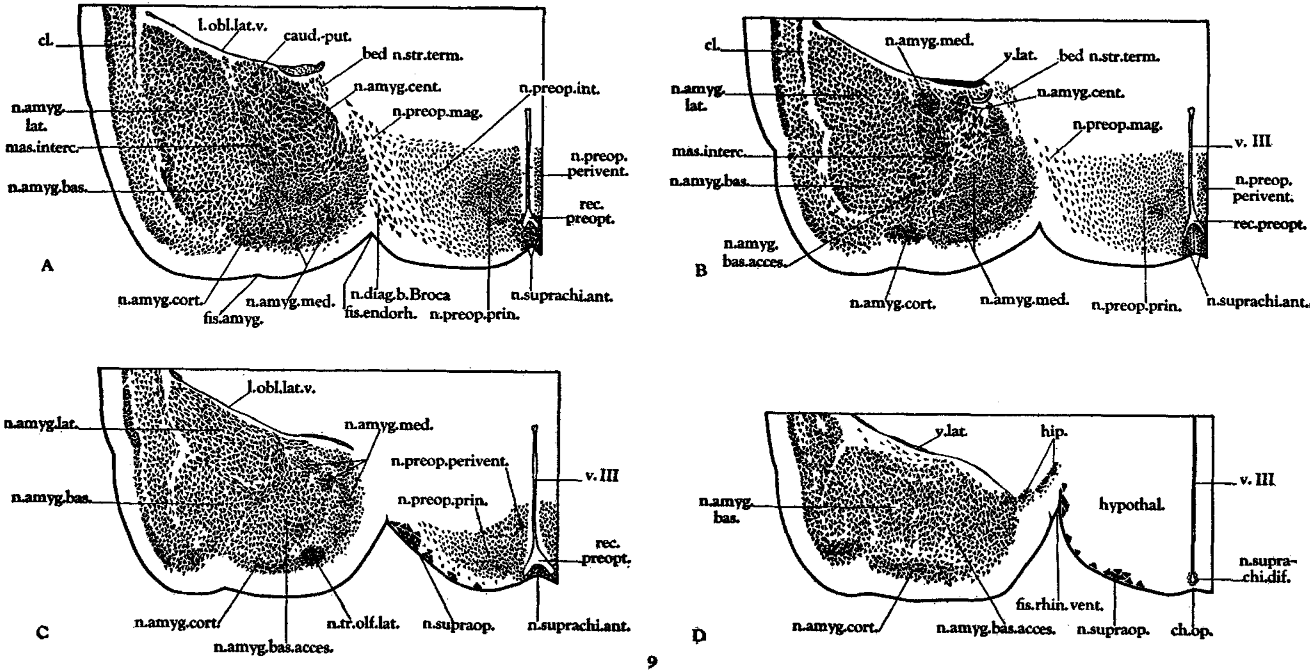

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Fig. 9 A series of small drawings from transversely sectioned material, to show the relations of the caudal portion of the amygdaloid complex and the preoptic area. Toluidin blue preparations. × 17.5. A, a section through the caudal end of the caudate-putamen complex. B, a section through the frontal end of the accessory basal amygdaloid nucleus. C, a section through the nucleus of the lateral olfactory tract. D, a section through the most caudal portion of the amygdaloid complex.

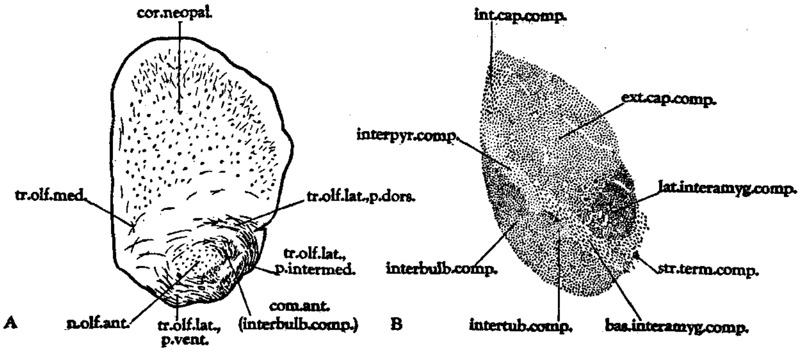

Fig. 10 A, a transverse section through the olfactory bulb and the overlying neopallial cortex of the bat, to show the olfactory tracts. Pyridine silver preparation. × 15. B, a drawing of a sagittal section through the anterior commissure of the bat to show its various components. The orientation of the commissure is the same as in figure 16, C and D. Pyridine silver preparation. × 80.

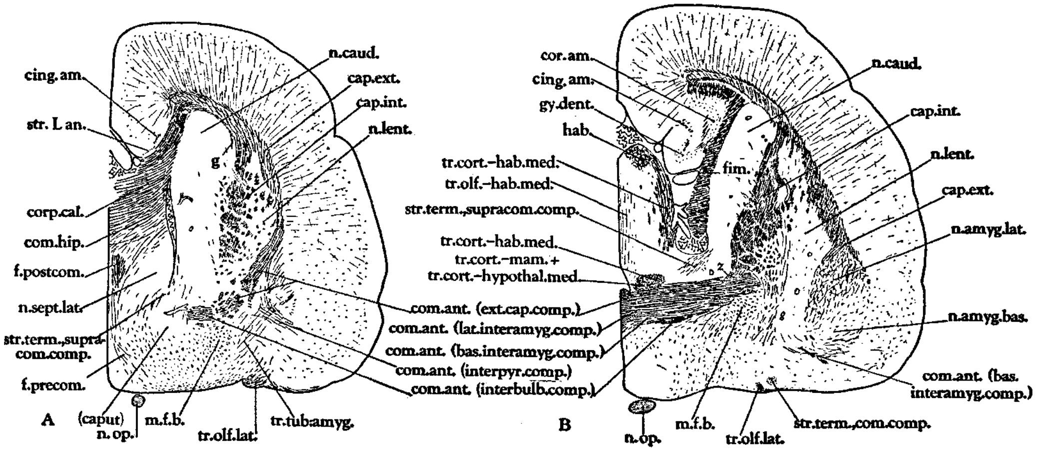

Fig. 11 Transverse sections of the telencephalon of the free-tailed bat to show fibers entering the internal capsule (g, in 11A) on its medial side, where, farther caudalward, fibers enter the anterior commissure (z, in 11B). Pyridine silver preparations. × 15. A, a section passing through the dorsal commissural systems and just frontal to the anterior commissure. B, a section passing just caudal to the middle of the anterior commissure.

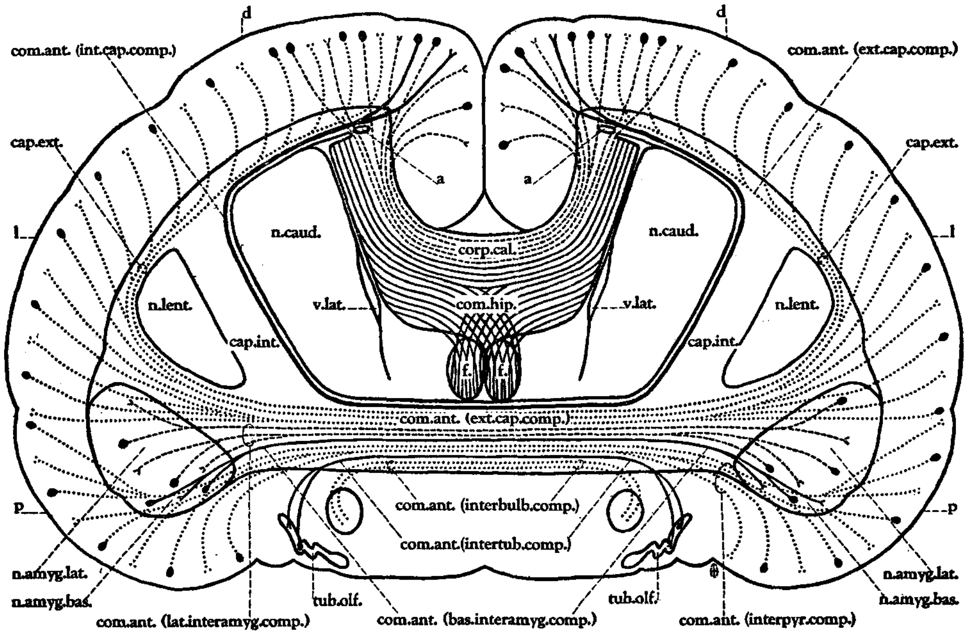

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Fig. 12 A diagram of a transverse section through the telencephalon of the free-tailed bat to illustrate the commissures of the hemispheres.

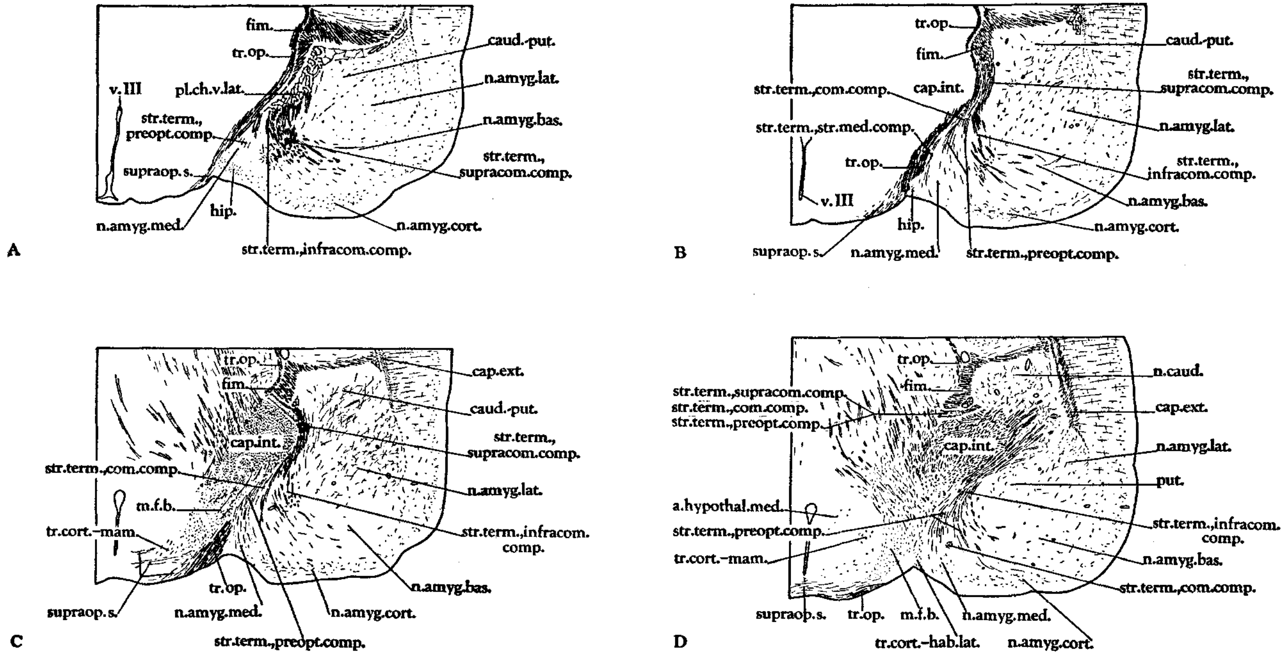

Fig. 13 A series of transverse sections through the forebrain of the free-tailed bat to show the relations of the stria terminalis to the amygdaloid complex. These are arranged in order, with the drawing of the most caudal section first, so as to follow the plan of description in the text: A, a section through the caudal end of the cortico-medial amygdaloid complex; B, a section 0.09 mm. frontal to A; C, a section 0.08 mm. frontal to B; D, a section 0.17 mm. frontal to C. The following figure (fig. 14) illustrates the relations of the stria terminalis to the hypothalamic and preoptic regions. Pyridine silver preparations. × 15.

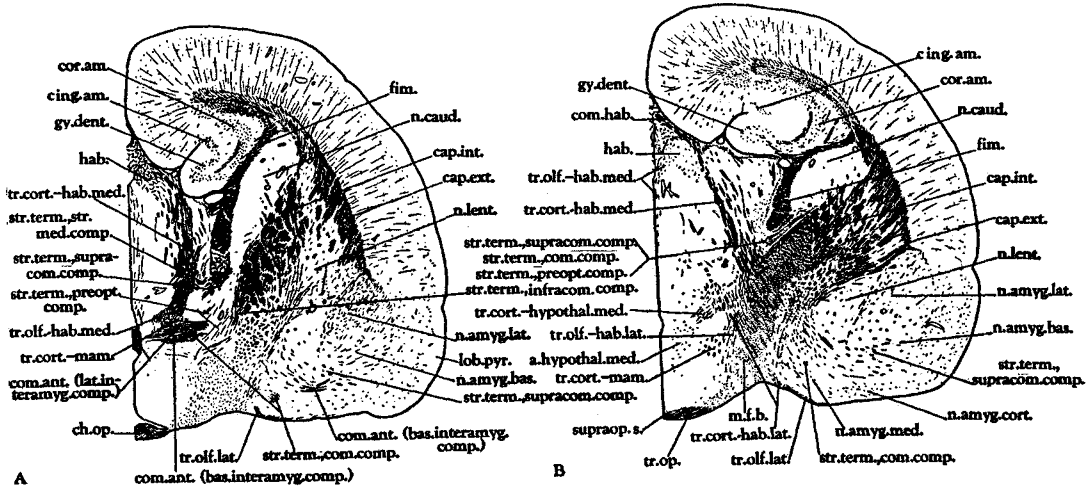

Fig. 14 Transverse sections through the forebrain of the free-tailed bat to show the relations of the stria medullaris, the stria terminalis, and the fornix system. Pyridine silver preparations. × 15. A, a section passing through the most caudal fibers of the anterior commissure and through the optic chiasm. B, a section passing through the frontal end of the habenular commissure and just caudal to the optic chiasm, a distance of 0.25 mm. caudal to A.

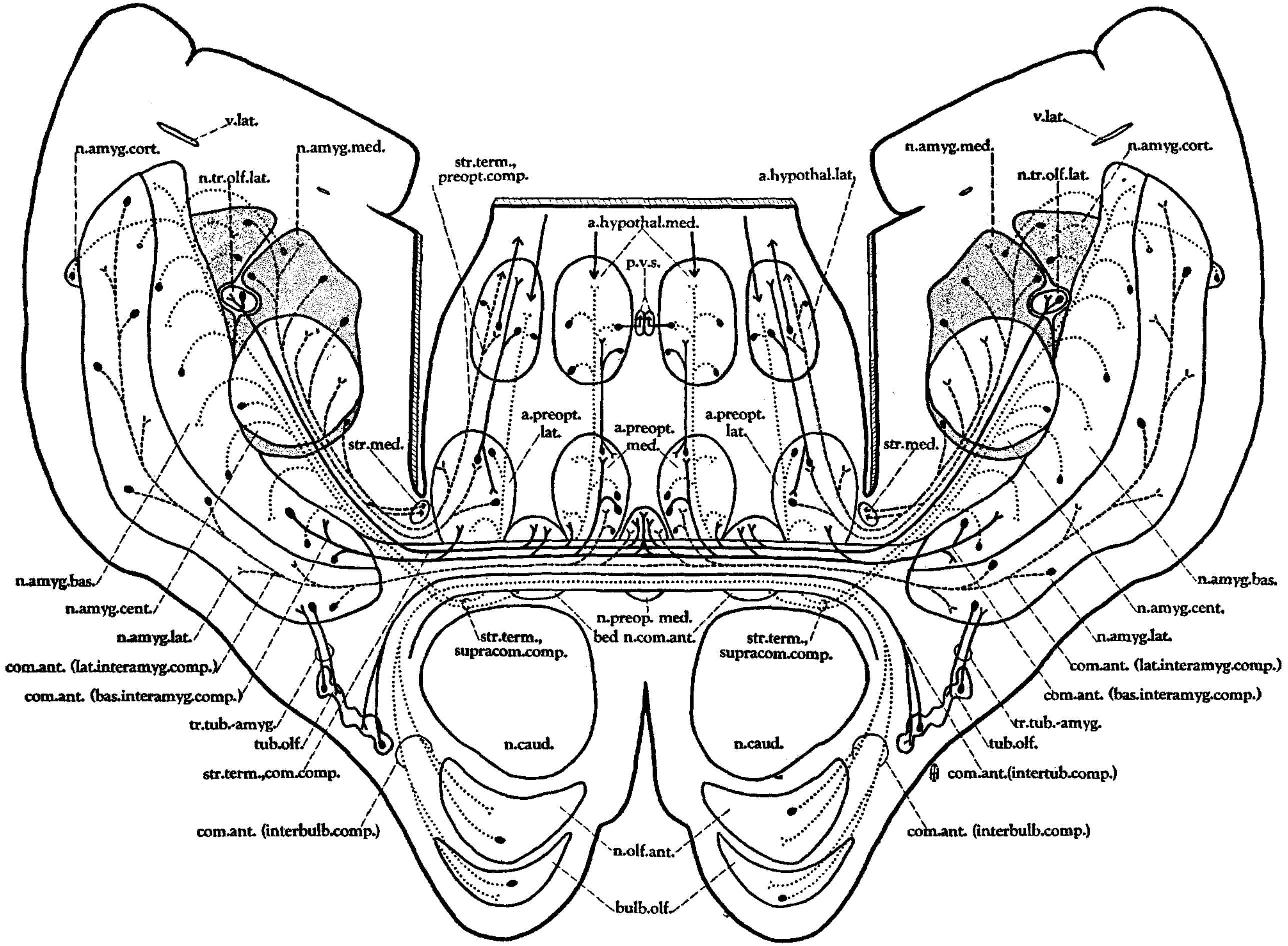

Fig. 15 A diagram of a horizontal section through the telencephalon of the free-tailed bat to show the relative position and the major connections of the amygdaloid complex. From Ariëns Kappers-Huber-Crosby's The Comparative Anatomy of the Nervous System of Vertebrates Including Man. Courtesy of The Macmillan Company.

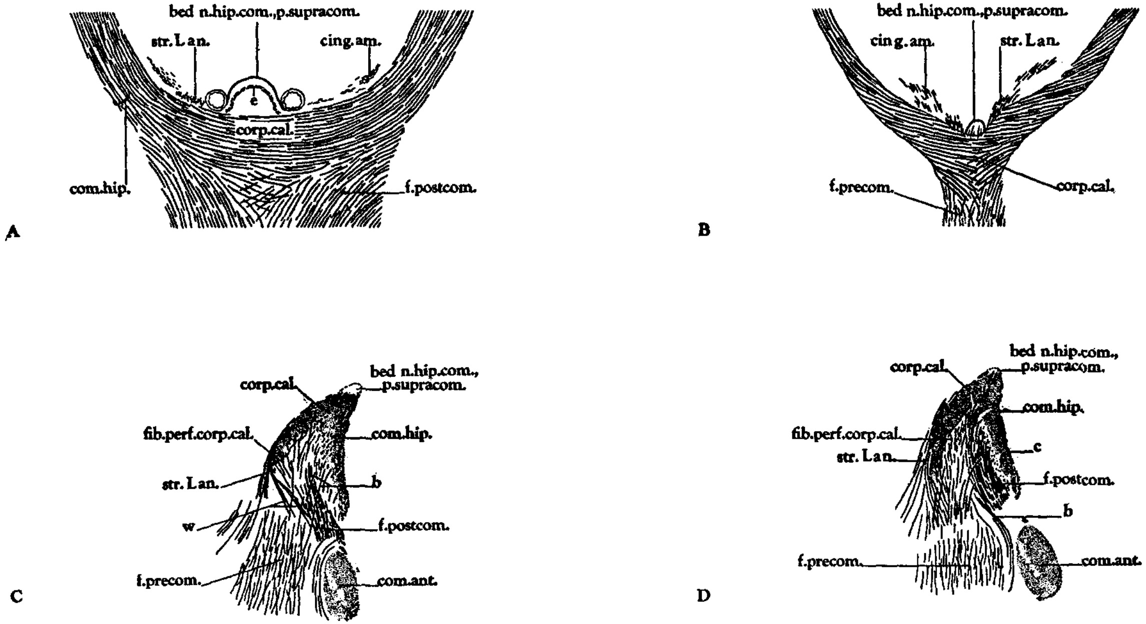

Fig. 16 A group of small drawings to show the fornix system and the relations of its fibers to the commissures of the hemispheres. Pyridine silver preparations. A, a transverse section through the region of junction of the corpus callosum and the hippocampal commissure. × 37.5. B, a transverse section toward the frontal end of the corpus callosum. × 37.5. C, a sagittal section through the commissures of the hemispheres close to the midline. × 17.5. D, a sagittal section through the commissures about 30 μ farther from the midline than the previous drawing. × 17.5. In figure 16, B and D, fibers from the frontal end of the supracommissural portion of the bed nucleus of the hippocampal commissure may be seen to join the stria of Lancisius. In figure 16, C and D, such fibers cross through the region of junction of the two commissural systems, as well as passing caudal to the hippocampal commissure.