

THE NUCLEI AND FIBER PATHS OF THE AVIAN DIENCEPHALON, WITH CONSIDERATION OF TELENCEPHALIC AND CERTAIN MESENCEPH- ALIC CENTERS AND CONNECTIONS

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NINETEEN PLATES (FORTY-ONE FIGURES)

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INTRODUCTION

This contribution constitutes one of a series of studies, dealing with the diencephalon, planned and directed by the authors and carried out in the Laboratory of Comparative Neurology of the Department of Anatomy, University of Michigan. These studies, as projected, include a study of the thalamus of primates, more particularly man, the material for which is in process of preparation. In this series of studies it is our aim to give as complete and accurate an account, as the material permits, of the normal nuclear arrangement and fiber connections in the forms considered, since in our opinions such detailed knowledge is fundamental for at least four types of investigations.

1. The forebrain is limited and modified in its development by the degree and type of development of the diencephalon and tectum. In turn the degree of organization of these latter regions is determined by the differentiation of striatal and cortical centers. Consequently, a knowledge of diencephalon and tectum is a prerequisite for an understanding of the forebrain. The pattern of the nervous system is both an expression and a reflection of the activities of the animal, and the more plastic types of behavior are generally recognized as the resultants of activities of the suprasegmental structures (forebrain and cerebellum) and their concomitants, tectum and thalamus. The finer gradations in behavior have their basis in the less noticeable, but not less important differences in structural pattern. Consequently, the first justification for a more detailed study of the nuclear masses and fiber connections of diencephalon and tectum is that such a study may provide useful morphologic data for a comparison of the behavior of animals of various types.

2. The detailed study of the diencephalic and tectal centers in a series of animals provides the clues for a better understanding of the course of phylogenetic development. A knowledge of this development has much more than academic interest, for it is reasonable to suppose that changes in the nervous system, however they may be brought about, operate

now, as in the past, within the limits of well-defined laws and that an understanding of the course of development is necessary for a knowledge of the operation of these laws.

3. A thorough knowledge of normal anatomic structure is vital in experimental work. At present there is great interest in experimental investigations. This finds expression in work on the nervous system as well as on other structures of the body. Many such experimental observations are of great importance. They have given interest and life to the anatomy of the nervous system. They have explained the anatomic structures in terms of their functional significance and have removed many known anatomical facts from the realm of theoretical to that of practical importance. Too much cannot be said in favor of properly controlled physiologic experimentation as applied to the nervous system. It must be emphasized, however, that a thorough knowledge of normal anatomical structure is an indispensable prerequisite for satisfactory experimental work. Thus, below the sulcus medius in the avian diencephalon, approximately fifteen nuclear groups, distinguishable not only on the basis of cell character, but in terms of specific fiber connections (and hence functional connections), are definable. Between such nuclear groups are conducting pathways, sometimes in synaptic relation, but frequently independent of the nuclei in question. It is reasonable to suppose that selective experimental destruction or stimulation based on accurate knowledge of the location of the nuclear groups and of the paths involved may lead to precise and at least relatively constant results. It is equally obvious that destruction of an area without adequate knowledge of its detailed structure is very apt to involve parts of several nuclear masses and unrelated fiber tracts and to lead to untrustworthy and conflicting results. Moreover, postmortem examinations of the material, while absolutely necessary as control observations, can never replace a knowledge of normal structure and relations. Crucial results follow only precise, clear-cut lesions. Degeneration preparations likewise are inadequate alone, although

extremely useful in conjunction with other evidence, when areas as complicated as those of the diencephalon are involved, since they show only the outgoing pathways, but not the complicated system of incoming impulses which gives the cell group in question its specific character.

4. This series of investigations has, as its ultimate goal, a study of the human thalamus and tectum. Technically, such a study presents many difficulties. The material is not so easily obtained in fresh condition, injection methods are in the main impossible, the sections are large, and necessarily the series are long and represent a great involvement of time and material. Further must be considered the highly complicated character of the areas in human and the great multiplicity of finer nuclear divisions and finer connections which are difficult to follow, but certainly of true functional significance. To these difficulties is added the fact that experimental checking must be made on other animals and its results carried over into human physiology and psychology. Such comparison is fruitful only when, for the experimental animal and for human, the anatomic structure of the nervous system and its physiologic manifestation, behavior, are thoroughly known and when the relations of the two in the phylogenetic scale are clearly understood.

The major reasons for the present study of bird diencephalon and tectum and incidentally of bird forebrain have been given. It may not be beside the point to emphasize that the present study was not undertaken with the idea of contributing to the knowledge of bird brain as such. So far as the present paper makes such contributions, they are incidental. Its purpose is rather to provide an anatomic basis for work on behavior in birds, since such work should enrich our knowledge of the general processes of learning and reasoning and of psychological activities in general; to add some small part of the story of the phylogenetic development of the nervous system; to provide an adequate anatomic basis for experimental work on diencephalon and tectum in a form easily available for experimental purposes; and, above all,

to build another step in the stairway to a more complete and adequate knowledge of these higher centers in man.

MATERIAL AND METHODS

The observations here recorded are based on a study of forty-five series of avian brains, mainly prepared for this investigation. As may be noted from a study of the table listing these series, certain of them were prepared for a study of the nuclear patterns and cytoarchitectures, others more particularly for the determination of fiber connections of both medullated and non-medullated tracts. Observations made by a study of homologous series, prepared by different methods, supplement one another to a gratifying extent, and it has been found very helpful and often essential to have at our disposal homologous series prepared by the same method and cut in cross, sagittal, and frontal planes.

The series prepared for cytoarchitectonic study and determination of nuclear patterns were fixed in a trichloroacetic-mercury-alcohol solution and stained in toluidin-blue solutions after a method described by one of us (Huber, '27). For the chromsilver series the entire brain with the brain stem was stained after the pyridine-silver method, embedded in paraffin, and cut serially in the plane desired; the sections were fixed to slides and mounted in Canada balsam under cover-glasses. The Weigert series available were prepared by Professor McCotter and placed at our disposal. A single series to enable study of cell form was prepared after the chrom-mercury method of Cox, embedded in paraffin, cut serially, fixed to slides, and mounted in Canada balsam without the use of cover-glass.

We desire to express our deep appreciation for the opportunity given one of us (Doctor Crosby) to study avian-brain series in the Central Institute for Brain Research at Amsterdam, Doctor Ariëns Kappers, director, through whose courtesy numerous photomicrographs of sections of avian brains were prepared for us which have been found helpful in this study.

The series of avian brains used in the preparation of this contribution we list as follows :

<i>No.</i>	<i>Plane of section</i>	<i>Thickness of section</i>	<i>Method of preparation and staining</i>
<i>English sparrow (Passer domesticus)</i>			
1 Sparrow, series A	Cross	40 μ	Toluidin blue
2 Sparrow, series B	Cross	40 μ	Toluidin blue
3 Sparrow, series C	Cross	40 μ	Toluidin blue
4 Sparrow, series A	Sagittal	40 μ	Toluidin blue
5 Sparrow, series B	Sagittal	40 μ	Toluidin blue
6 Sparrow, series C	Sagittal	40 μ	Toluidin blue
7 Sparrow, series A	Frontal		Toluidin blue
8 Sparrow, series B	Frontal	40 μ	Toluidin blue
9 Sparrow, series C	Frontal	40 μ	Toluidin blue
10 Sparrow, series A	Frontal		Toluidin blue
11 Sparrow, series A	Cross	15 μ	Chromsilver
12 Sparrow, series B	Cross	15 μ	Chromsilver
13 Sparrow, series C	Cross	15 μ	Chromsilver
14 Sparrow, series D	Cross	15 μ	Chromsilver
15 Sparrow, series A	Sagittal	10 μ	Chromsilver
16 Sparrow, series B	Sagittal	15 μ	Chromsilver
<i>Dove (Columba domestica)</i>			
17 Dove, series A	Cross	40 μ	Toluidin blue
18 Dove, series B	Cross	25 μ	Toluidin blue
19 Dove, series A	Sagittal	40 μ	Toluidin blue
20 Dove, series B	Sagittal	50 μ	Toluidin blue
21 Dove, series C	Sagittal		Toluidin blue
22 Dove, series D	Sagittal		Toluidin blue
23 Dove, series E	Sagittal		Toluidin blue
24 Dove, series A	Frontal	40 μ	Toluidin blue
25 Dove, series B	Frontal	50 μ	Toluidin blue
26 Dove, 10 days old	Cross	20 μ	Toluidin blue
27 Dove, 8 days old	Cross	20 μ	Toluidin blue
28 Dove, 1 day old	Cross	15 μ	Toluidin blue
29 Dove, series A	Cross	20 μ	Chromsilver
30 Dove, series B	Cross	20 μ	Chromsilver
31 Dove	Sagittal	15 μ	Chromsilver
32 Dove, 1 day old	Cross	20 μ	Chromsilver
33 Dove, 1 day old	Cross	20 μ	Chromsilver
34 Dove, 1 day old	Cross	20 μ	Chromsilver
35 Dove	Cross	50 μ	Chrom-mercury (Cox)

No.	Plane of section	Thickness of section	Method of preparation and staining	
<i>Chicken (Gallus domesticus)</i>				
36	Chicken	Cross	25 μ	Toluidin blue
37	Chicken, series A	Sagittal	50 μ	Toluidin blue
38	Chicken, series B	Sagittal	40 μ	Toluidin blue
39	Chicken	Cross	50 μ	Weigert
40	Chicken	Sagittal	50 μ	Weigert
41	Chicken	Frontal	50 μ	Weigert
<i>Duck (Anas domestica)</i>				
42	Duck	Cross	50 μ	Toluidin blue
43	Duck	Frontal	50 μ	Toluidin blue
<i>Parrakeet</i>				
44	Parrakeet	Cross	40 μ	Toluidin blue
45	Parrakeet	Sagittal	40 μ	Toluidin blue

Based on ascertained facts, homologies of avian forebrain and diencephalic structures have been made with those of the reptilian forebrain and diencephalon, wherever such homologies seemed justified. The series of sections of reptilian brains, including those placed at our disposal by Prof. C. Judson Herrick, of the University of Chicago, listed by Huber and Crosby ('26) in their study of the thalamic and tectal structures of the American alligator, have been freely drawn upon in making such homologies.

The drawing for each figure accompanying this contribution was made from a single section. The section was projected on the drawing paper at a magnification of 40 diameters. The outline and necessary details were sketched in pencil, and during the preparation of the final drawing, the respective section was studied under higher magnification and, where essential, further details added.

The figures giving the form of the several avian brains studied were made by photographing all of the brains sketched at exactly natural size on a single negative the size of a lantern slide. A lantern-slide picture was then made and used to project on drawing-paper at a definite magnification the photograph in question, from which projection the outline of the drawing was made. The relative size and the relative projection of the respective structures, therefore, are not subject to error.

Two points with regard to the labeling of the figures must be emphasized. In the first place, because of the relative complexity of the field, it has been impossible to label all the structures recognizable in a given plane. Frequently, a particular tract or nucleus is designated only on alternate drawings. In the second place, it has been necessary for general orientation to label certain tracts on the drawings of all material and a considerable number of nuclear masses on those figures which primarily illustrate the fiber paths. Structures thus labeled for orientation are, as a rule, not referred to in the plate and figure numbers to be found in the text. Text references are made to such figures as particularly illustrate the points which it is wished to emphasize. Such a method, in our opinion, makes for clearness and economy of time.

REVIEW OF AVIAN-BRAIN LITERATURE

To give a detailed account of the literature concerned with bird thalamus, midbrain, and tectum is entirely beyond the limits of the present paper. Within our knowledge there exist approximately a hundred contributions which are concerned wholly or in part with some phase of the subject, and there are undoubtedly others which have escaped our attention. As complete references as possible will be made to earlier papers under the description of each nuclear mass or fiber tract. The following account treats only of the literature on avian forms and is intended as a brief résumé of the lines of advancement of our knowledge of the form and structure of the bird brain and the methods used in studying it. References to the literature on the brains of other forms will be found in the descriptions of the various regions and in the discussion.

Many figures and more or less detailed accounts of the gross relations in the avian brain are to be found in the literature. The earlier papers, some of which are not readily available, are concerned almost exclusively with macroscopic descriptions. Brief mention of these papers is to be found

in the work of Bumm ('83), Edinger, Wallenberg, and Holmes ('03), and Schroeder ('11). Later papers frequently contain references to the gross structure, although they usually combine macroscopic with microscopic or experimental work. The following observers, among others, have paid considerable attention to gross relations: Turner ('91), C. J. Herrick ('93), Mrs. Gage ('95), Münzer and Wiener ('98), Kalischer ('01, '05), Edinger, Wallenberg, and Holmes ('03), Hunter ('23), and Craigie ('28). Lopicque and Girard ('05, '06) computed the weight of the brain and of various portions of it in large and small birds. Among other interesting facts they appear to have found that the percentage weight of the hemispheres increases and that of the optic lobe decreases with an increase in brain weight.

Stieda ('69) was the first observer who had at his disposal anything approaching adequate microscopic material of avian brains. His observations were based mainly on the study of a series of chicken brains, but certain goose, sparrow, and duck series were available. At present his work is chiefly of historic interest. The most important of the early accounts is that of Bumm ('83). This observer, to whom further reference will be made, identified some of the major fiber paths of the forebrain, such as the lateral forebrain bundle (Hirnschenkel) and the septo-mesencephalic tract (Scheidewandbündel) to the midbrain. Considering the technical methods at his disposal, the paper is exceedingly well done.

The optic lobes of the bird early aroused much interest, probably by reason of their great relative size, their ventrolateral position, and the size of the optic tracts and eyes. Bellonci ('88) studied the development of these lobes and their adult structure in chicken. He identified seven layers in them. The same region was studied in sparrow material by Ramón y Cajal ('91), who increased the number of layers to fifteen. van Gehuchten ('92) subdivided the region into three layers, while von Kölliker ('96), on the basis of Weigert material, described six layers. Ris ('99) gave an extremely

detailed account of the cell structure of the optic lobes based on Golgi material, in which account he made use of the subdivisions as given by von Kölliker.

In addition to these observations on optic tectum and to quite extensive experimental observations which will be noted later, a goodly number of papers dealing in whole or in part with the normal anatomy of the bird forebrain, thalamus, or tectum made their appearance in the twenty years following Bumm's publication. Among these there may be mentioned the work of Turner ('91), which contains an account of certain of the more conspicuous forebrain tracts, and that of Edinger ('95), dealing with the question of the presence in birds of an optic cortical center. In 1896, Jelgersma's account of a connection between the basal striatal areas and the oculomotor centers made its appearance. Somewhat later, Boyce and Warrington ('98) published a paper on experimental lesions in the bird brain, but preceded the report of their experimental work by an account of some of the more prominent paths of the normal brain. In 1899, the Edinger and Wallenberg paper on thalamus appeared, from which later studies of bird thalamus take their departure. Schulgin's paper ('85), on the phylogeny of the bird's brain, and that of Westphal ('98), on acoustic, midbrain, and diencephalic centers, made their appearance during this period. All of these papers contributed somewhat to the slowly accumulating knowledge regarding the avian central nervous system and kept alive an interest in avian morphology and physiology which culminated in the work of Edinger, Wallenberg, and Holmes ('03) on the forebrain of the bird—a contribution which we are pleased to recognize as an excellent research and which constitutes one of the very best descriptions of the avian brain. It is one of the classic papers of the literature of comparative neurology. It is based on a rich collection of material and its anatomic findings are checked by the use of embryological material and by experimental work. All later studies of avian forebrain are of necessity based upon it. Frequent mention of this paper will be found

in the text of the present article. A brief résumé of the more important features may be obtained from the seventh edition of the Edinger text ('08).

During this period various observers, among whom we may mention Holmes ('03), Ramón y Cajal ('08), and Wallenberg ('00), became interested in the avian cochlear centers and in their secondary connections with the midbrain centers. Apparently, general agreement exists as to the presence of such a secondary ascending tract, although there is difference of opinion as to its nuclei of origin.

As was stated above, the Edinger, Wallenberg, and Holmes paper ('03) contains a brief survey of the embryological development of the avian brain, and particularly of the forebrain. This phase of the work was carried on by Mesdag, who gave, in 1909, a description of the development of the nuclear masses of the brain of the hen, including an account of the development of the striatal and thalamic centers. Reference must be made in this connection to the paper of Schroeder ('11), who studied the tracts in the brains of chick embryos taken at one-day intervals from the first appearance of medullation to the twentieth day. His material included brains of nine-, ten-, twenty-, fifty-two-day, and adult chickens. The paper is concerned with the various fiber paths of the forebrain; it also contains a discussion of the development of the myelin sheaths. Only indirectly concerned with the problems of the present paper is the well-known contribution of Bok ('15) on the development of the avian cranial nerves and their central paths. This paper includes a presentation of the writer's theory of stimulogenous fibrillation. Rose ('14) studied in great detail the cytoarchitecture of the forebrain nuclear masses, including their development, in a wide range of material. He compared these various centers with respect to their form and size, their degree of differentiation, their persistence or disappearance, and the number of layers of which they were composed. He emphasized that for all of the orders considered there is a common ground-plan. He dis-

cussed the criteria of histological differentiation and was particularly interested in those determining cortex. Palmgren ('21), in his paper on the development and morphology of the cerebellum and of the midbrain, dealt with avian as well as other vertebrate brains. Three years later, there appeared a paper by Rendahl ('24) along somewhat similar lines, dealing with the diencephalon of chicken, in which he discussed the segmental pattern underlying thalamus development, and with this pattern as a basis makes certain divisions of the diencephalon—the synencephalon and the parencephalon posterior and anterior—which will be referred to later (p. 69). This paper gives an excellent account of the nuclear pattern of the avian diencephalon. It also includes a comparison of the bird diencephalon with that of reptiles and mammals.

A résumé of the results of the various studies on bird brain up to the time of its publication is to be found in Ariëns Kappers' "Vergleichende Anatomie des Nervensystems" ('20-'21). Shortly after the appearance of this work, its author published an account ('22) of the development of the striatal complex in birds and compared its various nuclear masses with homologous cell groups in mammals and man. This paper presents the terminology of this writer, which is now receiving general acceptance and is gradually replacing the older nomenclature. The terminology used by us in this paper is based thereon and is discussed under the description of the various nuclear masses.

Hunter's study of the brain of the New Zealand kiwi (*Apteryx australis*), published in 1923, is of particular interest because of the small size of the optic system and the relatively large size of the olfactory system in this bird. The parts of the striatum are named according to the Ariëns Kappers nomenclature. The significance of the blood supply to the striatum—a topic already discussed by Elliot Smith ('19) for reptiles—receives considerable attention.

With the increase in knowledge of the finer anatomy of the forebrain and thalamus of fishes, reptiles, birds, and mammals the interest in attempting to homologize the avian

centers with those in other forms has increased and has found expression particularly in the contributions of Ingvar ('23), Herman ('25), Craigie and Brickner ('27), and Ariëns Kappers ('22 and '28). Ingvar's paper contains an account of certain of the more prominent nuclear masses and fiber paths in the avian diencephalon. However, its greatest interest lies in the writer's discussion of the factors determining the specific nuclear configuration in birds and his attempts at homologizing certain avian and mammalian cell masses. It is an interesting and suggestive contribution. In the publication of Herman ('25) there is presented a comparison of the reptilian striatum with that of birds, mammals, and man. Craigie and Brickner ('27) have attempted to homologize the nuclei and tracts of the teleostean and avian midbrain and thalamus, and the details on which these homologies are based are to be found in two separate papers, one by Craigie ('28) on the brain of the humming bird and the other by Brickner ('29) on that of a teleost. Craigie's paper has been of particular interest to us and is referred to frequently in the following account. The last discussion of the bird forebrain is to be found in the published lectures of Ariëns Kappers ('28) given at Stockholm. It is noteworthy that, since the appearance of the paper by Doctor Ariëns Kappers on the bird striatum in 1922, workers at the Institute for Brain Research at Amsterdam have made a very considerable contribution to our knowledge of the bird brain—a contribution which has been made possible not only by the rich collection of material in the laboratory, but also by the knowledge and inspiration of its director.

Thus far we have been considering the literature concerned primarily with the development and normal structure of the avian forebrain, thalamus, and midbrain. It is not our purpose to enter here into a detailed account of the experimental work, yet no report on the literature could be considered adequate which does not contain some reference to the fundamental contributions in this field. Among the early workers must be mentioned Singer ('81), Singer and Münzer ('90),

Sandmeyer ('91), and Boyce and Warrington ('98), all of whom were interested in the possibility of direct connections between the forebrain and the spinal cord. Sandmeyer ('91) believed that such a connection existed. The other groups of observers denied the presence of such a direct fiber tract, since spinal-cord sections, taken a reasonable time after extirpation of the hemispheres, were normal.

Another group of workers, among whom were Bellonci ('88), Perlia ('89), Singer and Münzer ('90), Edinger ('95), Wallenberg ('98 c), Kalischer ('00, '01, '05), and Kosaka and Hiraiwa ('15), became interested in the relations and terminations of the optic fibers and the possible presence of optic centers in the forebrain. In 1888, Bellonci gave an excellent account of the optic tracts and associated fiber bundles in various vertebrates. In 1889, Perlia, working on cuckoo, chicken, and sparrow, by operative procedure, demonstrated the complete decussation of the optic nerves in birds and the presence of a medial and a lateral optic tract on either side of the diencephalon. He related the latter with the optic lobes, the former he traced dorsalward and caudalward to its termination in a nuclear mass which he termed the nucleus of the medial optic root. In his paper Perlia referred to a statement by von Gudden to the effect that two types of fibers are present in the optic nerve, fine centripetal ones concerned with the passage of the light impulses from the retina to the brain and coarse centrifugal ones involved in pupillary reactions. Perlia regarded the medial optic bundle as probably representative of the second type of fibers. Perlia also stated that, in 1882, Stilling carried optic fibers to the frenulum veli medullaris, but was unable to identify their nucleus of termination. The nucleus associated with the medial optic root has been described by many workers, among others by Bellonci ('88), Singer and Münzer ('90), and Jelgersma ('96), as ganglion opticum basale, by Wallenberg ('98), who followed Edinger in terming it ganglion isthmi, and recently by Craigie ('28), who considered it one portion of the ganglion-isthmi complex. Jelgersma ('96), who found

its cells degenerated after enucleation of the bulb, regarded the optic fibers leading from it as centrifugal in character. Wallenberg gave further proof of its centrifugal course by proving that direct injury to the nucleus was followed by degeneration of the tract.

To Wallenberg we owe much of our experimental evidence for the direction of conduction, position, and function of various tracts of the avian brain. In addition to the paper above mentioned on the median optic bundle, Wallenberg has given accounts of the central termination and secondary paths of the acoustic nerve ('98 a, '00), of the quinto-frontal path from the chief sensory nucleus of the trigeminal to the basal forebrain region ('98 b, '03), of the bulbo-thalamic tract (possibly the medial lemniscus) from the posterior funicular nuclei to the central part of the thalamus, including nucleus rotundus and the tuber cinereum, with a crossed component in the commissura transversa ('04), and of the secondary connections of the trigeminal centers with the ganglion lateralis mesencephali ('04). In 1906, he gave an extremely interesting account of the various components of the septo-mesencephalic tract. As collaborator with Edinger ('99 and '03), Wallenberg carried out the experimental side of the work and added greatly to the value of their contributions. The above brief résumé indicates only superficially the manner in which this notable experimental neurologist has contributed to our knowledge of the avian brain.

Kosaka and Hiraiwa ('15) described the optic connections in the dove; particularly noteworthy is their account of the basal optic root. The question of the localization of visual and other functions within the bird forebrain has aroused great interest, and among the many investigators in this field we may mention work of Ferrier ('86), Edinger ('95), Kalischer ('00, '01, '05), and Rogers ('22). Edinger ('95) believed that the occipital pole of the forebrain was an optic center and that its chief association path was the occipito-mesencephalic tract. Kalischer ('00) localized within the hemisphere in dove and duck, by means of electrical stimula-

tion, centers for the movements of the extremities, jaws, and tongue and a center concerned with the closing of the eyes. He considered the posterior pole a visual region. By extirpation methods ('00) he established similar centers in parrots. In 1905, Kalischer published a brief description of the normal anatomy of the forebrain of parrot, followed by an account of physiological experimentation involving extirpation and electrical stimulation. He believed himself able to localize a number of functions in the forebrain of the parrot, including a speech center ('05, p. 67). At the conclusion of the paper there is to be found a discussion of the functions of the various parts of the forebrain. However, not all observers have been able to obtain such definitely localized centers in the avian forebrain. Thus Boyce and Warrington ('98) found that injury to any portion of the hemisphere produced a deficiency in sight, although the defects were most marked after removal of the entire hemisphere or removal of its occipital portion. The region on the lateral surface of the hemisphere appeared to be related to deglutition, which act might be accompanied by pecking and rotation of the head and neck. Stimulation of the brain surface did not produce movement, and removal of one hemisphere caused no observable motor defects. After removal of the hemisphere, the birds were found to be inert, sat with the eyes closed and with feathers ruffled, and manifested great lack of interest. Later, such birds became restless, were able to avoid obstacles and to maintain their equilibrium. It is of interest to note that these investigators observed that injury of the optic vesicle produced motor disturbance and weakness on the side opposite to the lesion, so that the bird thus operated upon was unable to stand or to lie on its back.

Rogers has carried on a series of experimental observations on bird brains, using various physiologic methods. In the space available we can do little more than indicate the trend of his results. Removal of the cerebral hemispheres (Rogers, '19) without involvement of the thalamus gives the classic picture of a decerebrated bird, the animal remaining at rest

and showing the fluffed feathers. However, when the crop becomes empty, the animal begins to move about, to stretch and preen, and to react to slight stimulations on the nares. When sufficient food and water are obtained, the animal returns to the quiescent state. Normal temperature, perfect equilibrium, and satisfactory functioning of the digestive system are characteristic of such animals, and apparently their normal length of life has not been curtailed. Decerebrated birds give only avoiding reactions toward other birds. Removal of the hemispheres causes a permanent though slight fall of arterial blood pressure (Rogers, '20, '21 a) and leads to the erection of the feathers, though this condition may be modified. Electrical stimulation of the cortex has little effect on the smooth muscle of the feathers, but stimulation of the basal hemisphere areas produces depression of the feathers, indicating a functional tone relation between the pinnamotor nerves and the basal regions of the hemispheres (Rogers, '22). Removal of the entire surface of the fore-brain to the depth of about $\frac{1}{3}$ mm. does not prevent mating on the part of the female (Rogers, '19). The entire courting cycle is gone through with, but the female does not incubate the eggs. Removal of the entire supraventricular cortex and a portion of the medial cortex, but with the anterior one-third uninjured, is followed by the normal courting cycle and mating of the female. She will incubate the eggs, but for the most part fails to feed the young.

Destruction of the thalamus as well as the hemispheres produces much more profound results. The animal is quiet, is not aroused by starving, loses weight rapidly, and is unable to maintain normal body temperature. A great loss of body water and diuresis (Rogers, '24 a and b) follow complete thalamic destruction and the arterial blood pressure falls lower than when the injury is limited to the hemispheres. Pigeons in which the thalamus has been destroyed do not show disturbance of muscular activity, rigidity, or incoordination if the midbrain remains intact. Birds thus injured have their feathers flattened against the body. They cannot be

kept alive for any great length of time. Particular emphasis has been laid on the loss of the ability to maintain body temperature after injury to the diencephalic region, particularly the hypothalamic portion (Rogers, '21 b and '23). Rogers ('19) has shown that, when normal body temperature is maintained by artificial means, the bird manifests spontaneous movements and responds to external stimuli much as does a decerebrated bird with the thalamus intact, while a dose of pilocarpine administered to a decerebrated bird with the thalamus intact causes a fall in temperature associated with flattened feathers. All of these results suggest, as does experimental work on mammals, that the regions in the central part of the diencephalon, and particularly the hypothalamic regions, exert some directive influence over certain lower centers which form the preganglionic neurones of the sympathetic nervous system.

GROSS STRUCTURE

With all the excellent descriptions of the gross structure of the avian brain at present available in the literature (Bumm, '83; Turner, '91; C. J. Herrick, '93; Münzer and Wiener, '98; Edinger, Wallenberg, and Holmes, '03; Edinger, '08; Ariëns Kappers, '21; Hunter, '23; Craigie, '28, and others), a detailed account of such relationships is unnecessary. However, there are certain features which deserve brief mention by reason of their fundamental relation to our problems.

Observers in general have called attention to the relatively great reduction of the avian olfactory centers as compared with those of either reptiles or mammals. However, the amount of this reduction varies greatly in different birds. Edinger, Wallenberg, and Holmes ('03) called attention to the fact that the olfactory bulbs were relatively larger in goose, hen, and stork than in certain other birds. Hunter ('23) noted that the olfactory bulbs were relatively large in the New Zealand kiwi (*Apteryx australis*) and Craigie ('28) found the olfactory bulbs in the humming bird somewhat

large. Reference to our own material (pl. 1, figs. 1 and 2) indicates that there is wide variance in the size of the olfactory bulb in different birds, those of the chicken, dove, and duck (pl. 1, fig. 1, A, B, D) being relatively large for avian brains, much larger than those of the parrakeet (not illustrated), while the olfactory bulb of the sparrow (pl. 1, fig. 1, C; fig. 2, A and B) is a small, unpaired median structure, closely fused to the basal surface of the hemispheres. The olfactory bulbs of the duck and chicken project forward, while those of the dove are concealed by the frontal pole of the hemispheres. The reduction concerns itself not only with the primary olfactory centers of the bulb, but also with the secondary and tertiary olfactory centers of the hemisphere. Consequently, that portion of the medial wall occupied by the *pars dorsomedialis hippocampi* of reptiles is very thin in most birds and consists chiefly of fiber bundles, while the septal structures (including the parolfactory areas of Johnston, '15) suffer a decrease which appears as a reduction of the ventromedial hemisphere wall. However, as in the case of the olfactory bulbs, the amount of the reduction is variable, being relatively less in those birds in which the number of olfactory fibers is greater and the bulbs are larger. The materials used by both Hunter ('23) and Craigie ('28) emphasize this point, and our own material confirms it.

The forebrain in birds is relatively large, but its massive and compact character is given by the striatal and associated centers, and is not due, for the most part, to cortical development. The region occupied in most higher vertebrates by non-olfactory cortical laminae is very thin in birds, and consequently, in regions overlapped by such areas where a ventricle is present, the brain wall is very thin and the ventricle lies near the surface. However, in the dorsomedial portions of the hemisphere there is a definite thickening of the wall clearly visible in the gross material in most birds and usually termed the 'Sagittalwulst.' This is separated from the more lateral portions of the hemisphere by a depression, the *vallecula* (pl. 1, fig. 1). Both the 'Sagittalwulst'

and the vallecule were recognized by early workers on the avian brain (as, for example, Turner, '91; C. J. Herrick, '93; Edinger, Wallenberg, and Holmes, '03, and many others). The relative size and shape of the forebrain varies greatly in different birds—a fact which Edinger, Wallenberg, and Holmes ('03) emphasized and which receives frequent confirmation from figures published in the literature. Reference to plate 1, figure 1, of the present paper illustrates this point clearly and further explanation is unnecessary.

Large eyes and relatively very large optic nerves are present in most birds. Consequent to this great development of the optic nerves, as Edinger, Wallenberg, and Holmes ('03), Ingvar ('25), and others have pointed out, there results a downward growth of the optic tectal centers from their primitive position on the dorsal midbrain wall to a lateral and, in some birds, to practically a ventrolateral position (pl. 1, figs. 1 and 2). This shift in position, which varies in degree with different orders, is evident macroscopically, but one of its most important results, the accompanying changes in diencephalic nuclei and tecto-thalamic (and thalamo-tectal) connections, needs microscopic material for its demonstration. Contributory evidence that the migration is due to effect of the optic nerves is to be found in Hunter's work on the kiwi ('25). In this bird the optic nerves and optic chiasma are small, as are also the thalamic and midbrain centers. From his figures it would appear that the tectal centers are situated much farther dorsalward than in the brains at our disposal; intermediate in position between that occupied by them in a typical reptile or typical bird. In most birds the tectal regions, like the forebrain, are proportionately larger than in reptiles.

The extent of the lateral ventricle varies greatly in different birds. Craigie emphasized the fact that it extends lateralward in the humming bird in a manner suggestive of the relations in reptiles. It presents quite marked lateral extension in many of the bird brains at our disposal (chicken, dove, and sparrow); in the parrakeet in particular it is confined largely to the medial wall of the hemispheres.

MICROSCOPIC MATERIAL

A. Nuclear masses of the avian forebrain

OLFACTORY BULBS. In the gross material (pl. 1, fig. 1, C; fig. 2, A and B) and in the microscopic sections (pl. 2, fig. 3, E) the olfactory bulb of the sparrow appears as a small unpaired, cellular mass, which lies in intimate relation with the ventral brain surface, although separated from it by a sulcus for some little distance anteriorly. The olfactory fila not only enter it from the end and ventral side, but also swing up to the dorsal surface, passing between the hemisphere proper and the bulb. The lateral ventricles project down toward the mass on either side, suggestive of the arrangement for dual olfactory ventricles found in most vertebrates. However, in our sparrow material the ventricles do not appear to enter the bulb. This agrees with the statement of Turner ('91) that the lateral ventricles terminate in the crus region in those avian forms in which only a single bulb is found. Mitral and granule cells are present and a glomerular zone is found. The number of mitral cells, however, is not large, and the cells themselves, while easily recognizable from the granular cells, because of their greater size, do not form a distinct layer such as occurs in most vertebrates and in certain other birds (pl. 2, fig. 3, A, B, C), but are situated at the lower border of the granular layer and somewhat intermingled with its lowermost cells (pl. 2, fig. 3, E). Scattered cells external to the mitral cells represent the outer granular layer of the alligator.

In the parrakeet the (pl. 2, fig. 3, D) olfactory bulbs are small, paired structures on the ventromedial part of the forebrain toward its cephalic end. Olfactory terminal fibers and the processes of the mitral cells form a distinct glomerular layer at the outer surface. Among the cell processes are the scattered cells of the outer granular layer. The mitral cells lie along the outer border of the inner granular layer and, as in the sparrow, do not form a distinct layer, although they are distinguishable by reason of their greater size. The

ventricle extends downward toward the edge of the granular layer (pl. 2, fig. 3, D), but does not actually extend out into the bulb.

The olfactory bulbs of dove, chicken, and duck are larger and much better developed than those of parrakeet and sparrow. They are paired and, in general, have the characteristics of the olfactory bulbs of reptiles and mammals. They are very similar to those previously described for alligator, but lack the long olfactory crura characteristic of the bulbs of these reptiles. An olfactory ventricle is present on each side, continuous with the lateral ventricle of the hemisphere. In each olfactory bulb of the duck (pl. 2, fig. 3, A) there is clearly demonstrable a glomerular layer, an outer granular layer, a mitral cell layer, and an inner granular layer, the mitral layer being distinctly separable from the inner granular layer. The number of mitral cells is much greater than in sparrow or parrakeet, the layer being usually several cells thick. The cells of the inner granular layer are arranged in rows—a condition also found in alligator. Conditions essentially similar to those in duck are demonstrable in chicken (pl. 2, fig. 3, B); the differences consist in a slightly greater massing of the mitral cells and in an even more regular arrangement of the cells of the granular layer. In dove (pl. 2, fig. 3, C) the mitral cell layer is distinct from the inner granular layer in most regions, but in certain places there is a slight tendency for the two to fuse. The more superficial cells of the inner granular layer show the characteristic linear arrangement, but the periventricular cells are more scattered. On the whole, the bulb in dove is intermediate in type between that of duck and parrakeet, but with much greater resemblance to that of the former than to that of the latter. The olfactory bulbs in dove are near the anterior end of the hemisphere and extend farther cephalad than those of sparrow. The bulbs in duck and chicken project somewhat in front of the hemisphere, but then lie between the two hemispheres and unite with them at the ventral part of each medial side.

BASAL CENTERS OF THE VENTROMEDIAL FOREBRAIN WALL. The secondary olfactory centers along the medial, basal portions of the avian forebrain do not appear as yet to have received adequate description. In part at least they are included in the mesostriatum of Edinger, Wallenberg, and Holmes ('03). Rose ('14) differentiated along the ventral surface an area praepyramiformis and in the medial wall, between the two ventricles, an area which he termed septum pellucidum. Craigie ('28) identified medial and lateral septal nuclei in the humming bird, which we suppose to be homologous with those described in the present account under the same name, although the form relations are somewhat different in the birds studied by us and direct comparisons are consequently difficult. But while a detailed description for this region appears lacking in birds, there are a number of studies of reptilian forms which are sufficiently related in general type of differentiation to give material aid to an analysis of the areas. Most workers on reptiles have agreed that in the more cephalic portions of this medial basal wall are to be found secondary basal olfactory centers (usually termed nucleus olfactorius anterior—Herrick ('10), Crosby ('17), Hines ('23), and others—or nucleus olfactorius medialis, Johnston ('15)) and a tuberculum olfactorium, while farther caudalward are the medial and lateral septal or parolfactory nuclei, the nucleus of the diagonal band of Broca, and the bed nuclei of the commissures. On the whole, these centers are not as developed in avian as in reptilian forms and in some birds are greatly reduced. The following account is based on sparrow material, with only brief reference to the other bird brains available.

Before beginning the discussion some reference must be made to the nomenclature. As is well known, there has been much discussion as to the correct nomenclature to be used with reference to certain precommissural areas of the basal hemisphere wall. Those using the term septal have as their justification the earlier usage of the term in this connection, and their meaning is perfectly clear when they attach the

definitive term of precommissural. Those who use the term parolfactory are thinking in terms of human and higher mammalian anatomy and would restrict the use of septum to the homologues of the septum pellucidum areas in these forms. Personal preference inclines us to use of the term parolfactory, but the question of nomenclature does not seem to us to be of vital significance in this connection, and because of its general use and to avoid discussion or misinterpretation the term septal has been employed in the labels of the figures, although in the text both names are used.

In sparrow, at the level of the olfactory bulb, along the course of the lateral olfactory tract, there is found an ill-defined nuclear mass consisting of cells scattered along the course of the fiber bundles (pl. 2, fig. 3, E). At about the level of the caudal end of the bulb, this group of cells becomes cortex-like in appearance and extends along the medial portion of the ventral surface of the brain and constitutes the area praepyriiformis of Rose ('14). Internal and external to it are scattered cells which we have grouped with it. This band of cells turns slightly dorsalward at the medial border of the hemisphere, but does not extend upward along the medial surface. Caudalward it is soon replaced by a band of scattered cells and fibers which, likewise, soon disappear. The area praepyriiformis (or lobus olfactorius anterior) of Rose in the sparrow (pl. 2, fig. 4) is very suggestive both in position and general relations at least of part of the tuberculum olfactorium of alligator (Crosby, '17) and of Sphenodon (Hines, '23, and Craigie, '26), but we are not entirely convinced of this homology (p. 32).

In the sparrow, at the anterior end of the hemisphere, the accessory hyperstriatum ('Sagittalwulst') extends to the base of the forebrain on the ventromedial side. At a level approximately through the middle of the olfactory bulb it gradually recedes from the ventral surface, and its place is taken in part by the nucleus olfactorius anterior, which nucleus is, in general, the avian homologue of the reptilian nucleus olfactorius anterior (pl. 2, fig. 4). At the level of

the bulb this nucleus lies near the midline, in relation dorsalward, at about the level of the lower angle of the ventricle, with the forward prolongation of the hippocampal formation. Dorsolaterally, it is at first not clearly definable from the 'Wulst' area, but gradually becomes separated from it by the intervention of the hyperstriatum. At first the nucleus is band-like in form, but soon acquires a roughly planoconvex outline, with the straight portion parallel to the medial surface of the hemispheres. Caudalward, it disappears at about the level where the cortex-like band of the area praepyriiformis passes over into the more scattered cells of its posterior portion.

Behind the praepyriiform area there is a cell thickening around the ventral pole of the ventricle which extends dorsalward for a short distance along the medial and lateral ventricular walls, but is separated from the medial surface by a cell-free zone. This cell thickening extends caudalward as a distinct nucleus group for about 0.25 mm. At its posterior end it then becomes somewhat elongated and is continuous with a band of cells which extends to the ventral side of the brain. This band is to be found in only a few sections and then disappears. The nuclear mass itself gradually goes over into the medial continuation of the paleostriatum, which at this level lies ventral to it and forms the posterior portion of the nucleus accumbens. This complex is homologous with nucleus accumbens of alligator, which in this reptilian form consists of two portions, an anterior part composed of relatively small cells which occupy the lateral and medial side of the lower ventricular wall and which are intermingled with cells of somewhat larger size which represent a direct continuation of the paleostriatal region of the hemispheres around the ventricular wall to the medial surface. The two masses are intimately interrelated in the reptilian forms and in the majority of birds with which we are familiar. In the sparrow the anterior part is particularly well developed and relatively distinctly separable from the posterior part (pl. 3, figs. 5 and 6; pl. 4, fig. 9). Whether the two portions should

be regarded as separate nuclear masses on the basis of mammalian homologies, and, if so, to which of the two portions the classic term nucleus accumbens should be applied, it is impossible to state for the moment.

In the basal hemisphere wall, near the caudal termination of the anterior part of nucleus accumbens, a small nuclear mass makes its appearance near the medial surface of the hemisphere and soon becomes infiltrated with larger cells which extend down at the medial side of the septo-mesencephalic tract (even mingling with its fibers). They swing around the ventromedial border of the hemisphere and constitute the nucleus of the diagonal band of Broca (pl. 3, figs. 6 and 7) as that was identified for reptiles by Johnston ('15), Crosby ('17), Hines ('23), and others.

The anterior end of the septal or parolfactory area, in reptiles divisible into lateral and medial parolfactory or septal nuclei, is difficult to analyze to our satisfaction in the sparrow material. It makes its appearance, at about the same level as the nucleus of the diagonal band of Broca, as scattered cells along the medial ventricular wall (pl. 3, fig. 6). These gradually increase in number and form a relatively well-developed nuclear mass just medial to the ventricular wall. On the medial side a small band of cells appears extending down into it from the overlying hippocampal formation. In its more cephalic part (pl. 4, fig. 9) its ventrolateral portion is not sharply differentiable from the posterior part of nucleus accumbens present at the level. Ventromedialward, it is in relation with the diagonal band of Broca. We are inclined to think that some cells of the medial portions of the septal or parolfactory area are continuous on the medial side of the septo-mesencephalic tract, but cannot confirm this conclusively. In the most posterior portion of the area two nuclear masses are more readily demonstrated (pl. 5, fig. 10). Thus there appears a definite cell group which gradually takes on a circular outline in cross-sections, but with a strand of cells continuing dorsalward near the brain surface which we suppose to be the nucleus parolfactorius or

septalis medialis. This continues caudalward, and at the level of the anterior commissure lies mainly ventral to the lateral parolfactory area and dorsal to the bed nucleus of the so-called pallial commissure and to the bed nucleus of the anterior commissure (pl. 5, fig. 10). Near the posterior end of the anterior commissure the nuclear mass in question becomes greatly reduced and becomes intermingled with the cells of the lateral continuation of the bed nucleus of the pallial commissure, and disappears at about the level of the posterior end of the anterior commissure. This medial septal (parolfactory) nucleus is probably comparable with the nucleus of that name described by Craigie ('28) for the humming bird, although in the sparrow it occupies, in general, a more ventral position. The lateral septal or parolfactory nucleus of the sparrow, at first indistinctly separable, in our material, from the medial nucleus of that area, in sparrow enlarges farther caudalward to the extent sufficient to produce a definite ventricular swelling. As the diencephalic region is approached the nucleus decreases in size and (pls. 5 and 6, figs. 11 and 12) disappears at about the level of the foramen.

In sparrow, as in reptiles, both anterior and pallial commissures, the latter comparable in part at least with the hippocampal commissure of reptiles, have bed nuclei (pl. 5, figs. 10 and 11; pl. 6, fig. 12). The bed nucleus of the pallial commissure is U-shaped with lateral extensions which send a small band of cells dorsalward, just ventral to the medial parolfactory nucleus and a larger band ventral- and caudalward along the medial cortico-habenular component of the stria medullaris (pl. 5, fig. 11). This latter continues caudalward in sparrow into the area ventralis anterior (pl. 5, fig. 11), as does its homologue (the so-called bed nucleus of the hippocampal commissure) in alligators (Huber and Crosby, '26). The cells of the bed nucleus of the commissure are readily distinguishable in both reptiles and birds, by reason of their small size and the intensity with which they have taken the stain. The term bed nucleus of the anterior com-

missure is applied to those cells immediately surrounding it (pl. 5, fig. 10). They are similar to the cells of the preoptic area as in the alligator.

In the parrakeet the region immediately behind the olfactory bulb is characterized, along the ventromedial angle of the hemisphere, by small cells which swing from the region of the angle, dorsomedialward on the one hand and lateralward on the other (pl. 2, fig. 3, D). These are the homologues of the secondary basal olfactory centers at the anterior end of the reptilian hemisphere (nucleus olfactorius anterior, alligator, Herrick, '10; Crosby, '17; probably nucleus olfactorius medialis of turtle, Johnston, '15). Slightly farther caudad, but still considerably in front of the anterior commissure, a narrow band of cortex-like cells replaces in part and, particularly on the median surface, the secondary olfactory center described above. This band-like mass of cells may possibly be the homologue of a part at least of the praepyriiform area described for birds by Rose, but of this there is uncertainty. It falls within the general area occupied by the tuberculum olfactorium in reptiles. In general, the parolfactory or septal area is much smaller in parrakeets than in our other bird material. At the anterior end of the hemisphere the medial ventricular wall is very thin, it is only in more posterior areas (in the plane of our sections, just in front of the level of the anterior commissure) that a slight thickening of the lower part of the ventricular wall can be seen. Gradually this widens out, and medial and lateral septal or parolfactory nuclei can be recognized. The nucleus accumbens is present in parrakeet in relations similar to those in alligator, the two portions being more or less continuous as a single nuclear mass. Bed nuclei of the commissures are present as in sparrow.

In dove the secondary olfactory areas of the hemisphere project out into the crus and extend forward beyond the caudal limit of the mitral cells on both the lateral and the medial sides. The lateral portion (area praepyriiformis) consists of a thick band of deeply staining cells which extends

for only a short distance lateralward. Medialward it becomes continuous with more scattered cells which lie along the ventricle of the crus and posterior part of the bulb. A similar group of cells with less definite arrangement extends along the medial surface of the hemisphere (nucleus olfactorius anterior) and projects out into the crus and bulb on the medial side (pl. 2, fig. 3, C). Cephalad to the ventricle the two bands are continuous. Behind the ventricle the lateral portion of the nucleus swings medialward along the ventral surface of the brain, but soon disappears. The medial portion remains for some time along the medial surface of the ventricle. A second cortex-like band, similar to that described in parakeet, is present also in dove. The septal areas are larger in dove than in sparrow. The nucleus accumbens is a more or less homogeneous nuclear mass, although careful examination reveals that the two constituents are present. Medial and lateral parolfactory or septal nuclei, a nucleus of the diagonal band, and the bed nuclei of the commissure are easily demonstrable. No essential differences from the conditions described for dove have been observed in the chicken and duck material, although there are some minor differences in details. The area praepyramiformis is particularly clear in duck—a condition which, according to Rose ('14), is characteristic of *Natatores*.

The differentiation within the ventromedial quadrant of the avian hemisphere may be briefly summarized as follows. In duck, dove, and sparrow the basal wall of the hemisphere near the region of the olfactory bulb is differentiable into a medial nucleus olfactorius anterior and a ventrolateral area praepyramiformis. In parakeet they are represented by a band of scattered cells. These are secondary olfactory centers and are least well developed in parakeet, better developed in sparrow, and most clearly evident in dove, chicken, and duck, where the olfactory bulbs are larger and the number of secondary olfactory fibers consequently greater. In reptiles the basal wall of the anterior part of the hemisphere is occupied by a cortex-like band of cells (with associated scattered cells)

which has generally been recognized as tuberculum olfactorium. The area in birds from the base of the bulb to the level of the parolfactory or septal nuclei is occupied by the area praepyramiformis and farther caudalward by a faint band of cells. Between the two areas are scattered cells and fibers. Just how much of this area is to be homologized with the reptilian tuberculum olfactorium is uncertain.

In all the birds studied a nucleus accumbens is recognizable. In most birds this is chiefly a continuation of the paleostriatal portion of the hemisphere around the ventral angle of the ventricle, but in many birds, as in alligator, there is a more anterior portion which is intrinsically a part of the nuclear mass, but which appears to be associated particularly with a periventricular fiber band. In sparrow this portion forms the main mass of the nucleus.

Medial and lateral septal or parolfactory nuclei are demonstrable in all birds studied by us, but relatively less clear in parakeet and sparrow than in those having larger olfactory tracts. Typical bed nuclei of the commissures are present and the posterior prolongation of the bed nucleus of the pallial commissure into the anterior portion of the diencephalon has been particularly emphasized for sparrow. The above account indicates that all centers typical of the basal medial wall of the hemisphere of reptiles are present in birds (although in some cases in somewhat reduced form), with the possible exception of the tuberculum olfactorium, and that this latter is probably present in anlage.

BASAL CENTERS OF LATERAL FOREBRAIN WALLS. Many of the earlier observers (Stieda, '69; Bumm, '83; Turner, '91; C. J. Herrick, '93; Edinger and Wallenberg, '99, and others) have contributed facts of importance and of interest to our knowledge of the avian forebrain. However, most of the modern work takes its point of departure from the most excellent account of the avian forebrain given by Edinger, Wallenberg, and Holmes in 1903. These observers divided the lateral wall of the hemisphere into dorsal and ventral portions. To the ventral part belonged the olfactory apparatus, the mesostri-

atum, the basal nucleus, and the lobus parolfactorius of their terminology. The dorsal part contained a pallium—with frontal, parietal, temporal, and occipital portions—and a basal part consisting of hyperstriatum, ektostriatum, and epistriatum. They found the olfactory apparatus of minimal development and were unable to identify an Ammon's formation or a fornix. The lobus parolfactorius and the nucleus basalis were regarded as direct forward prolongations of the mesostriatum. In the midst of the mesostriatum they differentiated a large-celled nuclear mass which they termed nucleus entopeduncularis, and they traced a caudal continuation of this nucleus along the lateral forebrain bundle (*brachium cerebri* of their terminology) to the midbrain region. They stated that the position of the mesostriatum suggested its possible homology with the globus pallidus and that the epistriatum might be the homologue of the amygdaloid nucleus. Both of these homologies are at present receiving rather general acceptance.

In 1905, Kalischer followed some earlier experimental work on the localization of function within the forebrain of various birds by a study of the brain of the parrot. He preceded his account of the experimental work by a brief but clear description of the major features of forebrain architecture in this bird. He introduced a number of new terms. Thus the more ventral part of the hyperstriatal area of Edinger, Wallenberg, and Holmes ('03) (the neostriatum of the present paper) he termed the striatum and subdivided it into frontal and parietal portions. For the upper portion of the hyperstriatum of earlier workers he retained the name of hyperstriatum. Here likewise he spoke of frontal and parietal portions. However, these secondary subdivisions were dependent upon the position of the areas with reference to the skull, rather than expressions of different cytological structure. An 'Unterwulst' and a 'Wulst' region, a pallium and an ektostriatum were recognized, together with various other centers and certain fiber bundles. The paper has certain excellent illustrations.

In 1914, Rose undertook a cytological study of the nuclear centers of the avian forebrain. He used letters to designate the various areas. His contribution, which is both interesting and instructive, consisted in the main of further subdivisions of the main nuclear masses described by Edinger, Wallenberg, and Holmes ('03). He was able to differentiate nucleus basalis (field B) from the rest of the mesostriatum and questioned the presence of a lobus parolfactorius in the sense of the earlier workers. The secondary subdivisions which Rose obtained within the basal regions of the lateral wall have interested us particularly and have led, in part, to our present summary of the forebrain masses, since we believe that such differentiation must indicate functionally different areas, with specific fiber connections. The terminology of Rose is referred to under the descriptions of the various nuclear masses of the dorsal and lateral wall. The contribution of Rose may, in many ways, be regarded as representing the most careful study of the nuclear configuration of the avian striatal complex that has ever been made.

Within the last twenty years there have been made many studies on the avian forebrain in various forms, and, as an inevitable result, there has developed a cumbersome and confusing terminology. In an attempt to bring order out of this confusion, various terminologies have been suggested and of these, that given by Ariëns Kappers appears at present to be most generally accepted, at least for reptilian and avian forms. An account of this terminology as applied to reptilian, avian, and mammalian forebrains is to be found in the 1922 and 1928 contributions of this author. In the former paper he divided the striatal complex into a paleostriatum, a hyperstriatum inferius and superius, and an archistriatum. The paleostriatum consisted of two divisions, a paleostriatum primitivum and a paleostriatum augmentatum, which is the homologue of the mesostriatum of earlier writers. The archistriatum is the nucleus amygdalae. Later ('28), Ariëns Kappers changed the avian name, hyperstriatum inferius, to the mammalian term neostriatum. The region dorsal to it he

termed simply the hyperstriatum. He regarded the neostriatum as homologous with caudate and putamen, the paleostriatum as homologous with globus pallidus and with certain vestiges of gray sometimes separate from and sometimes associated with the mammalian caudate. In the year 1922, Ariëns Kappers suggested that hyperstriatum superius might be represented in the mammalian claustrum, but in the 1928 account he stated definitely that, although the two structures were similar in position, he did not regard them as homologous.

Hunter ('23) gave an interesting account of the development of the various parts of the forebrain in kiwi. He and Herman ('25) used the nomenclature of Ariëns Kappers ('22). Within the year, Craigie ('28) also used this terminology in his account of the brain of the humming bird. However, curiously enough, a misunderstanding as to the application of the term hyperstriatum (or hyperstriatum superius) appears to have arisen. The following quotations may serve to illustrate the differences in opinion. The first is from Craigie's account of the humming-bird brain ('28, p. 385):

Herman considers the dorsal part of the neostriatum of *Varanus*, which he believes to receive no thalamo-striatal fibers, as the probable homologue of the hyperstriatum superius of Kappers ('22). Doctor Kappers himself, however, informs the writer that his hyperstriatum superius is the Unterwulstregion of Schroeder (area B of Rose), which is undeveloped in the humming bird and in *Varanus*. His neostriatum includes both the parts described by Herman in *Varanus*, which correspond with those in birds as outlined above. Hunter ('23) seems to adopt the same view as Herman. The writer is anxious to avoid multiplying synonyms, but acts here in accordance with the personal statement of Doctor Kappers. It must be noted that the lamina medullaris hyperstriati of Kappers is not the same as the lamina medullaris hyperstriatica of Schroeder, but is the latter's Unterwulstlamella.

In direct contradistinction to this statement are the following quotations from the 1922 paper of Ariëns Kappers. In the text, page 139, is the following statement: "These divisions I shall call hyperstriatum superius¹), and hyperstriatum inferius²)." The footnotes read in part as follows:

1) This was called by Schroeder pars fronto-dorsalis hyperstriati. It consists of the areae A, C, and D, of Rose's. . . .

2) This corresponds with the areae G¹, G², G³ of Rose's and with the striatum parichale (parietale) of Kalischer. . . .

Evidently, there is misunderstanding here as to the use of the terms hyperstriatum and neostriatum. In our opinion, the areas indicated in the figures of both the 1922 and 1928 papers bear out the interpretation that the term hyperstriatum was applied to the fields A, C, and D of Rose. Whether it was intended to include B it is impossible to determine from the figures.

The use of different names for the same forebrain centers and, what is even more distressing, the use of the same name for different centers have led to much misunderstanding. Thus the term hyperstriatum may include fields G, D, C, and possibly A, of Rose (Edinger, Wallenberg, and Holmes, '03; Ariëns Kappers, '22; Hunter, '23, and others); it may mean the field D, and probably the field C, of Rose (Schroeder, '11; Ariëns Kappers, '28); it may mean only the field D of Rose, while field C of Rose is termed the Unterwulst (Kalischer); it may be applied to field B of Rose (Craigie, '28). This is only one example of the confusion in terminology. We are not primarily interested in forebrain morphology, but rather in the connections of forebrain and diencephalic centers, but in order to be certain that our use of the terminology may be clear, a brief description of the striatal complex seems advisable. To the best of our knowledge, we are basing our nomenclature on that of Ariëns Kappers ('28), but are making such additions as the secondary differentiations of the regions demand.

Nucleus basalis (pl. 3, figs. 5 and 6; pls. 4 and 5, figs. 9 and 10). The nucleus basalis as here described for sparrow is directly homologous with the field R figured by Rose ('14) for tit-mouse and regarded by him as homologous with the nucleus basalis of other accounts. In sparrow this nucleus mass makes its appearance at the level of the area praepyramiformis and continues caudalward in the plane of the sections from

which the drawings were made to about the level of the dorsal supra-optic decussation. At first it is merely a narrow band of small cells along the lateral side of the paleostriatum. It gradually increases in size and becomes somewhat crescentic in outline (pl. 3, fig. 5), then decreases again, and at its posterior end consists only of a few cells scattered along the inner border of the tractus fronto-archistriaticus et neostriaticus (pl. 3, fig. 6; pl. 4, fig. 9). During much of its posterior extent it is embedded in the nucleus tractus fronto-archistriatici.

This nucleus has been figured and described by Rose ('14) for a number of avian types, and it is not necessary here to redescribe it in the material at hand. However, an account of this nucleus in chicken, where the form relations are somewhat different, may be of value in interpreting certain of the earlier accounts. In chicken, nucleus basalis consists of a small-celled nuclear mass situated along the lateral surface of the more cephalic part of the hemisphere in the position figured for it by Rose ('14, tafel 10, fig. 91). Gradually the nucleus becomes separated from the surface and is pushed dorsalward by the intervention of the more lateral part of the paleostriatal area which is separated here from the medial part of that area by the lamina medullaris externa or dorsalis. At this level the small-celled nucleus basalis lies directly ventral to the neostriatum. Soon the medial and lateral portions of the paleostriatum fuse into a single nuclear mass and the nucleus basalis gradually becomes smaller and triangular in outline. Its posterior end comes into relation with the nucleus tractus fronto-archistriatici.

The nucleus basalis was described in the Edinger, Wallenberg, and Holmes paper ('03) as the lateral forward extension of the mesostriatum or the paleostriatum of the later terminology. Such a forward lateral extension of the paleostriatum is not present in sparrow, but is to be found in chicken and in certain other avian forms, such as dove. The area labeled the lateral mesostriatum in the 1903 account probably contains both this lateral extension of the striatal

area and the nucleus basalis of the present account. Certainly, this latter nucleus is the nucleus figured by Schroeder ('11) and receives the connections considered characteristic of nucleus basalis by Edinger, Wallenberg, and Holmes. The above considerations justify the statement that in sparrow and in chicken, and in certain other avian forms likewise, the nucleus basalis is not a direct anterolateral continuation of the mesostriatum or paleostriatum, but is a distinct nuclear mass. This agrees with the conclusions of Rose. This latter observer was unable to identify the nucleus in parrots. It has not been possible, in the parrakeet material at hand, to identify it with certainty.

Paleostriatum (pl. 3, figs. 5 and 6; pls. 4, 5, 6, figs. 9 to 12; pls. 7, 8, 9, figs. 14 to 18; pls. 10, 11, figs. 20 to 23). The paleostriatum, homologous with the mesostriatum of many workers (in part with that of Edinger, Wallenberg, and Holmes, '03, and with that of Hunter, '23, and of Craigie, '28), according to the nomenclature of Ariëns Kappers ('22, '28), is divisible into a paleostriatum augmentatum (pl. 3, figs. 5 and 6; pls. 4 to 6, figs. 9 to 12; pls. 7 to 9, figs. 14 to 18; pls. 10, 11, figs. 20 to 23) and a paleostriatum primitivum (pl. 3, fig. 6; pls. 4 to 8, figs. 9 to 12, 14, 16; pls. 10, 11, figs. 20 to 23). However, it does not include the paleostriatum primitivum to which Craigie ('28) refers, for he evidently means by this term the nucleus basalis of the Edinger, Wallenberg, and Holmes terminology and the field R of Rose. Ariëns Kappers refers to the term paleostriatum primitivum as applied to a basal nucleus, but his account and, in general, his figures show ('28, p. 48, figs. 9A and 9B) that the nucleus to which he has reference is the nucleus entopeduncularis of Edinger, Wallenberg, and Holmes ('03) and corresponds, then, to the present usage.

In transverse sections of the sparrow material, taken at the posterior end of the olfactory bulb, a small round nuclear mass makes its appearance in the medial portion of the neostriatum frontale and just lateral to the lower third of the ventricle. It soon becomes separated by a definite fiber lamina from the surrounding nuclear masses. This is the

anterior portion of the paleostriatum augmentatum. Followed caudad, the nucleus assumes a somewhat triangular outline, but with rounded corners. Still farther caudad, it increases rapidly in size and extends ventralward until it is separated by a narrow fiber band from the periphery. Edinger, Wallenberg, and Holmes ('03) designated this anterior continuation of the paleostriatum (mesostriatum of their terminology) the nucleus parolfactorius, but at present there appears to be no reason for such a nomenclature. Traced farther caudad, the paleostriatum loses its triangular outline and becomes, in reality, a four-sided structure, as can be seen in the regions where it spreads along the ventral surface (pl. 3, fig. 5). Histologically, the paleostriatum augmentatum consists of closely packed, rather faintly staining cells, small for the most part, but with a scattering of deeper-stained, larger elements. At the level where the septomesencephalic tract is swinging down toward the basal portion of the hemisphere, the lateral forebrain bundle and associated tracts appear as compact fiber masses in the midst of the paleostriatum. In the midst of the forebrain bundles, as they are thus surrounded by the paleostriatum augmentatum, are scattered cells—in part arranged in small groups—which form the so-called entopeduncular nucleus of Edinger and the field J of Rose (pl. 3, fig. 6). This is the paleostriatum primitivum of the Ariëns Kappers account ('28, p. 48, fig. 9B; see also p. 49). Its cells are both large and small, but the large are the more characteristic. These latter belong to the motor type of cell as described by Malone ('10); they are similar to the cells of the nucleus entopeduncularis diencephali with which, as Edinger, Wallenberg, and Holmes ('03) pointed out, they are more or less continuous. The nuclear mass of the paleostriatum primitivum and its associated fiber bundles increase rapidly in size and occupy a larger and larger field around which the paleostriatum augmentatum extends (pls. 5 and 6, figs. 10 to 12). At certain levels this latter nucleus has somewhat the shape of a letter C with the open part directed toward the midline (pl. 5, figs. 10

and 11; pl. 6, fig. 12). However, the outline varies with the plane of the section, but the paleostriatum augmentatum partly encircles the paleostriatum primitivum until behind the level of the interventricular foramen. The latter nucleus then gradually surrounds the central fiber and cell mass, which diminishes rapidly, but is still present in sections passing through the habenula (pl. 8, fig. 16). In the meanwhile the paleostriatum augmentatum decreases in size and caudad to the forebrain bundle remains as a somewhat irregularly rounded nuclear mass near the ventromedial surface of the hemisphere, dorsomedial to the tractus fronto-epistriaticus (pls. 8 and 9, figs. 17 and 18). This nucleus decreases rapidly and disappears in our material in sections just caudad to the posterior commissure.

According to Ariëns Kappers ('22), the paleostriatum, as a whole, is represented by the globus pallidus of man and by "eventual vestiges of gray substance occurring in and mesially to the capsula interna (underneath the fiss. neo-paleostriatica) including a vestige of gray substance which is a continuation of the latter and (as in birds) lies underneath the caudate nucleus; the substantia paleostriatica caudata, which in some animals may be separated from the caudate nucleus by a continuation of the lamina medullaris externa and of the fiss. neo-paleostriatica." It will be recalled that, in 1903, Edinger, Wallenberg, and Holmes raised the question of a possible homology of their mesostriatum with globus pallidus. We regard the large-celled portion, the paleostriatum primitivum, as the homologue of globus pallidus. We are less certain of the homologies of the paleostriatum augmentatum. As Ariëns Kappers ('22 and '28), Gurdjian ('28), and others have pointed out, the caudate and putamen are parts of a single nuclear mass; the paleostriatum augmentatum may represent that portion (in higher forms usually associated with caudate) which is continuous around the ventricle with nucleus accumbens.

Ektostriatum (pl. 3, fig. 6; pls. 4 to 6, figs. 9 to 12; pls. 10 and 11, figs. 20 to 22). This nuclear mass, for which no

mammalian homology has been suggested, but which has been recognized by most workers on avian brains (Edinger, Wallenberg, and Holmes, '03; Schroeder, '11; Rose, as field S, '14, and many others), lies dorsal to the external medullary lamina, medial to the nucleus basalis of Edinger, Wallenberg, and Holmes ('03) or field R of Rose ('14) and projects into the intermediate part of the neostriatal area. It contains small cells intermingled with some larger ones, the number of the latter depending upon the avian form in question. This nucleus is interpolated in the course of certain of the major components of the lateral forebrain bundle (p. 115).

Neostriatum (pls. 2 and 3, figs. 4 to 6; pls. 4 to 11, figs. 9 to 23). The term neostriatum is used here for the lower part of the hyperstriatum of Edinger, Wallenberg, and Holmes ('03), for the striatum of Kalischer ('05), for the field G (including G, G¹, G²) of Rose ('14), for the hyperstriatum inferius of Ariëns Kappers ('22), and for the neostriatum of his later account ('28). It is the neostriatum inferius of Craigie ('28). The neostriatum is the largest of the basal nuclei of the forebrain, as Rose has already pointed out. Beginning at a level only slightly behind the frontal pole of the hemisphere, it extends caudalward as a continuous nuclear mass to form ultimately the larger portion of the great protuberance which bulges out into the occipital pole of the ventricle. The mass, as a whole, is limited on its ventral side throughout most of its extent by the external medullary lamina of Ariëns Kappers or the dorsal medullary lamina of Edinger, Wallenberg, and Holmes ('03) and Schroeder ('11). It lies ventral to the hyperstriatum ventrale and dorsal to the paleostriatum and ektostriatum. Medially, it approaches the ventricle, however, separated from it at the anterior end of the hemisphere by the hyperstriatum ventrale and other intervening cell masses and by the periventricular cortex-like band in the more caudal regions. At its anterior end the neostriatum is bounded laterally by the thin superficial cortex-like layer. The tractus fronto-archistriaticus and its associated nucleus lie in close relation to the

main mass of the neostriatum. Observers in general do not appear to have recognized further subdivisions of the area, but Rose divided the nuclear mass (G) into three portions, G, G¹, G². The divisions of Kalischer ('05) into striatum parietale and striatum frontale appear to be based rather on topographic relation to the skull than on cytoarchitectonic differences. Such subdivisions can be seen in our own material, although the demonstration of them is far from easy, particularly in the transverse sections. They are more evident in the sagittal sections where obliquely running fiber bundles aid in their demarcation. They are differentiable on the basis of cytological characteristics, and they have, to some extent, characteristic fiber connections. For purposes of description they have been termed in the present paper the neostriatum frontale, intermediale, and caudale. The latter portion has been subdivided into a pars anterior and a pars posterior. In addition to these portions, the more lateral part of the field, lying in association with the tractus fronto-archistriaticus, has been called the nucleus of that tract.

The neostriatum frontale (pls. 2 and 3, figs. 4 to 6; pl. 4, fig. 9; pls. 10 and 11, figs. 21 to 23) makes its first appearance in the midst of the hyperstriatum ventrale, dorsoventrale (pl. 2, fig. 4). Rose ('14) regarded the two areas as here continuous with each other, but they are fairly distinct from the beginning in the sparrow material, due to a slight difference in their staining qualities. Soon the neostriatum frontale swings lateralward and occupies the ventrolateral portion of the hemisphere. With the appearance somewhat farther caudad of the anterior end of the paleostriatum (nucleus parolfactorius of Edinger, Wallenberg, and Holmes, '03), the neostriatal area becomes separated from the paleostriatum by the dorsal or external medullary lamina. The division between the two is clearly indicated by the fissura neopaleostriatica of Ariëns Kappers ('22 and '28) in certain birds. It is indicated by a change in the ependyme, and at certain levels a very slight indentation, much less evident, for example, in the sparrow than in the dove. The fissura

neohyperstriatica (pl. 3, fig. 6) indicates, along the ventricular wall, the line between the neostriatum and hyperstriatum ventrale at certain levels.

The neostriatum increases in size as it is followed caudad and extends nearer the ventricular wall, separated from it only by a periventricular band of cells and fibers. The exact boundary between the frontal and intermediate portions is very difficult to determine in our preparations of sparrow, and we are uncertain as to whether or not the intermediate part always intervenes between the periventricular band and the frontal division of the inferior neostriatal area. It is possible that the latter approaches the ventricular wall for a few sections before it is pushed aside by the intermediate portion. Certainly, in front of the cephalic end of the ektostriatum, the neostriatum intermediale has made its appearance on the medial side of the frontal division of the nucleus. This frontal part now rapidly decreases in size, but extends caudalward along the lateral wall, indistinctly separated from nucleus tractus fronto-archistriatici et neostriatici. We are of the opinion that we have carried this part farther caudalward than did Rose, but of course sagittal sections, on which he has figured his subdivisions, show this caudal prolongation only if taken at appropriate levels. This portion consists of medium-sized and rather large cells, intermingled with some smaller ones. In general, the cells are rather larger than those of the succeeding portion, and distinctly less closely massed.

The neostriatum intermediale (pl. 3, fig. 6; pls. 4 to 8, figs. 9 to 12 and 15; pls. 10 and 11, figs. 20 to 23), which is the field G of Rose, begins relatively far forward and near the ventricle. It increases rapidly in size and soon makes up the major portion of the neostriatum. It is replaced by the caudal portion of the nucleus which overlaps it in the posterior half of the hemisphere. This intermediate portion has closely packed medium-sized cells. The caudal portion—which gradually replaces it—forms that subdivision of the neostriatum which projects into the occipital pole of the ventricle.

The neostriatum caudale (pls. 5 and 6, figs. 10 to 12; pls. 7 to 11, figs. 15 to 23), or the field G² of Rose, consists of a part anterior to the tractus archistriaticus dorsalis and a part posterior to this fiber bundle. The pars anterior (pl. 11, fig. 22) resembles somewhat in general character the neostriatum frontale, at least its cells are more evenly distributed and not so closely packed as those of the neostriatum intermediale. The pars posterior (pl. 11, fig. 22, for example) contains cells similar to those of pars anterior, but intermingled with these in its most caudal part are large cells similar to, and in part continuous with, those of the periventricular band and which extend forward dorsal to the lamina hyperstriatica (pls. 8 and 9, figs. 16 to 18; pl. 11, fig. 22).

In the more lateral part of the neostriatum frontale, in a plane through the more posterior portion of the nucleus basalis, lies the nucleus tractus fronto-archistriatici et neostriatici (pl. 3, fig. 6; pls. 4 and 5, figs. 9 and 10; pl. 13, figs. 28 and 29). The cephalic end of this nuclear mass is not differentiable from the neostriatal area, but as the bundles of the tract gradually accumulate it becomes distinctly separated from the surrounding gray. On its medial side it is in close relation with the nucleus basalis (pl. 3, fig. 6). Whether it were better to consider this area an entirely distinct center or to regard it as a differentiated portion of the neostriatum frontale we are not prepared to discuss.

Hyperstriatum (pls. 2 and 3, figs. 4 to 6; pls. 4 to 7, figs. 9 to 15; pls. 10 and 11, figs. 20 to 23). The term is used here for the area described by Ariëns Kappers ('22) as the hyperstriatum superius and for which he later used the name hyperstriatum alone (p. 35 of the present paper). Used thus, it is comparable with the fields A, C, and D of Rose ('14) and presumably with the neostriatum superius of Craigie ('28). Its ventral portion is homologous with the hyperstriatum of Kalischer ('05), but its dorsal part (field C of Rose) is the 'Unterwulstregion' of this observer. However, this general area is divisible, as the work of Rose indi-

cated, into three secondary areas which we have termed hyperstriatum ventrale (field D of Rose), hyperstriatum dorsale (field C of Rose), and nucleus intercalatus hyperstriatum (field A of Rose). The hyperstriatum ventrale can be subdivided into two nuclear masses which have been termed hyperstriatum ventroventrale and hyperstriatum ventrodorsale. These two nuclear masses of the ventral hyperstriatum have not been previously described.

At the frontal end of the hemisphere the dorsoventral part of the ventral hyperstriatum and the dorsal hyperstriatum occupy the ventrolateral portion of the lateral wall (pl. 2, fig. 4). They both consist of deeply staining, relatively large cells. After the appearance of the neostriatum, the above-mentioned hyperstriatal areas are pushed dorsalward. The dorsoventral portion takes on something of a sickle shape, but with a much enlarged lateral portion, while the dorsal part is band-like in appearance (pl. 3, fig. 5). The two are distinctly separated medialward, but lateralward they are more or less continuous with each other and with the overlying accessory hyperstriatum and with the cortex-like band at the periphery of the forebrain (pl. 3, fig. 5). Gradually the hyperstriatum dorsale becomes smaller and acquires a somewhat unequally triangular outline, with one of the acute angles of the triangle directed toward the ventricle and continuous with the periventricular gray of the region and with the other acute angle contiguous and often apparently continuous with the cortex-like band at the periphery. Then the hyperstriatum dorsale flattens out into a narrow band which, at the ventricular side, goes over into a periventricular band of cells which lies between the ventricle and the hyperstriatum ventrale, dorsoventrale (pl. 3, fig. 6). The hyperstriatum dorsale disappears cephalad to the decussation of the anterior commissure. For some distance in front of its termination it is clearly separable from the dorsoventral part of the hyperstriatum ventrale (pl. 4, fig. 9).

The dorsal part of the hyperstriatum ventrale, the hyperstriatum ventrale, dorsoventrale, is the only part of that

area present at the anterior end of the hemisphere (pl. 2, fig. 4). However, gradually in the more ventral part of the area the cells become somewhat less closely packed together. Here the number of small cells increases, while that of the large cells decreases. The cells in this area, which is here designated hyperstriatum ventrale, ventroventrale (pl. 3, figs. 5 and 6; pls. 4 to 6, figs. 9 to 12; pls. 10 and 11, figs. 20 to 22), usually are arranged in rows more or less perpendicular to the underlying fronto-occipital tract. Their arrangement suggests the presence of intervening fiber bundles, and these, the silver preparations show, are actually to be found radiating through the field. The ventroventral portion suggests in general cell character the underlying neostriatal areas. Gradually the hyperstriatum ventroventrale increases until it occupies much of the medial portion of the area and extends lateralward for some distance under the dorsoventral part, which at this level is confined to the most dorsal and to the dorsolateral regions of the hyperstriatum ventrale (pl. 5, fig. 10). In the plane in which our cross-sections are cut (and more particularly in the series from which the drawings were made) the ventroventral portion reaches its greatest extent in sections passing immediately in front of and through the cephalic end of the nucleus accumbens. Behind this point this hyperstriatal area decreases rapidly, so that only a final trace remains in sections behind the anterior commissure. In front of the decussation of this commissure a sickle-shaped mass of small cells is present in our preparations in the hyperstriatum dorsoventrale, but near the border of the hyperstriatum ventroventrale (pl. 3, fig. 6). In the preparations from which the drawings were made this sickle-shaped mass persists for about 0.8 mm., however retaining its characteristic outline only throughout the middle portion of its extent. Behind the level of the anterior commissure the dorsoventral part of the hyperstriatum persists as a comma-shaped structure, the larger end of which is directed toward the outer side of the hemisphere. Along the edge of the ventricle it acquires a cortex-like band which is con-

tinuous with the accessory hyperstriatum (pl. 5, figs. 10 and 11). Gradually the dorsoventral part diminishes in size, its medial portion is lost, and only its lateral part remains as a definitely stained, large-celled mass external to the neostriatal area. This part, in turn, decreases rapidly at the level of the interventricular foramen and disappears at about the plane of its caudal border.

In sagittal sections (pl. 11, figs. 22 and 23; pl. 18, fig. 38) hyperstriatum dorsale and ventrale appear as two oblique bands running dorsocaudad from more frontal to more caudal regions across the hemisphere above the hyperstriatum ventrale through about the anterior two-thirds of the hemisphere. The hyperstriatum dorsale is the shorter of the two and consequently ends farther cephalad.

Nucleus intercalatus hyperstriati (pls. 2 and 3, figs. 4 to 6; pl. 4, fig. 9; pls. 10 and 11, figs. 20, 22, and 23). This nucleus has been recognized and described by Rose ('14), who termed it field A. No other account of this cell mass is to be found in the literature. It consists of very small, round cells which appear first at the anterior end of the hemisphere between the hyperstriatum dorsale and the accessory hyperstriatum. Nucleus intercalatus hyperstriati continues caudalward between these two hyperstriatal areas. It disappears at about the level of the termination of the hyperstriatum ventrale, ventroventrale. During the more caudal part of its course the nucleus is continuous with a scattered band of cells on the medial ventricular wall which swings around the dorsal angle of the ventricle to become continuous with the hyperstriatum dorsale. This entire band of cells undoubtedly represents neurones interpolated in the course of a fiber bundle (lamina suprema), and we are inclined to regard it as an interstitial nucleus for the tract rather than as a distinct hyperstriatal nuclear center.

Hyperstriatum accessorium (pls. 2 and 3, figs. 4 to 6; pls. 4 and 5, figs. 9 to 11, *a*; pl. 6, fig. 12, *a*). The dorsomedial portions of the cephalic pole of the avian brain are occupied by the so-called 'Wulst' region of many observers (as, for exam-

ple, Kalischer, '05). It constitutes the field B of Rose. The 'Unterwulst' region of Kalischer is the field C of Rose, but does not appear to be entirely homologous with the 'Unterwulst' region of Schroeder, so far as we can judge by comparison with our own material of chicken. The name of accessory hyperstriatum, as the term is used in the present paper, refers to the field B of Rose ('14), except that it does not include the peripheral cortex-like layers. It is the region to which Craigie would probably apply the term hyperstriatum superius (Craigie, '28).

In the gross material the accessory hyperstriatum with its associated cortex-like layers together with the hyperstriatum dorsale forms an eminence on the dorsomedial surface of the cephalic part of the hemisphere, which is frequently called the 'Sagittalwulst' and which is separated from more lateral areas by a depression known as the vallicula (Edinger, Wallenberg, and Holmes, '03, and many others; see also pl. 1, figs. 1 and 2). In the cell preparation of the sparrow's brain, in transverse sections passing through the frontal pole of the hemisphere, the accessory hyperstriatum extends from the dorsal to the ventral surface of the brain, being much wider on the upper than on the under side (pl. 2, fig. 4). Very soon it is replaced by the growth of the hyperstriatal areas, so that it comes into relation with the ventricular region and is ultimately confined to the dorsomedial portion of the hemisphere (pl. 3, fig. 5, etc.). It consists of smaller, usually less deeply staining elements, mingled with larger, more deeply staining cells. At the cephalic end of the hemisphere it extends over the dorsomedial angle. Its separation from the underlying entorhinal area is indicated by a sulcus of variable depths in different birds (particularly deep in duck, for example). However, gradually with the dorsal growth of the entorhinal area the accessory hyperstriatal area no longer extends over the angle of the ventricle, but is found farther lateralward and the paraentorhinal area intervenes between the entorhinal and accessory hyperstriatal masses (pl. 3, fig. 6, etc.). From this point

caudad there is a gradual decrease in size of the latter area. It lies in intimate relation (pl. 3, fig. 6; pl. 4, fig. 9) with the overlying corticoid layer, and there are places where the two cannot be sharply delimited in the sparrow material. Near its caudal termination the accessory hyperstriatum is particularly closely related lateralward to the cortex-like layer of the dorsal wall. A posterior prolongation of this area (pls. 5 to 8, figs. 10 to 12, 15, 16) runs back dorsal to the ventricle wall, as Rose found to be the case in his material. This portion shows a modified cytological character and is labeled *a* in the figures.

Archistriatum (pls. 8 to 11, figs. 16 to 19, 21, and 22). The archistriatum (or secondary epistriatum of the terminology of Ariëns Kappers, '08, '22, '28) is the epistriatum of Edinger, Wallenberg, and Holmes ('03) and of Schroeder ('11), and the field K of Rose. Hunter ('23) and Craigie ('28) have followed the nomenclature of Ariëns Kappers. The work of many observers (Johnston, '15 and '23; Ariëns Kappers, '22; Berkelbach van der Sprenkel, '26; Craigie, '28, and many others) indicates that the suggestion of Edinger, Wallenberg, and Holmes ('03), as to the possible homology of this nuclear mass with the amygdaloid complex of higher forms, is correct.

The more cephalic portion of the archistriatum or amygdaloid complex makes its appearance in the series of sparrow brain cut in a transverse plane through the middle of the habenulae. At this level it lies in the ventromedial portion of the hemisphere at the ventral angle of the lateral ventricle, ventral to the neostriatum and dorsomedial to the occipito-mesencephalic tract and the paleostriatum augmentatum (pl. 8, fig. 16). It increases relatively rapidly in size and, with the corresponding decrease of the paleostriatal area, spreads lateralward over the occipito-mesencephalic tract and is broken up into bands of cells intercalated between fiber bundles from this tract (pl. 8, fig. 17). On its ventromedial side near the inner surface of the hemisphere a compact nuclear mass appears, which is probably the homologue of the nucleus

taeniae of Edinger, Wallenberg, and Holmes ('03). Near the posterior end of the paleostriatal area, the archistriatum proper divides into a ventral portion formed of deeply staining cells intercalated among the fiber bundles of the tractus occipito-mesencephalicus and a dorsal crescentic-shaped mass of rather large cells, not particularly distinct at this level in neurone type from that of the ventral part, but separated from it by a definite lamina of very small cells. In plate 9, figure 19, the beginning of this dorsal crescent is to be seen; it is more conspicuous in sections taken farther caudalward. At no great distance behind the posterior pole of the paleostriatum augmentatum the larger bundles of the occipito-mesencephalic tract disappear. With their disappearance the more ventral part of the nucleus becomes more compact and the number of smaller cells therein increases. Gradually the dorsal part loses its crescentic outline, widens out, and occupies more and more of the archistriatum. The gradual increase of this dorsal part is associated with a corresponding decrease of the ventral part, until at the posterior end of the nucleus only the dorsal mass remains. The division of this cell complex into dorsal and ventral portions has been made for descriptive purposes. No homologies with nuclear masses of the amygdaloid group as described for other forms are here intended. It may well be that these subdivisions are due merely to the arrangement of the bundles of the occipito-mesencephalic and dorso-archistriatic tracts and, beyond that, have no fundamental significance. Comparison with conditions in certain birds such as dove suggests that such may well be the case, but it is a question which it is not possible at present to decide.

Nucleus taeniae (pl. 9, fig. 18). This nucleus, recognized by various observers (Edinger, Wallenberg, and Holmes, '03, and others), makes its appearance near the cephalic pole of the archistriatum with which it is in intimate relation. It lies ventromedial to this nuclear complex, dorsomedial to the occipito-mesencephalic tract, ventrolateral to the ventral tip of the lateral ventricle, and just internal to the medial surface

of the hemisphere. It soon develops into a distinct nuclear mass sharply separable from the surrounding areas. Its cells are of medium size, with some admixture of smaller elements. As the more posterior regions of the hemisphere are reached (in our series in transverse sections through the hemisphere, cerebellum, and the nuclei of the oculomotor nerve, pl. 9, fig. 18), the nucleus taeniae decreases in size and gradually disappears.

COMPARISONS OF BASAL CENTERS OF THE LATERAL FOREBRAIN WALL OF SPARROW WITH THOSE OF CERTAIN OTHER BIRDS AND ALLIGATOR. Lack of space prevents a detailed account of the various nuclear groups of the paleostriatal, neostriatal, hyperstriatal, and archistriatal areas in the material available to us for study. Moreover, comparison with the figures given by Rose ('14) and with other descriptions in the literature renders any further account unnecessary. However, a brief comparison of certain of the areas in the various forms may be of some interest.

All of these nuclear groups are distinguishable in duck, dove, and parrakeet as well as in sparrow, although there is some variation in relative as well as actual size. In parrakeet there is a particularly marked resemblance to the sparrow, but the greater relative size of the forebrain as compared with the remainder of the nervous system means particularly an increase in the neostriatal and hyperstriatal complex in the parrakeet. This increase is a slightly greater one in the hyperstriatal than in the neostriatal part of the hemisphere. In our material of the parrakeet the division between dorsal and ventral portions of the hyperstriatum is not as clear as in the sparrow. The three parts described for the neostriatum of the sparrow are evident in the sagittal material of the parrakeet.

In duck the neostriatum is increased relatively as well as actually and so forms a somewhat larger proportion of the lateral wall complex than in sparrow, while in dove the size relation between the neostriatal and hyperstriatal regions resembles more nearly that in sparrow.

While the accessory hyperstriatal area is large at the anterior end of the dove brain, it appears to decrease relatively somewhat more rapidly than in sparrow, so that it is proportionately much smaller at the level where the septo-mesencephalic tracts are running ventralward (Rose's figure, pl. 1, fig. 3). In our material it has disappeared before the level of the anterior commissure is reached. In duck the accessory hyperstriatal area forms the dorsomedial angle as in dove and in sparrow, but then is pushed lateralward by the upward growth of the dorsomedial hemisphere areas. The relations of the accessory hyperstriatal area in chicken show marked resemblance to those described for dove. The accessory hyperstriatal area in duck remains quite large for a long distance through the hemisphere, being of considerable size at the level of the posterior commissure. Beyond this level it diminishes, however, being overlapped by a corticoid lamina, and disappears before the posterior end of the third nucleus at the plane of our series.

The position of the archistriatum shows an interesting variability in the avian forms available for study. In the brains of the duck, chicken, dove, and parrakeet the archistriatum appears first on the lateral side of the paleostriatum and extends medialward behind that nuclear mass; this, it will be noted, is the direct opposite of the relations of the archistriatum as described for sparrow.

There are, of course, minor differences in size of striatal areas and in their form relations. However, the most surprising results of a comparison are not the differences, but the clearness with which a common pattern may be demonstrated.

Herman ('25) contrasted avian and reptilian striatal masses, basing his reptilian studies largely, although not exclusively, on *Varanus*. It is not our purpose to go into a detailed account of such homologies, but certain comparisons of homologous structures in sparrow and alligator may have some value. The brain of the alligator has been used, because this is the reptile with which we are most familiar

and one which is generally recognized as rather closely related to avian forms. The paper specifically referred to is that on alligator forebrain published in the spring of 1917 by the junior observer. During the last eleven years there have been many contributions to our knowledge of the nuclear masses and fiber connections of the reptilian brain. A better understanding of the homologies existing between reptilian and amphibian and reptilian and mammalian structures is the logical result. The contributors to this knowledge are far too numerous to list; particularly prominent among them are Herrick ('10, '24, '25), Johnston ('15, '23), Elliot Smith ('19), and Ariëns Kappers ('21, '22, '28) and the younger workers, Marion Hines ('23), Herman ('25), and Cairney ('26). This available store of knowledge, together with much better cell preparations and added experience, permits us to suggest certain homologies which the junior member did not attempt at the time of writing the earlier paper. The better material also permits more careful delimitation of the extent of the cortical mass along the dorsomedial wall (p. 59).

The non-olfactory part of the lateral wall of the alligator hemisphere is divisible into a ventrolateral, an intermedio-lateral, and a dorsolateral area. The ventrolateral area in the alligator forebrain is divisible into two parts, which in the earlier account were called large- and small-celled portions. The large-celled part contains medium-sized cells with an admixture of certain larger, deeply stained elements; the small-celled part consists mainly of small scattered cells intermingled with the fiber bundles of the lateral forebrain tract. Occasionally in this latter nuclear area, a few very large, faintly staining cells can be found, but in the material at our disposal, which is that of baby alligators, they are not sufficiently plentiful to give character to the field. However, they are much more plentiful and characteristic in birds where they form the typical neurones of the paleostriatum primitivum. The so-called large-celled part in alligator is the paleostriatum augmentatum of the sparrow. The ventro-

lateral area in alligator becomes, then, the paleostriatum in birds. Bounding this area dorsalward is a fiber lamina which Herman ('25) homologized with the external medullary lamina in birds. The sulcus on the ventricular wall separating the ventrolateral from the intermediolateral area is the avian *fissura neopaleostriatica* of Ariëns Kappers (referred to previously). Above the dorsal medullary lamina is the intermediolateral area of the alligator. We are unable to trace this as an independent area for any great distance in the alligator material at present available. Laterally and posteriorly, it goes over without sharp demarcation into the dorsolateral area. However, it marks the beginning of a differentiable neostriatal area, as that term is used for the avian brain. Dorsally, the area is separated on the medial side from the dorsolateral area by a cell-free lamina. At some levels there is a slight indication of a sulcus comparable to the *fissura neohyperstriatica* of the bird, although it is not equally clear in all sections. The dorsolateral area with its intimate relation, at the anterior end, to the overlying general cortex is comparable to the hyperstriatal areas of the sparrow. To attempt to carry the homology further for this area is to leave rather evident facts for what verges on speculation. It may be suggested that the medial portion in reptiles at the level of the infolding probably represents the more dorsal hyperstriatal areas in birds, while the reptilian lateral and ventral portions are included in the avian ventral hyperstriatal area. However, this last statement needs further proof.

The basal forebrain areas receiving olfactory impulses directly or indirectly from the olfactory bulb fall into the usual groups of medially and laterally situated centers in the alligator. A comparison of the medial centers with those in sparrow has been given in the present paper under the discussion of the avian basal centers of the medial forebrain wall. The lateral non-cortical centers were described previously in alligator under the name of the nucleus of the lateral olfactory tract. This consisted of two parts, an

anterior portion situated lateral to the intermediolateral area and not sharply separated from the surrounding areas at all levels and a posterior portion lying toward the caudal part of the hemisphere, as far back as sections through the habenula. The two portions were connected by scattered cells intercalated in the course of a fiber tract. The posterior part of the nucleus olfactorius lateralis is probably homologous with the nucleus of that name in turtle (Johnston, '15); the anterior part is the anterior amygdaloid nucleus of Cairney. The posterior portion is represented by the archistriatum in birds. The anterior part of the nucleus olfactorius lateralis of the earlier account is the avian nucleus basalis. It is probably the nucleus olfactorius lateralis of *Sphenodon* (Hines, '23; Cairney, '25). The scattered cells connecting the two are not present in birds. A discussion of the relations of the lateral olfactory tract to this nuclear mass is to be found under the description of the fronto-archistriatic tract. Previously, the pyriform-lobe cortex was described as coming down over the posterior end of the nucleus of the lateral olfactory tract. It does have this relation in part, but through some of its extent in this region is represented more by a corticoid than by a true cortical layer. Nucleus taeniae is homologous with the ventromedial nucleus of the alligator.

The above account indicates that the pattern along which the bird forebrain is to develop is already outlined in the reptilian brain. The avian forebrain represents very largely the increase of basal centers and the decrease of cortical centers already present as more or less distinct areas in this reptilian form.

CORTICAL AREAS. Not all observers are agreed as to the amount of cortex present in the avian brain. The differences of opinion are based largely on differences in definition of cortex. Thus Edinger, Wallenberg, and Holmes ('03) found cortex over the dorsal three-fourths of each hemisphere, but none on the ventral one-fourth. Great atrophy or absence of cortex was noted by them for the greater part of the

medial hemisphere wall. The ventricle separated the cortical from non-cortical or striatal areas in the mediodorsal and occipital regions, but elsewhere the cortex was mingled with the basal nuclei of the hemisphere.

Rose ('14) regarded pyramidal-shaped cells and clear evidence of layer formation as necessary criteria for cortex. Brodmann ('09) divided the cortex into heterogenetic and homogenetic types, of which the latter presents six typical layers and the former does not. Neopallium belongs to the homogenetic type, and since obviously six-layered cortex is not present in birds, Rose maintained that there is no avian neopallium. Archipallium is represented, however, in the entorhinal and hippocampal formations. Rose also regarded septum pellucidum and area praepyriiformis as cortical.

Hippocampus (pls. 2 and 3, figs. 4 to 6; pls. 4 to 9, figs. 9 to 19; pl. 10, fig. 20). In our sparrow material toward the anterior end of the hemisphere, just in front of the anterior pole of the ventricle, a rather heavily stained band of cells makes its appearance and soon occupies the region between the ventricle and the medial surface of the brain (pl. 2, fig. 4). This is the anterior continuation of the hippocampal area (cornu Ammonis of Rose) which extends forward, as in reptiles, toward the region of the olfactory bulb. At this level it is composed of small granular elements. As the ventricle extends downward in our sections the hippocampal formation is limited ventralward by the extent of the ventricle. Its ventral extremity lies close to the ventricular wall; farther dorsalward it is separated from the ventricle by scattered cells intermingled with fibers; on the medial side is a cell-free area. Soon the hippocampal formation occupies only the upper portion of the area internal to the ventricle; the area ventral to it, which, in reptiles, is occupied by a band of hippocampal cells, in birds is filled with fiber bundles only, and in consequence is very thin (pl. 3, fig. 5). The mass is triangular in outline, with the apex pointed ventralward and the two sides bounding the angle more deeply stained than the intervening cells. The more scattered cells of the ento-

rhinal area of Rose dorsal to it at the anterior end become fused in part with the hippocampal portion, so that at all levels it is not possible to establish an absolutely definite boundary between the two areas in our material. In our transverse sparrow material in sections passing through the optic chiasma, the hippocampal formation extends ventralward again toward the septal or parolfactory region (pl. 3, fig. 6). Just ventral to this formation is a band of cells, similar in appearance to those of the hippocampus, but possibly lighter in staining character (pl. 3, fig. 6). This band is separated from the hippocampus by a cell-free zone and is more or less fixed with the septal or parolfactory region ventral to it. It appears to occupy the position of the cells called by Johnston ('15) and Crosby ('17) the primordium hippocampi and regarded by Hines ('23) as the source of the fascia dentata. Both this last-described cell group and the ventral extension of the hippocampus persist for only a relatively short distance, then the area becomes relatively cell-free again and very thin. The hippocampal formation can be followed for a considerable distance toward the caudal end of the hemisphere (pl. 8, fig. 17), appearing to extend ventralward again at the level of the nucleus taeniae, toward that nuclear mass. It disappears in a plane near the caudal end of that nucleus.

Entorhinal area of Rose (pl. 3, figs. 5 and 6; pls. 4 to 9, figs. 9 to 18; pl. 10, fig. 20), which is the hippocampus pars dorsalis of the reptilian forebrain. This area is situated toward the anterior end of the hemisphere between the hippocampal area, or cornu Ammonis of Rose, and the accessory hyperstriatal area. It has its beginning as scattered cells which, from their lighter staining character, are quite easily distinguishable from the bordering areas. It increases rapidly and its cells become definitely pyramidal in character (pl. 3, figs. 5 and 6). It forms a long ovoid mass, not always definitely separable from the hippocampal area below. For some distance the entorhinal area does not quite reach the dorsal surface, but does so within the posterior third of the hemisphere, behind the

level of the accessory hyperstriatal area. It can be delimited dorsally, at certain levels, by a slight sulcus on the dorso-medial surface (pl. 5, fig. 11). However, this is not equally clear at all levels in our material. Cephalically, it is bordered dorsally and medially by the accessory hyperstriatum, but gradually it is separated from this latter region by a mass of cells (area paraentorhinalis), pyramidal in character and at first of the same general appearance as the entorhinal area, but more or less separable from it, through the massing of the cellular elements (pl. 3, fig. 6; pls. 4 to 8, figs. 9 to 16). Whether the two should be regarded as differentiated portions of the same area or as separate areas we are not at present prepared to say.

We have identified similar areas in duck, dove, and parakeet. In view of the figures of Rose and our own account of sparrow, a detailed account of these appears unnecessary. Yet there are a few points of difference which we should like to emphasize.

At the level of the olfactory bulbs in various birds, the medial hemisphere wall is occupied by cellular elements which are directly continuous on the dorsal side with the pars dorso-medialis hippocampi and on the ventral side, with more or less transition, into the parolfactory or precommissural septal area. The degree of development of this medial wall varies with different birds. In dove the wall is relatively thick. The scattered cells in the upper portion between the surface and the ventricular wall soon give place to the characteristically deeply staining cells of row-like arrangement which constitute the hippocampus proper, or cornu Ammonis of Rose. Cells belonging to this layer are to be found throughout nearly the extent of the hemisphere in dove. However, the layer is best developed in the more cephalic portions. Its more ventral portion, beginning from the ventral side, gradually thins out at the level of the decussation of the anterior commissure. The hippocampus, however, extends back toward the caudal end of the hemisphere. As a consequence of the disappearance of this ventral part of the hippocampal area,

the ventricular wall becomes very thin in the region and is occupied by fiber bundles with just a few scattered cells.

Rose stated (p. 342) with regard to the cornu Ammonis formation in parrots, "bei den Papageien ist dieselbe überhaupt nicht festzustellen." An entorhinal area was found by him and is clearly present in our material. He spoke of it as being present 'an kleiner Strecke.' In the parrakeet studied by us it appears to extend throughout the greater part of the hemisphere, although it is smaller than in dove. In parrakeet the medial wall of the hemisphere between the ventricle and the medial surface is exceedingly thin and the cephalic continuation of the dorsomedial wall is extremely small and represented only by cells intermingled with fiber bundles. Nevertheless, this is undoubtedly to be regarded as that anterior continuation of the hippocampal areas present in many birds and reptiles.

The cornu Ammonis, or hippocampus of birds, is represented in reptilian forms by the pars dorsomedialis hippocampi (Meyer, '92; Herrick, '10; Crosby, '17; Hines, and others). Certain observers, such as Meyer ('92) and Levi ('94), have regarded this dorsomedial area as homologous with the human fascia dentata; Cajal ('11) and Elliot Smith ('10) considered this homology doubtful, although the latter observer thought the area might be differentiating in that direction (a point of view advocated in the earlier paper, Crosby, '17). Miss Hines ('23), from a study of the development of the region in man, came to the conclusion that the dorsomedial hippocampal area of reptiles becomes the human hippocampus.

The avian entorhinal area or 'Hippocampusrinde' of Rose is comparable, then, with the pars dorsalis hippocampi of reptiles (Meyer, '92; Herrick, '10; Crosby, '17, and others) and apparently with the subiculum of Johnston ('15). In this connection we should like to call attention to the labeling of these areas in the paper on alligator forebrain (Crosby, '17). The leaders for the label pars dorsalis hippocampi (*H.p.d.*) on the figures 5, 6, and 7 are placed at the upper border of

the dorsal part of the hippocampus. It was thought at the time that this would limit the dorsal extent of that cell mass. However, this was not made clear in the figure descriptions or text and apparently has led to the misconception that, histologically, the pars dorsalis extends over the dorsal angle of the hemisphere. However, such is not the case. For the greater part of the more cephalic portion of the hemisphere the general cortex occupies this angle and extends along the dorsomedial wall for a short distance. The line between the two areas is marked by a slight sulcus, which is evident in material now available where the shrinkage is less and which is similar to the one mentioned above for sparrow. If the leaders on the three figures of alligator brain, referred to above, are lowered about 4 or 5 mm., they will fall well within the main portion of the pars dorsalis hippocampi.

Paraentorhinal area (pl. 3, figs. 5 and 6; pls. 4 to 8, figs. 9 to 17). The paraentorhinal area is a layer of pyramidal-shaped cells which appears in sparrow between the entorhinal and accessory hyperstriatal areas in our sections in a plane passing through the septo-mesencephalic tract as it courses ventralward and through the optic chiasma. It occupies the region of the angle and consists of pyramidal cells similar to those of the entorhinal region. It widens out somewhat laterally with the decrease of the accessory hyperstriatal area, but then narrows down with the widening of the ventricle and the thinning of the whole peripheral wall. It is still evident in a few sections at the level of the nucleus of the fourth, but soon after disappears. It may be differentiated secondarily into two portions (probably *x* and *y* of Rose). Its mammalian homologue, if any, is unknown.

A paraentorhinal area is present in dove in the same relative position as in sparrow, but extending somewhat farther over the medial angle, and somewhat less clearly separable from the entorhinal portion. Gradually it spreads laterally and with the disappearance of the accessory hyperstriatum it becomes continuous with the rest of the cortex-like lamina of the dorsal wall, which shows a relatively high degree of

development as compared with the development of homologous regions in sparrow and particularly in parrakeet. Where one should draw the line between paraentorhinal and other areas is not clear from this level caudad. Evidences of this nuclear mass can be seen in the caudalmost regions. A paraentorhinal area is present in chicken, which, as in dove, swings lateralward into relation with the dorsal superficial corticoid lamina and continues in this position back to the posterior pole.

In parrakeet the paraentorhinal area is along the lower border of the dorsal angle of the hemisphere and gradually swings to the dorsal angle between the entorhinal and accessory hyperstriatal areas as in other birds. It is not evident as far cephalad in our parrakeet material as in the forms previously described by us. Behind the accessory hyperstriatum, which extends far caudad in these forms, it becomes continuous with the mediodorsal periventricular layers of the dorsal wall.

The paraentorhinal area appears relatively farther caudad in duck than in dove and sparrow. It is more dorsomedial than dorsal throughout most of its extent. Its cell layers are continuous with those of the entorhinal region, the line being indicated by a sulcus on the medial surface and a corresponding decrease in thickness of the layers. Behind the accessory hyperstriatum the area is continuous with the general periventricular cell structure. It is to be noted that at this posterior end the periventricular cells of the dorsal wall show considerable tendency toward cortex formation.

Dorsolateral surface area (pls. 2 and 3, figs. 4 to 6; pls. 4 to 11, figs. 9 to 23). Over the surface of the hyperstriatum from the lower border of the hemisphere, dorsally and dorso-medially, there is a thin layer of cells separated from the surface by a narrow marginal zone. This cortex-like lamina is not so clear in the more cephalic portions of the hemisphere, but by the time the olfactory bulb is reached in our transverse sections, it has formed a distinguishable layer except in the more ventrolateral portions of the hemisphere.

It is fused on its inner side with the underlying hyperstriatal areas. It extends around the dorsomedial angle at the cephalic end of the hemisphere (pls. 2 and 3, figs. 4 and 5) and occupies the region dorsal to the entorhinal area. Gradually the dorsolateral surface area is pushed away from the midline with the greater development of the entorhinal and paratorhinal areas, so that it extends only over the upper part of the lateral and the more lateral portions of the dorsal surface of the forebrain (pl. 3, fig. 6; pls. 4 to 11, figs. 9 to 23). These dorsolateral cortex-like bands are continuous with the hyperstriatum dorsale and ventrale. As the ventricle extends lateralward it cuts off more and more of the surface layer (with part *a* of the accessory hyperstriatum) from the main hyperstriatal mass. Toward the posterior end of the hemisphere, where the accessory hyperstriatal portion has disappeared, the cortex-like lamina becomes very thin and is intermingled with the periventricular layer. Both are represented only by scattered cells, and the wall separating the ventricle from the surface of the brain becomes exceedingly thin (pl. 9, fig. 19). This account is based on sparrow.

The arrangement of the various parts of the dorsolateral areas has been studied in the avian brains at our disposal. They show much variation in development and might well repay a careful analysis, but that is beyond the scope of the present paper, the goal of which is the avian diencephalon.

Whether or not one regards the outer corticoid layer as true cortex or even primordial cortex (varying with the bird form considered), depends on the definition of cortex, as stated at the beginning of this account. If pyramidal cells and clear evidence of layer formation are regarded as a necessary prerequisite, the superficial zone of the dorsolateral area of the sparrow hemisphere cannot, at least for the most part, meet the requirements.

PERIVENTRICULAR AND INTERCALATED GRAY. We finally wish to call attention to an indefinite layer of periventricular gray which is to be found in relation with the ventricles of the forebrain. That on the striatal side of the ventricle (latero-

ventral periventricular gray) will be considered first. At the anterior end of the forebrain the periventricular gray is composed of long, somewhat rod- or spindle-shaped cells, intercalated in the course of dorsoventrally running fiber bundles (pl. 3, figs. 5 and 6). This band lies definitely in relation, on the dorsal side, with the accessory hyperstriatal and dorsal and ventral hyperstriatal areas. Near the posterior end of the dorsal hyperstriatal area the periventricular gray becomes infiltrated with larger cells apparently directly continuous with this hyperstriatal area (pls. 4 and 5, figs. 9 and 10). Then the inner layer of the ventral hyperstriatal area takes on a cortex-like appearance and the smaller cells of the lateroventral periventricular gray become intermingled with it (pls. 5 and 6, figs. 11 and 12). Gradually the periventricular layer, just beneath the ventricle, and in relation with the neostriatal area, becomes infiltrated with larger cells, so that the inner part of this striatal area presents the appearance of a corticoid lamina continuous on the side away from the ventricle with the remainder of the cell mass (pls. 8 and 9, figs. 16 to 19). This lamina is continuous dorso-lateralward with the ventral hyperstriatal area to the caudal end of that nuclear center. Behind this point the periventricular gray persists as a more or less definite lamina, clearer in some sections than in others, to a transverse plane through about the middle of the nucleus taeniae (pl. 9, fig. 18). Situated dorsal to this latter nucleus and forming in its middle portion a conspicuous bulge on the ventricular wall is a nuclear mass which we have labeled *m* on plate 9, figure 18. *m* is not, at all levels, distinct from the overlying neostriatum, although through its central portion it forms a clearly delimitable cell mass. Ventrally, it lies in close relation with nucleus taeniae. At present its place in the general nuclear plan of the hemisphere is not known, but at certain levels the periventricular gray lies in intimate relation with it. Likewise, a distinct lamination of the neopallial layer extends medialward from it, forming the lower border of the neostriatum, but this latter lamina soon disappears. Behind the

level of *m*, the periventricular layer persists and as the posterior end of the hemisphere is reached gradually becomes more conspicuous. Lateralward, it lies in evident relation with the overlying corticoid surface layer of the hemisphere (pl. 9, fig. 19). Medialward, at the caudal end of the hemisphere, a cell thickening at the ventromedial pole of the ventricle lies in relation with the posterior end of this periventricular gray.

A similar periventricular band (the mediodorsal periventricular gray) is to be found under the dorsolateral surface layer throughout much of its extent (pl. 3, figs. 5 and 6; pls. 4 to 9, figs. 9 to 18). As the more posterior regions of the hemisphere are reached, both the dorsolateral surface area and the periventricular gray become very small and ultimately practically fused and both appear to be represented by scattered cells along the very thin outer ventricular wall in the caudal part of the hemisphere (pl. 9, fig. 19).

Whatever further its functions may be, it is evident from its arrangement that the periventricular gray represents neurones intercalated in the course of fiber bundles. We shall take occasion to discuss this later with reference to the related fiber systems. Similarly intercalated cells are to be found in relation with other fiber systems of the avian forebrain. Attention has been called to the nucleus intercalatus hyperstriati (field A of Rose). Intercalated cells are also clearly present in the course of the dorsal medullary lamina, the ektostriatum and even the archistriatum primitivum partakes in part of the nature of intercalated cells in the course of the lateral forebrain system. All of these suggest that the number of relatively short neuraxes and of neurone chains of several links are factors to receive consideration in the study of the behavior of avian forms.

PREOPTIC AREA (pls. 3 and 4, figs. 7 to 9). In the sparrow the preoptic area begins as a mass of small cells grouped around the third ventricle in the region anterior to the entrance of optic fibers into the brain. These fine cells mark the cephalic end of the nucleus preopticus medialis, which is,

in all probability, the homologue of the mammalian nucleus of that name (Gurdjian, '27), but which is comparable to the nucleus periventricularis preopticus (Huber and Crosby, '26) or nucleus preopticus (Cairney, '26) of reptiles. This nucleus passes over without sharp demarcation into the more highly organized infundibular areas behind it.

External to the medial preoptic nucleus are the more scattered cells of the lateral preoptic area (pl. 4, fig. 9), which, as in mammals (Gurdjian, '27), are intermingled somewhat with the fiber bundles of the region. At the more anterior levels of the nucleus preopticus medialis four other nuclear masses, more or less distinctly associated with it, can be identified; these are the nucleus magnocellularis interstitialis, the nucleus of the diagonal band of Broca, the nucleus preopticus anterior, and group 'a,' an area which is probably comparable with a group termed 'a' by Röthig ('11) in *Emys* and by ourselves in alligator ('26). Nucleus magnocellularis interstitialis (pl. 3, fig. 7; pl. 4, fig. 9) is represented in sparrow by a small group of large cells which lies dorsal to the underlying optic chiasma and dorsolateral to the angle of the ventricle, partly in association with the tractus septo-mesencephalicus and partly with the forebrain bundle. The nucleus preopticus anterior consists of a band of cells intermingled with the medial optic nucleus, but easily distinguishable by the larger size and deeper staining qualities of its cells (pl. 3, fig. 7). At first it is somewhat spoon-shaped, the bowl of the spoon enclosing the nucleus preopticus medialis, gradually the lower portion becomes separated and forms a distinctly stained round mass which soon disappears. The handle shortens and disappears, except for a small band of cells which becomes continuous with the bed nuclei of the commissures (particularly the portion between the anterior and pallial commissures). The thickening of the cells of the preoptic area at the angle of the ventricle (pl. 3, fig. 7; pl. 4, fig. 9) corresponds to the group 'a' (*gr.a.*) of alligator. Between the medial preoptic nucleus and the ventricular wall is a row of scattered cells, intercalated in the course of a fiber

tract (pl. 4, fig. 9). These become continuous with the stratum cellulare internum (pl. 4, fig. 9) of the infundibular region and are regarded as the preoptic exponent of that system. They are probably the homologue of the mammalian preoptic periventricular nucleus of mammals (Gurdjian, '27), though not that of reptiles.

In dove, nucleus preopticus medialis consists of fine, densely packed cells situated on either side of the ventricular wall in the preoptic region. This layer of cells becomes directly continuous with a cell column which is found in a similar position in the infundibular region. External to the medial preoptic nucleus are scattered cells which form the lateral preoptic nucleus, which is really formed of scattered cells intermingled with fiber bundles. The nucleus preopticus medialis in the duck is not columnar in arrangement, but consists of an irregularly shaped cell mass just above the chiasma.

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. A group 'a' can be recognized similar in its relations to that described for sparrow. The stratum cellulare internum has essentially similar relations. It lies close to the ventricular wall in the region between the anterior commissure and the optic chiasma as a band of deeply staining cells continuous dorsally with some smaller cells of a similar arrangement. Gradually it extends farther dorsalward until, in the region of the hippocampal commissure, it forms a narrow band of scattered cells and fibers which extends from slightly below the ventral border of the hippocampal commissure to almost the lower limit of the ventricular wall. The upper part of this stratum cellulare internum is continuous posteriorly with the deeply staining thickly set cells of the nucleus internus inferior anterior (possibly the nucleus labeled 'n' by Rendahl; the homology is uncertain), which lies in a curve corresponding to the indentation of sulcus medius of the diencephalon and with the

stratum cellulare internum ventrale of the infundibular region.

The parrakeet preoptic area resembles most closely that of the sparrow, the same nuclei being recognized in the former as in the latter bird. There are some slight differences in form relations, but these do not appear to be of sufficient significance, with our present knowledge, to justify a detailed description for parrakeet.

Before closing the account of the preoptic areas, attention must be called to a curiously arranged, deeply staining group of cells, which are most highly developed in the material available in the chicken brain (pl. 4, fig. 8), although representatives of them have already been mentioned in the above discussion under the name of nucleus magnocellularis interstitialis. In chicken this system forms the most conspicuous nuclear constituent of the preoptic area, is found through practically its whole extent and becomes continuous caudally with certain diencephalic centers. To the entire nuclear mass the name of nucleus magnocellularis interstitialis has been applied. In chicken the anterior portion of the preoptic area is occupied by a mass of scattered cells, large in size and deeply staining, which occupies the ventromedial portion of the brain wall just cephalad to the optic chiasma and medial to the septo-mesencephalic tract with which it lies in close relation. They spread out lateralward along the course of the septo-mesencephalic tracts and form ultimately a cluster of deeply staining cells from the region of those tracts to the medial surface of the hemisphere, along the ventral wall. Similar cells extend dorsomedially along the course of the fibers and a band follows the preoptic ventricle dorsally in the midline (nucleus magnocellularis). The part of the cell mass directly associated with the septo-mesencephalic tracts (nucleus magnocellularis interstitialis intermedialis) forms a quite evident nuclear group which extends back along the tract into the anterior end of the diencephalon—in our sections to transverse planes passing through the posterior region of the optic chiasma and the anterior com-

missure. Considerably before this level has been reached, a small group of the cells separates off from the main mass in order to accompany the septo-mesencephalic tract lateralward. This group (nucleus magnocellularis interstitialis lateralis) extends slightly farther caudalward than the nucleus magnocellularis interstitialis intermedialis. Radiating out from the nucleus magnocellularis interstitialis toward the deeper regions of the diencephalon are lines of cells (nucleus magnocellularis interstitialis dorsalis) which ultimately are arranged as scattered groups of cells along the course of the forebrain bundles in the form of nucleus prestriaticus of Rendahl. The scattered cells of the nucleus magnocellularis interstitialis medialis are among the cells of the stratum cellulare internum and, in part, the medial preoptic nuclei. Some of them even lie internal to the former nucleus and so very close to the ventricular wall. They are present in varying amounts in different sections. In many other birds there is a scattered cell group associated with the septo-mesencephalic tract which is probably the homologue of the nucleus magnocellularis interstitialis lateralis just described. An account of the caudal extension of this nuclear group within the diencephalon is to be found on page 91.

B. Diencephalic and certain mesencephalic centers

In an earlier section of the paper reference has been made to the literature dealing with the diencephalon. In the account which follows this brief introduction, under the description of the various diencephalic nuclei, reference to the earlier account of respective nuclei will be made whenever it is possible to homologize our results with those of former workers. We shall here mention briefly some of the more outstanding contributions to our knowledge of the avian diencephalon. The work of Edinger and Wallenberg ('99) constitutes the point of departure for much of the later work on nuclear configuration and fiber connections within the diencephalon of birds. It must be supplemented by some of the earlier work on optic relations and centers (Bellonci, '88;

Perlia, '89; Singer and Münzer, '90, and others) to which reference has been made previously (p. 16). Reviews of the earlier work are to be found in the texts of Edinger ('08) and of Ariëns Kappers ('21). In 1909, Mesdag published an account of the development of the nuclei of the brain in chick embryos, and this included a brief description of certain of the thalamic centers. Ingvar's paper on the evolution of the thalamus, which will be considered later, appeared in 1923. In 1924, two papers dealing with avian diencephalic centers made their appearance; one by Groebbels, the other by Rendahl. Groebbels, who based his work on dove and chicken, gave an account of a number of thalamic and midbrain centers and of certain of their fiber connections. Rendahl concerned himself with the question of segmentation within the diencephalon, arriving at the conclusion that it represented three neuromeres. The areas respectively derived from them he termed, in part following Kupffer, parencephalon anterius and posterius and the synencephalon. Then he traced the progressive development of the nuclear masses in each of these segments through various embryonic and young stages of chick brain to adult conditions. For the details of the distribution of the nuclear groups direct reference should be made to his contribution. The paper is very well done. Our own observations for the most part accord extremely well with the results of Rendahl, although we have not followed his nomenclature. The last account of avian diencephalic centers to come to our attention is that of Craigie ('28), who has described a number of nuclear groups and fiber paths in the brain of the humming bird. Certain variations in pattern and in form relations and in some cases differences in interpretation of the details of the cytoarchitectonic structure of the region have made necessary a description of the area in sparrow and dove and some reference to nuclear grouping in other available material, in order to make clear our account of the relations of the fiber paths to the specific nuclear areas.

Area ventralis anterior (pls. 5 and 6, figs. 10 to 12). The bed nuclei of the commissures become continuous with a some-

what scattered mass of cells which runs forward into the anterior end of the diencephalon medial and dorsomedial to the occipito-mesencephalic tract. This is comparable to the area ventralis anterior of alligator and is so named here.

Nucleus dorsomedialis anterior (pls. 6 to 8, figs. 13 to 16). The dorsomedial part of the anterior thalamic region is occupied by a nuclear mass made up of medium-sized, deeply staining cells, showing, however, no massing of the elements such as distinguishes the neighboring nuclear mass, nucleus dorsolateralis anterior. Nucleus dorsomedialis anterior was designated the area dorsalis by Rendahl ('26) and was described by him in chicken. In our own chicken material it is present in substantially the relations given by Rendahl, occupying the dorsomedial area of the thalamus from a plane near the foramen of Monro to the habenular region medial to nucleus dorsolateralis anterior and extending to the ventricular wall until about the level of the posterior end of the habenula. It is then separated from this wall by the periventricular gray. Its cellular elements are of medium size and scattered, although occasionally they show some secondary grouping (as, for example, a mass of cells in the midst of the general nuclear mass at the level of the habenula, which is possibly the nucleus 1 mentioned and figured by Rendahl).

In the sparrow, nucleus dorsomedialis anterior appears slightly in front of the region of the foramen of Monro. At first it extends back as a slightly curved mass with nucleus dorsolateralis anterior in the hollow of the curve (pl. 7, fig. 15). Then it becomes triangular in outline. Gradually the nuclear mass decreases in size until it disappears at about the level of the middle of the habenular ganglion. In the duck, nucleus dorsomedialis anterior is a relatively large area, similar in general relation to that described for sparrow and chicken, but separated a little farther cephalad from the ventricular wall by the periventricular gray than in the latter form. Its cells are distinctly scattered as compared with those of the nucleus dorsolateralis anterior. It disappears

at about the same level as in the sparrow. In our series of one-day dove the area is actually as well as relatively smaller than in the duck and slightly smaller than in the sparrow. The cell character is likewise somewhat different, a greater number of smaller cells being found scattered among the larger ones, so that the nuclear mass presents here a greater contrast to nucleus dorsolateralis anterior than in the other forms studied. In the adult dove the nuclear mass, beginning at about the foramen, as in other forms assumes soon a relatively round outline in cross-section and then becomes irregularly ovoid in shape, with the lateral part becoming slightly narrower. The position of the nucleus is marked by a distinct bulge in the ventricular wall. Gradually the lateral border becomes less clearly defined, the nucleus decreases in size and is not differentiable in our material after the plane of the anterior third of the habenula. In the adult dove the cells are large and the group has more the character of that found in other adult avian material, particularly that in chicken.

In the parrakeet, nucleus dorsomedialis anterior begins, as in the other forms, near the level of the foramen. It consists of medium-sized cells less densely arranged than those forming nucleus dorsolateralis anterior. It is curved on the side toward this latter nucleus, so that it caps it to some extent. It is relatively smaller than in chicken and duck, and in the series at present available cannot be distinguished as a definite nuclear mass behind the level of the anterior end of the habenula.

Nucleus dorsolateralis anterior (pls. 6 to 8, figs. 12 to 17). Nucleus dorsolateralis anterior pars medialis in the sparrow begins at about the level of the interventricular foramen as a densely stained mass of cells just lateral to the nucleus dorsomedialis anterior. The cells forming the mass are multipolar, medium-sized, and closely packed together. At first the mass is slightly triangular, but soon becomes oval in outline (pl. 7, fig. 15). It then increases in size, particularly on its medial side, and forms an irregularly triangular or almost rectangular mass (pl. 8, fig. 16). It reaches its great-

est size, in the series from which the drawings were made, in a plane through the posterior part of the nucleus rotundus (pl. 7, fig. 15). Farther caudad it becomes more nearly oval again and gradually becomes smaller. It disappears in a plane passing through about the middle of the habenula, its place being taken by nucleus dorsalis posterior. Surrounding the main mass of this nucleus, but particularly numerous on the lateral side where the major bundles of the forebrain lie, are neurones, less deeply stained, and more nearly oval in outline which present consequently a different cytological picture (pls. 7 and 8, figs. 15 and 16). These are intercalated in the course of fiber bundles, particularly of the component of the lateral forebrain bundle which supplies the medial portion of the nucleus dorsolateralis anterior. Laterally, these more scattered cells are continuous with a similarly stained but more compactly arranged nuclear mass which for the present has been termed nucleus dorsolateralis anterior pars lateralis (pl. 7, fig. 15). The inclusion of this relatively distinct nuclear mass within the general area of nucleus dorsolateralis anterior appears to be justified on the ground that they share an area which in several other birds at least is represented by a common nuclear mass. This point will become clear when the relations in other birds are discussed. Behind the pars lateralis of the nucleus dorsolateralis anterior, the less deeply staining cells associated with it continue on the dorsal side of the area, but gradually grow less with the increased size of the nucleus dorsalis posterior and soon become intermingled with this latter nuclear mass, so that their exact posterior termination cannot be established in our sparrow material.

Nucleus dorsolateralis anterior pars lateralis (pl. 7, fig. 15) begins in sparrow at a plane through the anterior part of the diencephalon and passes through the anterior portion of nucleus rotundus in front of the cephalic limits of the nucleus dorsomedialis anterior and nucleus dorsolateralis anterior pars medialis. It lies between the nucleus superficialis parvocellularis lateralward and the forebrain bundles swinging

toward nucleus rotundus medialward and is dorsolateral to nucleus rotundus. It consists of rather deeply staining, medium-sized cells and at all levels is not sharply delimitable from the nucleus superficialis parvocellularis. Posteriorly, it goes over without sharp demarcation, in our sparrow material, into the intercalated cells associated with the forebrain bundle and into nucleus dorsolateralis posterior. Nucleus dorsolateralis anterior pars lateralis with the associated scattered cells about the pars medialis and the nucleus dorsolateralis posterior form an encircling cell layer around nucleus dorsolateralis anterior pars medialis.

Nucleus dorsolateralis posterior (pl. 6, fig. 13; pl. 8, fig. 17). In sparrow, as the habenular area is reached, the more scattered cells surrounding the deeply stained mass of the nucleus dorsolateralis anterior pars medialis gradually become more compact, perhaps more particularly on the lateral side. As the pars medialis disappears, these other cells gradually encroach upon the area formerly occupied by it, and by the time the posterior end of the habenula is reached occupy much of the dorsal part of the diencephalic wall. They persist to levels through the posterior commissure. The area has been termed nucleus dorsolateralis posterior (pl. 8, fig. 17). The grouping of its cells suggests that it may be capable of still further subdivision.

The dorsolateral nuclei in dove, chicken, parrakeet, and duck. In the dove, the nucleus dorsolateralis anterior cannot be subdivided into a pars lateralis and a pars medialis. A more or less homogeneous nuclear mass occupies the region between the nucleus dorsolateralis anterior and the nucleus superficialis parvocellularis. In the dove, as in sparrow, nucleus dorsolateralis anterior begins at about the level of the interventricular foramen. For the first part of its extent it occupies the region just lateral to the nucleus dorsomedialis anterior. In its upper part the cells are of medium size and rather closely packed together, and at the anterior end, where the fiber tracts (forebrain bundles) come into relation with the nucleus, show an arrangement into groups with

spaces for the fiber bundles between them. The nucleus is largest at the plane of the anterior end of the habenula where it extends immediately under the habenula almost to the midline. Ventromedialward at this level, however, there is a nuclear group (nucleus dorsalis posterior) resembling in general character the cells of the nucleus dorsomedialis anterior and not sharply defined from them. With the increases in size of this latter group, nucleus dorsolateralis anterior is gradually restricted to the more dorsolateral portion of the area originally occupied by it and disappears slightly behind the level of the habenula. In the one-day, eight- and ten-day doves the relations are essentially the same, again the more ventral cells of the group appearing slightly larger and also those cells which lie in relation with the fiber tracts. This nucleus presents essentially the same appearance and relations, with some minor variations, in the duck as in the dove.

Rendahl described this whole nuclear complex in chicken under the name of A_2 . This includes nucleus dorsolateralis anterior pars medialis, probably also pars lateralis, and nucleus dorsolateralis posterior. In our own material there is no evident division into a pars medialis and a pars lateralis in chicken. While the separation into a nucleus dorsolateralis anterior and posterior is very indistinct in this bird and probably would not be made on the basis of chicken material alone, a careful comparison with the dove series shows that suggestions of such a division may be seen in chicken.

In parrakeet nuclear groupings more nearly resembling those in sparrow are to be found. The nucleus appears first at the anterior end of the diencephalon in a position similar to pars lateralis in sparrow, but gradually the mass develops medialward and there is no sharp division between lateral and medial portions at all levels. Gradually the nucleus dorsolateralis posterior swings in from the lateral side. The nucleus dorsolateralis anterior decreases in size and disappears.

A comparison of the conditions in the various avian forms may make the preceding account clearer and easier to relate

to the literature. That part of the thalamus, roughly between the ventricular wall and the nucleus of the septo-mesencephalic tract, has been repeatedly termed nucleus dorsalis. This nucleus dorsalis is divisible in all the bird brains at our disposal, and obviously in Rendahl's material as well, into a medial and a lateral portion. The medial part is in all probability the medial portion of the nuclei dorsalis anterior and posterior of Edinger and Wallenberg. It is represented in the more anterior regions of the diencephalon by the area dorsalis of Rendahl or the nucleus dorsomedialis anterior of our account. (Probably posteriorly it contains, in part at least, the nucleus internus superior of Rendahl. This will be discussed later.) The lateral portions of the nucleus dorsalis anterior and posterior are two relatively distinct nuclear masses in the dove, which was the form on which Edinger and Wallenberg ('99) worked. They can be seen quite readily in duck; but much less easily in chicken, so that there was abundant reason for regarding them as a single nuclear mass, as Rendahl has done for that form. In sparrow not only are both anterior and posterior divisions of the nucleus dorsolateralis (of our terminology) present, but in the anterior part there is a differentiated portion indicated by a group of neurones of special stain and character which is looking toward greater differentiation of the nucleus dorsolateralis anterior and which has been termed for greater ease of description, *pars medialis*, while to the less differentiated more lateral part the name of nucleus dorsolateralis anterior *pars lateralis* has been applied. In parrakeet the process of differentiation appears to have gone still further. Most of the nucleus consists of deeply staining closely arranged neurones, and the *pars lateralis* is small and difficult to distinguish. Thus there is a common plan of the dorsal nuclear group throughout the avian forms considered, the differences being largely those of degree than of fundamental pattern.

The whole area was termed nucleus dorsalis by Edinger ('08), Ariëns Kappers ('21), and Groebbels ('24). We have

been unable to satisfactorily homologize our groups with those of Craigie, but undoubtedly the nuclei anteriores thalami, pars supracommissuralis, and pars postcommissuralis of the humming bird fall within the nuclei dorsales of other avian forms.

Nucleus superficialis parvocellularis (pls. 5 to 9, figs. 10 to 18). This name was given by Rendahl ('24) to the band of gray forming the greater part of the lateral portion of the dorsal diencephalon. As used by him, the nucleus included the nucleus lateralis of earlier workers (p. 77) and the 'Kern des Scheidewandbündels' of Edinger and Wallenberg ('99, p. 255, fig. 5), or—as this latter cell mass is sometimes called—the nucleus of the septo-mesencephalic tract, together with some other associated gray. We have retained the name of nucleus lateralis, because in most of our material it is a differentiable nuclear group. As to the most suitable name for the remainder of the area we are in considerable doubt. It is associated with the septo-mesencephalic tract and in synaptic relation with it, but, likewise, it has connections with other fiber systems. Since to Rendahl belongs the credit of recognizing the extent of this nuclear mass and since our findings can be most readily homologized with his figures and descriptions of this nuclear mass, for the present at least the name of nucleus superficialis parvocellularis will be used for the area (exclusive of nucleus lateralis). Nucleus superficialis parvocellularis appears first in the dove material as scattered cells about the level of the anterior end of nucleus dorsolateralis anterior and continues posteriorly to the level of the posterior commissure. Within the cell mass and at the side of it are to be seen the cross-cut and obliquely cut bundles of the tractus septo-mesencephalicus. At the level of the anterior end of the habenula the nuclear mass becomes intermingled with larger, deeper-staining cells which in a measure form an appendage to the nucleus lateralis (see the description of that nucleus). This latter nucleus occupies the dorsolateral surface of the diencephalon, just dorsomedial to the small-celled superficial nucleus. Just external to the

latter nucleus is a very thin superficial layer, which is evidently intercalated in the course of fiber bundles.

In sparrow essentially the same pattern is found, although there are some minor variations. The name, nucleus tractus septo-mesencephalici, is more appropriate here by reason of the presence of medium-sized and relatively large cells in the nuclear mass. The nucleus, irrespective of the terminology used, consists of a circular or oval mass of cells situated at the anterior end of the diencephalon, continuous at its upper border with the band of cells which are the probable homologue of nucleus lateralis of other forms. Gradually the nucleus in question becomes triangular and ultimately band-shaped; swinging dorsalward, it can be followed to the level of the posterior commissure. The relations of the nucleus in parrakeet resemble those described for sparrow. In duck the conditions are essentially the same, the size and appearance of the nucleus resembling more particularly that of dove.

Nucleus lateralis (pl. 8, fig. 16). The name, nucleus lateralis, was given by Edinger and Wallenberg ('99) to a nuclear mass situated dorsomedial to the nucleus tractus septo-mesencephalici (Kern des Scheidewandbündels of their nomenclature). They homologized it with the 'Kern der Decussatio inferior' of Münzer and Wiener ('98). It is probably, although not certainly, the nucleus lateralis anterior identified in *Pratincola rubicola* by Ariëns Kappers ('21, p. 875, fig. 468). Groebbels ('24) considered it the homologue of the geniculatum laterale externum of his terminology.

This latter homology does not appear to us tenable so far as conclusions may be based on the comparison of figures of the two groups of workers. The corpus geniculatum laterale externum of Groebbels lies ventrolateral to nucleus rotundus, while the nucleus lateralis of Edinger and Wallenberg lies in the dorsal portion of the thalamus, dorsomedial to the nucleus tractus septo-mesencephalici, and further "liegt in den frontalen Thalamusabschnitten und erreicht dicht unter dem Epithalamus auf weite Strecken der Aus-

serand." A further complication in making accurate comparison is offered by their statement that "Der Kern ist in allen Abbildungen zu klein gezeichnet möglicherweise gehören ihm auch Teile des als Nucleus dorsalis ant. und post. lateralis bezeichneten Kernes an." Rendahl ('24) regarded the nucleus lateralis as the anterior part of his nucleus parvocellularis superficialis. The nucleus in question is not that labeled in penguin as nucleus lateralis by Ingvar ('24). Presumably, it is included in the area designated as lateral thalamus by Craigie ('28), although this latter homology is uncertain. We may now consider its relations in the material available.

In the sparrow, nucleus lateralis (pl. 8, fig. 16) is represented by a band of deeply staining cells situated along the dorsolateral margin of the diencephalon. This band is definitely differentiable from the smaller cells of the nucleus parvocellularis superficialis ventrally. Caudally, it continues as a poorly defined group composed chiefly of cells scattered among those of the small-celled superficial nucleus. In the parrakeet, larger, more deeply staining cells of the nucleus lateralis are discernible among the cells of nucleus parvocellularis superficialis, but the two are greatly intermingled, and in our present material it is not possible to draw any definite boundaries between them.

In the chicken, along the lateral surface of the dorsal part of the diencephalon, except in its more posterior portions, two nuclear bands are discernible. One consists of deeply staining, medium-sized or fairly large cells. This lies in the dorsal half of the area and is regarded as nucleus lateralis. The other is a band of very small cells to which we have specifically applied the term nucleus parvocellularis superficialis, which Rendahl used for the whole nuclear group.

In the dove, nucleus lateralis consists of a mass of deeply staining, medium-sized, multipolar cells beginning at about the level of the anterior end of the habenular nucleus and extending back to about the middle of the region. At first it is somewhat comet-shaped with a nearly round upper portion

and a tail which is intermingled with cells of the nucleus parvocellularis superficialis, but which we consider differentiable from the latter by reason of their deep staining and larger size (this probably accounts for Rendahl's homology quoted above). A little farther caudad, the tail portion disappears and the group is clearly defined as an irregularly round, rather closely packed mass which gradually decreases posteriorly. In the one- and eight-day doves the nucleus is not definitely definable from the nucleus parvocellularis superficialis, although in the latter there is an accumulation of deeper-staining cells in its dorsomedial portion which suggests the future position of nucleus lateralis. In the ten-day stage it is clearly present, though not so large as in the adult stage.

In the duck the nucleus lateralis has somewhat different form relations. It appears as a densely staining band of cells, the inner portion of which is more or less intermingled with the lateral part of nucleus dorsolateralis anterior and which extends internal to the stria medullaris, while the outer part gradually rounds off into a mass of cells which extends farther caudad, but which disappears before the habenula is reached. A small 'tail' of cells extends caudad from its outer portion into the region of nucleus superficialis parvocellularis. From the above description it will be seen that there is considerable variation in the degree of development of the nuclear group in the different birds studied.

Nucleus tractus habenulo-peduncularis (pls. 8 and 9, figs. 16 to 18; also in pl. 19, figs. 40 and 41, B and C). This nucleus is found at the level of the habenula. In dove (pl. 19, figs. 40 and 41, A, B, and C) it consists of a small group of cells dorsal to the nucleus rotundus and continuous with it. Gradually the main mass of cells assumes a triangular and then a more or less oval outline, and the neurones are so arranged that they show the presence of fiber bundles passing between them. The cells themselves are large and multipolar and resemble in general character those of nucleus rotundus, although on the whole they are possibly somewhat

smaller. Scattered neurones of the same type and some smaller elements can be followed for a short distance along the fiber bundles of the system associated with this nucleus and which run medialward and ventromedialward from it. Essentially the same relations are to be found in chicken, where the nucleus has been designated A_3 by Rendahl. The nuclear mass is present in duck, but in the material at present available it has not been possible to define it so clearly as could be done for dove. Possibly this is in part due to a lack of fiber-stained material of the brain of duck. In sparrow (pls. 8 and 9, figs. 16 to 18) the nucleus is clearly evident in essentially the relations described for dove. Curiously enough, it has not been possible as yet to locate the nucleus in the parrakeet material at our disposal. Nucleus tractus habenulo-peduncularis is associated with the habenulo-diencephalic and habenulo-peduncular systems in the bird. It is probably not homologous with the mammalian nucleus parafascicularis.

Habenula (pl. 6, fig. 13; pl. 8, figs. 16 and 17; pl. 19, figs. 40 and 41, A, B, and C). The medial and lateral habenular nuclei have been identified by the majority of workers on the avian brain (Edinger and Wallenberg, '99; Rendahl, '21; Groebbels, '24, and others). They were called the 'zentrale Zellpartie' (medial habenular ganglion) and the habenular ganglion (lateral habenular nucleus) by Münzer and Wiener ('98). Mesdag ('09) could find only one nuclear mass. In our material the relations are essentially the same as those described previously, so that no detailed account is considered necessary. Nucleus superficialis epithalamicus, first identified by Rendahl as a superficially placed, small-celled mass, can be found in all of our material. It probably represents an intercalated nucleus for stria medullaris fibers to the habenula.

Nucleus rotundus (pls. 5 to 7, figs. 10 to 15; pl. 10, fig. 20; pls. 14 to 16, figs. 31 to 34; pl. 19, figs. 40 and 41, A, B, and C). A very brief description of this nuclear group will suffice, since it is one of the most generally recognized of the nuclear masses in birds. Among earlier workers it was

known by various names: thus it was the corpus geniculatum externum of Turner ('91) and the zentralen Kern of Bellonci ('83). Practically all later workers in this field (Stieda, '69; Edinger and Wallenberg, '99; Edinger, '08; Ariëns Kappers, '21; Groebbels, '24, and others) have termed it nucleus rotundus; it was designated as nucleus A₁ in Rendahl's paper ('24) on the chicken. Contrary to what one might expect from the name and from the classical descriptions, the nucleus rotundus is, in several avian types at least, not round in cross-section except at the extremes of the mass. Rendahl described it as round for hen, and our own chicken material indicates that it does have approximately this outline at most transverse levels, but in the sparrow it shows a circular outline only at the caudal and cephalic ends. In the intermediate regions it has a straight inner border and a much-curved outer one and, except for a notch at the ventromedial border, has a planoconvex contour rather than a circular one. The above description of the sparrow, except for very minor differences, applies to the duck; in the dove the same conditions are found except that the mass has not varied so far from the circular contour. In this latter form the round outline found at the anterior end becomes irregularly oval with a projection extending dorsomedially from it in the dorsomedial portion; still farther caudad, it acquires a planoconvex outline with the straight portion on the medial side (not quite as evident as in the sparrow and the duck) and then reacquires a more or less circular outline before its termination. The shape of the nucleus is very suggestive of the nucleus ventralis of lower mammals (with which we agree with Ingvar ('23) that it is homologous) as well as the nucleus rotundus of reptilian forms. In parrakeet the nucleus rotundus is round at the anterior end, but farther caudad, at levels near the middle of the nucleus, it is irregular in outline—slightly concavoconvex. Still farther caudad, near its posterior end, it becomes oval or nearly circular again.

Nucleus subrotundus (pl. 7, fig. 15). A band of dark-staining, distinctly multipolar cells extends from the region just ventral to nucleus ovoidalis diagonally downward, accompanied in its course by a fiber band. This nuclear mass, given the name of nucleus subrotundus by Rendahl ('24), has essentially the same relations in all the avian forms studied by us.

Nucleus intercalatus (pls. 5 and 6, figs. 10 to 13). Medial to the nucleus rotundus are components of the lateral fore-brain bundle to the lateral geniculate nucleus and to the tectum. This bundle of fibers is the stilus corporis geniculati of Edinger and Wallenberg ('99). Among the fibers are a few scattered nerve cells as well as neuroglia cells. At its basal portion, just dorsal to the corpus geniculatum laterale, is a nuclear mass termed nucleus intercalatus by Edinger and Wallenberg. This cell mass had previously been termed nucleus interstriaticus by Münzer and Wiener ('98) and later was called nucleus ventralis by Edinger ('08) himself. Ariëns Kappers ('21) used the name of nucleus intercalatus as did Craigie ('28), while 'r' was used by Rendahl ('24) to designate the group. We are uncertain as yet of Groebbels' identification or nomenclature for this nucleus. Nucleus intercalatus is present in all the birds studied in essentially the same relations as those described by the other observers.

Nucleus ovoidalis (pls. 6 and 7, figs. 12 to 15). Nucleus ovoidalis is the nucleus anterior ventralis of Edinger and Wallenberg ('99) (although not the nucleus anterior of Edinger, '08) and is the nucleus B of Rendahl. The term 'ovoidalis' was proposed by Craigie ('28), who identified this nuclear mass in the humming bird. The nucleus in question is present in all of the available avian material in the form of a rather sharply delimited, oval mass consisting of medium-sized and large multipolar cells, rather closely packed together. Within the mass there are some secondary cell groupings, and a very definite fiber band passes ventralward and slightly ventrolateralward from it. In the dove, as in the hen, the nucleus lies rather near the midline, just ventral

to the plane of the medial sulcus between the nucleus rotundus lateralward and the nucleus internus medialward and dorsal to the forebrain bundle. In the sparrow (pl. 6, fig. 12; pl. 7, fig. 15) the nucleus lies considerably farther lateralward, being dorsolateral to the forebrain bundles. It lies in practically the same position in parrakeet. The position of the nucleus in the duck is intermediate between that in sparrow and in dove, resembling that in the former more than that in the latter. The nucleus, in each form, has maintained a constant position in reference to nucleus rotundus, and in each case there is a tail of cells like the tail to a comet which extends downward from it and which is accompanied by a fiber tract. This extension of cells has apparently been grouped by Rendahl with his nucleus subrotundus. Edinger and Wallenberg ('99) regarded this nucleus as the homologue of a part of the nucleus anterior of higher forms and considered the related fiber tract homologous with the Vicq d'Azyr bundle of mammals. This interpretation has been questioned by certain observers, as, for example, Rendahl ('24) and Craigie ('28). The evidence available does not favor such an interpretation.

Nucleus tractus tectothalamici cruciati (pl. 5, fig. 10). *Nucleus lateralis anterior* (pl. 4, figs. 8 and 9). At about the level where the preoptic area passes over into the diencephalon a small nuclear group makes its appearance in association with the tractus tecto-thalamicus cruciatus. To this nucleus has been given the name of nucleus tractus tectothalamici cruciati. In its more caudal portion it is not possible in the present material to delimit the nucleus sharply from the nucleus intercalatus. Just lateral and then slightly dorsolateral to this nucleus is the nucleus lateralis anterior of Edinger and Wallenberg ('99). This is a round or oval group of medium-sized cells which runs for only a short distance and then, particularly in sparrow, is replaced by the anterior end of nucleus rotundus. In dove it is relatively better developed and continues slightly farther caudalward. Groebbels ('24) has homologized this with his nucleus genicu-

latum laterale externum, but there is some uncertainty as to this homology, since he carries the latter nucleus back to the region of the posterior commissure ('24, p. 388, fig. 2).

Nucleus geniculatus lateralis (pls. 5 and 6, figs. 10 to 13; pl. 7, fig. 15). In dove and sparrow—in fact, in avian forms in general—a band of cells, consisting of a layer of large, more deeply staining cells bounded on both sides, but particularly on the ventrolateral side, by smaller, more scattered cells, is found in the ventral part of the diencephalon just dorsal to the optic tract, ventral and medial to the nucleus rotundus and ventral to the nucleus intercalatus. This mass of cells, which is here termed the nucleus geniculatum laterale, has been known by a variety of names, although the consensus of opinion appears to be, as we ourselves hold, that it is associated with optic impulses. Thus, Bellonci ('88), Münzer and Wiener ('98), and Edinger and Wallenberg ('99) spoke of it as nucleus geniculatus; Edinger ('96 and '08) and Ariëns Kappers ('21) called it corpus geniculatum laterale, and Rendahl termed it the medial superficial layer, but favored the name corpus geniculatum thalamicum. He considered it only in part homologous with the lateral geniculate of reptiles and mammals. Groebbels applied to it the name corpus geniculatum laterale internum. The cell arrangement suggests that of the lateral geniculate of alligator. It constitutes nucleus superficialis synencephali.

Nucleus superficialis synencephali (pl. 5, fig. 11; pl. 6, figs. 12 and 13; pl. 7, fig. 15). *Nucleus superficialis magnocellularis* of Rendahl (pls. 6 and 7, figs. 12, 13, and 15). Just lateral to the main mass of nucleus geniculatus lateralis is a small group of large cells which receive optic fibers and which appear to belong to the geniculate complex and are included in it by Craigie and Brickner ('28) and Craigie ('28). This group of cells extends dorsalward lateral to the nucleus superficialis magnocellularis and constitutes the nucleus superficialis synencephali of Rendahl, which is better developed in chicken than in sparrow.

In sections of sparrow diencephalon passing through the anterior end of nucleus ovoidalis a small triangular nucleus is found ventrolateral to nucleus rotundus and dorsolateral to the lateral geniculate nucleus. Gradually it swings ventralward and lies just lateral to the lateral geniculate nucleus in the position figured for the nucleus geniculatum laterale externum by Groebbels. Dorsalward, the nucleus goes over into a band of deeply staining cells which lie external to rotundus and dorsalward in relation with the medial optic bundle. This nucleus and the band associated with it have been termed by Rendahl the nucleus superficialis synencephali. They include the nucleus geniculatum laterale externum and the nucleus geniculatum tertium anterius of Groebbels ('24), (whether or not nucleus superficialis magnocellularis also is included in these nuclei of Groebbels we cannot determine from his figures). So far as can be judged, they are a part of the lateral geniculate complex of Mesdag ('09). For the present the name used by Rendahl has been retained until a better knowledge of mammalian conditions may make possible further homologies.

Just lateral to the lower portion of nucleus superficialis magnocellularis is a band of tectal gray (pl. 7, fig. 15; pl. 8, fig. 16). This lies along the inner portion of the tectum, but is divided at most levels into dorsal and ventral portions to permit the passage of fiber tracts to and from the inner part of the tectum. This band of cells has been figured by Rendahl ('24, p. 321, fig. 72) as a part of the tectal area and is so regarded and labeled (pl. 7, fig. 15, *tect.gr.*) in the present account. It undoubtedly receives optic fibers at its lower border and is possibly the lateral optic nucleus of Craigie and Brickner ('28) and Craigie ('28), although this latter homology is uncertain. Its lower portion is the geniculatum laterale tertium posterius of Groebbels ('24), if his figure (p. 388, fig. 2) has been correctly interpreted.

Nucleus postrotundus (pl. 8, fig. 16). The name postrotundus, as applied to avian brains, was first used by Ariëns Kappers ('24). His figures do not show the cytoarchitecture

of the region, and it is difficult to determine certainly to which of several nuclear groups he applied the name. The only other observer to use this name was Craigie ('28), who appears to have applied it to a part of the area designated as postrotundus by Ariëns Kappers. Again lack of cell pictures makes it difficult to establish homologies. In so far as we are able to determine, the nucleus so designated in the present paper is the nucleus postrotundus of Craigie. To the other nuclear group in the region, to which apparently no name has been applied, the designation of nucleus posteroventralis has been given.

Nucleus postrotundus, as the term is here used, consists of a mass of medium-sized cells applied directly to the posterior and posteromedial surface of nucleus rotundus. The mass assumes a triangular outline for a short distance, then gradually decreases in size and disappears at about the level of exit of the third nerve in our series.

Nucleus posteroventralis (pl. 7, fig. 15; pl. 8, fig. 16). In the description of nucleus rotundus it was stated that the cell mass had a fairly regular planoconvex outline in its posterior portion, except at its lower border where there was a notch. In this notch region are fine, small cells intermingled with some larger cells and fiber bundles. Rows of smaller cells continuous with this nuclear mass and associated with a fiber bundle extend dorsalward just medial to nucleus rotundus. As one passes caudalward this mass of cells increases with the decrease in size of nucleus rotundus (pl. 8, fig. 16). On approaching the mesencephalic regions the larger cells of the nuclear mass gradually become more scattered and more and more intermingled with the smaller cells of the region until at the plane of the posterior commissure the nuclear mass disappears. This may be nucleus ventralis of Groebbels' description; we have been unable to determine this point from either his figures or description. Nucleus posteroventralis is probably included by Rendahl with his nucleus rotundus. It does not appear quite as well developed in our chicken material as in the preparations of some of the other birds; neverthe-

less, it is differentiable as a small cell mass situated at the ventral angle of nucleus rotundus. This nucleus is also present in parrakeet in essentially the relations found elsewhere in the birds. It is possible that this is the nucleus to which reference is made by Craigie ('28, p. 398), but if so, no name is given for it.

Nucleus postero-intermedialis (pl. 8, fig. 16). Dorsomedial to the nucleus posteroventralis, medial to nucleus rotundus and postrotundus, although separated from them by fiber bundles and associated cells, and ventral to the occipito-mesencephalic tract is a large-celled, rather columnar-shaped nuclear mass which persists from the level of the more posterior part of nucleus rotundus to a plane just in front of the caudal end of the habenula. At present the homologies of this nucleus are unknown. It is here termed nucleus postero-intermedialis.

Entopeduncular nuclear group. Edinger and Wallenberg ('05) termed the paleostriatum primitivum of the present account the nucleus entopeduncularis and then traced scattered cells of the same nucleus along the lateral forebrain bundle in its course through the diencephalon. The paleostriatum primitivum is now rather generally regarded as the homologue of the globus pallidus, and the term nucleus entopeduncularis is usually applied to only the preoptic and diencephalic portions of the nucleus entopeduncularis of these early observers. This portion of the nucleus was described by Edinger and Wallenberg ('99) as beginning at the plane of the anterior commissure in the dove. This cell mass split into dorsal and ventral groups in correspondence with the formation of the dorsal and ventral divisions of the lateral forebrain bundle. The ventral nucleus was traced to the region of the ganglion (or nucleus) isthmi. A single nuclear mass was identified by Rendahl as nucleus entopeduncularis; however, he regarded nucleus praestriaticus of his terminology as a part of the entopeduncular group of Edinger and Wallenberg. An entopeduncular nucleus was also identified by Groebels ('24).

In sparrow, scattered cells accompany the lateral forebrain bundle in its course ventromedialward from the paleostriatum primitivum, and at the level of the anterior commissure a distinct entopeduncular nucleus can be identified connected to the paleostriatum primitivum by strands of cells intermingled with the forebrain bundles. This portion of the nucleus is particularly, although not exclusively, concerned with synaptic relations with fibers of the dorsal supra-optic system. It is comparable with the nucleus decussationis supra-opticae dorsalis of alligator, and is so termed here to differentiate it from other entopeduncular groups (pl. 5, fig. 10). Just ventral to this nucleus is a second cell group (pls. 5 and 8, figs. 11 to 15), similar in type, which is the entopeduncular nucleus proper or ventral superior entopeduncular nucleus, as it is termed here, to differentiate it from a smaller ventral inferior group of the same general type. The nucleus entopeduncularis ventralis superior of the above terminology is the group 'G' of Rendahl, which he regards, likewise, as entopeduncular. A small group of cells dorsomedial to this nucleus (not illustrated) is the homologue of the nucleus praestriaticus described by Rendahl for chicken. It is small in sparrow. Rendahl has called attention to the fact that, embryologically, the nucleus praestriaticus and the ventral entopeduncular group have different anlagen. Certainly, in the adult sparrow they have the appearance of being similar in character, but in chicken, nucleus praestriaticus is associated with nucleus magnocellularis interstitialis. In following the course of the forebrain bundles farther caudal at various levels scattered masses of entopeduncular cells are found in course. The groups are often quite distinct from each other.

The entopeduncular nuclear group is present in all the avian material available and the relations are essentially the same as in sparrow, although there are certain minor variations. Thus in dove the nucleus of the dorsal supra-optic decussation and the ventral entopeduncular group, with a secondary division into superior and inferior portions, are

clearly differentiable. A nucleus praestriaticus is also demonstrable. Since the variations in the entopeduncular and associated nuclear groups in the other birds studied present no facts of outstanding interest, further details regarding them will be omitted.

Associated with this entopeduncular group in general type of relation is a bed nucleus for the tractus thalamo-frontalis internus. This lies dorsomedial to the nucleus rotundus at the place of entrance of the tract into the nucleus dorso-lateralis anterior pars medialis in sparrow.

Diencephalic periventricular gray and hypothalamus. The periventricular gray in birds has been described more or less completely by a number of writers (Edinger and Wallenberg, '99; Edinger, '08; Groebbels, '23; Rendahl, '23, and others). The German writers, as, for example, Groebbels, speak in general of a 'zentrales Höhlengrau,' consisting of a medial cell column—nucleus magnocellularis strati grisei—and, situated lateral to it in the more caudal regions, a round cell mass which they term nucleus parvocellularis strati grisei. It is difficult, however, to homologize their nuclei with those present in the avian material available. Rendahl has given the most detailed account of this region, and it is his account that we have found most easy to substantiate. Frequent reference is made to it in the following pages.

The diencephalic periventricular gray cannot be sharply delimited cephalically from the periventricular preoptic areas. Certain of the cell masses, as, for example, the stratum cellulare internum, are directly continuous from one area to the other. Any line which in the following account we are able to draw between the respective areas is more or less arbitrary.

In the sparrow, at the posterior end of the preoptic region, ventral to the anterior commissure and its associated bed nucleus, is to be seen an indistinct nuclear mass directly continuous with the stratum cellulare internum (pl. 5, fig. 10). This is the nucleus internus inferior anterior of the present account. Farther caudally it is much more definitely delim-

ited (pl. 5, fig. 11; pl. 6, fig. 12). It can be followed in the diencephalon, where ultimately it becomes almost continuous with the nucleus internus inferior of Rendahl, or the nucleus internus inferior posterior of the present paper. This latter nucleus was described by Rendahl ('24) for hen as a 'ziemlich grossen kleinzelligen Kern,' which lies 'dicht an dem Ependym.' In our own material it appears to consist of an admixture of small and medium-sized cells. Nucleus internus inferior posterior is present in all the forms studied in a position just ventral to nucleus internus superior and often just internal to nucleus ovoidalis. Its shape changes with the shifts in position of this latter nucleus, being oval in the hen (Rendahl, '23) and irregular with an outer portion curved about nucleus ovoidalis in the dove (pl. 6, fig. 13). In the sparrow (pl. 7, fig. 15) one finds the dorsal and medial surfaces at right angles to each other with the ventrolateral border in the form of a curve. The nucleus is much larger here—a fact correlated with the much more lateral position of the nucleus ovoidalis. The arrangement of the neurones, particularly in this latter form, suggests that they are accompanied by fiber bundles.

In the dove, near the line between the preoptic and hypothalamic regions, there is a large-celled deeply staining nuclear mass which stands out both in cell type and in staining qualities from the remainder of the periventricular gray. This nuclear mass at its greatest extent runs ventralward from the medial diencephalic sulcus through about one-half of the hypothalamus, extending dorsoventralward. It is not a wide band, but extends to about the level of the anterior end of the habenula. So far as we have been able to determine, it does not correspond exactly to any hypothalamic nuclei previously described, although it is probably a part of nucleus magnocellularis strati grisei of Edinger and Wallenberg, and we have adopted their term for it. Posteriorly, it is continuous with the stratum cellulare internum and the nucleus internus inferior posterior. We regard it as homologous with the less-developed nucleus internus inferior anterior of

sparrow. This nucleus is likewise present in parrakeet, where it consists of a deeply staining, but small band of relatively large cells capped by a dorsal portion of spindle-shaped cells (the nucleus internus superior anterior), which latter resemble and are continuous with the nucleus internus superior. Ventrally, this band goes over into the stratum cellulare internum ventrale without having any such clearly differentiated ventral part as we found in chicken. Laterally, it is in close association with nucleus internus inferior posterior. The nucleus internus inferior anterior disappears in front of the level of nucleus ovoidalis, its place being taken by nucleus internus inferior posterior. The nucleus internus superior anterior mentioned above for parrakeet is likewise present in dove. In both these forms, and in duck as well, there is a definite layer of periventricular gray between the nucleus dorsomedialis anterior and the surface of the ventricle. This, to which the name of nucleus internus superior anterior has been applied, is represented only by relatively few scattered cells between the nucleus dorsomedialis anterior and the ventricle in the sparrow, and Rendahl ('24) has not demonstrated it in chicken. Farther caudally, however, there is a clearly developed band of periventricular gray in the region to which Rendahl has applied the name of nucleus internus superior, and it is so labeled in our figures.

Mention was made previously of the group of large cells to be found in the preoptic region in the chicken (p. 67). As the diencephalic regions are approached, this nuclear group, which for convenience has been termed, as a whole, nucleus interstitialis magnocellularis, forms a mass of cells which extends from just below the sulcus medius diencephali ventralward toward the lower end of the ventricle. This is termed nucleus magnocellularis interstitialis medialis (pl. 4, fig. 8, B, C, D). Nucleus magnocellularis interstitialis lateralis is continued from the preoptic area into the anterior end of the diencephalic region, lying dorsolateral to the dorsal division of the septo-mesencephalic tract (pl. 4, fig. 8, B). Nucleus magnocellularis interstitialis dorsalis is likewise present as

scattered cells lateral to nucleus magnocellularis interstitialis medialis (pl. 4, fig. 8, B, C, D). Nucleus magnocellularis interstitialis medialis consists in reality of two portions: medialis b, a more dorsal part of rather large, densely placed cells; and medialis c, a more dense, but smaller ventral portion with scattered cells between the two. Soon the cells disappear from the lower part of the ventricular wall, while in the more dorsal regions a band of scattered cells extends farther up along the ventricle. Gradually medialis c begins to overlap the other portions and becomes more or less continuous with nucleus magnocellularis interstitialis dorsalis. The mass on either side takes on an irregularly triangular shape with one angle dorsal, one ventral, and one lateral. The nucleus increases rapidly at the lateral angle, spreading lateralward along the course of the stria terminalis. At this time it has also spread dorsalward internal to nucleus dorso-medialis anterior. The whole mass (nucleus magnocellularis interstitialis medialis and nucleus magnocellularis interstitialis dorsalis) on both sides forms a sort of butterfly picture, with the antennae represented by the dorsal continuations, the wings by the lateral prolongations, and the body by the main nuclear mass. Then it decreases in size. Medialis b, which becomes definitely separable from the ventral portion, now appears homologous with the nucleus internus superior anterior of dove. Medialis c suggests the nucleus internus inferior anterior of parrakeet, dove, and certain other avian forms. While in chicken they represent differentiated portions of the nucleus interstitialis magnocellularis, in the other birds studied they are in themselves discrete nuclear masses where present.

The stratum cellulare internum of the avian preoptic area is directly continuous with the diencephalic stratum cellulare internum (pls. 5 to 8, figs. 10 to 16) and more particularly, but not exclusively, with its ventral portion. This diencephalic nuclear region, which was identified by Rendahl for chicken, lies just under the ventricular wall limited dorsally by the nuclei internus inferior anterior and posterior and

extending ventralward around the lower border of the ventricle to fuse with its fellow of the other side. It is not possible at all levels to differentiate between the dorsal and ventral divisions. After the appearance of the differentiated ependyme along the third ventricle wall, the dorsal internal stratum, in general, lies above and the ventral below it in sparrow, and in other birds as well, but there is no sharp line between the two in most of the material. The scattered cells lateral to the stratum just described and which lie in relation with the occipito-mesencephalic and forebrain systems have been termed stratum cellulare externum, and are so labeled here (pls. 5 to 7, figs. 10 to 14).

The ventral part of the periventricular diencephalic areas has been divided into a series of nuclear groups by Rendahl, and part of these have been designated by letters. The following account is based on sparrow. In this description due reference has been made to Rendahl's account wherever homologies were possible. However, to attempt to compare such small nuclear groups in one form with similar groups in another form is a hazardous undertaking where this comparison must be based entirely on relative position of the nuclei, and not at all on fiber connections.

The more ventral parts of the diencephalic areas along the ventricular walls external to stratum cellulare internum can be differentiated at their cephalic end into a larger medial and smaller lateral cell mass, differentiable from the scattered cells of the stratum cellulare externum by their deeper staining and greater compactness. The medial group (pl. 5, fig. 10) is in all probability a part of the nucleus periventricularis hypothalami, as the name has been applied to reptiles (Draco, de Lange, '13; Huber and Crosby, '26). It is probably K_1 of Rendahl. Since it represents only a part of that cell column, however, the term here applied is nucleus hypothalamicus anterior medialis (pl. 5, fig. 10). The smaller lateral group (pl. 5, fig. 10) is termed nucleus hypothalamicus anterior lateralis. Just dorsal to the supra-optic decussation is a large-celled, but small nuclear mass to which the name of

nucleus supra-opticus (pl. 5, fig. 10) has been given. This is possibly Kl_1 of Rendahl. Gradually nucleus hypothalamicus anterior medialis becomes broken up into three more or less distinct divisions (pl. 5, fig. 11). Of these the more dorsal has been termed pars dorsalis (Kc of Rendahl), the next, pars intermedialis (Ka of Rendahl), and the most inferior, pars ventralis (K_2). Nucleus supra-opticus has disappeared and the scattered cells of the more anterior portion of nucleus hypothalamicus inferior take its place. By the time the plane shown in figure 12, plate 6, has been reached, the dorsal part of nucleus hypothalamicus anterior medialis has almost disappeared and the posterior end of pars intermedialis has been reached, but the pars ventralis still remains. Ventralward, the scattered cells of the cephalic part of nucleus hypothalamicus inferior are still evident. Dorsal to this are the deeply stained cells of the nucleus hypothalamicus posterior lateralis. This nucleus is characterized particularly by the row-like arrangement of its cells and consists of dorsal and ventral portions. At the level of figure 15, plate 7, nucleus hypothalamicus inferior (m of Rendahl) has taken on its characteristic appearance. It is composed of a mass of small and medium-sized cells which surrounds the ventral part of the ventricle and then widens out on each side. Dorsal to it is the caudal portion of nucleus hypothalamicus anterior medialis pars ventralis. Not clearly distinct from it at this level is nucleus hypothalamicus posterior medialis. A few cells of nucleus hypothalamicus lateralis are to be found capping it lateralward. Lateral and ventrolateral to these areas are the scattered cells of the area h.d.Z. of Rendahl.

Dorsal to the ventral part of the nucleus hypothalamicus anterior medialis at this level is a rather large, not sharply delimited nuclear area to which the name of nucleus hypothalamicus dorsalis posterior is applied. Between the ventral supra-optic system and the area h.d.Z. of Rendahl is a large-celled nuclear mass apparently associated with the ventral supra-optic fiber system. To it the name of nucleus decussationis supra-opticae ventralis has been given. Gradually the

nucleus hypothalamicus medialis disappears and nucleus hypothalamicus posterior medialis becomes a discrete nuclear group. A reference to plate 8, figure 16, shows nucleus hypothalamicus posterior lateralis (nearly gone), nucleus hypothalamicus posterior dorsalis and nucleus hypothalamicus inferior still present. Behind this level the first two nuclei disappear. The somewhat scattered cells of the last-mentioned nuclear group become directly continuous with a somewhat more dense nuclear mass, which is divisible secondarily into dorsal and ventral portions. We are inclined to agree with Rendahl that these portions are to be regarded as homologous with the nuclear groups of the mammillary body and to term them nuclei mamillares medialis dorsalis and medialis ventralis. Ultimately, the dorsal nuclei fuse to form an unpaired median nucleus (pl. 8, fig. 17). The scattered cells of the nucleus mamillaris lateralis are to be found at the outer side of the dorsal nucleus of the medial group (pl. 8, fig. 17). It is to be emphasized that there is suggestive evidence by way of fiber connections for the homology of these nuclear groups with the mammillary nuclei of higher forms. However, such homology is at present largely conjecture and awaits further proof.

Nucleus principalis precommissuralis (pl. 7, fig. 15). This nucleus consists of large scattered cells lying lateral to the nucleus rotundus between that nuclear mass and the layer of tectal gray. It extends caudalward behind rotundus, but is gradually replaced by nucleus spiriformis pars lateralis. This nucleus is probably homologous with the 'grosszelliger Kern des Geniculatum' of the Edinger and Wallenberg account. The name here used is the one by which the nuclear mass was designated by Rendahl ('24).

Nucleus ectomamillaris. Nucleus externus (pls. 8 and 9, figs. 16 to 18). The nucleus ectomamillaris or the basal optic ganglion of Ariëns Kappers ('21, p. 870) has been described by various workers on the avian brain (Edinger and Wallenberg, '99; Groebbels, '24, and others). It lies on the ventral surface of the brain about halfway between the ventral inner

border of the tectum and the outgoing root of the IIIrd nerve. It is an irregularly spherical mass consisting of rather large scattered cells intermingled with smaller ones. The above account is based particularly on dove and sparrow, but it has a relatively similar position and appearance in all the forms studied. Between it and the tectum is the small poorly defined cell group which Rendahl called nucleus externus (ex).

Nuclei of the medial longitudinal fasciculus. Nucleus ruber. There is a group of nuclei situated near the line between the mesencephalon and diencephalon (the synencephalon of Rendahl) which has been relatively completely described by various observers. They fall outside of the primary interest of the present paper. Consequently, no further description of them need be given other than a brief statement of their positions, characters, and homologies. They fall into a medial group consisting of the three nuclei of the medial longitudinal fasciculus (Nc.f.d. 1 and 2 and Nc.m. of Rendahl) and the nucleus ruber. The position of the latter is indicated in part in plate 8, figure 17, and plate 10, figure 20. All of this medial group was identified in the avian forms studied, but further account of relations and connections of its nuclei cannot be given at this time. The lateral group consists of four chief nuclei which are generally grouped under the term of pretectal nuclear masses, since the greater number of them are concerned in interrelating the tectal regions with diencephalon and lower centers. These nuclei are nucleus pretectalis, nucleus subpretectalis, and nucleus spiriformis medialis and lateralis. The pretectal and spiriform nuclei have been described recently for humming bird by Craigie ('28).

Nucleus pretectalis (pl. 8, figs. 16 and 17; pl. 10, fig. 20; pl. 11, fig. 22). *Nucleus subpretectalis* (pl. 8, figs. 16 and 17). The first, nucleus pretectalis, has been described by all workers on avian material since the early account of Edinger ('96). Even before that time, Turner ('91) had mentioned it under the name of nidulus posterior. Nucleus pretectalis appears as a dark-staining cell group dorsal to nucleus spiri-

formis and immediately medial to the tectal area and not far ventral to the medial optic tract. It is interconnected with a larger mass of more scattered cells lying ventral to the nucleus spiriformis and dorsal to the nucleus externus (ex) of Rendahl and to the most ventral part of the tectum. This is nucleus subpretectalis of Rendahl and ourselves. It may be the nucleus hypothalamicus posterior of Groebbels. It is in all probability the homologue of the nucleus pretectalis of reptiles which has shifted ventralward in the avian brain due to the ventrolateral shifting of the tectum.

Nucleus spiriformis (pl. 7, fig. 14; pl. 8, figs. 16 and 17; pl. 9, fig. 18; pl. 10, fig. 20; pl. 11, fig. 22). Edinger and Wallenberg ('99) divided nucleus spiriformis into a medial and a lateral portion. The lateral portion is represented in the present material by large, deeply staining, multipolar cells lying just ventral to nucleus pretectalis, dorsal to nucleus subpretectalis and medial to the tectal centers, but separated from them by the interconnecting fiber tract mentioned as occurring between the pretectal and subpretectal groups. The medial portion of spiriformis (pl. 9, fig. 18) consists of a pyramidal mass of cells so placed that the peak of the pyramid points toward the midline. The cells of the medial portion are more closely packed together than are those of the lateral part. The pyramidal outline is evident only in certain sections. Elsewhere the nuclear mass is more irregular in shape with scattered cells. In the region of the posterior commissure it extends relatively nearer to the midline. Differentiation into the two parts of this nuclear mass has led to the application of a variety of terms to them. Thus Rendahl limited the name nucleus spiriformis to the lateral portion and applied the name nucleus dorsocaudalis to nucleus spiriformis medialis of Edinger and Wallenberg ('99). Groebbels ('24) called the medial portion nucleus commissurae posteriorae, if we have interpreted him correctly. The above account, based primarily on dove and sparrow, can likewise be documented in the other avian forms available for study.

Tectal and subtectal centers (pls. 5 to 11, figs. 10 to 22; pls. 14 to 17, figs. 30 to 37). The greater size of the eyes and of the optic fibers in birds is associated not only with highly developed diencephalic optic centers, but with a very large and a highly differentiated optic tectum. Our Weigert, Cajal, and toluidin-blue series show clearly the basis for the various subdivisions of the tectum, to which reference has already been made on page 12. The differences in opinion are due chiefly to differences in the technique employed rather than to any fundamental difference in pattern, as the material available, which consists of Weigert, Cajal, Cox, and toluidin-blue series, makes very evident. Since so many excellent accounts of the details of the layer arrangement in the region are available, and particularly since that of Ramón y Cajal ('91) is based on sparrow, a further description of the area is deemed unnecessary. The details are indicated in the figures and need not be further discussed for the present. The avian tectal centers show a shift from the dorsal position usual in vertebrates to a distinctly lateral (as in dove, duck, and chicken) or even ventrolateral position (as in sparrow and parrakeet). This second migration is due, undoubtedly, as Ingvar has pointed out, to the great influence of the mighty optic tracts and is to be regarded in all probability as an illustration of the neurobiotactic theory of Ariëns Kappers.

An inferior quadrigeminal body or inferior colliculus is not visible from the brain surface in any of the birds with which we are familiar. However, rolled in on the under surface of the optic ventricle and bulging into it from the ventromedial side is the so-called ganglion mesencephalicus lateralis pars dorsalis, which Ariëns Kappers ('21) and certain others are inclined to regard as a homologue of the inferior colliculus of higher forms—a homology which appears to us justifiable.

Nucleus mesencephalicus lateralis pars dorsalis (pls. 8, 9, and 10, figs. 17, 18, and 20). At about the level of the posterior commissure in our sections of dove there appears a thickening along the under wall of the optic ventricle con-

sisting of cells similar to those forming the IIIrd cell layer or periventricular layer, and continuous with this layer around the angles of the ventricle. Medialward, cells of similar type pass toward the midline, scattering more or less between the bundles of the dorsal and ventral divisions of the posterior commissure. Gradually the mass thickens somewhat. It consists of medium-sized cells which, in our preparations at least, are not very deeply stained and which, behind the level of the ventral part of the posterior commissure where the optic ventricles open out into the aqueduct, becomes continuous with the periventricular gray which runs toward the midline. At about the middle of the optic ventricle, in the midst of these more scattered cells, there appears an ovoid mass of deeply staining, medium-sized cells. This represents the cell mass of the nucleus proper, presumably the equivalent of the nucleus of the inferior colliculus of mammalian forms, while the more scattered cells form a sort of capsule around this more central mass. The IIIrd cell layer of the optic tectum soon forms a very definite layer around the central nucleus between it and the ventricular wall.

The central nucleus ultimately grows smaller, becomes slightly crescent-shaped in cross-sections, and then ultimately is represented by a small patch of cells which disappears, leaving caudad to it for a short distance the more scattered cells of the capsular portion. The above account is based on dove. Figures were not drawn to illustrate it, because the relations here are essentially the same as those in the other available avian material, if due account is taken of such slight variations as are produced by differences in the tilt of the ventricle in parrakeet and particularly in sparrow. Consequently, figure 18, plate 9, drawn from preparations of the brain of this latter bird, provides all the necessary illustration of this nucleus.

The above-described nucleus is the ganglion or nucleus mesencephalicus lateralis, pars dorsalis of Ariëns Kappers ('21), and that portion which is to be regarded as the homologue of the torus semicircularis of lower forms. This

investigator labeled a nucleus just ventral to this, the ganglion mesencephalicus lateralis pars ventralis. This latter nucleus consists of scattered cells intermingled with some larger cells. On the whole, so far as our preparations show, it is an undifferentiated nuclear mass broken into by fiber bundles. This portion of the nucleus, according to Ariëns Kappers, receives secondary V fibers.

Nucleus isthmi pars principalis (pls. 8 to 11, figs. 17 to 22). Curiously enough, for a number of years two distinct nuclear groups have been described under the name of nucleus, or more frequently ganglion, isthmi. The earlier workers, Bellonci ('88), Perlia ('89), Jelgersma ('96), Wallenberg ('98), and others, applied the term ganglion isthmi to a nuclear group situated in the dorsal region of the mesencephalon, medial to the tectum and at about the level of the nucleus of the third nerve. To this part of the nucleus Craigie ('28) recently gave the name of nucleus of the isthmo-optic tract ('nucleus tractus isthmo-opticus').

Ariëns Kappers ('21), in his discussion of the avian mid-brain and thalamus, gave an account of another portion of this nuclear group. His description, which is based, as he states, upon the work of Pedro and S. Ramón y Cajal and of Sala, concerns itself with a more ventrally situated group of nuclei. These lie ventral and ventrolateral to the nucleus mesencephalicus lateralis in their more cephalic portion. Farther caudalward, they lie ventrolateral to the nucleus of the isthmo-optic tract and ultimately become surrounded at their caudal end by the optic tectum. For this portion of the nucleus isthmi Craigie ('28) has suggested the name of *pars parvocellularis* or *pars principalis*. The former is inapplicable to our material, since the outer or superior portion is distinctly large-celled; the term *pars principalis* is open to question, but may be applied in the sense that this is the larger portion of the nucleus. The terms 'pars superior' and 'pars inferior' (Ariëns Kappers, '21, and others), which are sometimes applied to them, are likewise not generally applicable, since at some levels the superior part is ventral to

the inferior part. The names of *pars principalis parvocellularis* and *pars principalis magnocellularis* have been used for the two divisions of nucleus isthmi in this region (pls. 9 and 10, figs. 18 to 21). Associated with the *pars principalis* is another nuclear group, the nucleus *semilunaris* of Mesdag ('11), for which Craigie ('28) has suggested the name of *pars magnocellularis ventralis nuclei isthmi*.

Pars principalis magnocellularis nuclei isthmi (pls. 9 and 12, figs. 18 to 27) makes its appearance in the sparrow material in a plane passing through the middle of the habenular region dorsally and the hypophysis ventrally. The nucleus in question lies ventral and slightly ventromedial to the lateral mesencephalic nucleus. At first it is an irregularly oval mass, but soon it breaks up into an inner and an outer slightly curved band with the *pars principalis parvocellularis* making its appearance in the curve of the inner band (pls. 9 and 12, figs. 18 to 21). The magnocellular portion remains about the same size for a considerable distance, but the parvocellular portion increases greatly in size. The cells of this latter portion are actually medium-sized, only small in comparison with the other portion. They are arranged in rows which radiate dorsoventrally, and at some levels a hilus is apparent on the dorsal side. The shape of the nucleus is best seen from the figures, as is also its relation medialward to nucleus *semilunaris*. *Pars principalis parvocellularis* elongates and forms a long column of cells capped ventrolaterally by the nucleus *principalis magnocellularis*. Gradually the small-celled part decreases somewhat and the large-celled portion swings around it, in somewhat the shape of a flattened crescent, with its outer and inner bands of cells still discernible. Behind this level both portions of the *pars principalis* decrease rapidly, and first the small-celled and then the large-celled portion disappears.

Pars principalis magnocellularis and *parvocellularis* are present in all the available avian material and essentially similar, although exhibiting some differences in minor details. The greatest differences in form relations appear to be evi-

dent in the sparrow. This, in part, may be due to the plane of the section, but certainly some of the differences are not governed by this factor. In comparison with dove, the pars principalis parvocellularis and pars principalis magnocellularis nuclei isthmi of sparrow lie relatively somewhat nearer to each other. The large-celled mass appears to be differentiated into a more ventral band of intermingled larger and smaller cells and a dorsal portion consisting of scattered large cells which have not been demonstrated in dove. In our own preparations its half-moon shape is not so evident as was the case in the dove material, the whole nuclear mass being rather compact. It extends in both birds behind the level of the small-celled portion and still exists as a definite bar of cells, deep-staining and very conspicuous in the tectal region in sections passing through the exit of the trochlear nerve. Likewise, the smaller-celled portion never assumes so characteristic a half-moon shape in sparrow as it does in dove.

In chicken and in duck the relations resemble more nearly those in dove, though perhaps the semilunar shape of the nuclei, at least in the planes of our sections, is less evident in the duck than in the chicken and dove. Likewise, in parrakeet there is quite a marked resemblance to dove and no noteworthy differences so far as is known. Contrary to expectations, the conditions in parrakeet appear to resemble, in some respects, those in dove more nearly than those in sparrow, although the half-moon shape of the small-celled nucleus is somewhat less evident in parrakeet than in dove.

Nucleus semilunaris (pl. 9, fig. 18; pl. 10, fig. 20). Ariëns Kappers ('21) quotes Mesdag ('11) as dividing the nucleus semilunaris into lateral and medial portions, both of which received secondary eight and lateral lemniscus fibers. These two nuclei are not sufficiently clearly differentiated in the figures of either Mesdag or Ariëns Kappers to make possible exact homologies. The medial nucleus is believed to be the region described and labeled as nucleus semilunaris of the present account, and consequently the pars magnocellularis

ventralis nuclei isthmi of Craigie ('28). Unfortunately, it is not large-celled as compared with the rest of the nuclear masses of the complex in sparrow or certain other birds, so that the name *semilunaris*, although almost equally inappropriate, is retained to avoid the multiplication of synonyms. This nucleus is intimately associated with the *pars principalis nuclei isthmi* and is probably to be regarded as an integral part of that complex. The *pars lateralis nuclei semilunaris* of the earlier account has been christened *nucleus lemnisci lateralis* in the present paper.

In transverse sections passing dorsally through the posterior commissure and ventrally through the tegmentum in the region of the red nucleus, the nuclei in question are to be found. The more lateral, ventral, and ventromedial of these—the *nucleus lemnisci lateralis*—is a large-celled nuclear mass lying along the course of the lateral lemniscus. This nucleus extends dorsalward into the subtectal regions and so reaches a position medial to the *nucleus semilunaris* (*pars medialis* of the earlier workers) and ventromedial to the small-celled portion of *nucleus isthmi*. Farther caudalward, the *nucleus lemnisci lateralis* becomes larger and extends farther ventralward in the tegmentum. Here, and here only, its shape might justify the name *semilunaris*. Behind this level it continues back along the course of the lateral fillet as scattered large cells which, at the level of the trochlear nucleus, lie in the lateral part of the tegmentum just ventral to its union with the tectal centers. This nucleus disappears in front of the level of disappearance of the large-celled portion of *nucleus isthmi*. The medial portion of the *nucleus semilunaris* of earlier workers, or the *nucleus semilunaris* of the present account, consists of cells which make their first appearance just medial to the medial part of the small-celled portion of *nucleus isthmi*. These cells resemble in type the cells of the adjacent portion of *nucleus isthmi* and in places at the anterior end of this latter nucleus appear to be directly continuous with it. Followed caudalward, the nucleus increases somewhat in size, becomes more or less semilunar in

outline, and extends really along the border between the sub-tectal regions, lying dorsomedial to the nucleus lemnisci lateralis. Nucleus semilunaris disappears in front of the level of termination of nucleus lemnisci lateralis and in front of the trochlear decussation. At its posterior end its cells are somewhat more deeply stained than are those of the small-celled part of the nucleus isthmi.

The two nuclei are clearly developed in the other avian forms. In the dove the nucleus semilunaris is club-shaped throughout part of its extent, but never, so far as we can see, semilunar, while the nucleus lemnisci lateralis consists of a round mass of cells which is ventral and sometimes slightly ventromedial to the semilunar nucleus. Both of the nuclei are associated with lateral fillet fibers.

The two nuclei are present in parrakeet. The nucleus semilunaris consists of deeply staining cells which bear less resemblance here than in other forms to the small-celled mass of the nucleus isthmi, but which lie in close proximity to it. The nucleus lemnisci lateralis is irregular in shape, consisting of scattered cells along the course of the lemnisci fibers.

In duck the medial part of the semilunar nucleus is deeply stained and is almost S-shaped rather than half-moon-shaped. The lateral portion consists of scattered cells, ventral to the medial part and scattered along the course of the medial part. It is not possible at present to give the homologies in chicken.

Nucleus isthmo-opticus (pl. 9, fig. 19). The position of nucleus isthmo-opticus is best understood by reference to plate 9, figure 19. This nucleus has been identified by various observers and was recently described by Craigie ('28), so that a detailed account of it is unnecessary. However, it has certain morphologic characteristics which are of interest and concerning which little appears to have been written. In sparrow it consists of a round or oval nuclear mass, appearing slightly in front of the level indicated in the figure. This mass consists of an outer layer of compactly arranged cells surrounding an inner more scattered mass of neurones of similar type. At the level at which figure 19, plate 9, is taken,

the outer layer has thinned down to a single row of cells which is separated from the inner portion by a zone almost free of cells. Caudalward, the inner mass disappears first and then the outer, somewhat thickened layer.

In certain other birds the nuclear form is quite different. Thus in dove there is an outer more compact portion, but the inner portion is not represented, except for a very few scattered cells. Instead of presenting an oval outline, from the beginning the nucleus is greatly folded, so that it resembles in appearance a miniature inferior olive. The fiber bundles swing in between the folds.

The nucleus of the mesencephalic root of V. The cells of the mesencephalic root of V may be observed in a number of figures, for example, plate 9, figure 18. No formal account of them is here given, since they were fully considered and figured by Weinberg ('28) in his study of the mesencephalic root of V in various vertebrate forms. The account for bird is based on the same material as that listed in this communication.

COMPARISON OF AVIAN DIENCEPHALIC AND CERTAIN MESENCEPHALIC CENTERS WITH CORRESPONDING REPTILIAN CENTERS. It is not possible at present to homologize all the nuclear masses of the avian diencephalic, tectal, pretectal, and subtectal centers with those of either reptilian or mammalian forms. For the most part, the discussion of mammalian homologies will be postponed to a later paper. A brief comparison, however, of the avian centers with those of reptiles may have some value. The epithalamic centers of the avian and reptilian brains are directly comparable. The differences in the habenulae of the two forms are differences in size rather than in type of nuclear mass. Birds and reptiles alike have lateral and medial habenular nuclei, the latter nucleus divisible into dorsomedial and ventrolateral portions. Subhabenular nuclei are present in both forms. The variation in size of the habenulae in the various birds and their relatively greater extent in reptiles is associated with the greater development of the olfactory system in those forms having the larger habenular nuclei.

Extending from the medial wall of the avian hemisphere into the beginning of the diencephalon and lying in intimate interrelation with the bed nuclei of the commissures and tracts of the region is the area ventralis anterior. This is directly comparable to a similarly designated area in alligator. The more dorsal portion of the dorsal thalamus is occupied anteriorly in birds by the nucleus dorsomedialis anterior, the nucleus dorsomedialis lateralis, and nucleus superficialis parvocellularis (nucleus tractus septo-mesencephalici). Nucleus dorsomedialis anterior is comparable to the nucleus of that name described by Huber and Crosby ('26) for alligator and by Cairney ('27) for *Sphenodon*. In neither birds nor reptiles does this nuclear mass receive any appreciable number of forebrain fibers; it is similarly located in the two types.

The avian nucleus dorsolateralis anterior is divisible secondarily in sparrow into a pars lateralis and a pars medialis. In some birds it appears to be a more or less homogeneous nuclear mass. This nucleus is homologous with the nucleus of similar name in alligator and in *Sphenodon*, and is likewise a recipient of forebrain fibers. The reptilian equivalent of the avian nucleus superficialis parvocellularis cannot be established beyond question. We should like to suggest, however, that the following facts justify the consideration of nucleus ovoidalis of alligator and *Sphenodon* as the possible homologue of the avian nucleus in question. In the first place, the position of the two (dorsal to the forebrain bundle and lateral to nucleus dorsolateralis anterior) is approximately the same. Cairney traced fibers from the medial and possibly from the lateral olfacto-habenular tracts to the nucleus and found it to lie in relation with fibers which pass from the region of the pallial commissure to the medial forebrain bundle and hence to the hypothalamus. Thus the area is related with the basal olfactory centers of the medial wall. Further study of the alligator material available suggests (although it does not conclusively demonstrate) that there are fibers from the medial forebrain bundle (or asso-

ciated with it) which swing around the ventral side of the lateral forebrain bundle and into nucleus ovoidalis. Such fibers would be homologous with the tractus septo-mesencephalicus of birds and the nucleus with the nucleus of that tract or nucleus superficialis parvocellularis. Such fibers are small in number in reptiles as compared with the homologous avian tract, and their nucleus, if such ovoidalis proves to be, is confined to the anterior part of the diencephalon. Contributory evidence to the possible homology of nucleus ovoidalis with nucleus superficialis parvocellularis is to be found in the distribution of optic fibers to the area in both reptiles (*Sphenodon*, Cairney) and birds. Likewise, the homologies of the nucleus lateralis are uncertain, although its position suggests as a possibility its comparison with the differentiable lateral portion (Huber and Crosby, '26, p. 115, fig. 6b) of the nucleus dorsolateralis anterior of the alligator.

Nucleus dorsolateralis posterior of birds includes within it nucleus posterodorsalis and probably part at least of the medial nucleus of reptiles. It is probably homologous to some degree with the nucleus medialis of mammals, since it lies, as does the mammalian nucleus, in close relation with the nucleus tractus pedunculo-habenularis. In this laboratory Rioch has identified the last-named nucleus in mammals.

Fiber connections, as well as general form and relations, indicate strongly that not only is the avian nucleus rotundus the equivalent of the reptilian nucleus of that name, but that also it is homologous with the mammalian nucleus ventralis (as has been suggested by Ingvar, '24, and others). The capsule of cells about it in birds is comparable with the similarly arranged cells in reptiles and rodents (Gurdjian, '27). Behind the nucleus rotundus in birds is nucleus postrotundus. This receives forebrain fibers and is connected with the tectum—relations which suggest nucleus medialis posterior of the alligator—which is similarly situated and similarly connected. Ventral to postrotundus in birds is what is termed nucleus posteroventralis. Its position suggests the nucleus posterior centralis of alligator, but since as yet the connec-

tions of neither cell group are definitely known, aside from certain tectal connections, all homologies must be dispensed with for the present.

The avian nucleus geniculatus lateralis is directly comparable with that of alligator even to the arrangement of its cells in a definite band bounded on either side by a zonal layer. Curiously enough, the nucleus itself is relatively smaller in birds than in alligator. It is supplemented in the avian forms by several smaller nuclear groups, but even so, the indication is that the main effect of the increase in optic fibers as exhibited in bird is to increase the components to tectal and midbrain centers (such as nucleus isthmo-opticus) rather than to increase the diencephalic components. Functionally, this probably makes for more efficient light and visual reflexes, rather than for a high degree of forebrain correlation and control of responses to stimulation of the retina. The nucleus tractus tecto-thalamicus cruciati is the homologue of the nucleus of the same name in alligator.

The homologies here offered for nucleus ovoidalis must be regarded as tentative. This nucleus receives lateral forebrain fibers and is connected with the tectum by a fiber bundle which runs internal to the nucleus rotundus and then ventral to this nuclear mass. In alligator the nucleus diagonalis has similar connections and tectalward directed fibers ventral to the nucleus rotundus, which nucleus in reptiles is more dorsally situated than in birds. The ventral migration of the nucleus rotundus in avian forms would give to the path from nucleus diagonalis toward tectum approximately the tilt of the avian tractus nuclei ovoidalis. Consequently, we hold as probable the homology of nucleus ovoidalis with the main mass of nucleus diagonalis of alligator. The dorsally directed 'tail-like' portion of the comet-shaped nucleus in alligator is probably the equivalent of the avian nucleus subrotundus. Avian nucleus intercalatus is in a situation similar to that of the area ventrolateralis of the reptile and is probably homologous with it, at least in part.

The entopeduncular groups are somewhat more highly differentiated in birds than in reptiles, but are of essentially similar type and significance in the two forms. In each case the groups consist of scattered masses of cells of globus pallidus type, scattered among the fibers of the forebrain bundle. An especially differentiated portion of the system, nucleus decussationis supra-opticae dorsalis, is demonstrable in both birds and alligator.

The hypothalamic region and the diencephalic periventricular gray are comparable in a general way in birds and reptiles. There appears to be a higher degree of differentiation in birds than in reptiles, but on the whole the pattern is distinctly similar in the two forms. The so-called hypothalamic periventricular gray of the reptile contains within it at least the anlage of the avian nucleus hypothalamicus anterior medialis. Scattered cells internal to nucleus periventricularis hypothalami of the alligator are representative of stratum cellulare internum of birds. The reptilian anterior hypothalamic nucleus is the probable homologue of nucleus hypothalamicus anterior lateralis of birds, while the lateral hypothalamic nucleus is probably to be compared with the avian nucleus posterior lateralis, nucleus posterior dorsalis, and other hypothalamic areas as well. The nucleus internus inferior posterior of the sparrow appears to be represented by the area ventromedialis of the alligator. Nucleus hypothalamicus inferior ventralis of sparrow is found in anlage in the nucleus hypothalamicus ventralis of the alligator.

The nucleus ectomamillaris is more highly developed in birds than is its homologous nucleus, the reptilian nucleus of the basal optic root. In both types of animals, however, the known connections are similar. These connections are the basal optic root and connections with the nucleus of the third nerve. In birds the nucleus ectomamillaris is likewise connected with the tectum. A red nucleus and nuclei of the medial longitudinal fasciculus are found in both birds and reptiles.

The pretectal nuclei of birds are represented by nucleus pretectalis, nucleus subpretectalis, nucleus spiriformis with its lateral and medial portions, and functionally at least by nucleus principalis precommissuralis. Nucleus pretectalis and subpretectalis are interconnected by a definite fiber band, and so in a sense may be regarded as a single group. It is, in the main, nucleus subpretectalis, however, which in position and general relations is to be regarded as homologous with the reptilian nucleus pretectalis. Pars medialis of nucleus spiriformis is a nucleus of the posterior commissure comparable to that described by de Lange ('13) for turtle. It is probably the nucleus dorsalis of *Varanus* (Beccari, '23) and of alligator (Huber and Crosby, '26). Whether or not the pars lateralis of nucleus spiriformis is the nucleus spiriformis labeled by Edinger ('08, Bd. 2, S. 158) in *Varanus griseus* as nucleus spiriformis and identified as a small cell group closely related to nucleus pretectalis in alligator we are not at present prepared to state. Nucleus principalis precommissuralis suggests the nucleus lentiformis mesencephali of reptilian forms.

The optic tectum is even more highly developed in birds than in reptiles, having acquired more layers and an even greater relative size. The nucleus mesencephalicus lateralis pars dorsalis, the torus semicircularis or corpus posticum of lower forms is below the ventricle and so entirely hidden from the surface, as in most reptilian forms. Its differentiation in birds into a central nucleus surrounded by a cellular capsule continuous with the optic tectal layers suggests the differentiation in this region in the alligator.

Nucleus isthmi pars principalis is the nucleus isthmi of lower forms, such as reptiles and amphibians. In all of these it has substantially similar connections. In both reptiles and birds the nucleus consists of two portions. Nucleus isthmi pars principalis is much larger and more highly differentiated cytologically in birds than in lower forms. The discussion of its mammalian homologies will be deferred for the present. The equivalent of the avian nucleus isthmo-opticus, if such exists in either higher or lower forms, is at present unknown.

The above brief presentation of the homologies existing between reptilian and avian forms is not complete, many nuclei have received no consideration. It is in many respects to be regarded as tentative and subject to revision, as all such attempts must necessarily be with the present extent of our knowledge. Our desire will be accomplished if it proves somewhat suggestive and helpful. It emphasizes that there is in alligator and avian diencephalon a common pattern. Ingvar has emphasized that the modified position of the avian diencephalic nuclei is due to downward shifting of the tectum (due to optic influences), with the corresponding change in the tecto-thalamic paths and their related centers. A consideration of the above homologies will indicate that such a change in position due to tectal changes has been taken into account. Our results in general substantiate Ingvar's thesis that the diencephalic pattern in the birds is modified by the migration ventralward of the optic tectum.

C. Fiber paths

The following account is based primarily on a study of Cajal material, although the various tracts, so far as possible, have been checked also in Weigert preparations. Certain of the fiber tracts have been described as completely as need be in previous accounts. To such, brief mention only is given. Others have been described, but not in sufficient detail to fulfill our present purposes; here details have been added with more or less account of the general relations, depending upon the necessities of the description. As complete a description as the material permits is given of those fiber tracts which are believed to be new, or where details of their relations appear to have been established. The literature concerned with each fiber system is considered with the account of the paths and need not receive further attention here.

ASSOCIATION BUNDLES OF THE FOREBRAIN. The lateral wall of the forebrain is more or less sharply divided into various areas by the presence of definite fiber laminae. These are the ventral and dorsal medullary laminae (Edinger, Wallen-

berg, and Holmes, '03; Schroeder, '11, and many others), the lamina hyperstriatica of Schroeder ('11), which is formed largely by the fronto-occipital fiber bundle, the superior frontal lamina (the 'Frontalmark' of Edinger, Wallenberg, and Holmes, '03; the 'Untervulstlamina' of Schroeder, '11), and the supreme frontal lamina.

Ventral and dorsal medullary laminae (pls. 12 to 18, figs. 26 to 38). These have been described in detail by Schroeder and others and are indicated in the figures. No further account appears to be necessary. Their nuclear connections are summarized on pages 162 and 163.

Lamina hyperstriatica (pls. 12 to 18, figs. 26 to 38). This lamina likewise has received a detailed description from Schroeder ('11), but there are certain points with regard to its connections which it is desired to emphasize, so that a brief account of its most important constituent, or the dorsal association bundle (Bumm, '83), or the tractus fronto-occipitalis intrastriaticus (Edinger, Wallenberg, and Holmes, '03), will be briefly described. This tract, which is usually termed simply the tractus fronto-occipitalis, but which in sparrow and dove, at least, and probably in other birds might more accurately be named tractus parieto-occipitalis, extends in a frontocaudal direction from the parietal to the caudal region of the hemisphere. Figure 4, plate II, of the Edinger, Wallenberg, and Holmes paper ('03) illustrates the position of the tract. Schroeder ('11) described the tract as connecting the frontal and parieto-occipital parts of the striatum, as being related further to the ektostriatum, to the ventricular 'Marksschicht' of the striatum and as sending fibers to the region from which the dorso-epistriatic tract arises.

Before giving an account of the relations in sparrow it is necessary to emphasize the point that the direction of conduction along the fiber bundle is not known. For convenience it is described from in front caudalward, but this is not intended to imply that impulses necessarily pass in that direction over its fibers. It is probable that it may conduct in both directions. Reference to the terminology of the nuclear

masses as here used as compared with the nomenclature of various observers is to be found under the discussion of the nuclear masses of the hemisphere (pp. 51 to 55).

The fronto-occipital tract is related frontalward with the neostriatum intermediale of the sparrow (field G of Rose). In this nuclear mass can be seen bundles of the tract which break up into finer strands among its cells (pl. 18, fig. 38). These bundles are joined by more delicate fibers which are intermingled with the forebrain component which passes through the ektostriatum. Whether these finer fibers synapse in the ektostriatum, as Schroeder's account implies, or whether they pass through it with other forebrain bundles it is impossible to state at present. The bundles in the neostriatum intermediale tilt dorsocaudally and accumulate along the upper border of the nucleus separating it and, farther caudalward, the neostriatum caudale from the overlying ventral hyperstriatal area. These bundles form a conspicuous tract, best seen in sagittal sections (pl. 18, fig. 38). Fine fibers, relatively few in number, join the tract from the hyperstriatum ventrale, particularly from that portion which is contiguous to it. Caudalward, the bundle is separated on the lateral side from the neostriatum caudale by the tractus thalamo-frontalis medialis pars occipitalis, which runs from the posterior lateral part of the neostriatum caudale dorsalward and then forward along the tractus fronto-occipitalis for a short distance, after which it swings ventromedialward between the neostriatum intermediale and neostriatum caudale to join the lateral forebrain bundle. With this latter bundle are also fibers to the dorsal medullary lamina. Likewise, on its lateral side tractus fronto- or parieto-occipitalis lies in close relation with the caudal portion of the lamina frontalis superior (Frontalmark of Edinger, Wallenberg, and Holmes, '03) which is intimately associated with the periventricular gray in the region.

Lamina frontalis superior (pls. 12 to 14, figs. 24 to 31; pl. 17, fig. 37; pl. 18, fig. 38). *Lamina frontalis superior*, as has just been stated, is the Frontalmark of the earlier account

(Edinger, Wallenberg, and Holmes, '03). It is intercalated in the course of the field A of Rose ('14) or the nucleus intercalatus hyperstriati of our terminology. In the more anterior portions of the hemisphere the bundle with its associated nucleus separates the dorsal from the ventral hyperstriatum. It is composed in part of fibers of these neighboring areas which course in it for a short distance and then swing ventralward or dorsalward, as the case may be. However, in addition to these shorter fibers, this bundle mediates between the dorsal and ventral hyperstriatal areas, with their laterally lying, associated corticoid area, and the periventricular gray. It is associated with the periventricular system internal to the hyperstriatum ventrale and the neostriatum throughout much of the hemisphere. The number of fibers in this periventricular path varies somewhat at different levels, but the system is present to the caudal end of the hemisphere. This provides a connection, among other things, for the hyperstriatum dorsale and the ventral hyperstriatum into the tractus thalamo-frontalis medialis and tractus strio-hypothalamicus ventralis. Behind the level of the dorsal hyperstriatal area the lamina suprema takes on the character of a periventricular system and becomes intermingled with the lamina frontalis suprema and chiefly its caudal continuation, the dorsolateral periventricular fibers. Thus the two periventricular systems are found side by side (pls. 15 to 17, figs. 32 to 36).

Lamina frontalis suprema (pls. 12 to 15, figs. 24 to 32; pl. 17, fig. 37). The lamina frontalis suprema separates the dorsal from the accessory hyperstriatal area and, after the disappearance of the latter nuclear mass, the two become approximately a single fiber system. The frontalis suprema carries short fibers associated with the overlying and underlying areas and becomes continuous with the mediodorsal periventricular fibers of the outer or non-striatal ventricular wall, which, behind the level of the hyperstriatal area, is its caudal continuation (pls. 15 to 17, figs. 32 to 36).

CONNECTIONS OF THE EKTOSTRIATUM. The ektostriatum is essentially a nuclear mass intercalated in the course of fiber bundles. Fibers entering this nucleus become so intermingled with other systems that it is often impossible to determine the amount of synapse in the area, although in some cases bundles can be followed directly through where the tilt of the fibers is favorable. A brief summary of the fiber relations of this nuclear mass may illustrate the possibilities of connections of any fiber system associated with it. The nucleus and its associated bundles are situated along the dorsal medullary lamina, laterocaudad to the nucleus basalis and then lateral to the nucleus tractus fronto-archistriatici et neostriatici. It is associated ventromedialward with bundles which pass to and through the ventral medullary lamina, in synaptic relation in part at least with the large cells of the associated paleostriatum primitivum (globus pallidus, pl. 14, figs. 30 and 31) and perhaps to the paleostriatum augmentatum as well. These form a very considerable but scattered fiber system. With the entrance of the lateral and intermediate thalamo-striatal systems into the hemisphere, the ektostriatum—which receives the majority of the fibers of these systems as well as some fibers from the medial fronto-striatal tract—reaches its greatest size and the paleostriatum primitivum immediately ventromedial to it becomes practically a continuous band of fibers (with only scattered cells), so great are the number of bundles passing through it (pls. 14 and 15, figs. 30 to 32). Within the ektostriatum there is a complete tangle of cells and fibers, so that in the normal preparation it is not possible in this region to follow through distinct bundles.

The most cephalic portion of the ektostriatum is connected by a special bundle of delicate fibers with the dorsal hyperstriatum and with the superior and supreme frontal fiber laminae in the region of lateral fusion of the cell masses with the overlying corticoid lamina. This bundle (in figs. 28 and 29, pl. 13) runs dorsalward, caudal to the neostriatal division of the fronto-archistriatic tract, and then swings forward to

the regions mentioned above. At about this level first appear the more heavily stained and larger bundles which connect the more dorsal areas of the hemisphere. These latter bundles form great strands of fibers which run medialward to neostriatum intermediale and the overlying ventral hyperstriatum (between the cells of the hyperstriatum ventrale ventroventrale) and spread as a more or less continuous sheet of bundles lateralward and dorsalward to the hyperstriatum ventrale dorsoventrale, particularly in its more lateral part, to the dorsolateral corticoid layer in the region and to the superior frontal lamina (which in turn implies, at least, connections with the accessory hyperstriatum and with the periventricular cell lamina, pls. 13 to 15, figs. 28 to 32).

To summarize, then, connections of a fiber system to or from the diencephalon with the ektostriatum give the possibility of interrelations between the particular diencephalic center involved and the hyperstriatal and intermediate neostriatal areas of the hemisphere together with connections to the dorsolateral corticoid area and the periventricular telencephalic gray.

LATERAL FOREBRAIN BUNDLE. The avian lateral forebrain bundle shows a great increase in number of fibers and in richness of distribution over its homologue in reptiles, yet it is built on the same general plan as that fiber complex in the alligator brain. Various components of the system have been described by previous workers on avian forebrain, such as Bumm ('83), Edinger and Wallenberg ('99), Edinger, Wallenberg, and Holmes ('03), Schroeder ('11), Hunter ('23), Craigie ('28), and others. A general statement of the work up to the time of its publication is to be found in the reference book of Ariëns Kappers ('21, vol. 2). The present knowledge of the components of this tract has been slowly accumulating for many years and is based on the study of a wide range of material both from the standpoint of the methods employed and the kinds of birds considered. Certain observers have used embryonic material or that of young animals. Much of the work has been done on normal material

stained by the Weigert method or on degeneration preparations stained either by that method or by the Marchi technique. The use of silver-impregnation methods as applied to the forebrain has been limited in amount. Where such methods have been employed they have involved preparation of the material according to the Golgi rather than to the Cajal technique. Avian material has been greatly favored by the experimental physiologists, and naturally the behavior of the bird after stimulation of areas supplied by forebrain tracts or the extirpation of the same has held a foremost place in the interest of this group of observers.

In 1883, Bumm described the cerebral peduncle, indicating its separation into dorsal and ventral divisions. The analysis of the components in 1903 by Edinger, Wallenberg, and Holmes still remains the classic description on which all later work of necessity is based. These observers described the following components: 1) Tractus thalamo-frontalis and parietalis. This tract connected nucleus rotundus and the frontal and parietal forebrain areas, conducting in both directions. (It is the 'Rindenbündel' of Westphal, '98.) 2) Tractus thalamo-frontalis medialis. This latter tract mediated between nucleus dorsalis and the frontal areas of the hemisphere, probably also carrying impulses both ways. 3) Tractus thalamo-striatalis. They described this as connecting the thalamus with middle and caudal parts of the hemisphere, the fibers running over the anterior commissure. The exact origin and termination were apparently unknown. 4) Tractus strio-thalamicus dorsolateralis. This fiber bundle accompanied the tract last described. Its origin was in nucleus rotundus. 5) Tractus strio-mesencephalicus. This connected lateral temporal and occipital cortex and also the ektostriatum, with the tegmental regions. 6) Tractus occipito-mesencephalicus. This tract had been previously described by Edinger in 1895, when he demonstrated it by a study of material in which the occipital region of the hemisphere had been injured. It was discussed in his later work ('03, '08). Edinger believed this tract was a projection

tract associated with vision and that a destruction of it produced blindness. It is interesting in this connection that Boyce and Warrington ('98) found that an injury to any part of the hemisphere gave impairment of vision. Other workers have found that vision returned in a short time, the length of time depending apparently on the conditions of the experiment. The paths thus far described made up the dorsal peduncle of the Edinger, Wallenberg, and Holmes account. Four paths formed the ventral peduncle. These were, 1) tractus mesencephalicus ventralis from meso- and ektostriatum to the midbrain region; 2) tractus thalamo-parolfactorius; 3) tractus quinto-frontalis, and, 4) tractus fronto-bulbaris, the accompaniment of the quinto-frontal at least in duck. Tractus mesencephalicus had been previously degenerated by Münzer and Weiner ('98) and by Boyce and Warrington ('98). Tractus quinto-frontalis was described in great detail by Wallenberg in 1898 as an isthmo-striatal and later ('03) as a quinto-striatal tract. Wallenberg believed the tract ran forward from the sensory V nucleus and, after partial decussation in the region of the IVth nucleus, distributed in part to mesencephalic areas and in part continued without synapse directly forward to the ektostriatal and adjacent regions and to the frontal part of the forebrain lateral to the parolfactory areas. This implies, of course, a sensory connection other than olfactory to forebrain without synapse in the thalamus.

Schroeder ('11) divided the peduncle into strio-thalamic, strio-mesencephalic, occipito-mesencephalic, and strio-cerebellar paths. The strio-thalamic portion consisted of two divisions: 1) his so-called radiatio epithalamica which, according to his description, ran to the epithalamus (nucleus dorsalis of Edinger probably) from the lateral and, farther caudad, from the medial division, and, 2) the path described by him as passing in the lateral portion to nucleus rotundus and, farther caudad, to nucleus anterior thalami (nucleus ovoidalis of the present account). His strio-mesencephalicus reached nucleus spiriformis, while the strio-cerebellar which

ran ventral to the last-mentioned tract at the level of the third nerve entered the anterior cerebellar peduncle.

In general, the description given by Ariëns Kappers ('21) agreed with the Edinger, Wallenberg, and Holmes account, with some differences, however, in detail and nomenclature. He described a tractus thalamo-frontalis externus (parietalis and frontalis of Edinger, Wallenberg, and Holmes) between the lateral hyperstriatum and nucleus rotundus and a thalamo-frontal path (tractus thalamo-frontalis medialis of Edinger, Wallenberg, and Holmes) which consisted of two divisions: an occipital ramus connecting the nucleus anterior and nucleus dorsalis with the posterior hyperstriatum and a frontal ramus connecting these same nuclear groups with neopallial areas adjacent to the frontal parts of the hyperstriatum. The occipito-mesencephalicus was carried to nucleus spiriformis and to adjacent gray.

Three components of the lateral forebrain bundle were described by Hunter ('23): tractus thalamo-frontalis externus, from rotundus to the lateral part of the hyperstriatum; tractus thalamo-frontalis medius from nucleus dorsalis to the frontal and occipital parts of the hyperstriatum, and tractus strio-thalamicus internus, the main efferent path of the striatum passing to the ventral thalamus and midbrain. This latter path he regarded as consisting of a crossed bundle (the tractus strio-thalamicus cruciatus internus) and an uncrossed bundle (the tractus strio-thalamicus rectus).

In the Craigie and Brickner ('27) paper was figured a tractus thalamo-frontalis externus, obviously the homologue of the Edinger, Wallenberg, and Holmes tract of that name to nucleus rotundus. In the text the statement was made that nucleus rotundus received the lateral strio-thalamic tract. Nucleus anterior of Craigie and Brickner and nucleus ovoidalis received fibers of the medial thalamo-striatal path. A ventral peduncle was indicated in the figures.

Some brief mention should be made here of the results of certain physiologists. Kalischer ('00, '01, '05) believed that he could plot out certain definite regions in the forebrain

associated with specific activities. On the basis of experimental lesions and methods of electrical stimulation, he described motor areas for tongue and jaw, for extremities. A center concerned with the closing of the eye, as well as an optic center situated posteriorly, was located. In parrot, there were, he believed, centers concerned with speech. He regarded the extremity center as associated with tractus septo-mesencephalicus, the tongue and jaw with the dorsal fronto-thalamic, the optic with the occipito-mesencephalic. In contrast with his results, Boyce and Warrington ('98) had found no motor syndrome when they extirpated one hemisphere. The typical early syndrome after extirpation of both hemispheres was inertia, ruffled feathers, closed eyes, marked lack of attempts at initiating movements, etc., followed by continual movement, ability to maintain equilibrium, etc. In fact, Rogers ('22) reached the conclusion that extirpation of the more dorsal forebrain areas did not appear to lead to loss of any single function, but to that of certain complicated 'action systems,' therefore, relatively little can be said as to the rôle of any particular tract. Extirpation or removal of hemispheres led to erection of the feathers, and depression of the feathers was produced by stimulation of the basal forebrain areas. He regards this as indicative of a tonic functional relation between these basal regions and the pinna-motor centers.

Our silver material permits of the addition of considerable detail, especially in regard to the distribution within the forebrain and thalamic areas. It should be emphasized that by this technique one recognized the forebrain bundle not as made up of distinct and separate components, but as a broad fan-shaped mass of fibers connecting the major portion of the lateral wall with most of the dorsal thalamus, certain pretectal areas and portions of the ventral thalamus, subthalamus, and tegmentum. In this general complex there are degrees of medullation, differences in tilt of the fibers and in the compactness of the general arrangement which make it possible in most cases to identify the components described by previous workers.

In the sparrow, at the point of entrance to the diencephalon, the components are arranged in the following order, beginning from the lateral side and proceeding medialward: tractus thalamo-frontalis lateralis, tractus thalamo-frontalis intermedialis, tractus strio-tegmentalis (including the quinto-frontal tract and some dorsal supra-optic fibers), tractus thalamo-frontalis medialis, and tractus strio-hypothalamicus medialis. In the following account we have described only briefly those relations which have been generally recognized, but have emphasized such as are new.

Tractus thalamo-frontalis lateralis (pl. 14, figs. 30 and 31; pl. 15, fig. 32; pl. 16, fig. 34). Tractus thalamo-frontalis lateralis (tractus thalamo-striatalis of Craigie, '28) has its origin and, in part (according to Edinger, Wallenberg, and Holmes, '03), its termination in nucleus rotundus. It appears also to receive some fibers from the more lateral portion of nucleus dorsolateralis anterior and from the nucleus post-rotundus. The tract swings dorsalward and lateralward to form the most lateral component of the forebrain bundle. The fibers become so intermingled medialward with those of the tractus thalamo-frontalis intermedialis that it is not possible in the material at hand to distinguish definitely one from the other within the hemisphere, although the more lateral fibers are those definitely associated with nucleus rotundus and nucleus dorsolateralis anterior pars lateralis. Tractus thalamo-frontalis lateralis swings through the ventral medullary lamina and the paleostriatum augmentatum dorsal to it and so reaches the ektostriatal areas. The possibilities of its further connections either with or without a synapse in that area have been discussed on page 115. In addition to this connection with the ektostriatal region, there is a fiber bundle of the tractus thalamo-frontalis lateralis (pl. 14, fig. 30) which runs lateral to the ektostriatum and then courses dorsalward and in part forward, to the lateral part of the hyperstriatum ventrale dorsoventrale, to the overlying corticoid layer and probably to the hyperstriatum dorsale. The tract from the nucleus rotundus to the hemisphere is for the

most part heavily medullated and is easily identified in the Weigert material of *Cacatua* and *Palaeornis* available at Amsterdam and in our series of *Gallus domesticus*.

Tractus thalamo-frontalis intermedialis (pls. 14 and 15, figs. 30 to 33). Adjacent to the tractus thalamo-frontalis externus at the entrance to the hemisphere is the tractus thalamo-frontalis intermedialis, of which the direction of conduction is unknown. It consists of fibers to or from several distinct areas: 1) tectum; 2) nucleus geniculatum laterale; 3) nucleus intercalatus; 4) nucleus lateralis anterior of Edinger and Wallenberg; 5) nucleus tractus tecto-thalamici cruciati. The first group swings (figs. 31 and 32) from the tectum directly medialward somewhat ventral to the main tecto-thalamic paths and dorsal to the lateral geniculate and among the cells in part of the nucleus tractus tecto-thalamici cruciati. They are joined ventromedially by a few delicate fibers from that latter nucleus and then turn dorsalward, occupying a position among the cells of the nucleus intercalatus which lies as a broad cell band between the nucleus rotundus and the ventral peduncle of the forebrain bundle (pls. 14 and 15, figs. 31 and 32). Here they are joined by many fibers from the nuclear mass, so that the fiber tract becomes a broad band, reddish in color in the silver material and easily distinguishable. It swings dorsalward between the lateral and medial thalamo-frontal paths, but becomes separated from the medial by the ventral peduncle of the lateral forebrain bundle. After entrance to the hemisphere, it has not been possible to definitely delimit this bundle. Fibers from it pass to the ektostriatum, and, it is believed, to the neostriatum intermediale.

Tractus strio-tegmentalis et strio-cerebellaris (pls. 13 to 16, figs. 28 to 35; pl. 18, fig. 38). This composite bundle apparently receives fibers from the ektostriatal region and the dorsal medullary lamina. The major portion of its fibers appear to arise from the paleostriatum augmentatum, particularly from its more anterior portion, and from the paleostriatum primitivum. The fibers swing ventralward and ven-

trolateralward in the paleostriatal area and converge to form a fiber mass usually designated as the ventral medullary lamina. This receives fibers on its dorsal medial side from the neostriatum frontale and has connections with the overlying ektostriatum. This ventral medullary lamina goes over largely, if not entirely, into the strio-tegmental and strio-cerebellar tracts. As the bundles turn ventrocaudalward they come into intimate relation with the quinto-frontal tract (p. 126) which throughout much of its course through the diencephalon lies at the ventral border of the strio-cerebellar tract. The strio-tegmental path and the associated strio-cerebellar system enter the diencephalon between the internal and the intermediate fronto-thalamic paths and are intermingled in part with the fibers of the dorsal supra-optic decussation. Ventral to the internal thalamo-frontal system, the bundle is bordered medially and dorsomedially by the occipito-mesencephalic tract and the small medial forebrain bundle. It is separated from the dorsal portion of the peduncle by the nucleus of the dorsal supra-optic decussation which receives many fibers of that decussation and also collaterals of the forebrain tract. From this level the tract extends caudalward, giving off in course some fibers to stratum cellulare externum and the nucleus hypothalamicus posterior lateralis and possibly to other hypothalamic areas. Another tectal path, smaller in number of fibers, is given off toward the posterior end of the diencephalon—the homologue of the strio-tectal of alligator—the remainder of the bundle could be traced to the level of the red nucleus, appearing to contribute to the tegmental gray in the region of that nucleus. Certain of the more dorsal fibers are in relation with the entopeduncular nucleus. The most ventral part of the bundle, including the quinto-frontal component, could be traced to about the level of the nucleus of the fourth nerve. Certain of these more ventral fibers then swing dorsocaudalward to the cerebellum. This is the strio-cerebellar tract, described by Schroeder ('11) for chicken and by Craigie ('28) for humming bird. That the path is not so readily demonstrated in

the sparrow material is due not to its small size, but to the great richness of the impregnation in the region. It is very clearly demonstrable in the Weigert material of chicken, particularly in the sagittal series. This is not completely illustrated in the figures because the recent description appears to make such illustration unnecessary. The strio-tegmental of birds corresponds with the strio-tegmentalis dorsalis (the part associated with the nucleus entopeduncularis), strio-tectalis, and strio-tegmentalis ventralis of the alligator (Huber and Crosby, '26).

Tractus thalamo-frontalis medialis (*internus*, Ariëns Kappers, '21, and others) is a very conspicuous component of the forebrain bundle (pls. 14 to 16, figs. 30 to 35; pl. 18, fig. 38). Its main relations have been recognized for many years, although the details of its connections have not been so well known. It is divided into two portions, a pars frontalis (the tractus thalamo-striatalis medius of Edinger, Wallenberg, and Holmes, '03) and a pars occipitalis (probably the tractus thalamo-striatalis of these last-mentioned observers). The medullated components of the bundle, as well as certain other forebrain tracts, have been diagrammed by Ariëns Kappers, '21, page 1048, figure 549. They are also to be seen in the charts of this observer. The direction of conduction of the fiber system is not known, although, as the name implies, it is believed to run, in part at least, from the thalamus to the hemisphere. It is so described in the present account.

Tractus thalamo-frontalis medialis within the diencephalon is related to the nuclei dorsolateralis anterior and posterior and to nucleus ovoidalis (pls. 15 and 16, figs. 33 and 35). It swings lateralward and ventrolateralward from these nuclei and enters the hemisphere medial to the strio-tegmental tract (pl. 15, fig. 32). Certain of the fiber bundles run dorsomedialward and to some extent forward. These constitute the pars frontalis and this connects with the neostriatum intermediale and frontale (on its medial side), with the medial portion of the hyperstriatum ventrale (possibly indirectly after a

synapse in the neostriatum), and by a small component with the lateroventral periventricular gray on the outer or striatal side of the ventricle in front of the level of the anterior commissure. Moreover, the bundle courses through the paleostriatum augmentatum, where it appears to either give or receive fibers. The pars caudalis (pl. 18, fig. 38) is a large bundle which lies in the more caudal portions of the medial part of the hemisphere. Its fibers connect particularly with the neostriatum caudale, including its more posterior portion, and, to some extent, with the periventricular gray in the region underlying the neostriatum. Fibers join the bundle from the paleostriatum augmentatum and paleostriatum primitivum. It is our opinion that these may distribute in part at least with the strio-tegmental system, but the evidence for this is inconclusive. Thus, nucleus dorsolateralis anterior, nucleus dorsolateralis posterior, and nucleus ovoidalis are connected with the neostriatum intermediale and caudale, with the periventricular gray in both frontal and caudal regions of the hemisphere and probably, to some extent, with the paleostriatum. They are further connected either directly or indirectly with the ventral hyperstriatal areas. It is to be emphasized, however, that silver preparations show that, at least in sparrow and in dove, the bundles just discussed form a continuous band of fibers of which ramus frontalis and ramus occipitalis represent more dense and probably better-medullated portions.

Tractus strio-hypothalamicus medialis (pl. 13, fig. 29; pl. 15, fig. 32). Tractus thalamo-frontalis medialis is accompanied medialward by fibers from the medial part of the paleostriatum augmentatum, the dorsal medullary lamina, and the lateroventral periventricular gray, which swing down in thalamic levels into the hypothalamus—a so-called tractus strio-hypothalamicus medialis. It distributes to the nucleus hypothalamicus anterior lateralis and possibly to other hypothalamic areas.

The tractus strio-thalamicus rectus internus of Hunter's account ('23, figured also by Ariëns Kappers, '21 and '24)

is also a strio-hypothalamic system in the sparrow. To distinguish it from the portion described above it is termed *tractus strio-hypothalamicus medialis pars posterior*. There is a suggestion of a crossed component running with anterior commissure fibers (the *tractus strio-thalamicus cruciatus internus* of Ariëns Kappers and Hunter), but the evidence for this in the sparrow material is not conclusive.

TRACTUS QUINTO-FRONTALIS (pls. 12 to 16, figs. 26 to 35; pl. 18, fig. 38). At the anterior end of the hemisphere, in the region of the *neostriatum frontale*, scattered bundles of the lateral part of the quinto-frontal system are to be seen (pl. 12, fig. 26). Fibers are contributed to these bundles from the overlying hyperstriatal areas, but a considerable portion of the fibers appears to arise among the cells of the *neostriatum* itself. Gradually the bundles collect in the ventrolateral part of the area and accumulate about the nucleus basalis and build up a large fiber system intermingled with the small cells of this nuclear mass. To what extent there is synapse here it is impossible to say in the normal preparations. Just medial to this basal component of the quinto-frontal tract are fibers from the hyperstriatal and accessory hyperstriatal areas which form its dorsal component. This basal component in part joins the dorsal component directly and in part turns into the underlying *paleostriatum*. Gradually the fibers of the basal component accumulate at the lower side of nucleus basalis and form a dense fiber system which swings into the *paleostriatum*. The two components approach each other in the region below the ventral medullary lamina, where they are apparently joined by fibers associated with the *ektostriatum*. Gradually they come together to form a relatively distinct, reddish-staining bundle which joins the strio-tegmental and strio-cerebellar components of the lateral fore-brain bundle and runs in company with them through the diencephalon, occupying a position ventral to the strio-cerebellar system. The fiber bundles extend caudalward to the lower level of the mesencephalon to about the level of the fourth, where, in part, they decussate and ultimately come

into relation with the chief sensory nucleus of the trigeminus. The course of the fiber bundle is not illustrated beyond the diencephalon, since it is essentially that described so carefully by Wallenberg. For convenience it has been described from forebrain caudalward, but the direction of conduction, as this observer has shown, is from the nucleus of the trigeminal to the hemisphere.

Throughout most of its course the quinto-frontal path is so intermingled with the strio-tegmental system in sparrow that the two are not distinguishable from each other in normal preparations. The above homology is based on a comparison with the relations in other forms, and not on the ability to trace the path as a discrete bundle throughout all of its extent. The bundle is relatively more distinct in our dove material, and it has been possible to trace it from the chief sensory nucleus forward as a partly crossed and partly uncrossed bundle, but even in this bird in the diencephalic areas it becomes so closely allied to the strio-tegmental system as to make it impossible at every level to distinguish it with certainty from that latter path. Still, the account of Wallenberg affords so much help in dove that there is reasonable certainty for the identification of the bundle in this bird. The two components here described have been identified in the chicken by Schroeder ('11) and are present in Weigert material of this bird available for study in essentially the relations given by him. The method for positive identification of this tract from the surrounding fiber systems, however, is the degeneration technique employed by Wallenberg ('98 b). This is a very important fiber system, since it brings directly forward into the neostriatal regions of the hemisphere sensory impulses, presumably tactile, pain, and temperature sensations, without the use of intermediary neurones in the thalamus.

OLFACTORY TRACTS (pl. 12, figs. 24 to 26). The incoming olfactory fibers enter the single olfactory bulb of sparrow from all surfaces. They form, with the dendrites of mitral cells, a typical glomerular layer near the periphery. The

neuraxes of the mitral cells pass back into the hemisphere as the olfactory striae or tracts. Whether, as in teleosts (Sheldon, '12) and in the alligator (Crosby, '17), neuraxes of granule cells are also present in the olfactory tract is uncertain, but that such is the case is very probable. The more medial of the fibers, the homologue of the medial olfactory tract of other vertebrates, passes to the nucleus olfactorius anterior. This nucleus is connected with the band of cells representing the cephalic continuation of the hippocampal area in sparrow, but it is uncertain whether or not olfactory fibers from the bulb reach this latter area without a synapse in their course through the nucleus. In dove, where the medial bundle is larger, there is a greater suggestion of such a direct connection to this anterior continuation of the hippocampus, although the evidence is not conclusive. Likewise, it has not been possible to demonstrate an interbulbar component of the anterior commissure which is present in most vertebrates and affords a direct connection from one olfactory bulb to the other.

The lateral olfactory tract (pl. 12, figs. 24 to 26), on leaving the olfactory bulb, runs along the lateral surface of the hemisphere and comes into synaptic relation with the area prae-pyriformis and with the more scattered cells of the area immediately caudal to it. Fibers arising in these areas may join the bundle, which at the best is small, so that it is difficult to state what percentage of the fiber mass from this point on arises directly from the bulb. The bundle decreases in this region, but some few fibers, particularly the more external ones, can be traced caudalward into the tractus fronto-archistriaticus et neostriaticus (pl. 12, fig. 25), while others, and in general the inner fibers, swing dorsomedial into the lower part of nucleus basalis.

It must be emphasized that all of these components are extremely small. In only one series was it possible to follow the lateral olfactory tract into nucleus basalis and into the tractus fronto-archistriaticus, yet in that series the bundle was picked out in a way so as to admit of determining

its relations. In the available Weigert series of the avian brain the olfactory tracts are not stained. These connections in the bird are of special interest, since they evidence, on a diminutive scale, what is to be seen on a larger scale in reptiles. This point will be discussed more fully under the account of the fronto-archistriatic and neostriatic tract.

PALLIAL COMMISSURE; SEPTO-CORTICAL AND CORTICO-SEPTAL FIBERS; MEDIAL FOREBRAIN BUNDLE. A small pallial commissure (pl. 18, fig. 39) is present in the position usually regarded as the field of a hippocampal commissure in reptiles. Without degeneration preparations it is impossible to say to what extent these fibers come from the small region regarded as hippocampus in these forms. Normal preparations certainly suggest the strong possibility that other regions of the dorso-lateral wall may provide some of the fibers for this bundle. This is probably also the case in alligator.

Between the dorsomedial wall of the hemisphere and the underlying septal or parolfactory regions there are delicate fiber tracts comparable to the connections to be found in the region in reptiles. In the bird, as in the alligator, they consist of a medial (possibly parolfacto- or septo-cortical tract) and a lateral bundle (by analogy a cortico-septal bundle, pl. 14, figs. 30 and 31). From the parolfactory region delicate fibers join the forebrain bundle on its medial side, in close relation to the tractus strio-hypothalamicus medialis. They are small in amount, but represent the avian equivalent of the reptilian medial forebrain bundle (pl. 14, figs. 30 and 31).

TRACTUS FRONTO-ARCHISTRIATICUS ET NEOSTRIATICUS (pls. 12 to 17, figs. 26 to 37). This is a composite tract related to more than one area in both frontal and occipital regions. Anteriorly, a part of its fibers arise from the nucleus tractus fronto-archistriatici and from the nucleus basalis (pls. 12 to 14, figs. 26 to 30). These are joined by an extremely small component of the lateral olfactory tract (p. 128). To all of these components are added fibers from the neostriatum frontale and from the hyperstriatum ventrale pars dorso-ventrale (pl. 12, figs. 26 and 27; pl. 17, fig. 37), particularly

from the more lateral portion which is indistinctly fused with the dorsolateral corticoid lamina. This last component is relatively small. Joining these bundles from the neostriatum intermediale is a distinctly arched bundle which runs lateralward and then ventralward to unite with the other components. It is clearly seen in figure 37, plate 17. The fibers from the neostriatal and hyperstriatal centers reach the fronto-archistriatic tract by passing through the nucleus of that tract. To what extent they synapse here it is not possible at present to state. The combined bundles form a prominent fiber system which runs caudad along the ventrolateral wall of the hemisphere as a broad band of fibers (pl. 17, fig. 37). This fiber system distributes to the archistriatum and to the posterolateral part of the neostriatum (pl. 17, fig. 37).

Soon after the various components of the fronto-archistriatic and neostriatic tract have massed into a compact fiber bundle, small fascicles are given off from its under side which run ventromedialward and caudalward along the surface of the hemisphere and gradually accumulate into a definite fiber bundle at its ventromedial angle (pls. 13 to 17, figs. 28 to 36). In a transverse plane through the level of the anterior commissure this bundle turns dorsalward and distributes to the more anterior portion of the archistriatum. Some few fascicles appear to pass directly into the occipito-mesencephalic tract and interarchistriatic or anterior commissure.

The fronto-archistriatic and neostriatic tract is the fiber system described by Edinger and Wallenberg ('99), Schroeder ('11), and others as the fronto-epistriatic tract of avian forms. For this tract Ariëns Kappers ('22) has suggested the name cortico-archistriatic tract. The applicability of the term archistriatum is obvious, in view of the present nomenclature. For birds certainly, and, in our opinion, for certain reptiles, the term 'cortico' does not seem suitable, so the name of fronto-archistriatic is used here. This fronto-archistriatic tract is in part comparable with the bulbo-archistriatic tract of the earlier workers on reptiles, or the lateral olfactory tract as that name has been applied to

alligator. A comparison between the systems in birds and alligator is rather easily made. In alligator the secondary basal centers of the lateral hemisphere wall which received lateral olfactory fibers were termed collectively the nucleus of the lateral olfactory tract (Crosby, '17). As has been previously stated (p. 54), this consisted of an anterior portion internal to the pyriform-lobe cortex near the cephalic end of the hemisphere and a posterior portion near the caudal end of that region, the two being connected by scattered cells. The anterior portion is comparable, it is thought, to the nucleus of the lateral olfactory tract of Cairney ('26) in *Sphenodon*. The posterior portion is the nucleus of the lateral olfactory tract in turtle (Johnston, '15) and in *Sphenodon* (Hines, '23) and the anterior amygdaloid nucleus of Cairney ('26). Incoming lateral olfactory fibers in alligator distribute to the pyriform-lobe complex and to the lateral olfactory nucleus throughout its extent, save that the greater number reach the anterior part of the area and after synapse are joined by fibers the cells of origin of which are in the nucleus of the tract. Thus, the lateral olfactory tract of the alligator, as it approaches the posterior end of the hemisphere to distribute to the posterior part of the lateral olfactory nucleus (or its complement, the anterior amygdaloid nucleus) and to the dorsolateral area at its caudal end, consists largely, but not exclusively, of tertiary fibers, or even those of higher order. This can be readily seen from the diagram on page 401 of the alligator paper (Crosby, '17). How, then, does this compare with the fiber relations in birds? The anterior end of the lateral olfactory nucleus of alligator is the nucleus basalis of birds, and probably, where it lies in relation with the dorsolateral area, equivalent of the nucleus tractus fronto-archistriatici as well. Nucleus basalis, similar to the nucleus of the lateral olfactory tract, receives olfactory fibers. It and the nucleus tractus fronto-archistriatici et neostriatici contribute fibers to the fronto-archistriatic et neostriatic tract, which, as in alligator, are accompanied by a small but evident direct lateral olfactory component.

Caudally, this tract distributes to the amygdaloid complex and to the neostriatal areas, while the lateral olfactory tract of the reptile goes to the posterior end of the lateral olfactory nucleus which is a part of the amygdaloid complex and to the dorsolateral area. Obviously, the lateral olfactory tract proper of the bird is comparable to the lateral olfactory connections in alligator between the bulb and the anterior end of the lateral olfactory nucleus (and the pyriform lobe); the avian fronto-archistriatic et neostriatic tract is comparable to the posterior end of the alligator lateral olfactory system, that is, to the portion arising from the nucleus of the lateral olfactory tract plus the direct lateral olfactory fibers behind the level of that nucleus and terminating in the amygdaloid complex (lateral olfactory nucleus of Johnston, '15), posterior end of lateral olfactory nucleus (Crosby, '17), and in the overlying dorsolateral area. Another way of stating the same facts is to say that at least, in general, the bulbo-epistriatic system described for reptiles is the equivalent of the lateral olfactory system of alligator and is directly comparable to the lateral olfactory tract plus the fronto-archistriatic et neostriatic tract of sparrow. The differences in the reptilian and avian forms are matters of emphasis. In the former animals the olfactory component is large, the accompanying association or correlation fibers are small, while in birds the olfactory portion is so small as to be almost negligible, while the association fibers between the hyperstriatum ventrale and neostriatal areas at the anterior end of the hemisphere and the neostriatum (and archistriatum) in the posterior portion make up most of the bundle. The fronto-archistriatic and neostriatic system in birds is in many ways a ventral dorsocaudal association bundle comparable to the more dorsal fronto-occipital tract.

TRACTUS ARCHISTRIATICUS DORSALIS (pl. 17, figs. 36 and 37). This is the tractus epistriaticus dorsalis of Schroeder ('11), which connects the neostriatum caudale with the archistriatum. The bundles form a very distinct fiber system toward the posterior end of the hemisphere in sparrow where they

interdigitate with the fibers of the tractus fronto (or parieto) occipitalis. In addition to these coarser bundles there are innumerable fine fibers from the whole caudal region of the neostriatum and the posterior portion of the hyperstriatum ventrale which converge into the dorsal medullary lamina which in this region of the hemisphere is represented by a greatly thickened fiber layer among the cells of the dorsal portion of the archistriatum. In this same region are fibers of the occipito-mesencephalic and interarchistriatic or anterior commissure (that is, the stria terminalis complex) and bundles from the tractus archistriaticus dorsalis. Consequently, this portion of the nuclear area consists mainly of fibers with intercalated cells (pl. 17, fig. 37). It is evident from the above account that there is a very intimate relation between the archistriatal and neostriatal areas in sparrow and dove. Similar connections were described by Schroeder ('11) for chicken.

TRACTUS OCCIPITO-MESENCEPHALICUS (ET BULBARIS) AND COMMISSURA ANTERIOR OR INTERARCHISTRIATICA (pls. 15 to 18, figs. 32 to 39). The literature concerned with tractus occipito-mesencephalicus (stria terminalis) has been considered under the description of the lateral forebrain bundle, since the tract has been considered by many previous workers as a part of that complex. The fibers arise from the archistriatum and from the hyperstriatum caudale. They swing medialward, and certain of them which are true commissural bundles (commissura interepistriatica, anterior commissure) reach the archistriatal region of the other side (pl. 15, fig. 32). Many of them belong to a non-decussating type of fibers, and these swing medialward, dorsal to the forebrain bundle, take up their place at the dorsomedial angle of that bundle, and in this position proceed caudalward. At the level of the nucleus ovoidalis the fibers running ventrolateralward from that nucleus (tractus nuclei ovoidalis) lie lateral to the occipito-mesencephalic tract and to the ventral part of the forebrain bundle (pl. 16, fig. 34). The relation of the tractus occipito-mesencephalicus et bulbaris to nucleus ovoidalis varies some-

what with the shifts in position of the nucleus in the different avian forms. Thus, the tract is medial to the nucleus in sparrow, but more nearly ventromedial in the dove. Behind the level of the nucleus ovoidalis the occipito-mesencephalic tract shifts somewhat lateralward and comes into intimate relation with the medial part of the nucleus spiriformis. Behind the level of this nucleus the tract can be followed caudalward into the medulla. Its final termination is not known. In its course the tractus occipito-mesencephalicus et bulbaris gives off fibers to the bed nucleus of the anterior commissure, the lateral preoptic nucleus, the stratum cellulare externum, the area anterior ventralis, the nucleus internus inferior anterior (and possibly posterior), and the stratum cellulare externum. As others have found (Craigie, '28), the nucleus spiriformis pars medialis (or dorsomedialis) lies in intimate relation with the tract and probably receives fibers from it. The course of the bulbar portion of the tract has been emphasized particularly by Craigie ('28), who speaks of it as a strio-bulbar tract. The occipito-mesencephalic tract and the commissura interstriatica are essentially the stria terminalis complex of reptiles (Huber and Crosby, '26) and mammals, with the exception that the connections to the hypothalamus and preoptic regions are relatively reduced, while the more caudal portions of the bundle are increased.

Associated with the main bundles of occipito-mesencephalic and interarchistriatic fibers are more delicate fibers which in part synapse in the bed nucleus of the anterior commissure and in part join bundles from the medial portion of the lateral hemisphere wall and from the medial forebrain bundle. How much interchange of fibers there is in the region cannot be stated. The bundle includes fibers of the medial forebrain component, distributed to the lateral preoptic area (and possibly the medial wall as well), to the nucleus inferior internus anterior, and to nucleus hypothalamicus anterior lateralis and possibly to other hypothalamic centers. This may be the tractus strio-thalamicus internus rectus of Ariëns Kappers ('21) and Hunter ('23). It is suggestive of a part of the

bundle '3' described by Berkelbach van der Sprenkel as a component of stria terminalis and is here included with tractus strio-hypothalamicus medialis pars posterior.

TRACTUS SEPTO-MESECEPHALICUS (pls. 12 to 16, figs. 25 to 35). The tractus septo-mesencephalicus, or Scheidewand-bündel, was one of the first tracts to be recognized in the avian brain. The details of its connections and relations have received much study. Among those who have given descriptions of this fiber bundle are Boyce and Warrington ('98), Edinger, Wallenberg, and Holmes ('03), Kalischer ('05), and Wallenberg ('06). This latter observer recognized three portions—a ramus basalis frontalis, a ramus dorsalis, and a ramus basalis caudalis. Since we have little to add to the accounts already given, a very brief description of the general relations will be sufficient.

It may be said in the beginning that the term tractus septo-mesencephalicus, although in general use, is not very appropriate for the system in question, since the majority of the fibers arise in relation with the accessory hyperstriatal and associated areas of the anterior portion of the dorsomedial wall rather than with the septal or parolfactory areas, although a small number of fibers are contributed to the bundle in its course through the last-mentioned areas. The degeneration experiments of both Kalischer ('05) and Wallenberg ('06) indicate this beyond question. Fibers from the accessory hyperstriatum (frontal radiations *k*; for homologies see p. 54) swing to the surface and form a band of fibers in close association with a similar band from the dorso-lateral (corticoid) surface area (frontal radiation *h*). These form a peripheral band of fibers as far lateralward at least as the point of fusion of the superficial corticoid areas with the underlying hyperstriatal region (p. 45). These fibers course medialward along the surface, being added to continually from the underlying accessory hyperstriatal region until the dorsomedial angle of the hemisphere is reached, and then they turn ventralward and somewhat caudalward and run toward the ventromedial surface of the brain. In the

upper part of the hemisphere they receive fibers from the paraentorhinal and entorhinal areas (frontal radiations *l*) and from the small hippocampal region. The fibers form a relatively compact bundle which swings ventralward through the parolfactory or septal region where collaterals or possibly stem fibers pass to the areas in the region and bundles are added to the tract. The tractus septo-mesencephalicus comes into a position medial to the forebrain bundle and then makes a sharp turn and runs lateralward, ventral to the forebrain bundle, in such a manner that this latter system lies in the angle (pl. 13, fig. 29) formed by the septo-mesencephalic tract. This makes a very striking picture in the Weigert series of the parrakeet (*Cacatua* and *Palaeornis*) and of chicken. It is equally clear, but less noticeable because of the richness of the impregnation of other fiber systems in the Cajal preparations of sparrow and dove. From this position the major portion of the bundle runs lateralward, lateral and ventral to the lateral forebrain bundle, and the ramus basalis frontalis of Wallenberg is given off (pl. 13, fig. 29). This ramus distributes to the basal part of the lateral brain in relation with scattered cells which represent probably the lateral continuation of the nucleus of the diagonal band of Broca. This portion of the tract undoubtedly belongs to the fasciculus praecommissuralis of Elliot Smith, as Wallenberg suggested. It is probably the olfactory radiations of Zuckerkandl and corresponds with the diagonal band connection between the amygdaloid complex and the hippocampus described by Johnston ('15) for turtle.

The dorsal ramus of the tractus septo-mesencephalicus (pls. 14 to 16, figs. 30 to 35) swings somewhat farther caudalward and then gradually turns dorsalward, lateral to the forebrain bundle and dorsal to the optic tract. As it runs dorsalward it comes into relation with its nucleus, the position of the tract can be seen in plates 16 and 17, figures 34 and 35. It distributes to this nucleus throughout its extent. Some of its fibers appear to end in the nucleus lateralis. The more posterior bundles of the ramus dorsalis, accompanied by

fibers from the lateral nucleus, run through the pretectal nucleus, with some synapse, and caudal to that nucleus to the tectum. This is comparable with the portion described by Craigie ('28) as passing to the tectum, although because of differences in position of this latter center, his bundle courses posterolateralward through the lateral nucleus to the tectum, while in the sparrow the bundle runs ventrolateralward through the pretectal nucleus to the tectal region. Terminal fibers of the dorsal ramus of the septo-mesencephalic tract run to the habenula (p. 140). Concerning the ramus basalis caudalis of Wallenberg there appears to be some difference of opinion. Thus Schroeder ('11) homologized it with a bundle described by Jelgersma which ran with the ventral peduncle (strio-tegmental tract) to the oculomotor nucleus crossing en route. Wallenberg ('06), however, stated that the bundle of his description was probably homologous with the tractus cortico-septo-spinalis of Kalischer ('05) and that it ran caudalward to a varying distance without decussation. This ramus is the bundle provisionally termed tractus septo-hypothalamicus by Edinger, Wallenberg, and Holmes ('03) and is the bundle which had been described earlier by Boyce and Warrington ('98) under the name "chiasmal fibers of the tractus septo-mesencephalicus." In degeneration material the bundle terminated in the thalamus in dove, in the mid-brain in goose, and in the bulb in duck. The bundle described by Jelgersma decussated and ended in relation with the oculomotor nucleus (p. 138). In our own material of both sparrow and dove there are two bundles. The more lateral is the ramus basalis caudalis of Wallenberg. It represents the caudal continuation of the septo-mesencephalic tract and can be traced in our normal dove material to about the posterior end of the diencephalon, and in sparrow to a level slightly farther caudal. The position of the tract is shown in the figures (pls. 14 to 16, figs. 30 to 35) of the fiber preparations. Kalischer thought this tract comparable to the pyramidal system of mammals. Wallenberg suggested that it might be a portion of the fasciculus praecommissuralis or a part of

the fornix longus (as illustrated by Cajal). The latter homology appears to us to be the more probable.

TRACTUS INFUNDIBULI (tract of Jelgersma) (pls. 15 and 16, figs. 33 to 35). Jelgersma showed that the extirpation of the hemisphere produced the degeneration of a tract which he believed connected the basal forebrain areas ('Stammganglion') with the contralateral nucleus of the oculomotor nerve. He described and figured the tract as accompanying the inferior or ventral peduncle of the forebrain bundle, through the hemisphere and for some distance into the diencephalon. Then the bundle separated from the forebrain fibers, ultimately crossed and terminated in relation with the oculomotor nucleus. By certain observers this path has been regarded as in part at least comparable, and more particularly in a physiologic sense, with the pyramidal path of mammals (Schroeder, '11, p. 118).

It is with some hesitancy that an attempt is made to discuss the path on the basis of observations made only on normal preparations. It is believed that the tract arises, in part at least, from the region of the bed nuclei of the commissures and possibly from areas in the immediate vicinity, that it runs caudalward in company with the medial forebrain fibers and in such intimate relation with the ramus basalis caudalis of the septo-mesencephalic tract that the two form, in sparrow, almost a single system for a part of their course. Gradually the more medially situated fibers of Jelgersma's bundle swing medialward and caudalward as a distinct fiber mass, cross in the retro- (or post) infundibular commissure, and swing dorsalward to the region at least of the oculomotor nucleus. Whether or not fibers from the lateral side of the ventricle join this path cannot be stated.

We should like to suggest that the bundle of Jelgersma, while a distinct fiber path, may belong functionally with the ramus basalis caudalis of Wallenberg, in that it too represents a part of the extrammillary fornix system, or may represent the strio-oculomotor tract described for certain mammals.

STRIA MEDULLARIS (pls. 16, 18, and 19, figs. 34, 35, 38 to 41). The following account of the connections of the habenula is based on a study of the dove brain. This bird was chosen in preference to sparrow, because of the greater size of the olfactory system and consequently the better development of the paths in question. The comparisons with alligator material are based on the accounts of Herrick ('10) and Crosby ('17). Essentially similar connections were described by Hines ('23) for *Sphenodon*.

Tractus cortico-habenularis medialis and tractus septo- or parolfacto-habenularis (pl. 18, fig. 39). In the dove, the habenular tract from the medial hemisphere wall arises only to a small extent from the overlying cortical areas. In so far as it does so, it forms a medial cortico-habenular system. The greater part of the fibers arise from the lateral parolfactory or septal nucleus and particularly from the bed nuclei of the pallial commissure and the anterior commissure as well. Those from the bed nuclei form particularly the more ventral part of the system and that most closely associated with the medial olfacto-habenular component. The fibers from the bed nuclei as well as those from the parolfactory or septal area have been termed collectively the septo-habenular or parolfacto-habenular tract. The fibers arising from the bed nuclei are accompanied for a considerable distance by cells of these nuclei which thus form an intercalated nucleus for the tract. The medial cortico-habenular and septo-habenular tracts join to form the stria medullaris, the course of which will be discussed later.

Tractus taenio-habenularis (pl. 18, fig. 39). *Tractus taenio-habenularis* is comparable with the so-called *tractus cortico-habenularis lateralis anterior* of alligator. It arises in birds from the nucleus taeniae which is the avian homologue of the nucleus ventromedialis of alligator, from which the reptilian bundle takes origin. From nucleus taeniae the fibers swing dorsomedialward and forward along the ventromedial surface of the hemisphere to enter the stria medullaris.

Tractus archistriato-habenularis et precommissuralis (pl. 18, fig. 39). Tractus archistriato-habenularis is an amygdalo-habenular system comparable in part with the tractus cortico-habenularis posterior of alligator. In this latter animal the tract arises from the posterior portion of the nucleus olfactorius lateralis (comparable in part with the avian archistriatum) from the overlying pyriform-lobe cortex and from the lower part of the dorsolateral area. In the present material it has been possible to trace the bundle definitely only from the archistriatal region, hence the name applied to it.

From the avian archistriatum fiber bundles of this system swing directly medialward, dorsal to the stria terminalis fibers. Gradually they accumulate into a compact bundle, of orange color in contrast to the grayish-black color of the stria fibers, which extends forward and medialward (pl. 18, fig. 39). A few of the fibers can be traced into stria medullaris. This is the archistriato-habenular component of the bundle. Many of the fibers run forward to synapse in the bed nuclei of the commissures and to some extent in the parolfactory or septal area. This latter connection is the tractus epistriaticus precommissuralis of Schroeder ('11). It is termed here tractus archistriatico-precommissuralis in accordance with the nomenclature used elsewhere.

Tractus olfacto-habenularis medialis (pl. 18, fig. 39). As the stria medullaris swings dorsalward to assume its position along the dorsal wall of the diencephalon it is joined medialward by many small bundles which connect it with the preoptic and hypothalamic areas. These constitute functionally the equivalent of the tractus olfacto-habenularis medialis described for reptiles (Herrick, '10; Crosby, '17; Hines, '23). The habenula is connected with preoptic and hypothalamic areas by means of periventricular fibers. Because of the richness of impregnation of the periventricular system of fibers, it is extremely difficult to determine the exact nuclear relations of this olfacto-habenular system. The fibers are related to the medial preoptic nucleus, to the stratum cellulare externus, to the nucleus internus inferior anterior, and probably to other hypothalamic areas.

COMPONENT FROM SEPTO-MESENCEPHALIC SYSTEM TO HABENULA. Joining the tractus taenio-habenularis on its medial side at its entrance to the diencephalon is a component from the septo-mesencephalic tract to the habenula. This latter fiber bundle appears to arise, in part at least, directly from the tract. It receives contributory fibers from the nucleus superficialis parvocellularis and probably from the nucleus lateralis. A lateral olfacto-habenular tract comparable to that in alligator has not been identified in the present material.

The various components thus far discussed collectively form a fiber bundle, the stria medullaris, which swings along the dorsal surface of the diencephalon toward the habenular region. Certain small bundles of the tract, possibly the fibers of the medial cortico-habenular, swing medialward ahead of the other bundles and first enter the habenular nuclei distributing to the medial group. The more medial fibers appear to distribute on the same side. The more lateral fibers cross, at least in part, in the habenular commissure, which is small and situated at the posterior end of the habenular nuclei.

In sparrow all the major components here mentioned can be identified, but in some cases they are so small that it is not possible to follow them clearly throughout all of their extent.

TRACTUS HABENULO-PEDUNCULARIS (pl. 19, fig. 40 and fig. 41, A to D). Tractus habenulo-peduncularis in the dove is divisible into several portions. It consists primarily of two main divisions as it emerges from the ventral side of the habenula. The more medial of these is related to the medial habenular nucleus. This component is golden brown in color and the bundles are somewhat less densely packed than those of the lateral division. The latter consists of darker-staining (grayish black in our preparations) fibers which are related to the lateral habenular nucleus. The lateral division will be discussed first. In our observations we agree with the generally expressed opinions that in mammals the tract consists of an unmyelinated portion from the medial habenular nucleus and a myelinated portion from the lateral habenular nucleus (Foix and Nicolesco, '25, and others).

The fibers of the lateral division (pl. 19, fig. 41, A to D) swing ventrolateralward to a position dorsal to the nucleus rotundus. Here the outermost bundles run lateral to the nucleus along its outer capsule, toward tectal regions. Some of these fibers are believed to reach the area, although, due to the great number of fibers in the region, absolute certainty of this latter connection is impossible. Just internal to this component, fibers of the lateral division swing into and through nucleus rotundus and are to some extent in synaptic relation with this nuclear mass. Just internal to this small component to nucleus rotundus lies the main fiber mass of the lateral division of the habenulo-peduncular system. This main fiber mass consists in reality of two portions, a more lateral portion which swings ventromedialward between the nucleus tractus habenulo-peduncularis and nucleus rotundus and a more medial portion which passes through the former nucleus and is to a considerable degree in synaptic relation with it. This constitutes a habenulo-diencephalic tract. Fibers arising in this nucleus join other habenulo-peduncular fibers of the lateral division which run ventromedialward and then more directly caudalward, always approaching the ventricular wall. At the level of the nucleus of the oculomotor nerve the lateral division of the tractus habenulo-peduncularis lies slightly lateral to the medial division previously described. It joins this division as the two swing internal to the emerging oculomotor fibers, lying, in general, rather ventrolateral and then ventral to the medial portion. A few of the fibers of the lateral division decussate in close proximity to the crossing fibers of the infundibular tract of Jellgersma. Thus, the interpeduncular region of the opposite side may receive a part of this system.

The medial division of the habenulo-peduncular tract (pl. 19, fig. 41, A to D) arises from the medial habenular nucleus. It runs in part parallel to the lateral division in its course through the diencephalon, and its outermost fibers are likewise in synaptic relation with the nucleus tractus habenulo-peduncularis. Its inner fibers, however, pass medial to this

nuclear group. The most medial of all the fibers of this component do not run lateralward with the remainder of the bundle, but cut straight through the dorsal thalamus, forming a slight double curve with the convexity first medialward, and then slightly lateralward. The fibers then run ventralward through the bundles of the occipito-mesencephalic tracts. The figures (pl. 19, fig. 40 and fig. 41, A to D) in which the different bundles were plotted give a better idea of the scattered components of the medial habenulo-peduncular tract than it is possible to convey by a written description and should be consulted at this time. Gradually the various components of the system converge. The fibers of the medial division swing internal to the emergent roots of the oculomotor and distribute there to gray, which is considered to be interpeduncular in character. So far as the present evidence is concerned, the medial division of the habenulo-peduncular is homolateral, at least it has not been possible to demonstrate contralateral fibers. The finer details of the internuclear terminations are not demonstrable in our preparations.

OPTIC CONNECTIONS. In a previous section (p. 98) attention has been called to the fact that large eyes are present in the bird, as is to be expected in animals in which vision plays so important a rôle. With such large eyes there is a corresponding increase in the number of optic fibers and in the size and differentiation of the tectal centers. Apparently, this great importance of the incoming optic is associated not only with a shift ventralward of the optic tecta, but also with a great increase in the number of incoming (and outgoing) fibers associating tectum with forebrain, diencephalon, and lower centers. As further consideration of the fiber connections will show, the tectal portions of the mesencephalon constitute correlation centers of prime importance in the avian brain.

Optic tracts have been recognized since the earliest work on avian brain has been carried out. The finer details of their relations and terminations have been the subject of

considerable study and experimental work. Associated with this work are the names of such observers as Bellonci ('88), Perlia ('89), Wallenberg ('98, '98 c), Edinger, Wallenberg, and Holmes ('03), Kosaka and Hiraiwa ('15), and others. The following account reviews to a considerable degree previous findings, but adds certain further points. It is based primarily on sparrow, but has been supplemented and checked by such other material as is available.

There is complete decussation of optic fibers in the chiasma in birds. After crossing, the greater number of fibers run lateralward and slightly dorsolateralward along the surface and constitute the marginal optic tract (pls. 13 to 17, figs. 29 to 36). This has been described repeatedly; consequently, it is only necessary to say that it enters the tectum surrounding it on all sides and forms its most superficial fiber layer. In course it contributes small bundles to the lateral geniculate nucleus and to the nucleus superficialis synencephali.

Bundles of optic fibers, at first indistinguishable from the marginal bundle of the optic tract, form the medial and lateral divisions of the axillary or isthmo-optic tract (pls. 13 to 17, figs. 29 to 37). The medial division consists of small bundles which run through and on the lateral side of the lateral geniculate. In this connection attention is called again to the structure of the lateral geniculate of birds, which, as in reptiles (Ramón y Cajal, '96; Beccari, '23; Huber and Crosby, '26), consists of a central layer of cells the processes of which extend in both directions in relation to the optic tract and a zonal layer of scattered cells, particularly well developed on the ventral side.

But although the more medial fibers of the isthmo-optic bundle pass along this nuclear mass and even, in part, through it, they either do not contribute greatly to it or are joined by fibers from it, since the fasciculi remain relatively large and the exiting bundles do not appear to have diminished appreciably in their course. Lateral to the nucleus they join the lateral division of the axillary bundle, the whole isthmo-optic tract then running immediately internal to the

marginal optic tract. The isthmo-optic fibers run dorsalward, internal to the tectum, and reach a position just internal to the most dorsal part of the marginal optic bundle (pls. 15 to 17, figs. 32 to 37). In this position they give off a tiny bundle (augmented in some of our material—at least sparrow) by a few fibers from the marginal tract which swing into the diencephalon in relation with the nucleus superficialis parvocellularis and probably reach nucleus lateralis. In this portion this small strand of optic fibers is just lateral to the lateral septo-mesencephalic tract. This little strand is possibly the avian homologue of the scattered optic fibers which run to the dorsolateral part of the dorsal thalamus in alligator (Huber and Crosby, '26). In the meanwhile the main axillary or isthmo-optic bundle proceeds caudad. Gradually it is incorporated within the deeper layers of the dorsal tectal area near its connection with the tegmentum. In this position the bundle appears to contribute some fibers to the deeper parts of the tectum of the region—as to this point we are uncertain—but the major portion of the bundle continues caudad to about the level of the motor nuclei of the third nerve. Here, in sparrow and dove at least, it turns medialward and slightly ventromedialward to terminate in the convoluted nucleus (isthmo-opticus). The method of distribution of this tract to the above-mentioned nucleus is of interest. The fibers enter mainly from the dorsal side, and the nuclear mass is folded in to form a double-walled and, in part, convoluted hilus at the level of entrance of the fibers. Smaller strands of the optic fibers swing around the outside of the nuclear mass and enter at the periphery on the lateral, medial, and ventral sides. Nucleus isthmo-opticus is connected with the motor nuclei of the third and fourth by bundles of the radiations of Meynert. It is likewise connected with the optic tectum and the nucleus mesencephalicus lateralis (pars dorsalis of Ariëns Kappers, '21, inferior colliculus of higher forms).

Further confirmation of the distribution of the axillary or isthmo-optic and marginal tracts in bird is to be found in a

horizontal series of dove—toluidin-blue-stained—at our disposal. In this series the optic tract is lacking on one side and associated with this is the disappearance of the outer layer of the tectum and the absence of nucleus isthmo-opticus on the same side.

The axillary or isthmo-optic tract of this account is certainly the tractus isthmo-opticus of Craigie and Brickner ('27) and Craigie ('28); it is the medial optic tract of the 1903 account of Edinger, Wallenberg, and Holmes. It is probable that it includes at least the axillary tract described for alligator (see discussion of literature of this tract in 1926 paper, Huber and Crosby). It is possible that it is in part at least the equivalent of the axillary bundle of Wlassak ('93) (frog) and Herrick ('17) (*Necturus*), but the homologies here are not clear.

The basal optic root, which can be quite easily traced in through the decussating optic fibers in the bird, lies adjacent to and slightly at an angle with the course of the tractus tecto-thalamicus cruciatus. It is larger in avian than in reptilian forms and runs slightly dorsalward and then backward until it reaches the ganglion ectomamillare of the Edinger and Wallenberg terminology (the nucleus of the basal optic root of reptiles). This nucleus, as has been stated previously, forms a large cell mass at the level of exit of the third nerve, lying just lateral to its outgoing fibers. Not only can basal optic fibers be traced to the nucleus, but between this nucleus and the interstitial nucleus of Cajal and between it and the third nuclei there runs a definite band of fibers similar to that described for Reptilia (Beccari, '23; Huber and Crosby, '26). The tract runs medialward between the medial septo-mesencephalic tract and the forebrain bundle. It has been seen in parrakeet, sparrow, and dove.

SUPRA-OPTIC DECUSSATIONS. The dorsal supra-optic decussation and its associated tractus tecto-thalamicus cruciatus are present both in the silver material of dove and sparrow and the Weigert series of chicken. They are also very clear in the Weigert material of the Amsterdam collection, in such

forms as the parrakeets, *Cacatua rosicapita* and *Palaeornis*, and the owl, *Athena noctua*. The fibers of the ventral supra-optic decussation in general are represented by a white unstained area in the material prepared for medullated tracts with here and there scattered medullated fibers, and small bundles in the dorsal division of the ventral supra-optic. This ventral supra-optic decussation is clearly evident in the silver preparations.

Dorsal supra-optic system (pls. 14 and 15, figs. 30 to 33). The fibers of the dorsal supra-optic system cross in the chiasmal ridge just ventral to the third ventricle. They consist, in the silver preparations, of a wide band of fine grayish or reddish fibers (depending upon the series) which form at the region of decussation a relatively compact mass of fibers, but which break up after crossing into smaller bundles which radiate out through nearly all parts of the thalamic wall from the periventricular areas to the regions above the optic tracts. For convenience in description, this more or less continuous spray of fibers has been divided into three rather arbitrary portions: medial, lateral, and ventral divisions.

The medial division (pls. 14 and 15, figs. 30 to 33) forms a part of the periventricular system of fibers. Among the most cephalad of its fiber bands is a tiny bundle which crosses just below the ventricle and swings almost immediately dorsalward as a relatively compact little mass of fibers among the cells of the periventricular gray. It terminates in the nucleus internus inferior anterior (possibly the nucleus n of Rendahl). A second, larger bundle crosses the midline and runs caudad along the side of the ventricle. It is added to gradually by decussating fibers and apparently by fiber bundles from the nuclear group through which it passes (notably stratum cellulare externum). It terminates in part in nucleus internus inferior posterior (pl. 14, fig. 31). Some fibers run farther caudad, possibly to the nuclear masses of the median longitudinal fasciculus. The more posterior bundles, at least, and possibly the whole medial division is to be regarded as the avian homologue of the ansulate fibers described by Bellonci

('88) for reptiles. However, in dove and sparrow—possibly in all birds—the medial division is more intimately related to the remainder of the dorsal supra-optic system than are the reptilian ansulate fibers to that system in reptiles. Other fibers of the medial division of the dorsal supra-optic system run dorsalward and caudalward in the region between the ventricle and the forebrain bundles. In part, the fibers distribute to the areas through which they pass; in part, they swing caudalward and can be traced as rather darker-staining bundles throughout most of the extent of the diencephalon, forming a part of the present system, but distributing also to more lateral parts of the medial areas. Ultimately, we believe, some of them come into relation with the nuclei of the median longitudinal fasciculus in birds, as they do in reptiles (Beccari, '23), but, unfortunately, the evidence for this is not entirely conclusive. This medial portion includes Ganser's commissure of mammals.

The main mass—that is, the lateral portion—of the dorsal supra-optic system, the homologue of the dorsal supra-optic decussation in reptiles (de Lange, Ariëns Kappers, Huber and Crosby, and others) after crossing in the chiasmal ridge swings dorsolateralward partly medial to the forebrain bundles, but mainly intermingled with them. The more anterior bundles are particularly intimately associated with the lateral forebrain bundle, strands running between portions of this latter bundle and, in part, accompanying it into the lateral regions of the hemisphere. This is true in both the silver and Weigert material. Their final distribution could not be determined in any material available to us (although it is believed to be paleostriatum, at least in part); we feel assured that a satisfactory analysis of them would involve the use of degeneration material which at present is not at hand. Such a connection to forebrain through the dorsal supra-optic system was described by Edinger and Wallenberg ('03) for birds. We were unable to identify such a direct forebrain connection of the dorsal supra-optic decussation in our alligator material, although it was searched for carefully.

Just caudad to this more anterior group of the lateral division of the dorsal supra-optic, some fibers of the division are in synaptic relation with a nuclear mass comparable to the nucleus of the dorsal supra-optic system described for alligator and so termed for birds in the present paper. This nucleus lies in the angle between the main mass of the fore-brain bundle and the thalamo-striatal tracts joining that bundle at the level. With or without synapse in this nucleus, fibers pass to dorsal thalamic areas with the fibers of the medial thalamo-frontal tract. Some of the ventral fibers of the lateral division arch lateralward and enter the optic tectum. Others appear to run farther caudalward, but their ultimate termination is as yet unknown.

The ventral division of the dorsal supra-optic decussation has previously been described in reptiles as *tractus tecto-thalamicus cruciatus* (Huber and Crosby, '26). The following description of the tract is based on the sparrow material. Essentially similar relations can be demonstrated in such other of our avian material as shows this tract. In sparrow the fibers run directly lateralward, synapsing to some extent in a nuclear mass dorsal and in part cephalic to the more cephalic portion of the lateral geniculate nuclear group (pl. 14, fig. 31). This nucleus we have termed the nucleus of the crossed tecto-thalamic tract (*nucleus tractus tecto-thalamici cruciati*), following the terminology used by us ('26) for an apparently homologous nuclear group in the alligator. It probably belongs, in general, to the lateral geniculate complex, since short fibers relate it with that nucleus, and fibers of *tractus tecto-thalamicus cruciatus* appear to distribute to both nuclear groups to some extent. Some fibers run directly through the nucleus of the tract and, strengthened by fibers from it and from lateral geniculate, pass to tectum. This band of fibers between lateral geniculate and tectum is the avian homologue of the reptilian *tractus tecto-thalamicus ventrolateralis* (pl. 15, fig. 33). It carries fibers, crossed and uncrossed, between the lateral geniculate and *nucleus tractus tecto-thalamici cruciati* on the one hand and the tectum and

pretectal areas, probably, on the other. Its nearest mammalian equivalent is the peduncle of the superior colliculus.

Whether or not there are optic fibers in tractus tecto-thalamicus cruciatus is as difficult of determination in normal material of birds as it proved to be in reptiles. It has been described as containing more or less optic components in various forms. It is probably the tractus opticus commissuralis of chameleon (P. Ramón y Cajal, '96). Edinger ('99) identified the bundle in reptiles, but was uncertain as to whether it was optic or non-optic in character. It is our opinion that it is supra-optic rather than optic.

Ventral supra-optic system (pls. 14 to 16, figs. 30 to 35). The fibers of the ventral supra-optic system cross in two divisions, a dorsal and a ventral, as they did in alligator, although the divisions are not as clearly marked as in that latter form, nor is the dorsal division as distinctly separate from tractus tecto-thalamicus cruciatus as is the case with reptiles. Furthermore, both dorsal and ventral portions begin posterior to the cephalic end of the dorsal supra-optic system, but cross at the level of the optic decussation and slightly caudad to it. In this respect, also, they differ from the homologous tracts of the alligator, since in the reptilian forms the ventral supra-optic decussates in the chiasmal ridge cephalad to the dorsal supra-optic system.

The following account of the ventral supra-optic decussation is based on silver material of sparrow supplemented by similar preparations of dove. Dorsal and ventral divisions cross in the chiasmal ridge as a mass of fibers between the dorsal supra-optic system superiorly and the optic tracts inferiorly (pls. 14 and 15, figs. 30 to 32). The two divisions are not at first clearly differentiable from each other, but swing dorsolateralward just internal to the optic fibers until a region just dorsal to the lateral geniculate body is reached. Here the ventral supra-optic attains a position dorsal and dorsomedial to the nucleus and ultimately just dorsal to the basal optic root. By this time the two parts of the bundle can be recognized. Pars ventralis is composed of the more

ventrally crossing fibers which have accumulated into a compact (orange-colored in our preparations) bundle, lying lateral and slightly ventrolateral to pars dorsalis (pls. 15 and 16, figs. 32 to 35). This latter portion, consisting of the more dorsally and, in part, the more caudally crossing bundles, has accumulated medially—at first ventromedially and gradually dorsomedially—of the ventral divisions. In the particular preparations used it had a reddish color which aided in differentiating it. From this point on, the courses of the two divisions are specific for each; consequently, they are considered separately.

Pars dorsalis of the ventral supra-optic is the commissura transversa of Craigie's and Brickner's account. The distribution, as indicated in their figures, is only a small portion of the tract, probably the medullated part in the series considered. Pars dorsalis, having reached the above-described position, turns caudad and is visible in the preparations (pl. 15, fig. 32) as a group of cross-cut bundles just dorsal to pars ventralis and ventral to the more medial bundles of the lateral forebrain complex. In part in this position it is intermingled with other tracts. Gradually the bundles swing lateralward toward the tectum and, joining the other tecto-thalamic and thalamo-tectal tracts, enter the tectum on its ventral side. In one series it presents further relations which cannot be substantiated in our other material. We have some hesitation in presenting these connections, since our evidence is based on this one series which appears to be cut in a plane particularly favorable for making clear certain relations. From this series the dorsal division of the ventral supra-optic system appears to send fibers directly into the fiber mass from nucleus ovoidalis which has been regarded by certain observers as a thalamo-mamillary tract (Edinger, Münzer and Wiener). Other uncrossed fibers of the tract run with this dorsal division to the tectum (see description of tract, p. 153). Fibers from the dorsal division of the ventral supra-optic likewise are to be found on either side of the tract; the more medially directed ones we have been unable to

follow to their destination. The laterally directed larger bundles swing across the more posterior portions of nucleus rotundus, probably with some synapse there, and across nucleus spiriformis toward the tectum, close to the other tectothalamic tracts and to the ventral division. They synapse in part in pars principalis nucleus isthmi. Some fibers pass into the optic tectum.

Pars ventralis of the ventral supra-optic division (pls. 15 and 16, figs. 32 to 35) from its position ventral to the dorsal division swings lateralward as a distinct bundle in order to reach the optic tectum. Part of the fibers run directly across the lower part of nucleus rotundus and pass to the optic tectum. The main bundle turns caudad and sends radiating fiber bundles across the ventrolateral part of nucleus rotundus and nucleus principalis precommissuralis. To what extent the fibers terminate in these nuclei we cannot at present state. They are most evident in one series. The remainder of the bundle runs caudad in a position dorsal to the lateral geniculate (and in part separated from it by a tectal bundle) and ventral to the dorsal division. It decreases in course, fibers passing off dorsolaterally from it, the destination of which could not be determined; possibly pretectal or tectal areas. Some fibers appear to reach nucleus mesencephalicus lateralis. Pars ventralis of the ventral supra-optic tract gradually comes into closer relation with the main tecto-thalamic tract and runs caudad between that and the optic tract. It distributes to the deep medullary layer of the optic tectum.

TECTO-THALAMIC AND THALAMO-TECTAL TRACTS. *Tract from nucleus ovoidalis* (pls. 15 and 16, figs. 33 to 35; pl. 18, fig. 38). At one time this tract was termed the Vicq d'Azyr bundle by Edinger; earlier, this same homology had been made by Münzer and Weiner. On the basis of such an identification of the tract, these observers called the cell mass nucleus anterior ventralis. The nucleus anterior of Edinger's later description ('08), however, is the area dorsalis of Rendahl. Several observers have questioned the homology thus made for the tract; Ariëns Kappers called particular attention to

the fact that the observers themselves had proved that the direction of conduction was outgoing from the thalamic areas, while modern work on the *Vieq d'Azyr* bundle shows it to be mamillo-thalamic. Furthermore, the earlier workers were not able to carry it to the mamillary body. Most students of the avian diencephalon have retained the name of nucleus anterior—rather illogically it seems to us, since in neither sense (ventral nor cephalic) is it anterior in position nor is it the evident homologue of the mammalian nucleus of that name. Rendahl has raised the question of the advisability of such usage and has christened it, tentatively, nucleus B. Craigie and Brickner ('27) have suggested the name nucleus ovoidalis. No observer, to our knowledge, has traced the tract in question to its termination. The analysis of this fiber bundle is difficult. Experimental data would be of great value here.

From nucleus ovoidalis, joined by fibers from the nucleus subrotundus and from the area just internal to these, the nucleus internus inferior posterior, the fibers arch downward, passing at first almost directly ventralward, so that the tract appears in cross-sections as a longitudinally coursing bundle of fibers lying lateral to the nucleus rotundus and medial to the ventral peduncle of the forebrain bundle. Gradually the fiber bundle turns backward, running caudalward in the lower part of the region, and appears to come into positional relationship with the supra-optic system. Here, unfortunately, the tract from nucleus ovoidalis in most of our series disappears from view. The cells of nucleus subrotundus of Rendahl lie along the course of the tract, and they contribute fibers and possibly also receive collateral or terminal fibers from it. Two of the sparrow series afford some further clues. One cut obliquely, but approaching the horizontal plane, makes it possible to trace the tract lateralward into the region of the tecto-thalamic and thalamo-tectal tracts, which systems it appears to join. The second series is one cut more nearly transversely, but the plane is still oblique. In this latter series the fibers swing ventralward and reach, as

stated before, the region of the dorsal division of the ventral supra-optic system. Here certain bundles become continuous with fibers of the dorsal division, evidently forming a part of that decussation. Other bundles of the tract from nucleus ovoidalis accompany the dorsal division tectalward. The evidence for this latter point is not entirely conclusive. It has not been possible to follow the further distribution of the bundle.

The tract from nucleus ovoidalis apparently represents a part of the thalamo-tectal system, the work of Edinger and Wallenberg indicating that the direction of conduction is centrifugal with reference to thalamus. The tract represents a crossed and an uncrossed connection (with the emphasis on the uncrossed) between the nucleus ovoidalis and nucleus subrotundus on the one hand and the tectal and probably subpretectal areas on the other. It may have further connections.

Tectal connections of nucleus rotundus (tractus tecto-thalamicus and thalamo-tectalis nuclei rotundi) (pls. 15 and 16, figs. 33 to 35). This tract is usually designated as the tecto-thalamic tract of birds. It has been previously described by Edinger and Wallenberg ('99), Ariëns Kappers ('21), Craigie ('28), and others. The tract is present in the silver material available and in the Weigert series of *Gallus domesticus*, *Cacatua*, and *Palaeornis*. From the more anterior regions of the nucleus rotundus the fibers accumulate in the lower end of the nuclear mass until a fair-sized bundle is formed (pl. 15, fig. 33). As the fibers increase in number the ventral end of nucleus rotundus disappears and the scattered cells of nucleus posteroventralis take its place. Here the fiber bundle is large and is intermingled with cells of the latter nucleus with which it undoubtedly has some synaptic relations. This tecto-thalamic path is intermingled with fibers of the supra-optic systems, the dorsal division of the ventral supra-optic in particular passing directly across its ventral portion. In this position it is joined by other tecto-thalamic and thalamo-tectal paths, some of which are more

or less distinguishable—as, for example, the divisions of the ventral supra-optic system—while others become so intermingled as to be indistinguishable and build with the fibers from nucleus rotundus, nucleus posteroventralis, and nucleus principalis precommissuralis a common path between tectum and thalamus. Collaterals and probably stem fibers are given off in course to nucleus subpretectalis. The bundle proceeds from its position in the region of nucleus principalis precommissuralis ventrolateralward and caudalward and enters the tectal regions ventral to pars principalis of nucleus isthmi and in company still with the ventral supra-optic bundles. The tract distributes to the deeper medullary lamina of the tectum extending to its posterior end. In all probability it also carries impulses in the other direction. The dorsal thalamic centers, nucleus dorsolateralis anterior and nucleus tractus habenulo-peduncularis, contribute fine fibers to a bundle which gradually accumulates on the medial side of the tecto-thalamic path associated with rotundus and runs caudad with it to the tectum. This tract, which is termed tractus tecto-thalamicus and thalamo-tectalis dorsalis, receives additions from nucleus rotundus and particularly from the capsule surrounding it on the medial side. It does not show as a special tract equally well in all series.

Tractus tecto-thalamicus ventrolateralis (pl. 15, fig. 33). Where the tractus tecto-thalamicus cruciatus sends branches to the lateral geniculate, small bundles of fibers begin to accumulate. These fibers, which in part are directly related to the geniculate and in part are fibers of tractus tecto-thalamicus cruciatus, form a small and scattered, deeply staining bundle which runs lateralward to the optic tectum, passing in course through and ventral to the nucleus superficialis synencephali of Rendahl.

Tractus tecto-thalamicus et thalamo-tectalis nuclei ectomamillaris (pl. 16, fig. 35). This connection consists of a small fiber bundle which runs directly from the dorsolateral portion of the nucleus ectomamillaris dorsal to the nucleus externus of Rendahl and so enters the optic tectum. The direction of conduction is unknown.

Tractus tecto-thalamicus et thalamo-tectalis nuclei externi (pl. 16, figs. 34 and 35). Optic fibers come into relation with this nucleus. Arising from it is a rather deeply staining tract which runs to the tectum. In this nucleus the tract to the tectum is so intermingled with the incoming optic that it is not possible to determine whether or not optic fibers continue through into the tectal tract.

Tectal connections of the pretectal group of nuclei. In this list of tectal connections one must not fail to enumerate those from nucleus pretectalis, subpretectalis, and nucleus spiriformis. All three of these nuclei are intimately interrelated by broad fiber bands with the roof of the midbrain. Mention should also be made of the two tectal components previously described with the forebrain bundle; one running with the tractus thalamo-frontalis intermediaris; the other, with the ventral tegmental path. Likewise, the septo-mesencephalic tract through its dorsal division sends fibers to the pretectal nucleus and to the tectum (pl. 16, fig. 35). The intimate interrelation of tectal and thalamic and tectal and forebrain centers emphasizes how great is the interdependence of these parts in their advances in development. The direction of conduction of the above tracts needs to be checked as yet.

TRACTUS PRETECTALIS SUBPRETECTALIS (pl. 16, fig. 34). A very definite and broad band of fibers unites nucleus pretectalis with nucleus subpretectalis. It should be emphasized again that nucleus subpretectalis and nucleus pretectalis of avian forms represent a pretectal group of reptiles, the most important component of which is the so-called nucleus pretectalis. In the differentiation into the avian group the pretectal reptilian nucleus has become spread out to form both the pretectal and subpretectal masses interconnected by the delicate tractus pretectalis subpretectalis. In this connection may be mentioned the presence of fine fibers connecting the pretectal with the lateral part of the spiriform nucleus. The two parts of the spiriform nucleus are likewise interconnected by short fibers.

POSTERIOR COMMISSURE (pls. 17 and 18, figs. 36 and 38). The literature contains many references to the various components of the posterior commissure in birds (Ariëns Kappers, '21; Craigie, '28, and others) and in other forms. The system is very large in birds, but in general resembles that in alligator and in other reptiles. It will be unnecessary to describe the system in great detail, but there are certain components which we wish to emphasize because of their relation to tectal and pretectal centers.

The posterior commissure in sparrow may be divided into the classical dorsal and ventral divisions (pl. 17, fig. 36). The dorsal division is essentially a connection between the tectal centers of the two sides. The fibers accumulate, for the most part, just dorsal to the ventricle, swing across the midline, and reach the corresponding area of the other side. The ventral division connects, in general, with the region of the mid-brain below the ventricle. This includes the dorsal part of the lateral mesencephalic nuclear region (the homologue of the inferior colliculus) and the pretectal areas. These fibers form an almost continuous band extending from the midline to the tectal regions, except in so far as they are intermingled or pushed aside by the pretectal groups, particularly by nucleus pretectalis, nucleus spiriformis pars medialis (nucleus dorsocaudalis), and nucleus spiriformis pars lateralis. These posterior commissure fibers surround the nucleus pretectalis on all sides, forming a sort of capsule about it and separating it ventrally from nucleus spiriformis lateralis and medialis and laterally from the tectum (pl. 17, fig. 36). Certain bands of the commissure break up into delicate fibers among the cells of the mass and probably either arise or end there or do both. The nucleus spiriformis pars lateralis is connected to the pretectal areas of the opposite brain wall through the posterior commissure, a considerable bundle of the commissural fibers lying dorsal and lateral to it, and a smaller bundle passing medial and ventral to it between it and nucleus spiriformis medialis, which also appears to contribute to the commissure.

A special band of tectal and subtectal fibers passing to the posterior commissure collect from the tectum in the region of the nucleus principalis precommissuralis of Rendahl, from which nucleus they probably receive fibers. This bundle runs dorsomedialward behind the nucleus rotundus, through the area of nucleus postrotundus, and swings dorsalward to join the other components of the commissure. Tecto-bulbar fibers cross it in its course dorsomedialward.

The most medial fibers of the commissure swing around the periventricular gray and then in toward the midline where they end, in part directly in the median longitudinal fasciculus, and in part in its associated interstitial nuclei, particularly the dorsal one. These periventricular bundles carry with them apparently crossing fibers between associated periventricular gray. For further details with regard to the interrelations of the posterior commissure and the median longitudinal fasciculus and the associated interstitial gray reference should be made to the work of Wallenberg ('04), and Beccari ('23, for reptiles).

ASCENDING CONNECTIONS FROM LOWER CENTERS TO DIENCEPHALIC AND MESENCEPHALIC REGIONS. A communication to be published later from the Department of Anatomy, University of Michigan, will concern itself with the connections between the avian diencephalon and lower centers. Consequently, such connections will be touched upon only incidentally in the present communication. However, a brief summary of certain fundamental connections is included here in order that the nuclei of the diencephalon may be more fully discussed. Unless otherwise stated, the connections have been identified and their relations followed in the material at our disposal.

Fibers from the cochlear nuclei of the medulla, after decussation, swing forward as the lateral lemniscus to the lateral mesencephalic nucleus (pars dorsalis, Ariëns Kappers, '21, probably the inferior colliculus of mammals). In course they give collaterals (possibly stem fibers) to the associated nucleus of the lateral lemniscus and to the pars principalis of nucleus isthmi. This latter nuclear group is connected with the optic

tectum by isthmo-tectal and probably tecto-isthmal fibers, with the lateral mesencephalic nucleus by an isthmo-mesencephalic tract, and with the cerebellum. These connections have been mentioned by Ariëns Kappers ('21) and have been verified in the present material. Accompanying the lateral lemniscus are secondary trigeminal paths, the bulbo-mesencephalic paths of Wallenberg ('04), who traced them forward into the medial mesencephalic nucleus (nucleus mesencephalicus lateralis, ventral part, according to Ariëns Kappers, '21). These fibers have been identified in relation with those of the lateral lemniscus, but thus far it has not been possible to follow them through as an independent system in the material at hand.

In addition to the above connections, Wallenberg traced, by degeneration methods, ascending fibers arising from the nuclei of the posterior funiculi, decussating and then ascending along the ventromedial wall of the medulla. These fibers terminated in nucleus intercalatus, the medial capsule of nucleus rotundus, the red nucleus, and the nucleus of the strio-mesencephalic tract (nucleus superficialis parvocellularis). This bulbo-thalamic tract he homologized with the mammalian medial lemniscus. Running with this bundle he found fibers to the infundibular region, to the tuber cinereum and associated with the commissura transversa. These latter fibers formed a bulbo-hypothalamic tract which he regarded as comparable to the mamillary peduncle of higher forms. The quinto-frontal path of this worker has been considered earlier in this paper (p. 126). Wallenberg's work was carried out by the use of degeneration preparations. A study of his figures makes possible the differentiation of many of these components in the normal material of dove and chicken. We have not been able to follow clearly the component to commissura transversa. Because of the richness of the impregnation, it has not been possible as yet to follow the tracts completely in sparrow, but there can be no doubt as to their presence in general.

The descending pathways from the tectum to the lower centers have been described by numerous observers, chief

among whom are Edinger and Wallenberg ('99). In avian forms they resemble closely the tectal paths as observed for reptiles. They consist of a dorsal tecto-bulbar system which runs medialward from the tectum to a position ventral to the oculomotor nuclei, contributes fibers to these nuclei, then forms the dorsal tegmental decussation and turns caudalward. It is accompanied by uncrossed fibers. A large ventral tecto-bulbar system sweeps across the tegmentum as one of its most conspicuous fiber components, and after a partial decussation takes its position in the ventrolateral region of the mesencephalon and runs caudalward to the medulla. These tecto-bulbar systems constitute the main efferent pathways from the optic tectum.

TABULAR SUMMARY OF NUCLEAR MASSES WITH FIBER CONNECTIONS

<i>Nuclear masses</i>	<i>Forebrain</i>	<i>Fiber connections</i>
<i>a. Basal centers of the medial forebrain wall</i>		
Area praepyramidalis	Tractus olfactorius lateralis	
Bed nucleus, commissura anterior	Tractus occipito-mesencephalicus	
	Commissura anterior	
	Tractus septo-habenularis	
Bed nucleus, commissura pallii	Commissura pallii	
	Tractus infundibuli	
	Tractus septo-habenularis	
Bulbus olfactorius	Fibrae olfactoriae	
	Tractus olfactorius lateralis	
	Tractus olfactorius medialis	
Nucleus accumbens	Internuclear connections with paleostriatum and septum	
Nucleus of the diagonal band of Broca	Diagonal band	
	Tractus septo-mesencephalicus ramus basalis frontalis	
Nucleus olfactorius anterior	Tractus olfactorius medialis	
	Internuclear connection with area praepyramidalis	
Nucleus septalis lateralis	Tractus cortico-septalis	
	Tractus septo-corticalis	
	Tractus septo-habenularis	
	Medial forebrain bundle	
Nucleus septalis medialis	Tractus septo-corticalis	
	Tractus septo-habenularis	
	Tractus septo-mesencephalicus	
	Medial forebrain bundle	

<i>Nuclear masses</i>	<i>Fiber connections</i>
b. Basal centers of the lateral forebrain wall	
Archistriatum	Tractus olfactorius lateralis Tractus fronto-archistriaticus et neostriaticus Commissura anterior Tractus archistriatio-habenularis et precommissuralis
Ektostriatum	Internuclear connections with neostriatum Tractus fronto-occipitalis Fibers to and from dorsal and ventral medullary laminae Internuclear connections with paleostriatum augmentatum, neostriatum intermediale, and hyperstriatum ventrale Hyperstriato-ektostriatal fasciculus from the dorsolateral surface area, the superior and supreme frontal laminae, and the hyperstriatum dorsale to or through the ektostriatum Collateral and perhaps stem fibers of the lateral, intermediate, and medial thalamo-frontal tracts Tractus strio-tegmentalis et strio-cerebellaris (?)
Hyperstriatum accessorium	Lamina frontalis suprema Tractus septo-mesencephalicus Internuclear connections with dorsolateral surface area, entorhinal and paraentorhinal areas, and hyperstriatum dorsale
Hyperstriatum dorsale	Mediodorsal periventricular system Lamina frontalis superior Lamina frontalis suprema Internuclear connections with hyperstriatum ventrale, ektostriatum, nucleus basalis, dorsolateral surface area, and hyperstriatum accessorium
Hyperstriatum ventrale pars dorsoventrale	Tractus thalamo-frontalis lateralis Lateroventral periventricular system Tractus fronto-occipitalis Lamina frontalis superior Internuclear connections with dorsolateral surface area, hyperstriatum accessorium, hyperstriatum dorsale, hyperstriatum ventroventrale, and neostriatum
Hyperstriatum ventrale pars ventroventrale	Tractus thalamo-frontalis lateralis Tractus thalamo-frontalis medialis pars frontalis Tractus fronto-archistriaticus et neostriaticus Lateroventral periventricular system Tractus fronto-occipitalis Internuclear connections with ektostriatum and hyperstriatum ventrale pars dorsoventrale

<i>Nuclear masses</i>	<i>Fiber connections</i>
Neostriatum caudale	Tractus fronto-occipitalis Lamina medullaris dorsalis Tractus thalamo-frontalis medialis pars caudalis Tractus fronto-archistriaticus et neostriaticus Tractus archistriaticus dorsalis Medioventral periventricular system
Neostriatum frontale	Internuclear connections with archistriatum Tractus thalamo-frontalis pars frontalis Tractus quinto-frontalis pars basalis and pars dorsalis Tractus fronto-archistriaticus et neostriaticus Internuclear connections with dorsolateral surface area, hyperstriatum ventrale, ektostriatum, nucleus basalis, paleostriatum augmentatum
Neostriatum intermediale	Lamina medullaris dorsalis Tractus fronto-occipitalis Tractus fronto-archistriaticus et neostriaticus pars frontalis Tractus thalamo-frontalis intermedialis Tractus thalamo-frontalis medialis pars frontalis Internuclear connections with neostriatum frontale, hyperstriatum ventrale, ektostriatum, paleostriatum augmentatum, and neostriatum caudale Medioventral periventricular system
Nucleus basalis	Tractus fronto-archistriaticus et neostriaticus pars basalis Tractus quinto-frontalis pars basalis Tractus olfactorius lateralis Internuclear connections with neostriatum frontale and nucleus tractus fronto-archistriatici
Nucleus intercalatus hyperstriatici	Lamina frontalis superior
Nucleus taeniae	Tractus taenio-habenularis
Nucleus tractus fronto-archistriatici et neostriatici	Tractus fronto-archistriaticus et neostriaticus Internuclear connections with neostriatum frontale and nucleus basalis
Paleostriatum augmentatum	Dorsal and ventral medullary laminae Tractus strio-tegmentalis et strio-cerebellaris Tractus strio-hypothalamicus medialis Tractus thalamo-frontalis medialis (?) Decussatio supraoptica dorsalis pars lateralis (?) Internuclear connections with neostriatum, ektostriatum, paleostriatum primitivum, nucleus basalis, and probably archistriatum and nucleus accumbens Medioventral periventricular system

<i>Nuclear masses</i>	<i>Fiber connections</i>
Paleostriatum primitivum	Tractus strio-tegmentalis et strio-cerebellaris Lamina medullaris ventralis Internuclear connections with paleostriatum and entopeduncular nuclear groups

c. Cortical (corticoid) areas

Area entorhinalis of Rose (hippocampus pars dorsalis of reptiles)	Tractus septo-mesencephalicus Mediodorsal periventricular system Internuclear connections with hyperstriatum accessorium, area paraentorhinalis, hippocampus, and dorsolateral surface area
Area paraentorhinalis	Tractus septo-mesencephalicus Mediodorsal periventricular system Internuclear connections with area entorhinalis, hyperstriatum accessorium, and dorsolateral surface area
Dorsolateral surface area	Tractus septo-mesencephalicus Tractus thalamo-frontalis lateralis Internuclear connections with ektostriatum, hyperstriatum dorsale, and hyperstriatum ventrale pars dorsoventrale
Hippocampus	Tractus olfactorius medialis Tractus cortico-septalis Tractus septo-corticalis Commissura pallii (?) Internuclear connection with area entorhinalis

d. Preoptic area

Nucleus magnocellularis interstitialis pars preoptica	Intercalated in the course of various fiber bundles of the region
Nucleus preopticus anterior	Collaterals of tractus septo-mesencephalicus
Nucleus preopticus lateralis	Tractus occipito-mesencephalicus Medial forebrain bundle
Nucleus preopticus medialis	Tractus olfacto-habenularis medialis Collateral of tractus septo-mesencephalicus

Diencephalon

a. Epithalamus

Habenula	Stria medullaris, including tractus cortico-habenularis medialis, tractus taenio-habenularis, tractus archistriato-habenularis Tractus olfacto-habenularis medialis Commissura habenularum Habenular component of tractus septo-mesencephalicus pars medialis Tractus habenulo-peduncularis
Nucleus superficialis epithalamicus	Habenular component of tractus septo-mesencephalicus pars medialis

<i>Nuclear masses</i>	<i>Fiber connections</i>
<i>b. Thalamus (exclusive of pretectal group)</i>	
Area ventralis anterior	Tractus occipito-mesencephalicus Internuclear connections with the bed nuclei of the commissures [thalamus]
Nucleus decussationis supra-opticae dorsalis	Decussatio supraoptica dorsalis and dorsal Collaterals of tractus thalamo-frontalis medialis
Nucleus decussationis supra-opticae ventralis	Decussatio supraoptica ventralis
Nucleus dorsolateralis anterior pars lateralis	Tractus thalamo-frontalis lateralis Tractus thalamo-frontalis medialis Internuclear connections with nucleus superficialis parvocellularis, nucleus dorsolateralis anterior pars medialis
Nucleus dorsolateralis anterior pars medialis	Tractus thalamo-frontalis medialis Tractus tecto-thalamicus dorsalis Internuclear connections with pars lateralis, with nucleus dorsolateralis posterior and nucleus dorsomedialis anterior
Nucleus dorsolateralis posterior	Tractus thalamo-frontalis medialis Internuclear connections with nucleus dorsolateralis anterior pars medialis
Nucleus dorsomedialis anterior	Diencephalic periventricular system Internuclear connections with nucleus dorsolateralis pars medialis
Nucleus ectomamillaris	Tractus opticus basalis Tractus tecto-thalamicus and thalamo-tectalis pars ectomamillaris Connections with interstitial nucleus of Cajal and oculomotor
Nuclei entopedunculares	Tractus strio-tegmentalis et strio-cerebellaris
Nucleus externus of Rendahl	Tractus opticus Interconnected with tectum
Nucleus fasciculus longitudinalis medialis (in large part tegmental)	Fibrae ansulatae Commissura posterior pars ventralis Fasciculus longitudinalis medialis
Nucleus geniculatus lateralis	Tractus opticus Tractus tecto-thalamicus cruciatus Tractus tecto-thalamicus ventrolateralis Tractus thalamo-frontalis intermedialis Internuclear connections with nucleus tractus tecto-thalamici cruciati and nucleus externus
Nucleus intercalatus	Tractus thalamo-frontalis intermedialis Tractus bulbo-thalamicus (Wallenberg)
Nucleus internus superior	Periventricular system
Nucleus interstitialis magnocellularis diencephali	Interstitial cells in the course of subthalamic (and hypothalamic) fiber bundles and periventricular gray

<i>Nuclear masses</i>	<i>Fiber connections</i>
Nucleus lateralis	Tractus isthmo-opticus Internuclear connections with nucleus superficialis parvocellularis and lateral habenular nucleus
Nucleus lateralis anterior	Tractus thalamo-frontalis intermedialis
Nucleus ovoidalis	Tractus thalamo-frontalis medialis Tractus nuclei ovoidalis Tractus tecto-thalamicus dorsalis Internuclear connections with nucleus rotundus and nucleus subrotundus
Nucleus tr. hab. ped.	Tractus habenulo-peduncularis
Nucleus posterointermedius	(?)
Nucleus postrotundus	Tractus thalamo-frontalis lateralis Tractus tecto-thalamicus et thalamo-tectalis nuclei rotundi Internuclear connections with nucleus rotundus Tractus bulbo-thalamicus (Wallenberg) (?)
Nucleus posteroventralis	(?)
Nucleus prestriaticus	Tractus thalamo-frontalis lateralis
Nucleus rotundus	Tractus thalamo-frontalis lateralis Tractus tecto-thalamicus et thalamo-tectalis nuclei rotundi Tractus tecto-thalamicus dorsalis Decussatio supraopticae ventralis Tractus bulbo-thalamicus (Wallenberg) Internuclear connections with nucleus ovoidalis, nucleus subrotundus, and nucleus postrotundus
Nucleus subrotundus	Tractus nuclei ovoidalis Internuclear connections with nucleus ovoidalis
Nucleus superficialis magnocellularis	Collaterals of tecto-thalamic tracts Fibers to commissura posterior Internuclear connections with tectum, nucleus superficialis synencephali, and nucleus rotundus
Nucleus superficialis parvocellularis	Tractus septo-mesencephalicus pars dorsalis Tractus isthmo-opticus Internuclear connections with habenula, nucleus lateralis, nucleus dorsolateralis anterior pars lateralis, and tectum
Nucleus superficialis synencephali	Internuclear connections with tectum
Nucleus suprarotundus	Collaterals of tractus thalamo-frontalis lateralis
Nucleus tractus tecto-thalamici cruciati	Tractus tecto-thalamicus cruciatus Tractus thalamo-frontalis intermedialis

*Nuclear masses**Fiber connections*

c. Hypothalamus

h. d. Z.	Decussatio supraopticae ventralis
Nucleus hypothalamicus anterior lateralis	Tractus occipito-mesencephalicus Medial forebrain bundle
Nucleus decussationis supraopticae ventralis	Collaterals of the decussation
Nucleus hypothalamicus anterior medialis pars dorsalis	Tractus occipito-mesencephalicus Decussatio supraopticae dorsalis pars medialis Other portions of the diencephalic periventricular system Internuclear connections with nucleus hypothalamicus dorsalis posterior, nucleus internus inferior posterior, nucleus hypothalamicus anterior lateralis, pars intermedialis of nucleus hypothalamicus anterior medialis, and probably with other hypothalamic centers
Nucleus hypothalamicus anterior medialis pars intermedialis	Tractus occipito-mesencephalicus Tractus strio-tegmentalis et strio-cerebellaris Decussatio supraopticae dorsalis pars medialis and other fibers of the diencephalic periventricular system Internuclear connections with pars dorsalis and pars ventralis of the nucleus and with nucleus hypothalamicus anterior lateralis and other hypothalamic centers
Nucleus hypothalamicus anterior medialis pars ventralis	Decussatio supraopticae ventralis Diencephalic periventricular system Internuclear connections with pars intermedialis and adjacent areas
Nucleus hypothalamicus posterior dorsalis	Tractus occipito-mesencephalicus Internuclear connections with nucleus internus inferior posterior, nucleus hypothalamicus anterior medialis pars dorsalis, and other hypothalamic areas Diencephalic periventricular system
Nucleus hypothalamicus posterior lateralis	Tractus strio-tegmentalis et strio-cerebellaris Tractus septo-mesencephalicus ramus basalis caudalis Internuclear connections with adjacent areas
Nucleus hypothalamicus inferior	Probably, diencephalic periventricular fibers and internuclear connections with surrounding areas
Nucleus internus inferior anterior	Tractus occipito-mesencephalicus Tractus olfacto-habenularis medialis Diencephalic periventricular system Internuclear connections with adjacent areas

<i>Nuclear masses</i>	<i>Fiber connections</i>
Nucleus internus inferior posterior	Tractus occipito-mesencephalicus Decussatio supraopticae dorsalis pars medialis and other fibers of the diencephalic periventricular system Tractus nuclei ovoidalis Internuclear connections with nucleus ovoidalis and subrotundus and with adjacent hypothalamic regions
Nuclei mamillares	Tractus septo-mesencephalicus ramus basalis caudalis†
Stratum cellulare externum	Tractus strio-tegmentalis et strio-cerebellaris Tractus olfacto-habenularis medialis Medial forebrain bundle Tractus occipito-mesencephalicus Decussatio supraopticae dorsalis pars medialis Internuclear connections with adjacent areas
Stratum cellulare internum dorsale	Diencephalic periventricular system
Stratum cellulare internum ventrale	Tractus occipito-mesencephalicus Diencephalic periventricular system Internuclear connections with adjacent areas
<i>d. Pretectal areas</i>	
Nucleus pretectalis	Tractus septo-mesencephalicus pars dorsalis Tractus pretectalis subpretectalis Commissura posterior Internuclear connections with tectum, with medial and lateral portions of nucleus spiriformis, and with nucleus superficialis parvocellularis
Nucleus principalis precommissuralis	Decussatio supraopticae ventralis pars ventralis Commissura posterior pars ventralis Internuclear connections with tectum
Nucleus spiriformis pars lateralis	Commissura posterior pars ventralis Internuclear connections with pars medialis and nucleus pretectalis
Nucleus spiriformis pars medialis	Tractus tecto-spiriformis lateralis Tractus occipito-mesencephalicus Tractus tecto-spiriformis medialis Commissura posterior pars ventralis Internuclear connections with pars lateralis and nucleus pretectalis
Nucleus subpretectalis	Tractus pretectalis subpretectalis Internuclear connections with tectum

*Nuclear masses**Fiber connections**Mesencephalon**a. Tectum*

Optic tectum

Tractus opticus marginalis
 Tractus thalamo-frontalis intermedialis
 Tractus strio-tegmentalis et strio-cerebellaris
 (tectal division)
 Tractus septo-mesencephalicus pars dorsalis
 Tractus tecto-thalamicus ventrolateralis
 Tractus tecto-thalamicus cruciatus
 Decussatio supraopticae dorsalis pars lateralis
 Decussatio supraopticae ventralis pars dorsalis
 and pars ventralis
 Tractus tecto-spiriformis lateralis
 Tractus tecto-spiriformis medialis
 Internuclear connections with nucleus ectomamil-
 laris, nucleus externus, nucleus pretectalis,
 nucleus subpretectalis, nucleus superficialis
 magnocellularis, nucleus principalis precommis-
 suralis, and other diencephalic nuclei
 Tractus tecto-thalamicus dorsalis
 Tractus tecto-thalamicus et thalamo-tectalis nu-
 clei rotundi
 Commissura posterior pars dorsalis et pars ven-
 tralis
 Tractus tecto-bulbaris dorsalis
 Tractus tecto-bulbaris ventralis
 Connections to nucleus of the oculomotor
 Internuclear connections with nucleus isthmo-
 opticus and nucleus isthmi pars principalis

b. Subtectum

Nucleus isthmo-opticus

Tractus isthmo-opticus
 Internuclear connections with tectum, ocul-
 motor nucleus, and trochlear nucleus

Nucleus isthmi pars princi-
palis (magnocellularis et
parvocellularis)

Decussatio supraopticae ventralis pars dorsalis
 Lemniscus lateralis (at least collaterals)
 Tractus isthmo-cerebellaris
 Tractus isthmo-mesencephalicus

Nucleus mesencephalicus lat-
eralis pars dorsalis

Tractus isthmo-tectalis et tecto-isthmi
 Decussatio supraopticae ventralis pars vent'
 Lemniscus lateralis
 Tractus isthmo-mesencephalicus
 Internuclear connections with tectum

Nucleus semilunaris

Lemniscus lateralis
 Internuclear connections with nucleus isthm'
 principalis

A BRIEF SUMMARY OF AVIAN FIBER TRACTS AND THEIR
COMPARISON WITH SIMILAR TRACTS IN REPTILES

In most cases a comparison of the fiber tract in question with the homologous tract in reptiles has been given under the description of the fiber bundle. The following is intended as a brief summary of such relations, and the details of the comparison will not be repeated here.

The lateral wall of the forebrain of the bird is divided into relatively clearly defined areas by a series of fiber tracts or lamellae. Functionally, these lamellae consist of two types of fibers: They carry association fibers from one part of the hemisphere to another, bringing into relation neighboring areas and frontal and caudal regions of the same area. In part they represent the assembling of projection fibers which carry impulses to and from the forebrain by way of the lateral forebrain bundles. These lamellae are represented to some degree in the alligator forebrain, although in no case are they as clearly defined or as prominent as in birds. Thus, the alligator has fiber bundles which correspond directly with the dorsomedial lamina and for a short distance bundles which are equivalent to a part of the fronto-occipital system. Slight indications of a ventromedial lamina may be seen, although in the material available it is far from being clearly defined. The avian tractus archistriaticus dorsalis, which is really a correlation bundle confined to the hemisphere and so comparable with the laminae, is represented in the reptilian brain by short connections between the dorsolateral areas of the alligator (p. 54) and the nuclear homologues of the archistriatum.

The avian forebrain bundle consists of the dorsal and ventral portions typical likewise of reptiles. The dorsal portion consists of tracts connecting, 1) the nucleus rotundus with the neostriatum, with the neostriatum frontale, with the hyperstriatum dorsale and hyperstriatum ventrale, and with the dorsolateral surface area; 2) the nuclei dorsolateralis anterior and posterior and the nucleus ovoidalis with the neostriatum (both cephalic and caudal portions), with the hyper-

striatum ventrale and with the lateroventral periventricular gray; 3) the lateral geniculate nucleus, nucleus intercalatus, the tectum, and the nucleus tractus tecto-thalamici cruciati with the neostriatum intermediale, with the ektostriatum, and perhaps with the hemisphere areas. These three bundles, tractus thalamo-frontalis lateralis, tractus thalamo-frontalis medialis, and tractus thalamo-frontalis intermedius, respectively, have their homologues in the medial, anterior, and internal thalamo-striatal paths of the alligator and are equally well represented in the various parts of the dorsal peduncle of the lateral forebrain bundle in such mammalian forms as rodents (Gurdjian, '27). The differences in form relations which have necessitated differences in usage of such terms as medial and lateral have no real functional significance.

The ventral peduncle of the forebrain bundle carries in birds connections between striatal areas (particularly paleostriatum) and hypothalamic, tegmental, and cerebellar centers. Its representatives in reptiles are the tractus strio-tegmentalis dorsalis, tractus strio-tectalis, and tractus strio-tegmentalis ventralis of the alligator. A further tract in birds connecting the striatal areas and the ventrolateral periventricular gray is the tractus strio-hypothalamicus medialis. The lateral forebrain bundle, then, of birds is directly comparable with that of reptiles. The quinto-frontal tract, associated in avian forms with the forebrain bundle in its course through diencephalon and into hemisphere, as has frequently been pointed out (Wallenberg and others), is an important connection between the sensory nucleus of the fifth and the hemisphere.

The olfactory tracts and the secondary olfactory connections in birds are small as compared with the similar connections in reptiles. Their size varies with the development of the peripheral olfactory system in the particular bird under consideration, so that they are relatively large in duck, dove, and chicken and relatively very small in parrakeet and sparrow. In principle the olfactory connections are typical of those found in other vertebrates and particularly comparable

to those found in alligator. This has already been discussed (p. 132) and need not receive further consideration here. Tractus fronto-occipitalis of the bird and commissura interarchistriatica are the direct avian representatives of the stria terminalis and the anterior commissure of other vertebrate types, for tractus occipito-mesencephalicus connects the archistriatum or amygdaloid complex with the periventricular and hypothalamic areas of the diencephalon. Its backward continuation into the medulla, regarded by Craigie ('28) as a strio-bulbar tract, is merely a further constituent of the stria terminalis system, which in reptiles (turtle, Johnston; and alligator) reaches the tegmental region of the midbrain. The anterior commissure of birds is chiefly for interconnection of the amygdaloid complex and its relation to the basal medial wall of the hemisphere. The interbulbar part of this component appears to be very small in birds.

Tractus septo-mesencephalicus pars basalis caudalis and tractus infundibuli are to be regarded probably as the equivalent of the fornix longus system, although the complex may carry a few true fornix fibers from the hippocampus. Small bundles from the medial forebrain area swinging ventral to the lateral forebrain bundle and into the nucleus ovoidalis of the alligator are probably the homologues of the much more highly developed tractus septo-mesencephalicus pars dorsalis of the bird. The ramus basalis frontalis of the tractus septo-mesencephalicus is probably the diagonal band of Broca of other forms. It is to be emphasized that the septo-mesencephalic tract of both bird and alligator arises not only from the hippocampus area, but also from the whole dorsomedial hemisphere wall and carries other than impulses from olfactory projection cortex. It is suggested that the entorhinal area or its reptilian equivalent, hippocampus pars dorsalis, is probably olfactory association cortex, with the olfactory component relatively small in avian forms.

Stria medullaris in birds consists of components comparable in general terms to those demonstrated for reptiles by various observers, although in the material at hand it was

not possible to demonstrate a lateral olfacto-habenular tract. The size of the stria varies directly with the degree of development of the peripheral olfactory centers. In spite of the small size of the stria medullaris, the habenulo-peduncular tract is well developed and the habenula is related to the diencephalon and to the tectum. Before leaving the consideration of these fiber systems, associated more or less with olfactory impulses, there are certain points which should be reemphasized. The basal olfactory centers of the medial wall of the hemisphere, the stria medullaris and, to a considerable extent, the habenula and the hippocampus vary in size with the development of peripheral olfactory areas. The archistriatum or amygdaloid complex, the olfactory association areas of the dorsomedial wall, are doubtless affected to some extent by the peripheral development of the olfactory system. Nevertheless, they are well developed in avian forms, such as sparrow and parrakeet, where the incoming olfactory fibers are relatively very few in number. This indicates that they receive important connections of the non-olfactory type and may play an important rôle when their olfactory components are relatively insignificant. Thus the paths carrying impulses into and out of these centers are large even in the absence of any considerable incoming olfactory component. For example, the fronto-occipital path and the occipito-mesencephalic path to the anterior commissure, which are connections of the archistriatum, are more highly developed in sparrow with its single olfactory bulb than in alligator with its well-developed olfactory system. The septo-mesencephalic tract from the dorsomedial hemisphere wall and the bundles associated with it from the septum are more conspicuous and of greater extent in the sparrow than in reptilian forms. It is to be noted also that the habenula, which, through its connection with tectum and dorsal thalamus and with the olfactory centers by stria medullaris, is an olfactory somatic correlation center, discharges by a relatively highly developed path even in the absence of any considerable olfactory component. All of these facts indicate

that the size of a center and of its component paths is dependent upon all of the impulses brought into it, and that comparisons of relative sizes of areas with an idea of establishing functional relationships must be made with the utmost caution, unless all of the types of impulses which may reach them are understood and the relative development of each of these systems is taken into account.

The highly developed optic tracts in birds need no further consideration except to reemphasize that their added connections are primarily for establishment of more efficient reflex relations. The connections with tectum, ectomamillary nucleus, and nucleus of the basal optic root are largely, at least, for visual and light reflexes. The amount of connection into the hemisphere is not in proportion to the development of the rest of the optic system.

The supra-optic system of birds is directly comparable with that described previously for the alligator. One connection, which it was not possible to identify in the alligator material available, has been established for birds, namely, the commissural connections between the striatal and probably the paleostriatal areas of the two sides.

Tecto-thalamic and thalamo-tectal connections in birds are similar to those of alligator. Most of the major nuclei of the diencephalon (including nucleus rotundus, nucleus ovoidalis, nucleus geniculatus lateralis, nucleus intercalatus, nucleus ectomamillaris), the pretectal group, and other centers as well are interconnected with the tectum. The tectum plays a dominant rôle, in the behavior of the bird, through its diencephalic and forebrain relations and its connections with motor centers.

The posterior commissure interconnects tectal and pretectal areas. It carries fibers between the nucleus mesencephalicus lateralis pars dorsalis of one side and that of the other. It appears to carry fibers from one side to the contralateral medial longitudinal fasciculus of the other side. In all these relations it is similar to the reptilian posterior commissure. The ascending connections have been summarized on page 158 and need not be considered further here.

In conclusion, one may state that the fiber-tract system of the bird in all important particulars is directly homologous with that of alligator, and that the differences are differences of degree of development rather than differences in type of development. The larger striatum and larger tectum of the bird are associated with an increase in size of the lateral fore-brain bundle, tecto-thalamic and thalamo-tectal areas. The highly developed hyperstriatum accessorium of the bird and the development of the upper portion of the dorsomedial hemisphere wall have led to an increase in size of the septo-mesencephalic system, although the olfactory or fornix portion of that system is smaller than in reptiles. The basal olfactory areas and associated tracts are smaller in birds than in reptiles, except where they are dominated, as in the case of the archistriatum, by non-olfactory connections. The development of the archistriatum with the interconnections with neostriatum has led to a high degree of development of the stria medullaris system, while the avian habenulo-peduncular tract is large since it is a discharge system for olfactory somatic correlations, and the somatic component from tectum and diencephalon is large in birds.

GENERAL DISCUSSION AND CONCLUSIONS

Diencephalic, telencephalic, and certain mesencephalic nuclei of the avian brain, with their fiber connections and with homologies in the reptilian brain, have been summarized in preceding pages (51, 105, 160, 169). However, there are certain questions of broad, general interest which deserve further and special discussion in a final generalization and summary.

As is usually conceded, the striatal complex of birds is relatively very large, while the cortical areas, with the possible exception of the entorhinal and paraentorhinal areas, are small and lacking in differentiation. Ariëns Kappers and others have indicated that the hyperstriatal areas are to be regarded as vicarious cortex, and our own observations tend to confirm such conclusions. Moreover, the existing relations suggest that the dorsal and ventral hyperstriatal areas which

respectively are associated laterally with the dorsolateral corticoid surface area, together find representation in the primordial neopallium of the alligator and in at least the cephalic portion of the dorsal ventricular ridge of the turtle (Johnston, '15). The lamina frontalis suprema represents in such cases the place of entrance of association fibers from surface cortical or corticoid areas. Therefore, morphologically and functionally considered, the hyperstriatum of the bird's brain represents an evolution of structures and functions found in anlagen in the reptilian striatal complex, and is not to be regarded as a new creation. In both avian and reptilian forms, portions of the striatal complex represent an attempt at formation of the major centers of higher correlation within the forebrain, but along the ventricular wall rather than on the surface—an attempt which has attained much further development in the bird than in the reptile. In the avian hyperstriatal centers there is evidenced a certain localization, recognizable through distribution of lateral forebrain tracts, which in broad terms is suggestive of localization in the cortex of lower mammals. In this consideration it is to be understood that the multiplicity of internuncial connections and the lack of layer arrangement do not tend to further a high specificity of localization within the avian hyperstriatal complex. Therefore, in its inherent pattern this complex is so limited by position and structure that it does not possess the potentiality of attaining the specific localization reached in the cortex of higher mammals.

In birds the hippocampus is small. The entorhinal area of Rose, dorsal to the hippocampus and in intimate association with it, is probably hippocampal association cortex, with the olfactory component much less dominant here than in most other forms. The discharge path for the hippocampal and entorhinal areas, and for the paraentorhinal and a portion of the accessory hyperstriatal areas as well, is the septomesencephalic tract. This tract includes not only the equivalent of the mammalian fornix and fornix longus, but also other components, which have as yet no known representa-

tives in mammals. This septo-mesencephalic tract was regarded by Kalischer as the homologue of the mammalian pyramidal tract. However, as has been frequently pointed out, the position and general relations of this tract make doubtful such a direct homology, but this statement does not exclude the possibility of regarding a portion of the septo-mesencephalic tract as found in birds in the light of a vicarious system, substituting for a portion of the internal capsule as found in mammals. In both birds and mammals there are connections between striatal areas and lower centers represented in birds by the major portion of the lateral forebrain bundle and in mammals by ansa lenticularis and certain thalamo-striatal paths. In mammals the paths between basal and cortical centers (with the exception of hippocampus and immediately associated areas) course through the striatal regions. In birds representatives of such fibers are to be found in the components from the dorsolateral surface area (corticoid) and the hyperstriatal regions (vicarious cortex) to the lateral forebrain bundle; these are the true forerunners of the cortical projection paths of higher forms. The avian septo-mesencephalic system and its homologue in the alligator constitute a means of sending certain non-olfactory projection fibers with the olfactory projection systems, represented in the fornix, and such non-olfactory fibers are of appreciable number. Therefore, the septo-mesencephalic tract includes not only the avian representatives of the mammalian fornix and fornix longus, but also a projection system to diencephalic and mesencephalic centers which may be regarded as accessory to the avian lateral forebrain bundle and which in a sense is a substitute for a part of the mammalian internal capsule system.

The diencephalon in the bird, as in other vertebrate forms, is divisible into epithalamus, hypothalamus, dorsal thalamus, and ventral thalamus. The habenular nuclei of the epithalamus are relatively small in most avian forms, correlated with the relatively limited development of the peripheral olfactory system. Through their connections with tectum and

dorsal thalamus, their nuclei are centers of olfacto-somatic correlation. They discharge through a well-developed habenulo-diencephalic and a habenulo-peduncular system. The hypothalamus has been shown to be differentiable into various centers with connections and interrelations suggestive of those of certain mammalian forms. The intricate structural pattern and interrelations of the hypothalamic region are evidenced in the behavior of the animal which Rogers and others have shown to be seriously modified in certain directions after lesions in the region (p. 18).

The dorsal and ventral thalamic centers, on the whole, are comparable with those of reptiles and particularly those of alligator. A comparison of the areas in the two types indicates that the differences consist, on the one hand, of an increase in differentiation in birds correlated with a greater development of the striatal areas of the hemispheres and, on the other hand, of a displacement ventralward of the various thalamic nuclei associated with a ventral migration of the avian tectum and tecto-thalamic and thalamo-tectal tracts. This change of position of tectum and its effect on the thalamic nuclei have been considered previously by Ingvar ('23). The mammalian homologues of the avian thalamic nuclei, on the whole, have not been considered in the present account. However, there appears sufficient justification for the homology made by Ingvar and others of the avian nucleus rotundus with the mammalian nucleus ventralis. Such a homology offers considerable theoretic interest, for if it proves correct, it opens the old question concerning the presence of a neothalamus and an archithalamus in mammals. Edinger, followed by others, designated the lateral division of the thalamus as neothalamus and the medial division as archithalamus. Under such consideration the neothalamus would contain, among other centers, the ventral nucleus, the lateral geniculate, the lateral nucleus, the medial geniculate, and the pulvinar, while the archithalamus would contain the anterior and medial nuclei and associated nuclear areas. The lateral geniculate of submammalian forms, we, with others, concede

to be the homologue of at least the ventral nucleus of the lateral geniculate of lower mammals and possibly to contain the anlage of the dorsal nucleus as well (Sphenodon, Cairney, '26). Therefore, within the lateral division of the mammalian thalamus there is representation of primitive centers as well as new centers; for instance, such as pulvinar and at least the greater part of the lateral nucleus. In the mammalian medial division, which is represented in the dorsal nuclei and associated cell groups of reptiles and birds and the homologous cell groups in still lower vertebrates, there is great increase in both the number of centers and their differentiation. Thus, it may be said of the dorsal part of the thalamus of higher mammals that it does consist of neothalamic and archithalamic portions, but each of these portions finds representation in the lateral divisions of the thalamus and in the medial division as well. Phylogenetically considered, each has a primitive portion and each a newer portion.

The dorsal thalamus in its degree of development and in the pattern of that development reflects and at the same time makes possible the differentiation of the striatum and tectum. A considerable portion of its discharge paths to lower centers is by way of thalamo-tectal and then tecto-bulbar paths. The great size and layer differentiation of the tectum is due to a considerable degree to this interrelation with thalamic centers. Thus the reflex mechanisms and the paths for muscular coordination, which involve striatal connections including strio-cerebellar paths, are highly developed in the bird. The paths for optic reflex, embracing particularly tectal and other mesencephalic centers, are likewise conspicuous structures. The highly organized behavior on the instinctive and reflex planes, characteristic of birds, is reflected in the anatomic pattern of the tectum, thalamus, and forebrain. The close interrelation of the hyperstriatal (vicarious cortical) areas, and the surface corticoid areas, with the basal striatal centers, the lack of definite layer formation within the hyperstriatum, all tend to diminish the possibilities of definite

localization and relative independence of forebrain centers. The richness of fiber connections between the highly developed avian thalamus and the hyperstriatum makes possible the wealth of associations necessary for a highly organized behavior and, we postulate, particularly those associations which come to expression through a high degree of muscular coordination. If this latter conjecture receives more complete substantiation, it will of necessity be seen that the avian hyperstriatum partakes both of cortical and striatal characters, and that this dual rôle has dominated and directed the whole trend of anatomic and functional differentiation which finds its expression in the highly organized but relatively fixed behavior of birds. Correlated with this type of forebrain development there is to be found a specific differentiation of diencephalic centers, for there can be no forebrain localization without corresponding diencephalic localization, and this applies not only to birds, but to all vertebrate forms, including mammals. The great degree of differentiation of dorsal thalamic centers of higher mammals is the necessary accompaniment of the specificity of cortical centers in these forms.

Finally, attention is drawn to the fact that the development of higher centers in birds, as in other vertebrates, is dependent upon a corresponding development of various centers of the central nervous system and of such peripheral end organs as the eye and the ear. Birds differ from lower forms not only in the greater differentiation of telencephalic, diencephalic, and tectal areas, but in a correspondingly higher differentiation of bulbar, cerebellar, and such other mesencephalic centers as are related to these regions. Therefore, it is to be emphasized that there are phylogenetically old portions and phylogenetically new portions in all parts of the central nervous system. The appearance of a new center in any one segment is almost invariably associated with the appearance of correlated differentiation at several brain levels. Comparison of higher with lower forms indicates that, superimposed upon the more stable phylogenetic pattern, the further

specific development and differentiations appear in all affected parts of the peripheral and central nervous system. However, the projection and association areas of the cortex (and sometimes their more directly associated diencephalic centers) appear relatively late in phylogeny.

An extended morphologic study of the avian brain, as here recorded, would scarcely justify the effort expended, were it not clear that, when considered from the viewpoint of comparative neurology, such a study relates very definitely to the interpretation of the structure of the central nervous system of lower and higher forms. There is permitted a direct comparison of the avian and reptilian brains. Birds and mammals, as terminal branches of the phylogenetic tree, are not so directly comparable. Yet the very differences in the diencephalon, tectum, and forebrain of birds and mammals, associated with differences in behavior, lend special value to the study of these centers in the avian brain as one of the means by which the type of development and particularly the organization of the corresponding mammalian centers may be elucidated.

NOTE

After the manuscript had been sent to the editors, Craigie made a brief report at the Rochester meeting of the American Association of Anatomists (abstract, *Anat. Rec.*, vol. 42, p. 13) on cortical areas in *Apteryx*. He found, among other things, a distinct hippocampus with a fascia dentata well developed in the posterior part of the medial hemisphere wall, a much-reduced pyriform-lobe cortex with rhinal and amygdaloid fissures and in the ventrolateral part of the occipital pole and in a small area on the lateral hemisphere wall a neocortex of five or possibly six layers. He described for hippocampus "postero-ventrally . . . an arrangement of cell layers corresponding with the medial superposition in reptiles."

The present account of the dorsolateral surface or corticoid area is based primarily on sparrow, where the wall is very thin caudally. In chicken and duck the wall in the region is thicker and there is a suggestion of layer formation, although we would hesitate to identify six layers (p. 62). Quite probably, such may occur in *Apteryx*. The ventral portion of the dorsolateral corticoid area, for example, in dove, probably represents pyriform-lobe cortex. It is to be emphasized again that the entorhinal area of Rose is probably hippocampal association cortex.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

1 Dorsolateral views of avian brains; A, chicken (*Gallus domesticus*); B, dove (*Columba domestica*); C, sparrow (*Passer domesticus*); D, duck (*Anas domestica*).

2 A, lateral view of the brain of the English sparrow (*Passer domesticus*); B, ventral view of the brain of the English sparrow (*Passer domesticus*); *b.olf.*, unpaired median bulbus olfactorius.

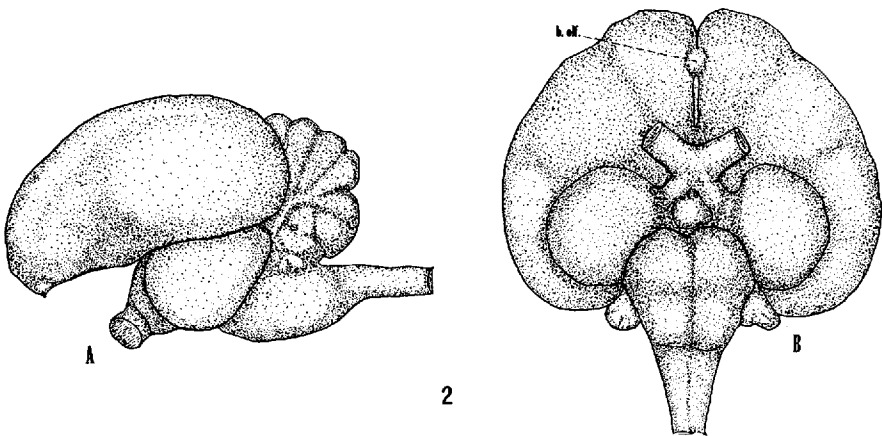
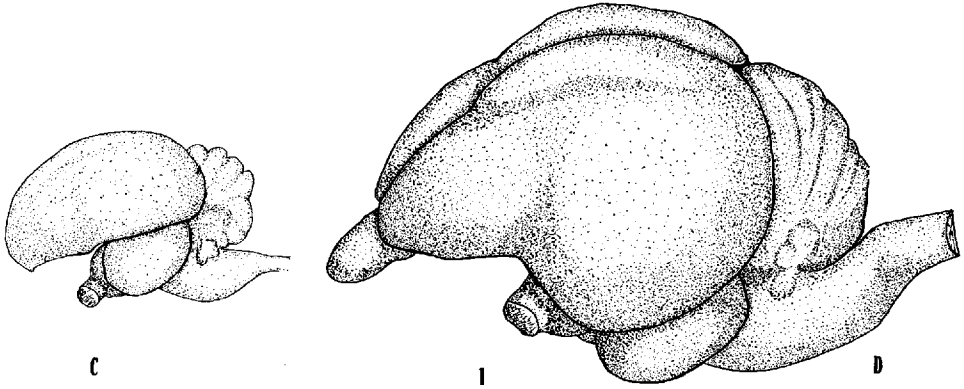
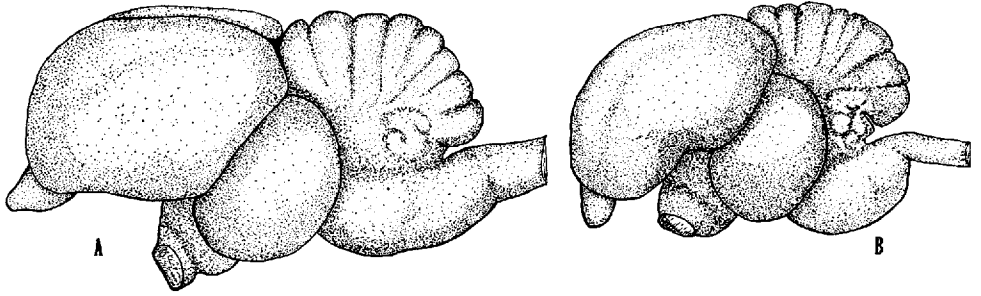


PLATE 2

EXPLANATION OF FIGURES

3 Transverse section through the olfactory bulbs of various birds. A, olfactory bulbs of duck; B, olfactory bulbs of chicken; C, olfactory bulbs of dove; D, olfactory bulbs of parrakeet; E, unpaired olfactory bulb of English sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

a.praepyr., area praepyiformis
glom.l., glomerular layer
in.gr.l., inner granular layer
m.c.l., mitral cell layer

n.olf.ant., nucleus olfactorius anterior
olf.vent., olfactory ventricle
out.gr.l., outer granular layer
vent., ventricle

4 Transverse section through cephalic end of the forebrain, at the level of the olfactory bulb; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

a.hip.f., anterior hippocampal formation
a.praepyr., area praepyiformis
d.l.s.a., dorsolateral surface area (corticoid)
glom.l., glomerular layer
hyperstr.acc., hyperstriatum accessorium
hyperstr.dors., hyperstriatum dorsale
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
in.gr.l., inner granular layer

interc.c.l.supr., intercalated cells of lamina frontalis suprema
l.vent., lateral ventricle
m.c.l., mitral cell layer
n.intercal.hyperstr., nucleus intercalatus hyperstriati
n.olf.ant., nucleus olfactorius anterior
neostr.fr., neostriatum frontale

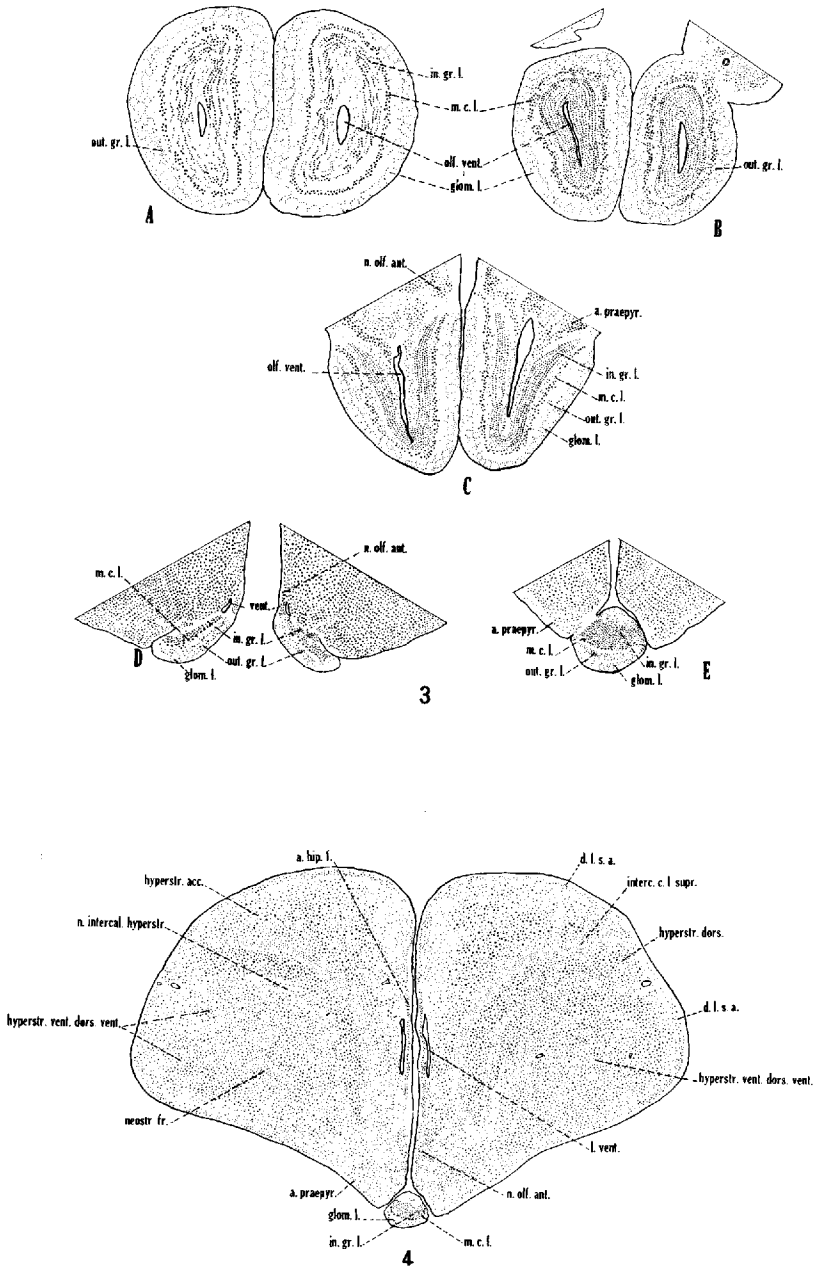


PLATE 3

EXPLANATION OF FIGURES

5 Transverse section through the cephalic end of the forebrain, at the level of anterior portion of nucleus accumbens and nucleus basalis; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a.entorh.</i>, area entorhinalis of Rose <i>a.praeepyrr.</i>, area praepyriiformis <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>f.neopaleostr.</i>, fissura neopaleostriatica <i>hip.</i>, hippocampus <i>hyperstr.acc.</i>, hyperstriatum accessorium <i>hyperstr.dors.</i>, hyperstriatum dorsale <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale ventroventrale <i>interc.c.l.supr.</i>, intercalated cells of lamina frontalis suprema <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis)</p>	<p><i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.accum.p.ant.</i>, nucleus accumbens pars anterior <i>n.bas.</i>, nucleus basalis <i>n.intercal.hyperstr.</i>, nucleus intercalatus hyperstriati <i>neostr.fr.</i>, neostriatum frontale <i>paleostr.aug.</i>, paleostriatum augmentatum</p>
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6 Transverse section through cephalic end of forebrain slightly caudal to plane of figure 5; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a</i>, a differentiated portion of hyperstriatum accessorium <i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>a.sept.</i>, area septalis <i>ch.op.</i>, chiasma opticum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>ektostr.</i>, ektostriatum <i>f.neohyperstr.</i>, fissura neohyperstriatica <i>f.neopaleostr.</i>, fissura neopaleostriatica <i>hip.</i>, hippocampus <i>hyperstr.acc.</i>, hyperstriatum accessorium <i>hyperstr.dors.</i>, hyperstriatum dorsale <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale ventroventrale <i>interc.c.l.supr.</i>, intercalated cells of lamina frontalis suprema <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis</p>	<p><i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.accum.p.post.</i>, nucleus accumbens pars posterior <i>n.bas.</i>, nucleus basalis <i>n.d.b.Br.</i>, nucleus of the diagonal band of Broca <i>n.intercal.hyperstr.</i>, nucleus intercalatus hyperstriati <i>n.tr.fr.archistr.</i>, nucleus tractus fronto-archistriatici et neostriatici <i>neostr.fr.</i>, neostriatum frontale <i>neostr.intermed.</i>, neostriatum intermediale <i>p.</i>, primordium hippocampi of Johnston <i>paleostr.aug.</i>, paleostriatum augmentatum <i>paleostr.prim.</i>, paleostriatum primitivum <i>s</i>, sickle-shaped area in hyperstriatum ventrale <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.sept.mes.</i>, tractus septo-mesencephalicus</p>
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7 Transverse section through the anterior portion of the preoptic area; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>ch.op.</i>, chiasma opticum <i>gr.a.</i>, group a of Röhlig <i>n.d.b.Br.</i>, nucleus of the diagonal band of Broca <i>n.magnocell.ints.</i>, nucleus magnocellularis interstitialis</p>	<p><i>n.preop.ant.</i>, nucleus preopticus anterior <i>n.preop.med.</i>, nucleus preopticus medialis <i>tr.sept.mes.</i>, tractus septo-mesencephalicus</p>
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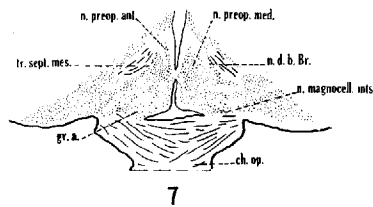
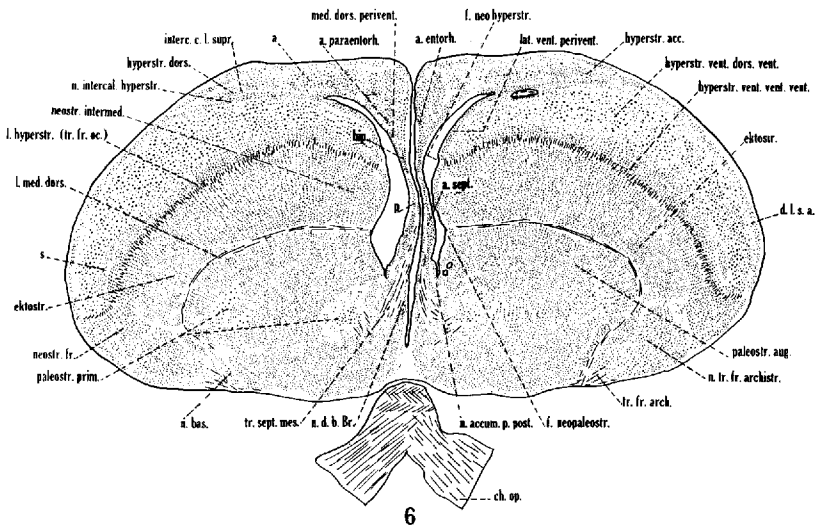
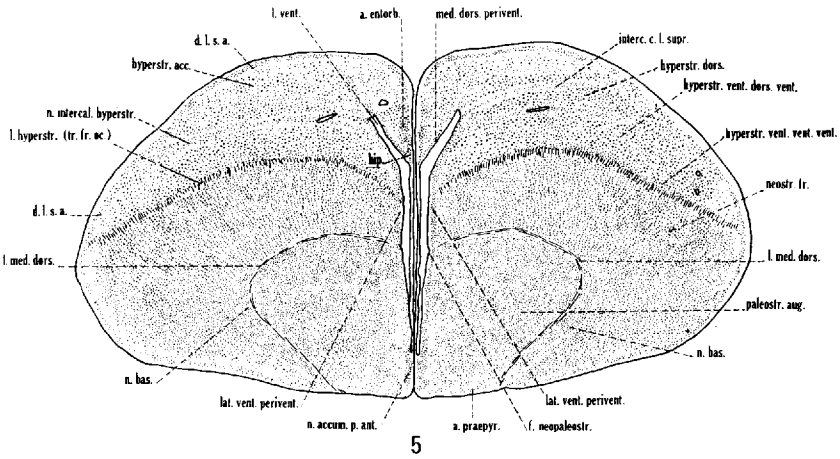


PLATE 4

EXPLANATION OF FIGURES

8 Four successive levels, A, B, C, D, illustrating position and relation of nucleus magnocellularis interstitialis; chicken. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>bedn.pal.com.</i>, bed nucleus of the pallial commissure <i>ch.op.</i>, chiasma opticum <i>dec.supraop.dors.</i>, decussatio supraoptica dorsalis <i>l.f.b.</i>, lateral forebrain bundle <i>n.gen.lat.</i>, nucleus geniculatus lateralis <i>n.hyp.ant.med.</i>, nucleus hypothalamicus anterior medialis <i>n.lat.ant.</i>, nucleus lateralis anterior <i>n.magnocell.ints.dors.</i>, nucleus magnocellularis interstitialis pars dorsalis <i>n.magnocell.ints.int.</i>, nucleus magnocellularis interstitialis pars intermedius</p>	<p><i>n.magnocell.ints.lat.</i>, nucleus magnocellularis interstitialis pars lateralis <i>n.magnocell.ints.med.</i>, nucleus magnocellularis interstitialis pars medialis <i>n.magnocell.ints.med.a.</i>, nucleus magnocellularis interstitialis pars medialis a <i>n.magnocell.ints.med.b.</i>, nucleus magnocellularis interstitialis pars medialis b <i>n.magnocell.ints.med.c.</i>, nucleus magnocellularis interstitialis pars medialis c <i>n.preop.med.</i>, nucleus preopticus medialis <i>tr.oc.mes.</i>, tractus occipito-mesencephalicus et bulbaris <i>tr.op.</i>, tractus opticus <i>tr.sept.mes.</i>, tractus septo-mesencephalicus</p>
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9 Transverse section through the forebrain at the level of the optic chiasma rostral to tectum; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a</i>, a differentiated portion of hyperstriatum accessorium <i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>ch.op.</i>, chiasma opticum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>ektostr.</i>, ektostriatum <i>f.neopaleostr.</i>, fissura neopaleoestriatica <i>gr.a.</i>, group <i>a</i> of Röthig <i>hip.</i>, hippocampus <i>hyperstr.acc.</i>, hyperstriatum accessorium <i>hyperstr.dors.</i>, hyperstriatum dorsale <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale pars dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale pars ventroventrale <i>interc.c.l.supr.</i>, intercalated cells of lamina frontalis suprema <i>l.f.b.</i>, lateral forebrain bundle <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray</p>	<p><i>n.accum.p.post.</i>, nucleus accumbens pars posterior <i>n.bas.</i>, nucleus basalis <i>n</i>, area of fusion of the intercalated cells of lamina frontalis suprema with nucleus intercalatus hyperstriati <i>n.intercal.hyperstr.</i>, nucleus intercalatus hyperstriati <i>n.lat.ant.</i>, nucleus lateralis anterior <i>n.magnocell.ints.</i>, nucleus magnocellularis interstitialis <i>n.preopt.lat.</i>, nucleus preopticus lateralis <i>n.preopt.med.</i>, nucleus preopticus medialis <i>n.sept.lat.</i>, nucleus septalis lateralis <i>n.sept.med.</i>, nucleus septalis medialis <i>n.tr.fr.archistr.</i>, nucleus tractus fronto-archistriatici et neostriatici <i>neostr.fr.</i>, neostriatum frontale <i>neostr.intermed.</i>, neostriatum intermediale <i>p.</i>, primordium hippocampi of Johnston <i>paleostr.aug.</i>, paleostriatum augmentatum <i>paleostr.prim.</i>, paleostriatum primum <i>str.cell.int.</i>, stratum cellulare internum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.sept.mes.</i>, tractus septo-mesencephalicus</p>
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PLATE 5

EXPLANATION OF FIGURES

10 Transverse section of the brain through anterior commissure and rostral portion of tectum; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

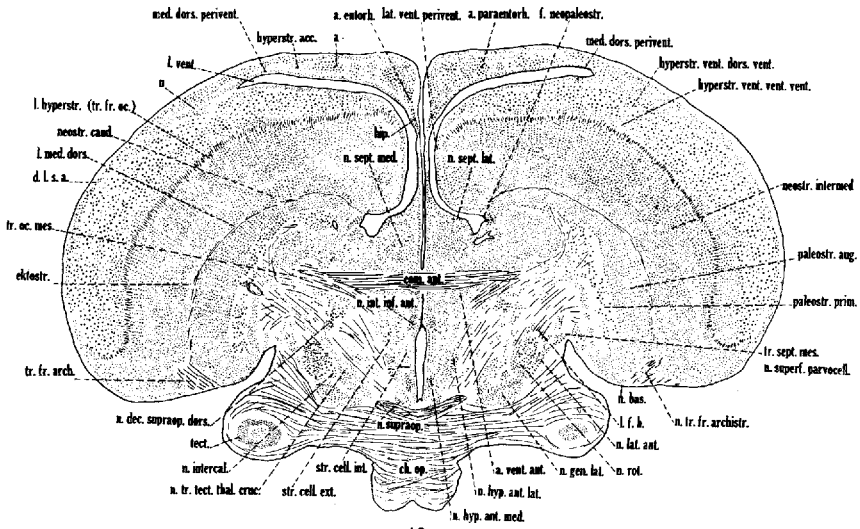
<p><i>a</i>, differentiated portion of hyperstriatum accessorium <i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>a.vent.ant.</i>, area ventralis anterior <i>ch.op.</i>, chiasma opticum <i>com.ant.</i>, commissura anterior <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>ektostr.</i>, ektostriatum <i>f.neopaleostr.</i>, fissura neopaleostriatica <i>hip.</i>, hippocampus <i>hyperstr.acc.</i>, hyperstriatum accessorium <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale pars dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale pars ventroventrale <i>l.f.b.</i>, lateral forebrain bundle <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n</i>, area of fusion of the intercalated cells of lamina frontalis suprema with nucleus intercalatus hyperstriati <i>n.bas.</i>, nucleus basalis <i>n.dec.supraop.dors.</i>, nucleus decussationis supraopticae dorsalis</p>	<p><i>n.gen.lat.</i>, nucleus geniculatus lateralis <i>n.hyp.ant.lat.</i>, nucleus hypothalamicus anterior lateralis <i>n.hyp.ant.med.</i>, nucleus hypothalamicus anterior medialis <i>n.int.inf.ant.</i>, nucleus internus inferior anterior <i>n.intercal.</i>, nucleus intercalatus <i>n.lat.ant.</i>, nucleus lateralis anterior <i>n.rot.</i>, nucleus rotundus <i>n.sept.lat.</i>, nucleus septalis lateralis <i>n.sept.med.</i>, nucleus septalis medialis <i>n.superf.parcocell.</i>, nucleus superficialis parvocellularis <i>n.supraop.</i>, nucleus supraopticus <i>n.tr.fr.archistr.</i>, nucleus tractus fronto-archistriatici et neostriatici <i>n.tr.tect.thal.cruc.</i>, nucleus tractus tectothalamici cruciati <i>neostr.intermed.</i>, neostriatum intermediale <i>neostr.caud.</i>, neostriatum caudale <i>paleostr.aug.</i>, paleostriatum augmentatum <i>paleostr.prim.</i>, paleostriatum primitivum <i>str.cell.ext.</i>, stratum cellulare externum <i>str.cell.int.</i>, stratum cellulare internum <i>tect.</i>, tectum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.oc.mes.</i>, tractus occipito-mesencephalicus et bulbaris <i>tr.sept.mes.</i>, tractus septo-mesencephalicus</p>
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11 Transverse section through brain slightly caudal to anterior commissure, giving the nuclear pattern in the more anterior portion of the diencephalon; sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

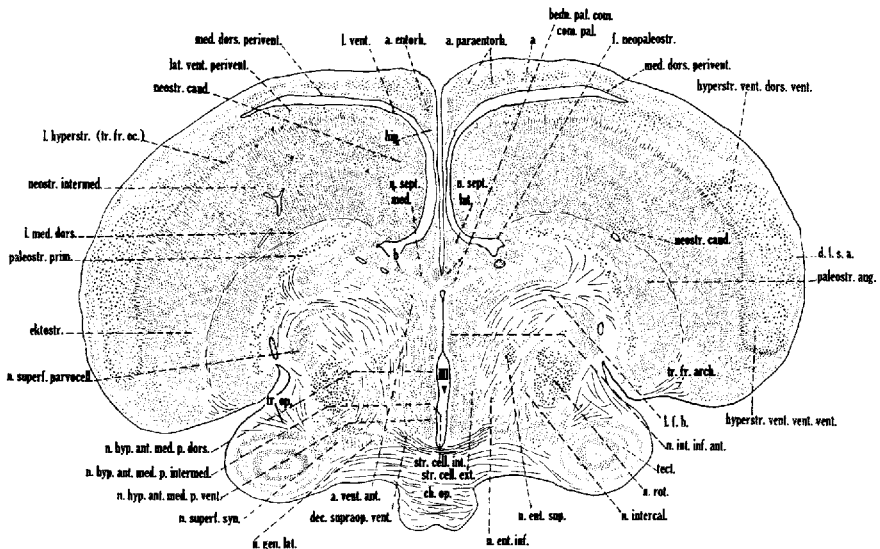
ABBREVIATIONS

<p><i>a</i>, differentiated portion of hyperstriatum accessorium <i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>a.vent.ant.</i>, area ventralis anterior <i>b</i>, lateral continuation of bed nucleus of pallial commissure <i>bedn.pal.com.</i>, bed nucleus of pallial commissure <i>ch.op.</i>, chiasma opticum <i>com.pal.</i>, commissura pallii <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>dec.supraop.vent.</i>, decussatio supraoptica ventralis <i>ektostr.</i>, ektostriatum <i>f.neopaleostr.</i>, fissura neopaleostriatica <i>hip.</i>, hippocampus <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale pars dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale pars ventroventrale <i>l.f.b.</i>, lateral forebrain bundle <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.ent.inf.</i>, nucleus entopeduncularis inferior</p>	<p><i>n.ent.sup.</i>, nucleus entopeduncularis superior <i>n.gen.lat.</i>, nucleus geniculatus lateralis <i>n.hyp.ant.med.p.dors.</i>, nucleus hypothalamicus anterior medialis pars dorsalis <i>n.hyp.ant.med.p.intermed.</i>, nucleus hypothalamicus anterior medialis pars intermediale <i>n.hyp.ant.med.p.vent.</i>, nucleus hypothalamicus anterior medialis pars ventralis <i>n.int.inf.ant.</i>, nucleus internus inferior anterior <i>n.intercal.</i>, nucleus intercalatus <i>n.rot.</i>, nucleus rotundus <i>n.sept.lat.</i>, nucleus septalis lateralis <i>n.sept.med.</i>, nucleus septalis medialis <i>n.superf.parcocell.</i>, nucleus superficialis parvocellularis <i>n.superf.syn.</i>, nucleus superficialis synencephali <i>neostr.caud.</i>, neostriatum caudale <i>neostr.intermed.</i>, neostriatum intermediale <i>paleostr.aug.</i>, paleostriatum augmentatum <i>paleostr.prim.</i>, paleostriatum primitivum <i>str.cell.ext.</i>, stratum cellulare externum <i>str.cell.int.</i>, stratum cellulare internum <i>tect.</i>, tectum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.op.</i>, tractus opticus <i>III v.</i>, third ventricle</p>
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G. CARL HUBER AND ELIZABETH CAROLINE CROSEY



10



11

PLATE 6

EXPLANATION OF FIGURES

12 Transverse section through brain of sparrow slightly caudal to plane of figure 11 and through the oral portion of nucleus dorsolateralis anterior pars lateralis and nucleus ovoidalis. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

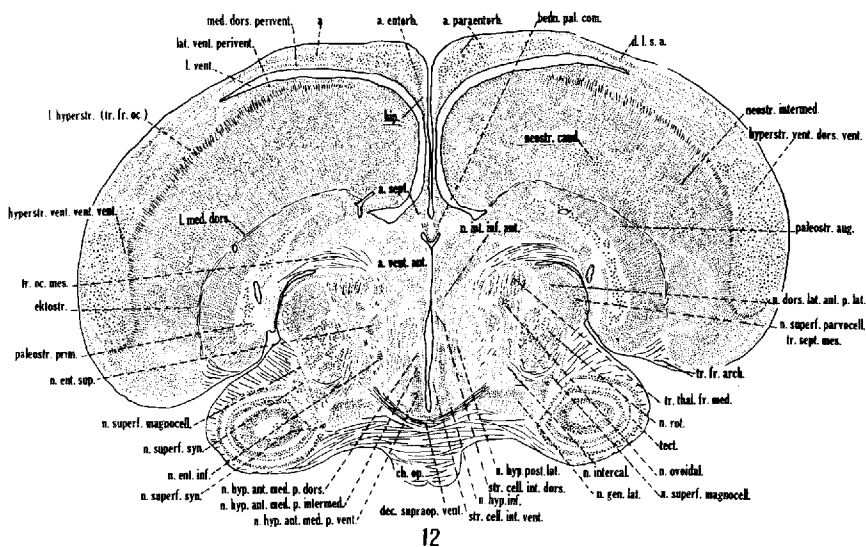
a., differentiated portion of hyperstriatum accessorium
a.entorb., area entorhinalis of Rose
a.paraentorb., area paraentorhinalis
a.sept., area septalis
a.vent.ant., area ventralis anterior
bedn.pal.com., bed nucleus of the pallial commissure
ch.op., chiasma opticum
d.l.s.a., dorsolateral surface area (corticoïd)
dec.supraop.vent., decussatio supraoptica ventralis
ektostr., ekstostriatum
hip., hippocampus
hyperstr.vent.dors.vent., hyperstriatum ventrale pars dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale pars ventroventrale
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.vent., lateral ventricle
lat.vent.perivent., lateroventral periventricular gray
med.dors.perivent., mediodorsal periventricular gray
n.dors.lat.ant.p.lat., nucleus dorsolateralis anterior pars lateralis
n.ent.inf., nucleus entopeduncularis inferior
n.ent.sup., nucleus entopeduncularis superior
n.gen.lat., nucleus geniculatus lateralis
n.hyp.ant.med.p.dors., nucleus hypothalamicus anterior medialis pars dorsalis
n.hyp.ant.med.p.intermed., nucleus hypothalamicus anterior medialis pars intermedialis

n.hyp.ant.med.p.vent., nucleus hypothalamicus anterior medialis pars ventralis
n.hyp.post.lat., nucleus hypothalamicus posterior lateralis
n.hyp.ant.med.p.vent., nucleus hypothalamicus anterior medialis pars ventralis
n.hyp.inf., nucleus hypothalamicus inferior
n.hyp.post.lat., nucleus hypothalamicus posterior lateralis
n.int.inf.ant., nucleus internus inferior anterior
n.intercal., nucleus intercalatus
n.ovidal., nucleus ovoidalis
n.rot., nucleus rotundus
n.superf.magnocell., nucleus superficialis magnocellularis
n.superf.parcocell., nucleus superficialis parvocellularis
n.superf.syn., nucleus superficialis synencephali of Rendahl
neostr.caud., neostriatum caudale
neostr.intermed., neostriatum intermediale
paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
str.cell.int.dors., stratum cellulare internum dorsale
str.cell.int.vent., stratum cellulare internum ventrale
tect., tectum
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.oc.mes., tractus occipito-mesencephalicus et bulbaris
tr.sept.mes., tractus septo-mesencephalicus
tr.thal.fr.med., tractus thalamo-frontalis medialis

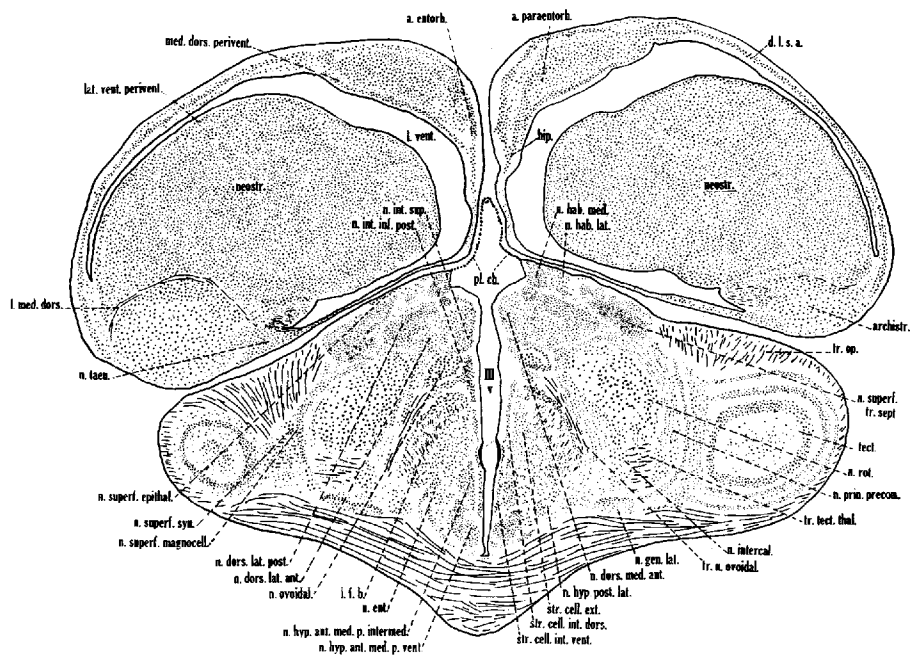
13 Transverse section through brain of dove, showing positions and relation of many of the more important diencephalic nuclei. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

a.entorb., area entorhinalis of Rose
a.paraentorb., area paraentorhinalis
archistr., archistriatum
d.l.s.a., dorsolateral surface area (corticoïd)
hip., hippocampus
l.f.b., lateral forebrain bundle
l.med.dors., lamina medullaris dorsalis
l.vent., lateral ventricle
lat.vent.perivent., lateroventral periventricular gray
med.dors.perivent., mediodorsal periventricular gray
n.dors.lat.ant., nucleus dorsolateralis anterior
n.dors.lat.post., nucleus dorsolateralis posterior
n.dors.med.ant., nucleus dorsomedialis anterior
n.ent., nucleus entopeduncularis
n.gen.lat., nucleus geniculatus lateralis
n.hab.lat., nucleus habenularis lateralis
n.hab.med., nucleus habenularis medialis
n.hyp.ant.med.p.intermed., nucleus hypothalamicus anterior medialis pars intermedialis
n.hyp.ant.med.p.vent., nucleus hypothalamicus anterior medialis pars ventralis
n.hyp.post.lat., nucleus hypothalamicus posterior lateralis
n.int.inf.post., nucleus internus inferior posterior
n.int.sup., nucleus internus superior
n.intercal., nucleus intercalatus
n.ovidal., nucleus ovoidalis
n.rot., nucleus rotundus
n.superf.epithal., nucleus superficialis epithalamicus
n.superf.magnocell., nucleus superficialis magnocellularis
n.superf.parcocell., nucleus superficialis parvocellularis
n.superf.syn., nucleus superficialis synencephali of Rendahl
n.taen., nucleus taeniae
neostr., neostriatum
pl.ch., plexus choroideus
str.cell.ext., stratum cellulare externum
str.cell.int.dors., stratum cellulare internum dorsale
str.cell.int.vent., stratum cellulare internum ventrale
tect., tectum
tr.n.ovidal., tractus nuclei-ovoidalis
tr.op., tractus opticus
tr.sept.mes., tractus septo-mesencephalicus
tr.tect.thal., tractus tecto-thalamicus et thalamo-tectalis
III v., third ventricle



12



13

PLATE 7

EXPLANATION OF FIGURES

14 Transverse section through brain of parrakeet, showing the positions and relations of some of the more important centers of the forebrain, thalamic, pre-tectal, and tectal areas. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. X 7.5.

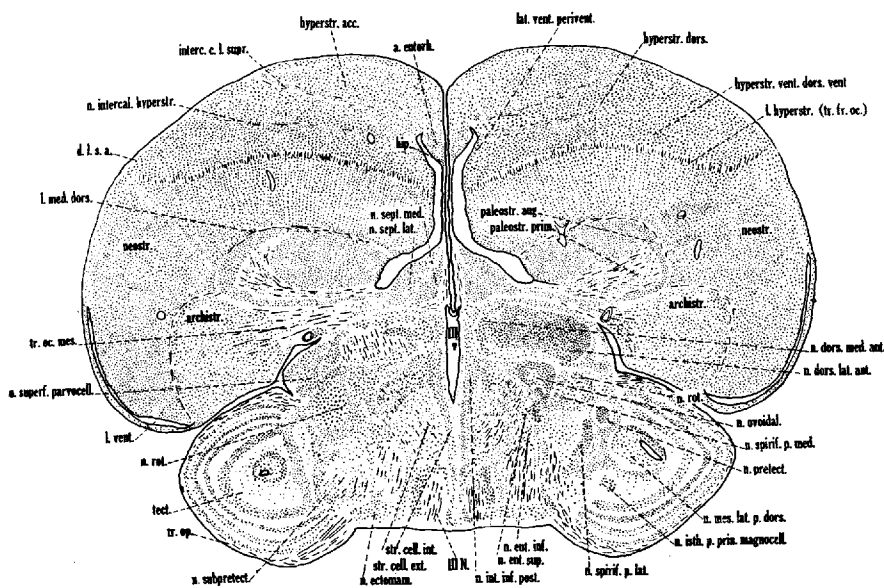
ABBREVIATIONS

a.entorh., area entorhinalis of Rose
a.paraentorh., area paraentorhinalis
archistr., archistriatum
d.l.s.a., dorsolateral surface area (corticoid)
hip., hippocampus
hyperstr. acc., hyperstriatum accessorium
hyperstr. dors., hyperstriatum dorsale
hyperstr. vent. dors. vent., hyperstriatum ventrale pars dorsoventrale
interc. c. l. supr., intercalated cells of lamina frontalis supra
l. hyperstr. (tr. fr. occ.), lamina hyperstriatica (tractus fronto-occipitalis)
l. med. dors., lamina medullaris dorsalis
l. vent., lateral ventricle
lat. vent. perivent., lateroventral periventricular gray
n. dors. lat. ant., nucleus dorsolateralis anterior
n. dors. med. ant., nucleus dorsomedialis anterior
n. ectomam., nucleus ectomammillaris
n. ent. inf., nucleus entopeduncularis inferior
n. ent. sup., nucleus entopeduncularis superior
n. int. inf. post., nucleus internus inferior posterior
n. interc. hyperstr., nucleus intercalatus hyperstriati
n. isth. p. prin. magnocell., nucleus isthmi pars principalis magnocellularis
n. mes. lat. p. dors., nucleus mesencephalicus lateralis pars dorsalis
n. ovoidal., nucleus ovoidalis
n. pretecl., nucleus pretectalis
n. rot., nucleus rotundus
n. sept. lat., nucleus septalis lateralis
n. sept. med., nucleus septalis medialis
n. spirif. p. lat., nucleus spiriformis pars lateralis
n. spirif. p. med., nucleus spiriformis pars medialis
n. subpretecl., nucleus subpretectalis
n. superf. parvocell., nucleus superficialis parvocellularis
neostr., neostriatum
paleostr. aug., paleostriatum augmentatum
paleostr. prim., paleostriatum primitivum
str. cell. ext., stratum cellulare externum
str. cell. int., stratum cellulare internum
tecl., tectum
tr. oc. mex., tractus occipito-mesencephalicus
tr. op., tractus opticus
III N., third nerve
III v., third ventricle

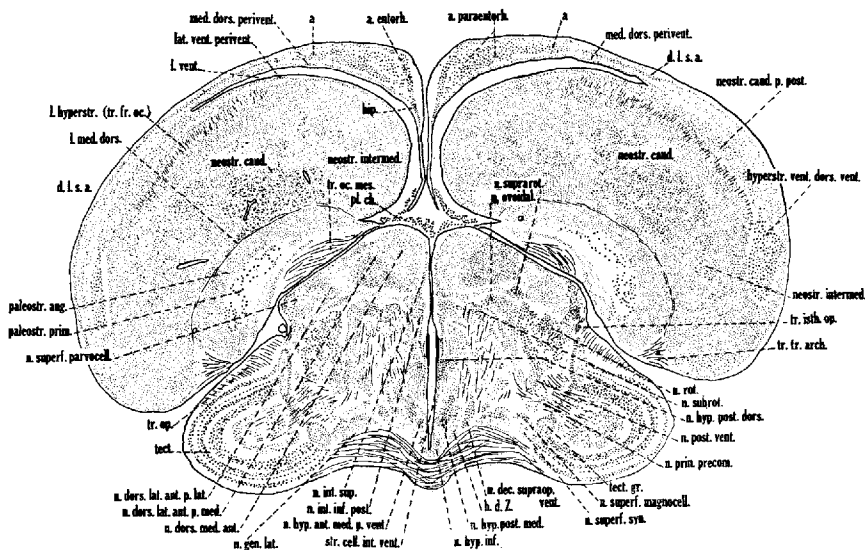
15 Transverse section through brain of sparrow at the level of the hyperstriatum ventrale pars dorsoventrale, indicating particularly the positions and relations of nuclear masses in the more dorsal portion of the thalamus. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. X 7.5.

ABBREVIATIONS

a, differentiated portion of hyperstriatum accessorium
a.entorh., area entorhinalis of Rose
a.paraentorh., area paraentorhinalis
d.l.s.a., dorsolateral surface area (corticoid)
h. & Z., h. & Z. of Rendahl
hip., hippocampus
hyperstr. vent. dors. vent., hyperstriatum ventrale pars dorsoventrale
l. hyperstr. (tr. fr. occ.), lamina hyperstriatica (tractus fronto-occipitalis)
l. med. dors., lamina medullaris dorsalis
l. vent., lateral ventricle
lat. vent. perivent., lateroventral periventricular gray
med. dors. perivent., mediodorsal periventricular gray
n. dec. supraop. vent., nucleus decussationis supraopticae ventralis
n. dors. lat. ant. p. lat., nucleus dorsolateralis anterior pars lateralis
n. dors. lat. ant. p. med., nucleus dorsolateralis anterior pars medialis
n. dors. med. ant., nucleus dorsomedialis anterior
n. ent. sup., nucleus entopeduncularis superior
n. gen. lat., nucleus geniculatus lateralis
n. hyp. ant. med. p. vent., nucleus hypothalamicus anterior medialis pars ventralis
n. hyp. post. dors., nucleus hypothalamicus posterior dorsalis
n. hyp. post. med., nucleus hypothalamicus posterior medialis
n. hyp. inf., nucleus hypothalamicus inferior
n. int. inf. post., nucleus internus inferior posterior
n. int. sup., nucleus internus superior
n. ovoidal., nucleus ovoidalis
n. post. vent., nucleus posteroventralis
n. prin. precom., nucleus principalis precommissuralis
n. rot., nucleus rotundus
n. subrot., nucleus subrotundus
n. superf. magnocell., nucleus superficialis magnocellularis
n. superf. parvocell., nucleus superficialis parvocellularis
n. superf. syn., nucleus superficialis syncephali of Rendahl
n. suprarot., nucleus suprarotundus
neostr. caud., neostriatum caudale
neostr. caud. p. post., neostriatum caudale pars posterior
neostr. intermed., neostriatum intermediale
paleostr. aug., paleostriatum augmentatum
paleostr. prim., paleostriatum primitivum
pl. ch., plexus choroideus
str. cell. int. vent., stratum cellulare internum ventrale
tecl., tectum
tecl. gr., tectal gray
tr. fr. arch., tractus fronto-archistriaticus et neostriaticus
tr. isth. op., tractus isthmo-opticus
tr. oc. mex., tractus occipito-mesencephalicus et bulbaris
tr. op., tractus opticus



14



15

PLATE 8

EXPLANATION OF FIGURES

16 Transverse section through brain of sparrow immediately caudal to nucleus rotundus. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a.</i>, differentiated portion of hyperstriatum accessorium <i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>archistr.</i>, archistriatum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>epiph.</i>, epiphysis <i>hip.</i>, hippocampus <i>hypoph.</i>, hypophysis <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.dors.lat.ant.</i>, nucleus dorsolateralis anterior <i>n.dors.lat.post.</i>, nucleus dorsolateralis posterior <i>n.dors.med.ant.</i>, nucleus dorsomedialis anterior <i>n.ectomam.</i>, nucleus ectomamillaris <i>n.ent.</i>, nucleus entopeduncularis <i>n.ex.</i>, nucleus externus <i>n.hab.lat.</i>, nucleus habenularis lateralis <i>n.hab.med.p.dors.lat.</i>, nucleus habenularis medialis pars dorsolateralis <i>n.hab.med.p.vent.med.</i>, nucleus habenularis medialis pars ventromedialis <i>n.hyp.post.dors.</i>, nucleus hypothalamicus posterior dorsalis <i>n.hyp.post.lat.</i>, nucleus hypothalamicus posterior lateralis</p>	<p><i>n.hyp.inf.</i>, nucleus hypothalamicus inferior <i>n.int.inf.post.</i>, nucleus internus inferior posterior <i>n.int.sup.</i>, nucleus internus superior <i>n.intramed.</i>, nucleus intramedialis <i>n.lat.</i>, nucleus lateralis <i>n.postrot.</i>, nucleus postrotundus <i>n.post.intermed.</i>, nucleus posterointermedialis <i>n.post.vent.</i>, nucleus posteroventralis <i>n.pretect.</i>, nucleus pretectalis <i>n.spirif.p.lat.</i>, nucleus spiriformis pars lateralis <i>n.subpretect.</i>, nucleus subpretectalis <i>n.superf.parvocell.</i>, nucleus superficialis parvocellularis <i>n.tr.hab.ped.</i>, nucleus tractus habenulo-peduncularis <i>neostr.caud.</i>, neostriatum caudale <i>neostr.caud.p.post.</i>, neostriatum caudale pars posterior <i>paleostr.aug.</i>, paleostriatum augmentatum <i>paleostr.prim.</i>, paleostriatum primitivum <i>pl.ch.</i>, plexus choroideus <i>str.cell.int.cent.</i>, stratum cellulare internum ventrale <i>tect.</i>, tectum <i>tect.gr.</i>, tectal gray <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.oc.mes.</i>, tractus occipito-mesencephalicus et bulbaris <i>tr.op.</i>, tractus opticus</p>
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17 Transverse section through brain of sparrow through posterior diencephalic and pretectal areas. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a.entorh.</i>, area entorhinalis of Rose <i>archistr.</i>, archistriatum <i>cer.</i>, cerebellum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>hip.</i>, hippocampus <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.dors.lat.ant.</i>, nucleus dorsolateralis anterior <i>n.dors.lat.post.</i>, nucleus dorsolateralis posterior <i>n.ectomam.</i>, nucleus ectomamillaris <i>n.ex.</i>, nucleus externus <i>n.hab.med.p.dors.lat.</i>, nucleus habenularis medialis pars dorsolateralis <i>n.int.inf.post.</i>, nucleus internus inferior posterior <i>n.isth.p.prin.parvocell.</i>, nucleus isthmi pars principalis parvocellularis <i>n.mam.med.dors.</i>, nucleus mamillaris medialis pars dorsalis</p>	<p><i>n.mam.med.vent.</i>, nucleus mamillaris medialis pars ventralis <i>n.mes.lat.p.dors.</i>, nucleus mesencephalicus lateralis pars dorsalis <i>n.pretect.</i>, nucleus pretectalis <i>n.rub.</i>, nucleus ruber <i>n.spirif.p.lat.</i>, nucleus spiriformis pars lateralis <i>n.spirif.p.med.</i>, nucleus spiriformis pars medialis <i>n.subpretect.</i>, nucleus subpretectalis <i>n.superf.parvocell.</i>, nucleus superficialis parvocellularis <i>n.tr.hab.ped.</i>, nucleus tractus habenulo-peduncularis <i>neostr.caud.</i>, neostriatum caudale <i>neostr.caud.p.post.</i>, neostriatum caudale pars posterior <i>paleostr.aug.</i>, paleostriatum augmentatum <i>pl.ch.</i>, plexus choroideus <i>tect.</i>, tectum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.oc.mes.</i>, tractus occipito-mesencephalicus et bulbaris <i>tr.op.</i>, tractus opticus</p>
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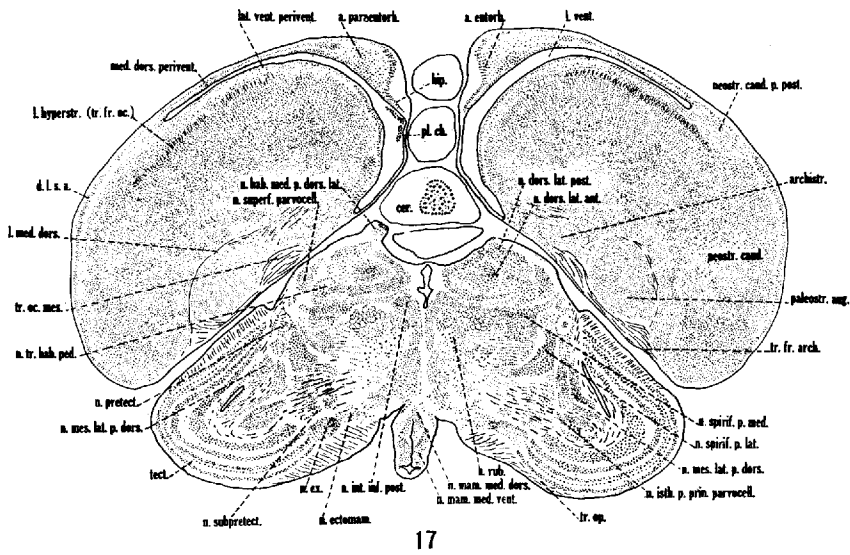
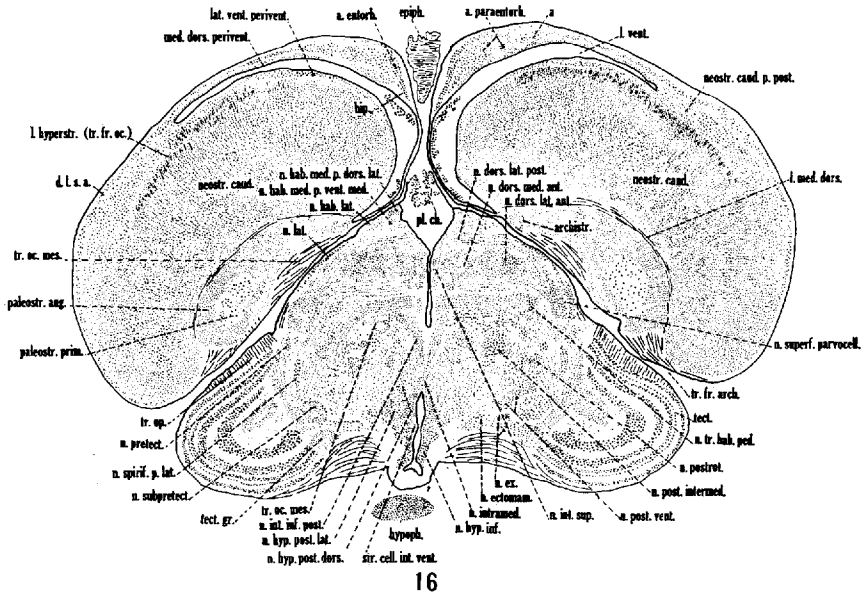


PLATE 9

EXPLANATION OF FIGURES

18 Transverse section through the brain of sparrow at the level of the posterior commissure and the level of the exit of oculomotor nerve. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>a.entorh.</i>, area entorhinalis of Rose <i>archistr.</i>, archistriatum <i>c.mes.V.</i>, cells of the mesencephalic root of the fifth nerve <i>cer.</i>, cerebellum <i>com.post.</i>, commissura posterior <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>hip.</i>, hippocampus <i>l.hyperstr. (tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle <i>m.</i>, differentiated area associated with periventricular gray <i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>med.dors.perivent.</i>, mediodorsal periventricular gray <i>n.dors.lat.post.</i>, nucleus dorsolateralis posterior <i>n.ectomam.</i>, nucleus ectomamillaris <i>n.ex.</i>, nucleus externus <i>n.isth.p.prin.magnocell.</i>, nucleus isthmi pars principalis magnocellularis</p>	<p><i>n.isth.p.prin.parvocell.</i>, nucleus isthmi pars principalis parvocellularis <i>n.mes.lat.p.dors.</i>, nucleus mesencephalicus lateralis pars dorsalis <i>n.rub.</i>, nucleus ruber <i>n.semilun.</i>, nucleus semilunaris <i>n.spirif.p.med.</i>, nucleus spiriformis pars medialis <i>n.superf.parvocell.</i>, nucleus superficialis parvocellularis <i>n.taen.</i>, nucleus taeniae <i>n.tr.hab.ped.</i>, nucleus tractus habenulo-peduncularis <i>neostr.caud.</i>, neostriatum caudale <i>neostr.caud.p.post.</i>, neostriatum caudale pars posterior <i>paleostr.aug.</i>, paleostriatum augmentatum <i>tect.</i>, tectum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.oc.mes.</i>, tractus occipito-mesencephalicus et bulbaris <i>tr.op.</i>, tractus opticus <i>III N.</i>, third nerve</p>
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19 Transverse section through brain of sparrow at the level of nucleus isthmo-opticus and nucleus of the fourth nerve. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<p><i>archistr.p.dors.</i>, archistriatum pars dorsalis <i>archistr.p.vent.</i>, archistriatum pars ventralis <i>c.mes.V.</i>, cells of the mesencephalic root of the fifth nerve <i>cer.</i>, cerebellum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>f.l.m.</i>, fasciculus longitudinalis medialis <i>hip.</i>, hippocampus <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.vent.</i>, lateral ventricle</p>	<p><i>lat.vent.perivent.</i>, lateroventral periventricular gray <i>n.isth.op.</i>, nucleus isthmo-opticus <i>n.isth.p.prin.magnocell.</i>, nucleus isthmi pars principalis magnocellularis <i>n.isth.p.prin.parvocell.</i>, nucleus isthmi pars principalis parvocellularis <i>n.IV N.</i>, nucleus of the fourth nerve <i>neostr.caud.</i>, neostriatum caudale <i>tect.</i>, tectum <i>tr.op.</i>, tractus opticus</p>
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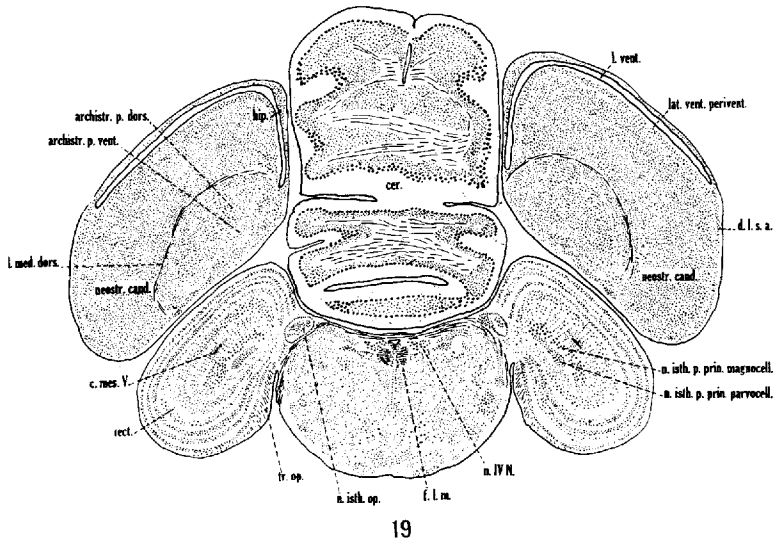
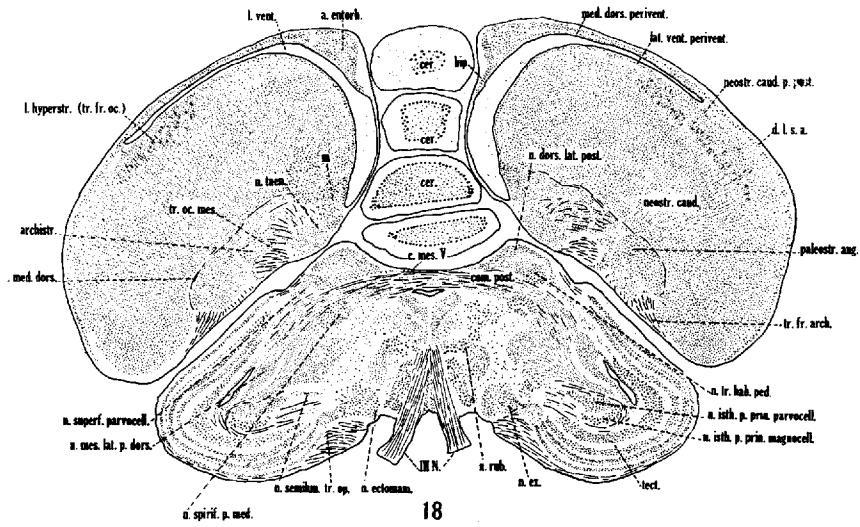


PLATE 10

EXPLANATION OF FIGURES

20 Horizontal section through brain of sparrow, indicating the positions and relations of many of the nuclear constituents of the forebrain, thalamic, and midbrain regions. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

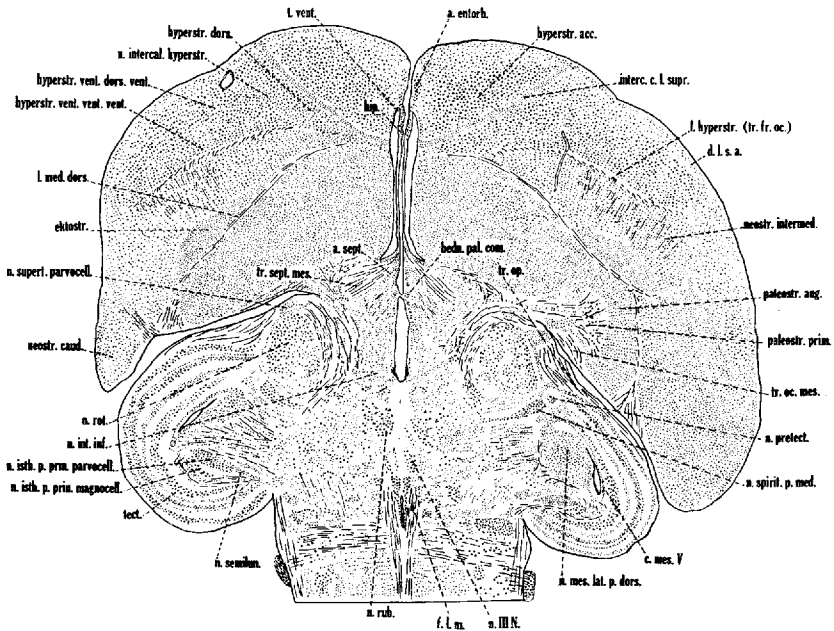
ABBREVIATIONS

<i>a.entorh.</i> , area entorhinalis of Rose	<i>n.isth.p.prin.magnocell.</i> , nucleus isthmi pars principalis magnocellularis
<i>a.sept.</i> , area septalis	<i>n.isth.p.prin.parvocell.</i> , nucleus isthmi pars principalis parvocellularis
<i>bedn.pal.com.</i> , bed nucleus of the pallial commissure	<i>n.mes.lat.p.dors.</i> , nucleus mesencephalicus lateralis pars dorsalis
<i>c.mes.V.</i> , cells of the mesencephalic root of the fifth nerve	<i>n.pretect.</i> , nucleus pretectalis
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>n.rot.</i> , nucleus rotundus
<i>ektostr.</i> , ektostriatum	<i>n.rub.</i> , nucleus ruber
<i>f.l.m.</i> , fasciculus longitudinalis medialis	<i>n.semilun.</i> , nucleus semilunaris
<i>hip.</i> , hippocampus	<i>n.spirif.p.med.</i> , nucleus spiriformis pars medialis
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>n.superf.parvocell.</i> , nucleus superficialis parvocellularis
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>n.III N.</i> , nucleus of the third nerve
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>neostr.caud.</i> , neostriatum caudale
<i>hyperstr.vent.vent.vent.</i> , hyperstriatum ventrale ventroventrale	<i>neostr.intermed.</i> , neostriatum intermediale
<i>interc.c.l.supr.</i> , intercalated cells of lamina frontalis suprema	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>paleostr.prim.</i> , paleostriatum primitivum
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>tect.</i> , tectum
<i>l.vent.</i> , lateral ventricle	<i>tr.oc.mes.</i> , tractus occipito-mesencephalicus et bulbaris
<i>n.int.inf.</i> , nucleus internus inferior	<i>tr.op.</i> , tractus opticus
<i>n.intercal.hyperstr.</i> , nucleus intercalatus hyperstriati	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus

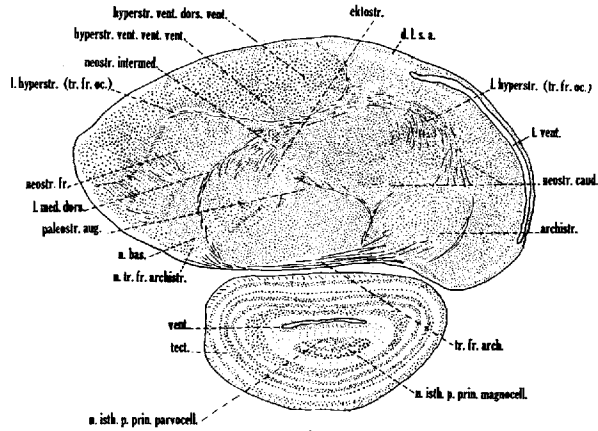
21 Sagittal section passing through lateral portion of the forebrain and tectum of the sparrow. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<i>archistr.</i> , archistriatum	<i>n.isth.p.prin.magnocell.</i> , nucleus isthmi pars principalis magnocellularis
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>n.isth.p.prin.parvocell.</i> , nucleus isthmi pars principalis parvocellularis
<i>ektostr.</i> , ektostriatum	<i>neostr.caud.</i> , neostriatum caudale
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>neostr.fr.</i> , neostriatum frontale
<i>hyperstr.vent.vent.vent.</i> , hyperstriatum ventrale ventroventrale	<i>neostr.intermed.</i> , neostriatum intermediale
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>tect.</i> , tectum
<i>l.vent.</i> , lateral ventricle	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>n.bas.</i> , nucleus basalis	<i>vent.</i> , ventricle in tectal region
<i>n.tr.fr.archistr.</i> , nucleus tractus fronto-archistriatici	



20



21

PLATE 11

EXPLANATION OF FIGURES

22 Sagittal section of brain of sparrow medial to figure 21, indicating particularly well the positions and extent of the several striatal regions of the forebrain. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

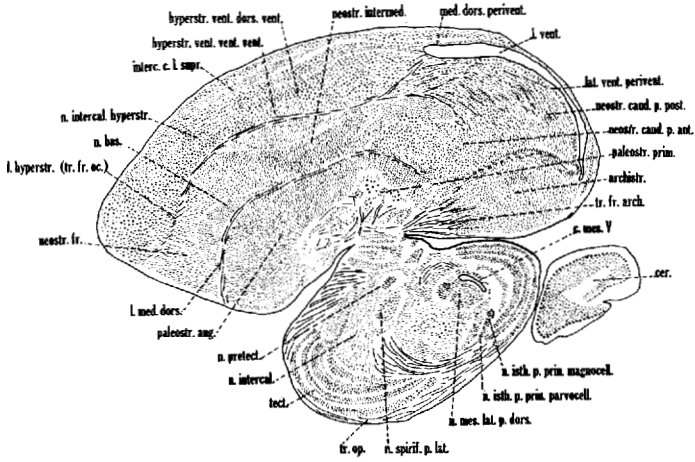
ABBREVIATIONS

<i>archistr.</i> , archistriatum	<i>n.isth.p.prin.magnocell.</i> , nucleus isthmi pars principalis magnocellularis
<i>c.mes.V.</i> , cells of the mesencephalic root of the fifth nerve	<i>n.isth.p.prin.parvocell.</i> , nucleus isthmi pars principalis parvocellularis
<i>cer.</i> , cerebellum	<i>n.mes.lat.p.dors.</i> , nucleus mesencephalicus lateralis pars dorsalis
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>n.pretect.</i> , nucleus pretectalis
<i>hyperstr.vent.vent.</i> , hyperstriatum ventrale ventroventrale	<i>n.spirif.p.lat.</i> , nucleus spiriformis pars lateralis
<i>interc.c.l.supr.</i> , intercalated cells of lamina suprema	<i>neostr.caud.p.ant.</i> , neostriatum caudale pars anterior
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>neostr.caud.p.post.</i> , neostriatum caudale pars posterior
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>neostr.fr.</i> , neostriatum frontale
<i>l.vent.</i> , lateral ventricle	<i>neostr.intermed.</i> , neostriatum intermediale
<i>lat.vent.perivent.</i> , lateroventral periventricular gray	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>med.dors.perivent.</i> , mediodorsal periventricular gray	<i>paleostr.prim.</i> , paleostriatum primitivum
<i>n.bas.</i> , nucleus basalis	<i>lect.</i> , tectum
<i>n.intercal.</i> , nucleus intercalatus	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>n.intercal.hyperstr.</i> , nucleus intercalatus hyperstriati	<i>tr.op.</i> , tractus opticus

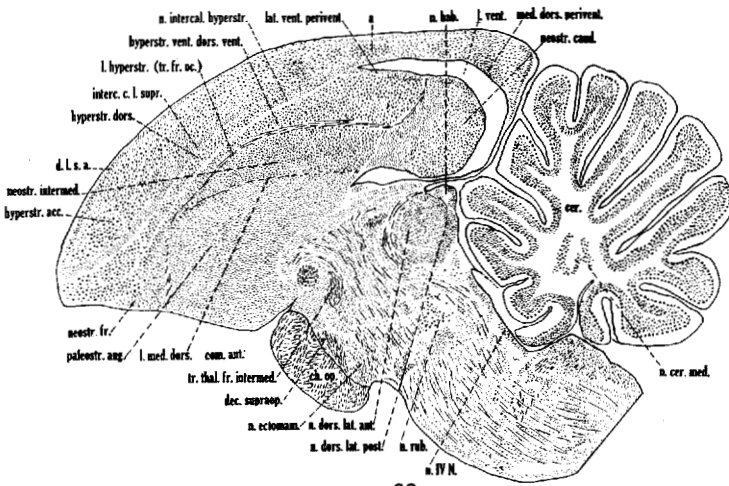
23 Sagittal section through brain of sparrow, medial to plane of figure 22, showing relations of striatal areas of the forebrain and certain diencephalic centers. Fixation, trichloroacetic-mercury-alcohol; toluidin-blue stain. $\times 7.5$.

ABBREVIATIONS

<i>a.</i> , differentiated portion of the hyperstriatum accessorium	<i>med.dors.perivent.</i> , mediodorsal periventricular gray
<i>cer.</i> , cerebellum	<i>n.cer.med.</i> , nucleus cerebellaris medialis
<i>ch.op.</i> , chiasma opticum	<i>n.dors.lat.ant.</i> , nucleus dorsolateralis anterior
<i>com.ant.</i> , commissura anterior	<i>n.dors.lat.post.</i> , nucleus dorsolateralis posterior
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>n.ectomam.</i> , nucleus ectomamillaris
<i>dec.supraop.</i> , decussatio supraoptica	<i>n.hab.</i> , nucleus habenularis
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>n.intercal.hyperstr.</i> , nucleus intercalatus hyperstriati
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>n.rub.</i> , nucleus ruber
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>n.IV N.</i> , nucleus of the fourth nerve
<i>interc.c.l.supr.</i> , intercalated cells of the lamina frontalis suprema	<i>neostr.caud.</i> , neostriatum caudale
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>neostr.fr.</i> , neostriatum frontale
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>neostr.intermed.</i> , neostriatum intermediale
<i>l.vent.</i> , lateral ventricle	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>lat.vent.perivent.</i> , lateroventral periventricular gray	<i>tr.thal.fr.intermed.</i> , tractus thalamo-frontalis intermedialis



22



23

PLATE 12

EXPLANATION OF FIGURES

24 Transverse section through the rostral end of brain of sparrow at the level of the olfactory bulb. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

<i>a.prae pyr.</i> , area prae pyriformis	<i>hyperstr.dors.</i> , hyperstriatum dorsale
<i>b.olf.</i> , bulbus olfactorius	<i>hyperstr.vent.</i> , hyperstriatum ventrale
<i>fr.rad.h.</i> , frontal radiation from dorsolateral surface area	<i>l.fr.supr.</i> , lamina frontalis superior
<i>fr.rad.k.</i> , frontal radiation from hyperstriatum accessorium	<i>l.fr.supr.</i> , lamina frontalis suprema
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>n.olf.ant.</i> , nucleus olfactorius anterior
	<i>tr.olf.lat.</i> , tractus olfactorius lateralis
	<i>tr.olf.med.</i> , tractus olfactorius medialis

25 Transverse section through the brain of sparrow at the level of the anterior end of the neostriatum. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

<i>a.prae pyr.</i> , area prae pyriformis	<i>l.fr.supr.</i> , lamina frontalis suprema
<i>b.olf.</i> , bulbus olfactorius	<i>neostr.</i> , neostriatum
<i>fr.rad.h.</i> , frontal radiation from dorsolateral surface area	<i>neostr.hyperstr.comp.n.bas.</i> , neostriatal-hyperstriatal component to nucleus basalis
<i>fr.rad.k.</i> , frontal radiation from hyperstriatum accessorium	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>tr.olf.lat.</i> , tractus olfactorius lateralis
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>tr.olf.med.</i> , tractus olfactorius medialis
<i>hyperstr.vent.</i> , hyperstriatum ventrale	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus
<i>l.fr.supr.</i> , lamina frontalis superior	

26 Transverse section through the brain of the sparrow at the level of the rostral end of paleostriatum augmentatum. Pyridine-silver preparation. $\times 7.5$.

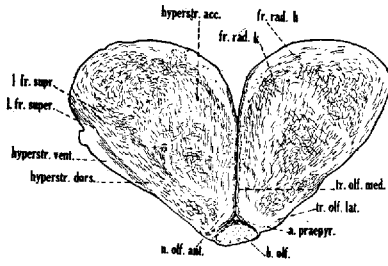
ABBREVIATIONS

<i>a.entorh.</i> , area entorhinalis	<i>med.dors.perivent.sys.</i> , mediadorsal periventricular fiber system
<i>fr.rad.h.</i> , frontal radiations from dorsolateral surface area	<i>n.bas.</i> , nucleus basalis
<i>fr.rad.k.</i> , frontal radiations from hyperstriatum accessorium	<i>neostr.</i> , neostriatum
<i>hip.</i> , hippocampus	<i>neostr.hyperstr.comp.n.bas.</i> , neostriatal-hyperstriatal component to nucleus basalis
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>hyperstr.vent.</i> , hyperstriatum ventrale	<i>tr.olf.lat.</i> , tractus olfactorius lateralis
<i>l.fr.supr.</i> , lamina frontalis superior	<i>tr.quint.fr.</i> , tractus quinto-frontalis (and associated fibers)
<i>l.fr.supr.</i> , lamina frontalis suprema	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>tr.thal.fr.med.p.fr.</i> , tractus thalamo-frontalis medialis pars frontalis
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>x</i> , composit bundle containing, among other fibers, tractus quinto-frontalis pars dorsalis
<i>l.vent.</i> , lateral ventricle	
<i>lat.vent.perivent.sys.</i> , lateroventral periventricular fiber system	

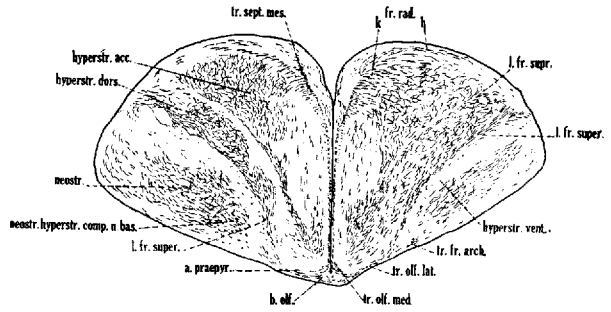
27 Transverse section through brain of sparrow at a level slightly caudal to figure 26. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

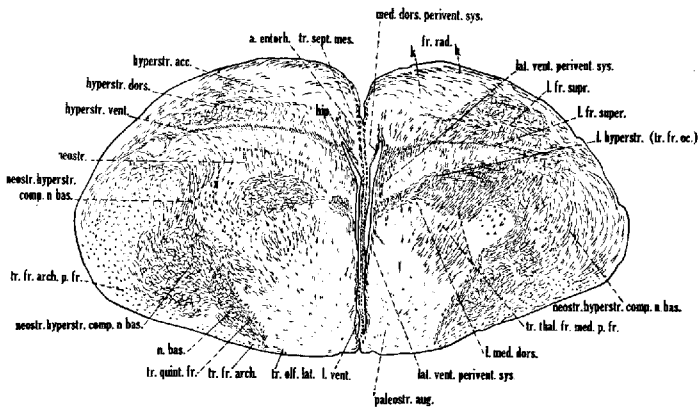
<i>a.entorh.</i> , area entorhinalis of Rose	<i>med.dors.perivent.sys.</i> , mediadorsal periventricular fiber system
<i>a.paraentorh.</i> , area paraentorhinalis	<i>n.bas.</i> , nucleus basalis
<i>ch.op.</i> , chiasma opticum	<i>neostr.hyperstr.comp.n.bas.</i> , neostriatal-hyperstriatal component to nucleus basalis
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>ektostr.</i> , ektostriatum	<i>tr.fr.arch.p.bas.</i> , tractus fronto-archistriaticus et neostriaticus pars basalis
<i>fr.rad.h.</i> , frontal radiations from dorsolateral surface area	<i>tr.fr.arch.p.fr.</i> , tractus fronto-archistriaticus et neostriaticus pars frontalis
<i>fr.rad.k.</i> , frontal radiations from hyperstriatum accessorium	<i>tr.quint.fr.p.bas.</i> , tractus quinto-frontalis pars basalis
<i>hip.</i> , hippocampus	<i>tr.quint.fr.p.dors.</i> , tractus quinto-frontalis pars dorsalis
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus
<i>hyperstr.comp.ektostr.</i> , hyperstriatal component to ektostriatum	<i>tr.str.hyp.med.</i> , tractus strio-hypothalamicus medialis
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>tr.thal.fr.med.p.fr.</i> , tractus thalamo-frontalis medialis pars frontalis
<i>hyperstr.vent.</i> , hyperstriatum ventrale	<i>x</i> , composit bundle containing, among other fibers, tractus quinto-frontalis pars dorsalis
<i>l.fr.supr.</i> , lamina frontalis superior	
<i>l.fr.supr.</i> , lamina frontalis suprema	
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	
<i>l.med.dors.</i> , lamina medullaris dorsalis	
<i>lat.vent.perivent.sys.</i> , lateroventral periventricular fiber system	



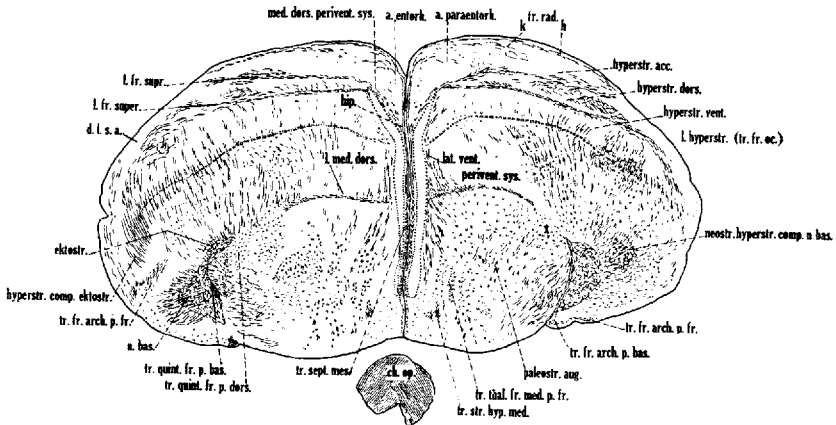
24



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PLATE 13

EXPLANATION OF FIGURES

28 Transverse section of brain of sparrow, passing on the left side through nucleus tractus fronto-archistriatici and ektostriatum and on the right side through nucleus basalis. Pyridine-silver preparation. $\times 7.5$.

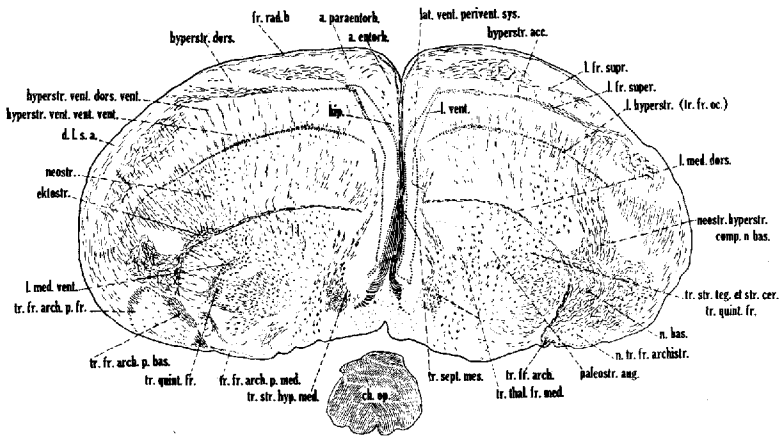
ABBREVIATIONS

<p><i>a.entorh.</i>, area entorhinalis of Rose <i>a.paraentorh.</i>, area paraentorhinalis <i>ch.op.</i>, chiasma opticum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>ektostr.</i>, ektostriatum <i>fr.rad.h.</i>, frontal radiations from dorsolateral surface area <i>hip.</i>, hippocampus <i>hyperstr.acc.</i>, hyperstriatum accessorium <i>hyperstr.dors.</i>, hyperstriatum dorsale <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale ventroventrale <i>l.fr.super.</i>, lamina frontalis superior <i>l.fr.supr.</i>, lamina frontalis suprema <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.med.vent.</i>, lamina medullaris ventralis <i>l.vent.</i>, lateral ventricle <i>lat.vent.perivent.sys.</i>, lateroventral periventricular fiber system</p>	<p><i>n.bas.</i>, nucleus basalis <i>n.tr.fr.archistr.</i>, nucleus tractus fronto-archistriatici et neostriatici <i>neostr.</i>, neostriatum <i>neostr.hyperstr.comp.n.bas.</i>, neostriatal-hyperstriatal component to nucleus basalis <i>paleostr.aug.</i>, paleostriatum augmentatum <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.fr.arch.p.bas.</i>, tractus fronto-archistriaticus et neostriaticus pars basalis <i>tr.fr.arch.p.fr.</i>, tractus fronto-archistriaticus et neostriaticus pars frontalis <i>tr.fr.arch.p.med.</i>, tractus fronto-archistriaticus et neostriaticus pars medialis <i>tr.quint.fr.</i>, tractus quinto-frontalis <i>tr.sept.mes.</i>, tractus septo-mesencephalicus <i>tr.str.teg.et str.cer.</i>, tractus strio-tegmentalis et strio-cerebellaris <i>tr.str.hyp.med.</i>, tractus strio-hypothalamicus medialis <i>tr.thal.fr.med.</i>, tractus thalamo-frontalis medialis</p>
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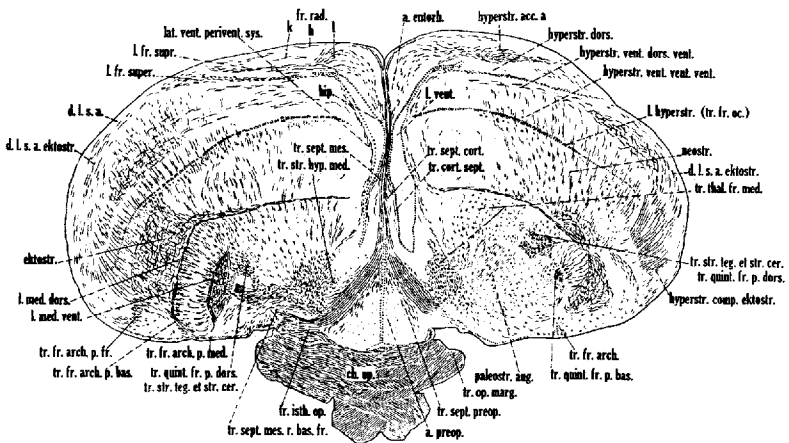
29 Transverse section through the brain of sparrow, passing through the preoptic area and optic chiasma. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

<p><i>a.entorh.</i>, area entorhinalis of Rose <i>a.preop.</i>, area preopticus <i>ch.op.</i>, chiasma opticum <i>d.l.s.a.</i>, dorsolateral surface area (corticoid) <i>d.l.s.a.ektostr.</i>, dorsolateral surface area component to ektostriatum <i>ektostr.</i>, ektostriatum <i>fr.rad.h.</i>, frontal radiations from dorsolateral surface area <i>fr.rad.k.</i>, frontal radiations from hyperstriatum accessorium <i>fr.rad.l.</i>, frontal radiations from lamina frontalis suprema <i>hip.</i>, hippocampus <i>hyperstr.acc.a.</i>, hyperstriatum accessorium; a, differentiated portion <i>hyperstr.comp.ektostr.</i>, hyperstriatal component to ektostriatum <i>hyperstr.dors.</i>, hyperstriatum dorsale <i>hyperstr.vent.dors.vent.</i>, hyperstriatum ventrale dorsoventrale <i>hyperstr.vent.vent.vent.</i>, hyperstriatum ventrale ventroventrale <i>l.fr.super.</i>, lamina frontalis superior <i>l.fr.supr.</i>, lamina frontalis suprema <i>l.hyperstr.(tr.fr.oc.)</i>, lamina hyperstriatica (tractus fronto-occipitalis) <i>l.med.dors.</i>, lamina medullaris dorsalis <i>l.med.vent.</i>, lamina medullaris ventralis <i>l.vent.</i>, lateral ventricle</p>	<p><i>lat.vent.perivent.sys.</i>, lateroventral periventricular fiber system <i>neostr.</i>, neostriatum <i>paleostr.aug.</i>, paleostriatum augmentatum <i>tr.cort.sept.</i>, tractus cortico-septalis <i>tr.fr.arch.</i>, tractus fronto-archistriaticus et neostriaticus <i>tr.fr.arch.p.bas.</i>, tractus fronto-archistriaticus et neostriaticus pars basalis <i>tr.fr.arch.p.fr.</i>, tractus fronto-archistriaticus et neostriaticus pars frontalis <i>tr.fr.arch.p.med.</i>, tractus fronto-archistriaticus et neostriaticus pars medialis <i>tr.isth.op.</i>, tractus isthmo-opticus <i>tr.op.marg.</i>, tractus opticus marginalis <i>tr.quint.fr.p.bas.</i>, tractus quinto-frontalis pars basalis <i>tr.quint.fr.p.dors.</i>, tractus quinto-frontalis pars dorsalis <i>tr.sept.cort.</i>, tractus septo-corticalis <i>tr.sept.mes.</i>, tractus septo-mesencephalicus <i>tr.sept.mes.r.bas.fr.</i>, tractus septo-mesencephalicus ramus basalis frontalis <i>tr.sept.preop.</i>, tractus septo-preopticus <i>tr.str.teg.et str.cer.</i>, tractus strio-tegmentalis et strio-cerebellaris <i>tr.str.hyp.med.</i>, tractus strio-hypothalamicus medialis <i>tr.thal.fr.med.p.fr.</i>, tractus thalamo-frontalis medialis pars frontalis</p>
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PLATE 14

EXPLANATION OF FIGURES

30 Transverse section through the brain of sparrow at the level of rostral end of tectum and the dorsal supra-optic decussation. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

a.entorh., area entorhinalis of Rose
a.preop., area preopticus
a.sept., area septalis
ass.f., association fibers
ch.op., chiasma opticum
d.l.s.a., dorsolateral surface area (corticoid)
dec.supraop.dors., decussatio supraoptica dorsalis
dec.supraop.dors.p.med., decussatio supraoptica dorsalis pars medialis
dec.supraop.dors.p.tect., decussatio supraoptica dorsalis pars tectalis
dec.supraop.vent., decussatio supraoptica ventralis
ektostr., ektostriatium
fr.rad.h., frontal radiations from dorsolateral surface area
fr.rad.k., frontal radiations from hyperstriatum accessorium
fr.rad.l., frontal radiations from lamina frontalis suprema
hyperstr.acc., hyperstriatum accessorium
hyperstr.dors., hyperstriatum dorsale
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.fr.super., lamina frontalis superior
l.fr.supr., lamina frontalis suprema
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.med.vent., lamina medullaris ventralis
l.vent., lateral ventricle
lat.vent.perivent.sys., lateroventral periventricular fiber system

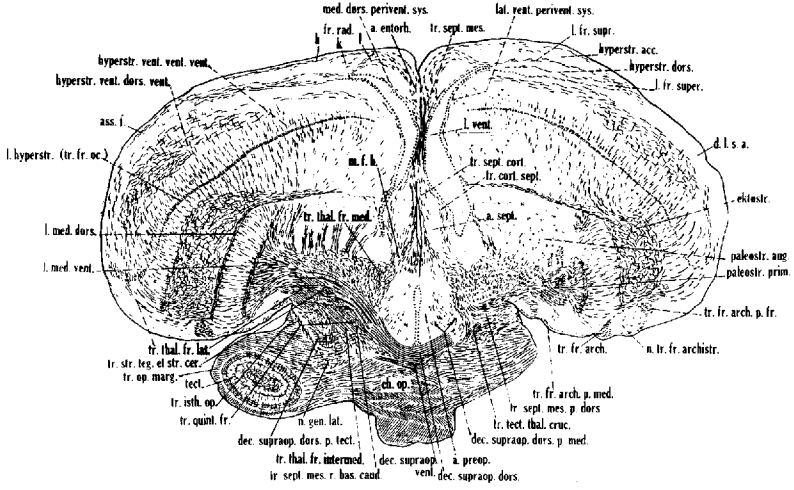
med.dors.perivent.sys., mediadorsal periventricular fiber system
m.f.b., medial forebrain bundle
n.gen.lat., nucleus geniculatus lateralis
n.tr.fr.archistr., nucleus tractus fronto-archistriatici
paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
tect., tectum
tr.cort.sept., tractus cortico-septalis
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.fr.arch.p.fr., tractus fronto-archistriaticus et neostriaticus pars frontalis
tr.fr.arch.p.med., tractus fronto-archistriaticus et neostriaticus pars medialis
tr.isth.op., tractus isthmo-opticus
tr.op.marg., tractus opticus marginalis
tr.quint.fr., tractus quinto-frontalis
tr.sept.cort., tractus septo-corticalis
tr.sept.mes., tractus septo-mesencephalicus
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.str.teg.et.str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.tect.thal.cruc., tractus tecto-thalamicus cruciatus
tr.thal.fr.intermed., tractus thalamo-frontalis intermedialis
tr.thal.fr.lat., tractus thalamo-frontalis lateralis
tr.thal.fr.med., tractus thalamo-frontalis medialis

31 Transverse section through brain of sparrow, passing through the rostral end of nucleus rotundus and nucleus geniculatus lateralis. Pyridine-silver preparation. $\times 7.5$.

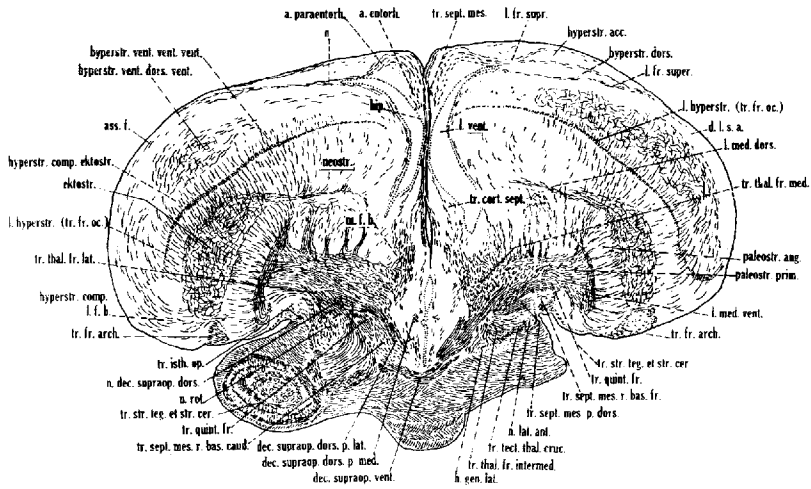
ABBREVIATIONS

a.entorh., area entorhinalis of Rose
a.paraentorh., area paraentorhinalis
ass.f., association fibers
d.l.s.a., dorsolateral surface area (corticoid)
dec.supraop.dors.p.lat., decussatio supraoptica dorsalis pars lateralis
dec.supraop.dors.p.med., decussatio supraoptica dorsalis pars medialis
dec.supraop.vent., decussatio supraoptica ventralis
ektostr., ektostriatium
hip., hippocampus
hyperstr.acc., hyperstriatum accessorium
hyperstr.comp.ektostr., hyperstriatal component to ektostriatium
hyperstr.comp.l.f.b., hyperstriatal component to lateral forebrain bundle
hyperstr.dors., hyperstriatum dorsale
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.fr.super., lamina frontalis superior
l.fr.supr., lamina frontalis suprema
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.med.vent., lamina medullaris ventralis
l.vent., lateral ventricle
m.f.b., medial forebrain bundle
n., region of fusion of laminae frontalis superior et suprema

n.dec.supraop.dors., nucleus decussationis supraopticae dorsalis
n.gen.lat., nucleus geniculatus lateralis
n.lat.ant., nucleus lateralis anterior
n.rot., nucleus rotundus
neostr., neostriatum
paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
tr.cort.sept., tractus cortico-septalis
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.isth.op., tractus isthmo-opticus
tr.quint.fr., tractus quinto-frontalis
tr.sept.mes., tractus septo-mesencephalicus
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.sept.mes.r.bas.fr., tractus septo-mesencephalicus ramus basalis frontalis
tr.str.teg.et.str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.tect.thal.cruc., tractus tecto-thalamus cruciatus
tr.thal.fr.intermed., tractus thalamo-frontalis intermedialis
tr.thal.fr.lat., tractus thalamo-frontalis lateralis
tr.thal.fr.med., tractus thalamo-frontalis medialis



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PLATE 15

EXPLANATION OF FIGURES

32 Transverse section through brain of sparrow, passing through anterior commissure and tectum. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

a.sept., area septalis
ass.f., association fibers
ch.op., chiasma opticum
com.ant., commissura anterior
d.l.s.a., dorsolateral surface area (corticoid)
d.l.s.a.ektotr., dorsolateral surface area component to ektostriatum
dec.supraop.dors.p.lat., decussatio supraoptica dorsalis pars lateralis
dec.supraop.dors.p.med., decussatio supraoptica dorsalis pars medialis
dec.supraop.vent., decussatio supraoptica ventralis
dec.supraop.vent.p.dors., decussatio supraoptica ventralis pars dorsalis
dec.supraop.vent.p.vent., decussatio supraoptica ventralis pars ventralis
dien.perivent., diencephalic periventricular fiber system
ektotr., ektostriatum
hyperstr.acc., hyperstriatum accessorium
hyperstr.comp.ektotr., hyperstriatal component to ektostriatum
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.med.vent., lamina medullaris ventralis
l.vent., lateral ventricle
lat.vent.perivent.sys., lateroventral periventricular fiber system

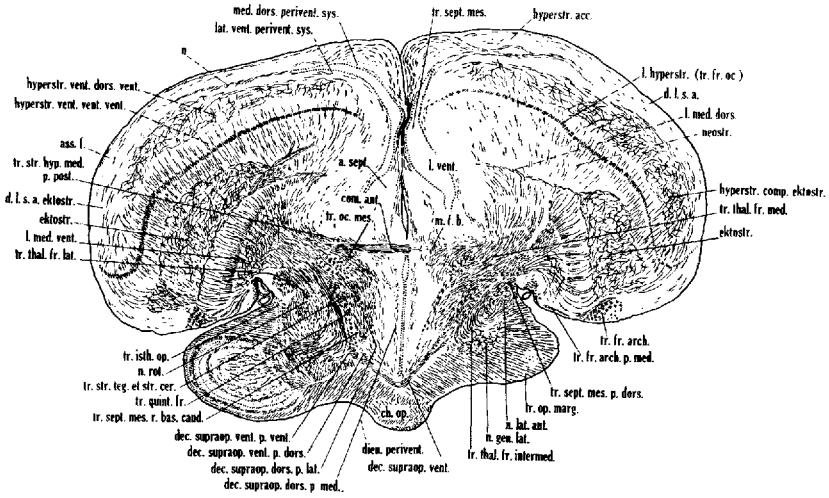
m.f.b., medial forebrain bundle
med.dors.perivent.sys., mediadorsal periventricular fiber system
n., region of fusion of laminae frontalis superior et suprema
n.gen.lat., nucleus geniculatus lateralis
n.lat.ant., nucleus lateralis anterior
n.rot., nucleus rotundus
neostr., neostriatum
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.fr.arch.p.med., tractus fronto-archistriaticus et neostriaticus pars medialis
tr.isth.op., tractus isthmo-opticus
tr.oc.mes., tractus occipito-mesencephalicus et bulbaris
tr.op.marg., tractus opticus marginalis
tr.quint.fr., tractus quinto-frontalis
tr.sept.mes., tractus septo-mesencephalicus
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.str.teg.et str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.str.hyp.med.p.post., tractus strio-hypothalamicus medialis pars posterior
tr.thal.fr.intermed., tractus thalamo-frontalis intermedialis
tr.thal.fr.lat., tractus thalamo-frontalis lateralis
tr.thal.fr.med., tractus thalamo-frontalis medialis

33 Transverse section through brain of sparrow slightly caudal to level of anterior commissure, showing numerous diencephalic fiber connections. Pyridine-silver preparation. $\times 7.5$.

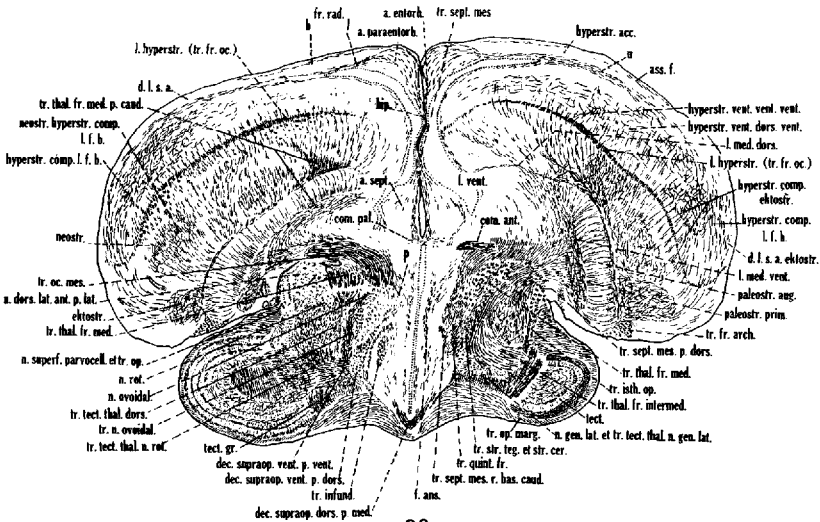
ABBREVIATIONS

a.entorh., area entorhinalis of Rose
a.paraentorh., area paraentorhinalis
a.sept., area septalis
ass.f., association fibers
com.ant., commissura anterior
com.pal., commissura pallii
d.l.s.a., dorsolateral surface area (corticoid)
d.l.s.a.ektotr., dorsolateral surface area component to ektostriatum
dec.supraop.dors.p.med., decussatio supraoptica dorsalis pars medialis
dec.supraop.vent.p.dors., decussatio supraoptica ventralis pars dorsalis
dec.supraop.vent.p.vent., decussatio supraoptica ventralis pars ventralis
ektotr., ektostriatum
f.ans., fibrae ansulatae
fr.rad.h., frontal radiations from dorsolateral surface area
fr.rad.l., frontal radiations from lamina frontalis suprema
hip., hippocampus
hyperstr.acc., hyperstriatum accessorium
hyperstr.comp.ektotr., hyperstriatal component to ektostriatum
hyperstr.comp.l.f.b., hyperstriatal component to lateral forebrain bundle
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.med.vent., lamina medullaris ventralis
l.vent., lateral ventricle
n., region of fusion of laminae frontalis superior et suprema
n.dors.lat.ant.p.lat., nucleus dorsolateralis anterior pars lateralis
n.gen.lat.et tr.tect.thal.n.gen.lat., nucleus geniculatus lateralis et tractus tecto-thalamicus nuclei geniculati lateralis

n.ovidal., nucleus ovoidalis
n.rot., nucleus rotundus
n.superf.parnocell.et tr.op., nucleus superficialis parvocellularis et tractus opticus
neostr., neostriatum
neostr.hyperstr.comp.l.f.b., neostriatal-hyperstriatal component to lateral forebrain bundle
p., fibers from *tr.oc.mes.* to *n.int.inf.post.*
paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
tect., tectum
tect.gr., tectal gray
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.infund., tractus infundibuli
tr.isth.op., tractus isthmo-opticus
tr.n.ovidal., tractus nuclei ovoidalis
tr.oc.mes., tractus occipito-mesencephalicus et bulbaris
tr.op.marg., tractus opticus marginalis
tr.quint.fr., tractus quinto-frontalis
tr.sept.mes., tractus septo-mesencephalicus
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.str.teg.et str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.thal.fr.intermed., tractus thalamo-frontalis intermedialis
tr.thal.fr.med., tractus thalamo-frontalis medialis
tr.thal.fr.med.p.caud., tractus thalamo-frontalis medialis pars caudalis
tr.tect.thal.dors., tractus tecto-thalamicus et thalamo-tectalis dorsalis
tr.tect.thal.n.rot., tractus tecto-thalamicus et thalamo-tectalis nuclei rotundi



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PLATE 16

EXPLANATION OF FIGURES

34 Transverse section of brain of sparrow through region of midthalamus. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

a.paraentorh., area paraentorhinalis
ass.f., association fibers
d.l.s.a., dorsolateral surface area (corticoid)
d.l.s.a.ektost., dorsolateral surface area component to ektostriatum
dec.supraop.vent.p.dors., decussatio supraoptica ventralis pars dorsalis
dec.supraop.vent.p.vent., decussatio supraoptica ventralis pars ventralis
dien.perivent., diencephalic periventricular fiber system
f.ans., fibrae ansulatae
fr.rad.h., frontal radiation from dorsolateral surface area
fr.rad.l., frontal radiation from lamina frontalis suprema
hip., hippocampus
hyperstr.comp.ektost., hyperstriatal component to ektostriatum
hyperstr.vent.dors.vent., hyperstriatum ventrale dorsoventrale
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.med.vent., lamina medullaris ventralis
l.vent., lateral ventricle
lat.vent.perivent.sys., lateroventral periventricular fiber system
n.dors.lat.ant.et tr.thal.fr.med., nucleus dorsolateralis anterior et tractus thalamo-frontalis medialis
n.dors.med.ant., nucleus dorsomedialis anterior
n.ectomam.et tr.op.r.op.bas., nucleus ectomamillaris et tractus opticus radix opticum basale

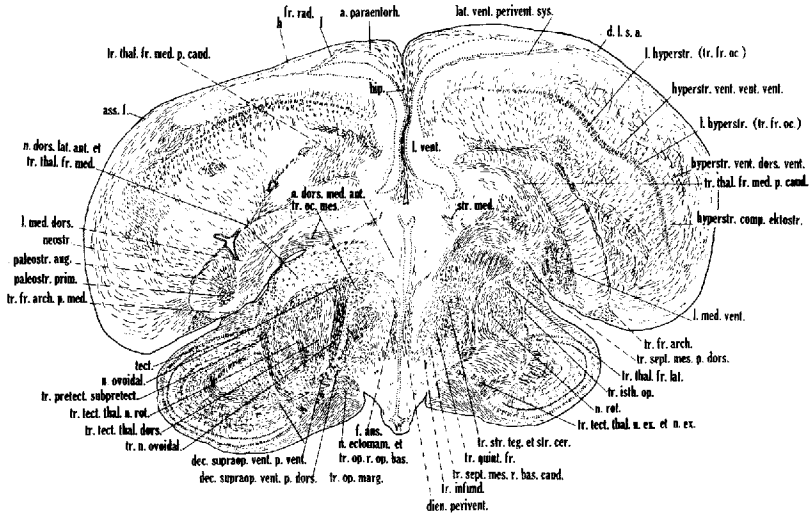
n.ovidal., nucleus ovoidalis
n.rot., nucleus rotundus
neostr., neostriatum
paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
str.med., stria medullaris
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.fr.arch.p.med., tractus fronto-archistriaticus et neostriaticus pars medialis
tecl., tectum
tr.infund., tractus infundibuli
tr.isth.op., tractus isthmo-opticus
tr.n.ovidal., tractus nuclei ovoidalis
tr.oc.mes., tractus occipito-mesencephalicus et bulbaris
tr.op.marg., tractus opticus marginalis
tr.pretect.subprelect., tractus pretectalis subpretectalis
tr.quint.fr., tractus quinto-frontalis
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.str.teg.et str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.tect.thal.dors., tractus tecto-thalamicus et thalamo-tectalis dorsalis
tr.tect.thal.n.rot., tractus tecto-thalamicus et thalamo-tectalis nuclei rotundi
tr.tect.thal.n.ex.et n.ex., tractus tecto-thalamicus et thalamo-tectalis nuclei externi et nucleus externus
tr.thal.fr.lat., tractus thalamo-frontalis lateralis
tr.thal.fr.med.p.caud., tractus thalamo-frontalis medialis pars caudalis

35 Transverse section of brain of sparrow through level of pretectal nuclei and decussation of tractus infundibuli. Pyridine-silver preparation. $\times 7.5$.

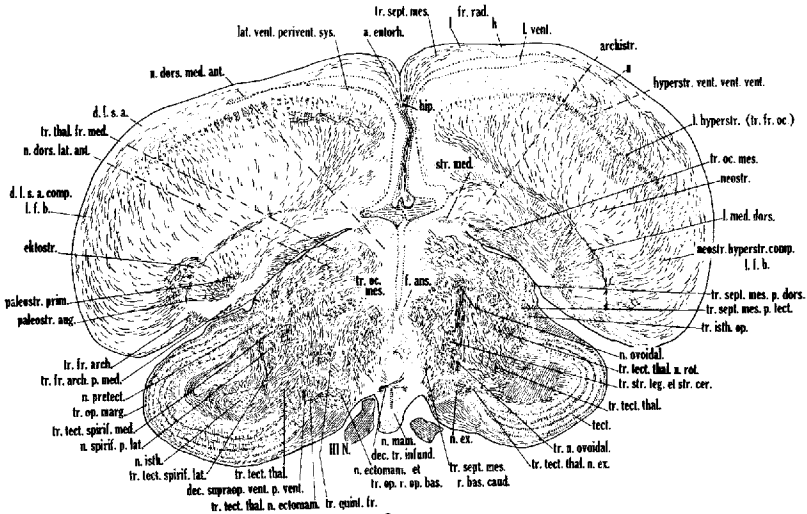
ABBREVIATIONS

a.entorh., area entorhinalis of Rose
archistr., archistriatum
d.l.s.a., dorsolateral surface area (corticoid)
d.l.s.a.comp.l.f.b., dorsolateral surface area component to lateral forebrain bundle
dec.supraop.vent.p.vent., decussatio supraoptica ventralis pars ventralis
dec.tr.infund., decussatio tractus infundibuli
ektost., ektostriatum
f.ans., fibrae ansulatae
fr.rad.h., frontal radiations from dorsolateral surface area
fr.rad.l., frontal radiations from lamina frontalis suprema
hip., hippocampus
hyperstr.vent.vent.vent., hyperstriatum ventrale ventroventrale
l.hyperstr.(tr.fr.oc.), lamina hyperstriatica (tractus fronto-occipitalis)
l.med.dors., lamina medullaris dorsalis
l.vent., lateral ventricle
lat.vent.perivent.sys., lateroventral periventricular fiber system
n., region of fusion of laminae frontalis superior et suprema
n.dors.lat.ant., nucleus dorsolateralis anterior
n.dors.med.ant., nucleus dorsomedialis anterior
n.ectomam.et tr.op.r.op.bas., nucleus ectomamillaris et tractus opticus radix opticum basale
n.ex., nucleus externus
n.isth., nucleus isthmi
n.mam., nucleus mamillaris
n.pretect., nucleus pretectalis
n.ovidal., nucleus ovoidalis
n.spirif.p.lat., nucleus spiriformis pars lateralis
neostr., neostriatum
neostr.hypostr.comp.l.f.b., neostriatal-hypostratial component to the lateral forebrain bundle

paleostr.aug., paleostriatum augmentatum
paleostr.prim., paleostriatum primitivum
str.med., stria medullaris
tecl., tectum
tr.fr.arch., tractus fronto-archistriaticus et neostriaticus
tr.fr.arch.p.med., tractus fronto-archistriaticus et neostriaticus pars medialis
tr.isth.op., tractus isthmo-opticus
tr.n.ovidal., tractus nuclei ovoidalis
tr.oc.mes., tractus occipito-mesencephalicus et bulbaris
tr.op.marg., tractus opticus marginalis
tr.quint.fr., tractus quinto-frontalis
tr.sept.mes., tractus septo-mesencephalicus
tr.sept.mes.p.dors., tractus septo-mesencephalicus pars dorsalis
tr.sept.mes.p.tecl., tractus septo-mesencephalicus pars tectalis
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.str.teg.et str.cer., tractus strio-tegmentalis et strio-cerebellaris
tr.tect.spirif.lat., tractus tecto-spiriformis lateralis
tr.tect.spirif.med., tractus tecto-spiriformis medialis
tr.tect.thal., tractus tecto-thalamicus et thalamo-tectalis
tr.tect.thal.n.ectomam., tractus tecto-thalamicus et thalamo-tectalis nuclei ectomamillaris
tr.tect.thal.n.ex., tractus tecto-thalamicus et thalamo-tectalis nuclei externi
tr.tect.thal.n.rot., tractus tecto-thalamicus et thalamo-tectalis nuclei rotundi
tr.thal.fr.med., tractus thalamo-frontalis medialis
III N., third nerve



34



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PLATE 17

EXPLANATION OF FIGURES

36 Transverse section through brain of sparrow through level of the posterior commissure. Pyridine-silver preparation. $\times 7.5$.

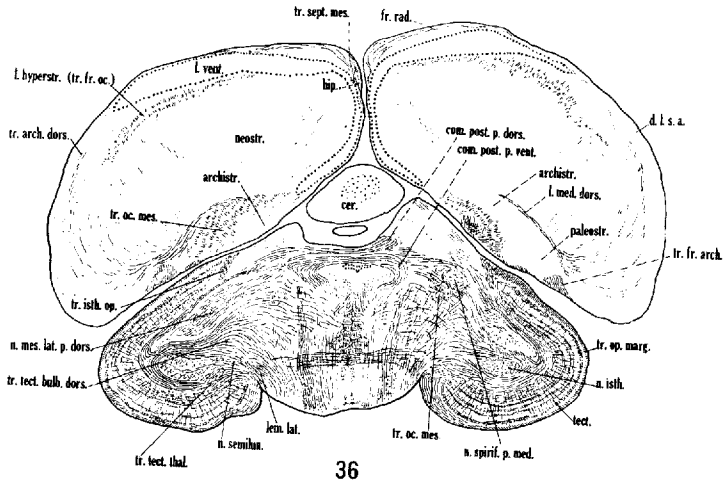
ABBREVIATIONS

<i>archistr.</i> , archistriatum	<i>n.spirif.p.med.</i> , nucleus spiriformis pars medialis
<i>cer.</i> , cerebellum	<i>neostr.</i> , neostriatum
<i>com.post.p.dors.</i> , commissura posterior pars dorsalis	<i>paleostr.</i> , paleostriatum augmentatum
<i>com.post.p.vent.</i> , commissura posterior pars ventralis	<i>tect.</i> , tectum
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>tr.arch.dors.</i> , tractus archistriaticus dorsalis
<i>fr.rad.</i> , frontal radiations	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>hip.</i> , hippocampus	<i>tr.isth.op.</i> , tractus isthmo-opticus
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>tr.oc.mes.</i> , tractus occipito-mesencephalicus et bulbaris
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>tr.op.marg.</i> , tractus opticus marginalis
<i>l.vent.</i> , lateral ventricle	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus
<i>lem.lat.</i> , lemniscus lateralis	<i>tr.tect.bulb.dors.</i> , tractus tecto-bulbaris dorsalis
<i>n.isth.</i> , nucleus isthmi	<i>tr.tect.thal.</i> , tractus tecto-thalamicus et thalamo-tectalis
<i>n.mes.lat.p.dors.</i> , nucleus mesencephalicus lateralis pars dorsalis	
<i>n.semilun.</i> , nucleus semilunaris	

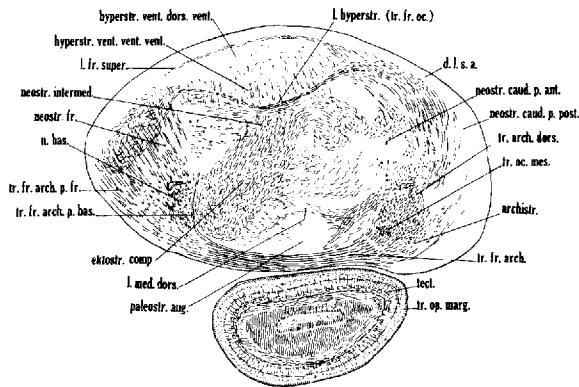
37 Sagittal section through brain of sparrow at a level including the tractus fronto-archistriaticus et neostriaticus. Pyridine-silver preparation. $\times 7.5$.

ABBREVIATIONS

<i>archistr.</i> , archistriatum	<i>neostr.caud.p.post.</i> , neostriatum caudale pars posterior
<i>d.l.s.a.</i> , dorsolateral surface area (corticoid)	<i>neostr.fr.</i> , neostriatum frontale
<i>ektostr.comp.</i> , ektostriatum with associated components	<i>neostr.intermed.</i> , neostriatum intermediale
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>paleostr.aug.</i> , paleostriatum augmentatum
<i>hyperstr.vent.vent.vent.</i> , hyperstriatum ventrale ventroventrale	<i>tect.</i> , tectum
<i>l.fr.super.</i> , lamina frontalis superior	<i>tr.arch.dors.</i> , tractus archistriaticus dorsalis
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>tr.fr.arch.</i> , tractus fronto-archistriaticus et neostriaticus
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>tr.fr.arch.p.bas.</i> , tractus fronto-archistriaticus et neostriaticus pars basalis
<i>n.bas.</i> , nucleus basalis	<i>tr.fr.arch.p.fr.</i> , tractus fronto-archistriaticus et neostriaticus pars frontalis
<i>neostr.caud.p.ant.</i> , neostriatum caudale pars anterior	<i>tr.oc.mes.</i> , tractus occipito-mesencephalicus et bulbaris
	<i>tr.op.marg.</i> , tractus opticus marginalis



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PLATE 18

EXPLANATION OF FIGURES

38 Sagittal section of brain of sparrow cut slightly lateral to the midsagittal plane. Pyridine-silver preparation. $\times 7.5$.

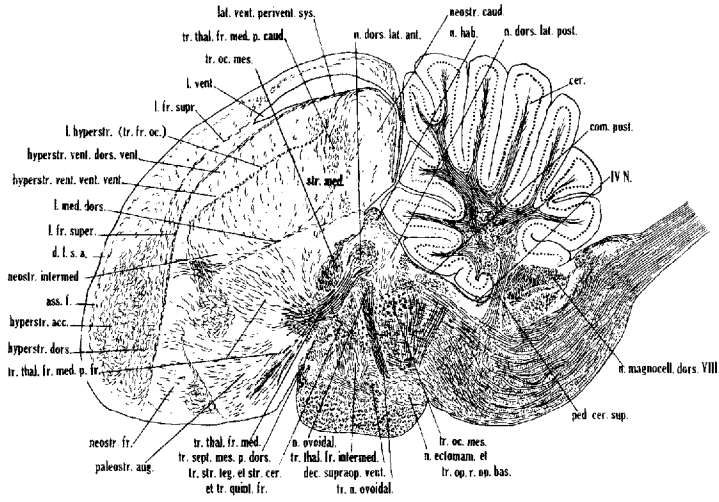
ABBREVIATIONS

<i>ass.f.</i> , association fibers	<i>n.magnocell.dors.VIII.</i> , nucleus magnocellularis dorsalis of the cochlear nerve
<i>cer.</i> , cerebellum	<i>n.ovidal.</i> , nucleus ovoidalis
<i>com.post.</i> , commissura posterior	<i>neostr.caud.</i> , neostriatum caudale
<i>d.l.s.a.</i> , dorsolateral surface area (cortico)	<i>neostr.fr.</i> , neostriatum frontale
<i>dec.supraop.vent.</i> , decussatio supraoptica ventralis	<i>neostr.intermed.</i> , neostriatum intermediale
<i>hyperstr.acc.</i> , hyperstriatum accessorium	<i>paleustr.aug.</i> , paleostriatum augmentatum
<i>hyperstr.dors.</i> , hyperstriatum dorsale	<i>ped.cer.sup.</i> , pedunculus cerebellaris superior
<i>hyperstr.vent.dors.vent.</i> , hyperstriatum ventrale dorsoventrale	<i>str.med.</i> , stria medullaris
<i>hyperstr.vent.vent.vent.</i> , hyperstriatum ventrale ventroventrale	<i>tr.n.ovidal.</i> , tractus nuclei ovoidalis
<i>l.fr.super.</i> , lamina frontalis superior	<i>tr.oc.mes.</i> , tractus occipito-mesencephalicus et bulbaris
<i>l.fr.supr.</i> , lamina frontalis suprema	<i>tr.sept.mes.p.dors.</i> , tractus septo-mesencephalicus pars dorsalis
<i>l.hyperstr.(tr.fr.oc.)</i> , lamina hyperstriatica (tractus fronto-occipitalis)	<i>tr.str.teg.et str.cer.et tr.quint.fr.</i> , tractus strio- tegmentalis et strio-cerebellaris et tractus quinto-frontalis
<i>l.med.dors.</i> , lamina medullaris dorsalis	<i>tr.thal.fr.intermed.</i> , tractus thalamo-frontalis intermedialis
<i>l.vent.</i> , lateral ventricle	<i>tr.thal.fr.med.</i> , tractus thalamo-frontalis medialis
<i>lat.vent.perivent.sys.</i> , lateroventral periventricular fiber system	<i>tr.thal.fr.med.p.caud.</i> , tractus thalamo-frontalis medialis pars caudalis
<i>n.dors.lat.ant.</i> , nucleus dorsolateralis anterior	<i>tr.thal.fr.med.p.fr.</i> , tractus thalamo-frontalis medialis pars frontalis
<i>n.dors.lat.post.</i> , nucleus dorsolateralis posterior	<i>IVN.</i> , fourth nerve
<i>n.ectomaxo.et tr.op.r.op.bas.</i> , nucleus ectomamillaris et tractus opticus radix opticum basale	
<i>n.hab.</i> , nucleus habenularis	

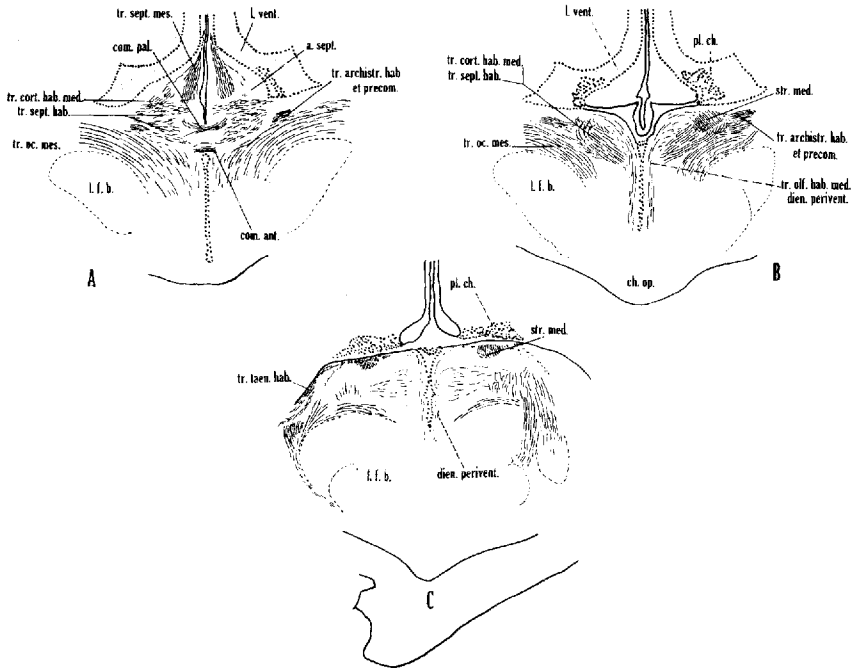
39 A series of three outline drawings (A, B, and C), from pyridine-silver preparations of the brain of dove, indicating the components of stria medullaris. $\times 7.5$.

ABBREVIATIONS

<i>a.sept.</i> , area septalis	<i>tr.archistr.hab.et precom.</i> , tractus archistriato-habenularis et precommissuralis
<i>ch.op.</i> , chiasma opticum	<i>tr.cort.hab.med.</i> , tractus cortico-habenularis medialis
<i>com.ant.</i> , commissura anterior	<i>tr.oc.mes.</i> , tractus occipito-mesencephalicus et bulbaris
<i>com.pal.</i> , commissura pallii	<i>tr.olf.hab.med.</i> , tractus olfacto-habenularis medialis
<i>dien.perivent.</i> , diencephalic periventricular fiber system	<i>tr.sept.hab.</i> , tractus septo-habenularis
<i>l.f.b.</i> , lateral forebrain bundle	<i>tr.sept.mes.</i> , tractus septo-mesencephalicus
<i>l.vent.</i> , lateral ventricle	<i>tr.taen.hab.</i> , tractus taenio-habenularis
<i>pl.ch.</i> , plexus choroideus	
<i>str.med.</i> , stria medullaris	



38



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PLATE 19

EXPLANATION OF FIGURES

40 Transverse section of brain of dove, pyridine-silver series, giving relative position of the habenulo-peduncular tracts. For details see figure 41. $\times 8$, approximately.

41 A series of four outline drawings (A, B, C, and D), from pyridine-silver preparations of the brain of dove, indicating the several components and the relations of the habenulo-peduncular system. $\times 7.5$.

ABBREVIATIONS

com.post., commissura posterior
l.f.b.vent.ped., lateral forebrain bundle ventral peduncle
n.hab.lat., nucleus habenularis lateralis
n.hab.med., nucleus habenularis medialis
n.ovidal., nucleus ovoidalis
n.rot., nucleus rotundus
n.tr.hab.ped., nucleus tractus habenulo-peduncularis
pl.ch., plexus choroidaeus

tr.hab.ped.p.lat., tractus habenulo-peduncularis pars lateralis
tr.hab.ped.p.med., tractus habenulo-peduncularis pars medialis
tr.hab.tect., tractus habenulo-tectalis
tr.infund., tractus infundibuli
tr.sept.mes.r.bas.caud., tractus septo-mesencephalicus ramus basalis caudalis
tr.n.ovidal., tractus nuclei ovoidalis
III v., third ventricle

