STUDIES OF THE VERTEBRATE TELENCEPHALON

I. THE NUCLEAR CONFIGURATION OF THE OLFACTORY AND ACCESSORY OLFACTORY FORMATIONS AND OF THE NUCLEUS OLFACTORIUS ANTERIOR OF CERTAIN REPTILES, BIRDS, AND MAMMALS

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EIGHTEEN FIGURES

INTRODUCTION

This paper is the first of a projected series of reports on the nuclear configuration and the fiber connections of the telencephalon in reptiles, birds, and mammals. It is hoped that such studies may aid in a better understanding of the morphologic pattern common to this forebrain region in all these forms, and that it may contribute somewhat to a further appreciation of some of those factors which, during the course of phylogeny, have led to modifications and variations of this common pattern resulting in the appearance of those differentiations and specializations of structure which characterize the various classes constituting these orders and in some instances individual members of these classes. Since in the course of phylogeny, the hemispheres begin their development under the influence of the olfactory system, it is fitting that studies of this type should begin with a consideration of the primary and secondary olfactory centers.

MATERIAL STUDIED

For the present study the G. Carl Huber collection was available, and was supplemented by series of the brains of the

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squirrel, mole, pig, macaque, and man prepared especially for this work on the telencephalon. The primate material was obtained through a grant from the Horace H. Rackham School of Graduate Studies of the University of Michigan, to which the authors wish to express their most sincere appreciation.

All of the material listed below is serially cut and, with the exception of a Weil series used in the study of the macaque brain, is stained in toluidin blue. Those forms in which transverse series of the brain material are available are marked with a single asterisk (*), those having transversely and sagittally cut series with a double asterisk (**), and those unmarked have material cut in all three planes. The series being employed in preparing the report on the fiber connections of these regions are not included here, although reference has been made to them in collecting the data for this paper.

The reptile series consist of preparations of the brains of turtles (Chelhydra serpentina*, Chrysemys marginata, Sternotherus odoratus**, Emys melageris*, Pseudemys elegans, and Graptemys pseudogeographica*), of snakes (Python molurus*, Natrix, Boa constrictor**, Thamnophis sirtalis, and Agkistrodon mokasen*), of crocodiles (Alligator mississippiensis), and of lizards (Phrynosoma cornutum, Anolis carolinensis, Varanus griseus*, Heloderma suspectum, and Holbrookia maculata**). The avian material includes series of the brains of a fairly wide range of birds (Passer domesticus, Platycercus**, Columba livia, Gallus domesticus, Anas domestica**, and Corvus brachyrhynchos*). From the mammalian preparations available, series of the brains of representative marsupials (Didelphis virginiana), rodents (Sciurus hudsonicus*, Mus[1]), carnivores (Mustela noveboracensis*), ungulates (Sus scrofa*), insectivores (Blarina brevicauda**, Scalopus aquaticus**), chiropteres (Tadarida mexicana), and primates (Macaca mulatta*, Homo sapiens*) were selected for study.

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[1] The mouse series were prepared from material furnished by Doctor Little and his co-workers and there is no record of the species available (see however Murray, '29, p. 313).

THE REPTILIAN OLFACTORY AND ACCESSORY OLFACTORY BULBS

General considerations

The olfactory and accessory olfactory bulbs of reptiles show a wide range in the degree of their development, depending upon the reptile considered. Thus the olfactory bulbs of various turtles and alligators are relatively large; those of certain lizards, such as Anolis, are small and poorly developed internally, but the bulbs of other lizards may show special modifications; and in snakes there is an exaggeration of the medial side of the bulb and a thinning of the lateral wall. In reptiles such as alligators and certain lizards, the bulbs are on long stalks; in other reptiles, for example snakes and turtles, they are close to the hemisphere wall. Obviously, the intrinsic differentiation of the bulb is dependent upon the richness of entering olfactory and vomeronasal impulses. In all the reptiles studied the ventricle is patent and continuous with the lateral ventricle.

Numerous figures and some descriptions of the gross relations of the olfactory bulbs are available both in texts on comparative neurology (Johnston, '06; Edinger, '08; Papez, '29; Ariëns Kappers, Huber, and Crosby, '36; and many others) and in many of the special papers dealing with reptilian forms, for example, those of Meyer (1892), de Lange '13), Crosby ('17), and Goldby ('34). It is somewhat interesting that in Rabl-Rückhard's (1878, 1894) early account the olfactory peduncle was identified as the olfactory nerve. The accessory olfactory bulbs are present in turtles, snakes, and certain lizards, but lacking in some of the lizards and in the alligators. Goldby ('34) has given an interesting illustration of the gross relations of the olfactory and accessory olfactory bulbs in the lizard (Lacerta viridis). The following descriptions of these areas may be regarded as fairly representative of the range of conditions found in reptiles.

Microscopic structure in turtles

In all the turtle material available the olfactory and accessory olfactory bulbs show a common pattern of development, although some differences in size. Except for minor variations, then, the following account of these structures in Pseudemys may be regarded as typical for the turtles available for study (p. 122; for an account of these regions in Graptemys see Crosby and Humphrey, '39, fig. 1).

The olfactory formation has been described for Cistudo carolina by Johnston ('15), who identified the vomeronasal nerve as the dorsal root of the olfactory nerve and so failed to recognize an accessory olfactory formation. In Chrysemys, however, a vomeronasal nerve was traced from the periphery to its termination in the accessory olfactory bulb by McCotter ('17).

PSEUDEMYS ELEGANS (A SLIDER OR COOTER). At the periphery of the bulb in Pseudemys (fig. 1, A and B) a layer of olfactory nerve fibers breaks up into relationship with the mitral cell dendrites to form the glomerular layer. Scattered neurons lying in relation to these synapsing fibers appear to be comparable to the periglomerular cells described for other forms. Occasionally these granule cells, together with a few displaced mitral cells (fig. 1, B), group along the inner border of the glomeruli, foreshadowing the mammalian external granular layer, but such a layer is not very sharply differentiated here (fig. 1, A and B) although somewhat more evident in sagittal than in cross sections. Internal to these neurons is the external molecular or plexiform layer, formed, in large part, of the peripherally extending dendrites both of the mitral cells and of those neurons of the internal granular layer, which, in some reptiles at least, send processes to the olfactory glomeruli. Scattered among these fibers are displaced mitral cells (fig. 1, A and B) which have wandered out from the mitral cell layer under the influence of the incoming olfactory stimuli. The mitral cell layer consists of triangularly shaped, larger neurons, two or three or more cells thick (fig. 1, A and B). Internal to this layer is the internal plexiform or molecular layer, made up largely of dendritic processes of cells of the inner granular layer and of neuraxes of mitral and granule cells, but not everywhere sharply delimited, since scattered granule cells of the type characteristic of the internal granular layer are found among its fibers. The internal granular layer (fig. 1, A and B) is formed of round or oval cell bodies of neurons, grouped in broken strands, often one cell thick, which are concentrically arranged around the ventricle. The dendrites of these neurons spread out in the internal granular layer and, in part, continue out toward the periphery of the bulb. Their neuraxes either join the olfactory tract or redischarge into the mitral cell layer.

The accessory olfactory formation of Pseudemys elegans (fig. 1, A and B) occupies the dorsal portion of the bulb and the crus and projects out to form a true accessory olfactory bulb which shows an arrangement of layers similar to that of the olfactory formation. The granular layer of the accessory olfactory bulb is merely part of the general bulbar layer and not separate from that of the olfactory formation and it disappears caudalward to give place to the secondary centers of the hemisphere (fig. 1 B). The accessory olfactory formation of Emys is illustrated in figure 8 A.

Microscopic structure in the alligator

The available material of the olfactory bulb of Alligator mississippiensis verifies the detailed study of this region by Crosby ('17; see also Ariëns Kappers, Huber, and Crosby, '36) and no further account is necessary here. In this reptile no accessory olfactory bulb has been demonstrated.

Microscopic structure in lizards and snakes

The order Squamata is made up of two suborders, the lizards (Sauria) and the serpents (Serpentes). In the lizard material (p. 122) the extremes in development of the accessory olfactory and olfactory formations are found (see also Crosby and Humphrey, '39). The grouping for description is based on the presence or absence of an accessory olfactory bulb.

Lizards with no accessory olfactory bulbs. AMERICAN CHAMELEON (ANOLIS CAROLINENSIS), SPOTTED LIZARD (HOLBROOKIA MACULATA), AND THE HORNED TOAD (PHRYNOSOMA CORNUTUM).

ABBREVIATIONS

a.prepyr., prepyriform area of Rose
ant.cont.hip., anterior continuation of hippocampus
ant.cont.pyr.lobe, anterior continuation of lobus pyriformis
b.v., blood vessel
bulb.olf., bulbus olfactorius
bulb.olf.acc., bulbus olfactorius accessorius
com.ant., commissura anterior
com.ant.,interbulb.comp., commissura anterior, interbulbar component
dors.vent.ridge, dorsal ventricular ridge
ep., ependyma
f.olf., formatio olfactoria
fil.olf., fila olfactoria
fil.vom., fila vomero-nasalis
fis.circ.rhin., fissura circularis rhinencephali
fis.endorh., fissura endorhinalis
g.cor., general cortex
hip., hippocampus
hyperstr., hyperstriatum
hyperstr.acc., hyperstriatum accessorium
hypopal., hypopallium of Elliot Smith
isl.Cal., island of Calleja
l.glom., lamina glomerularis
l.gran.ext., lamina granularis externa
l.gran.int., lamina granularis interna
l.,mit.c., layer of mitral cells
l.molec.ext., lamina molecularis or plexiformis externa
l.molec.int., lamina molecularis or plexiformis interna
l.outw.mit.c., layer of outwandered mitral cells
lob.pyr., lobus pyriformis
mit.c., mitral cell
n.ac., nucleus accumbens
n.caud., nucleus caudatus
n.olf.ant., nucleus olfactorius anterior
n.olf.ant.,p.dors., nucleus olfactorius anterior, pars dorsalis
n.olf.ant.,p.ext., nucleus olfactorius anterior, pars externa
n.olf.ant.,p.lat., nucleus olfactorius anterior, pars lateralis
n.olf.ant.,p.med., nucleus olfactorius anterior, pars medialis
n.olf.ant.,p.post., nucleus olfactorius anterior, pars posterior
n.olf.ant.,p.vent., nucleus olfactorius anterior, pars ventralis
n.olf.ant.,p.vent.(sub.), nucleus olfactorius anterior, pars ventralis subventricularis
n.olf.ant.,p.vent.(supra), nucleus olfactorius anterior, pars ventralis supraventricularis
n.sept.-hip., nucleus septo-hippocampalis
n.vom., nervus vomero-nasalis
neopal., neopallium
neostr., neostriatum
outw.mit.c., outwandered mitral cells
p.g., griseum periventriculare
paleostr., paleostriatum
sept., septum
str.alb., stratum album
tr.olf.lat., tractus olfactorius lateralis
tub.olf., tuberculum olfactorium
tub.olf.,plex.l., tuberculum olfactorium, lamina plexiformis
tub.olf.,polym.l., tuberculum olfactorium, lamina polymorphica
tub.olf.,pyram.l., tuberculum olfactorium, lamina pyramidalis or corticalis
v.lat., ventriculus lateralis
v.olf.,ventriculus olfactorius
X, indentation indicating area of fusion of the olfactory bulbs of the crow
Y, area first denuded of olfactory formation rostrocaudally

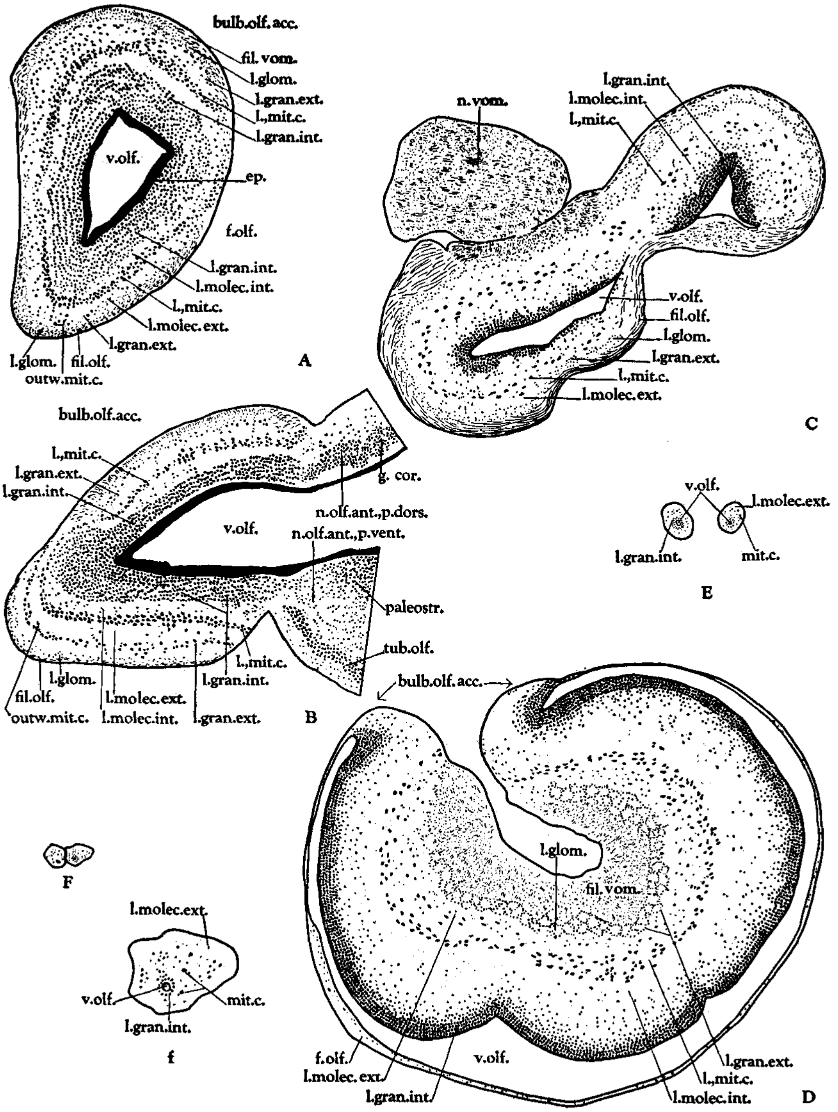

Fig. 1 Drawings illustrating the right olfactory and, if present, the right accessory olfactory formation as seen in transversely cut (A, C to F) and sagittally cut (B) sections of the brains of the turtle, Pseudemys elegans (A and B), the Gila monster, Heloderma suspectum (C and D), the horned toad, Phrynosoma cornutum (E), and the American chameleon, Anolis carolinensis (F). Toluidin blue preparations. Figures A to F are drawn at a magnification of 25 and figure f at a magnification of 100.

In Anolis the olfactory stalk is very small, with a patent ventricle, in the walls of which are a few scattered neurons constituting a forward continuation or crural representative of the nucleus olfactorius anterior. The bulb itself (fig. 1, F and f) is tiny, and shows a very primitive organization for it consists of a mass of medium sized, centrally placed neurons (a primitive lamina granularis interna) surrounded by a molecular layer in which there are occasional smaller granule cells and a few larger neurons, the representatives of the mitral cells, which do not form a distinct layer here. Outside of these is an almost cell free external molecular layer. The entering fila olfactoria do not show in this material. Figure 1 F shows this bulb at 25 magnification—that of the rest of the series— and figure 1 f at 100 magnification. With minor differences the pattern seen in Anolis is repeated in the horned toad, Phrynosoma (fig. 1 E) and in Holbrookia and a comparable organization was described in Chameleon vulgaris by Shanklin ('30). No accessory olfactory bulb has been differentiated in the material of Anolis, Holbrookia, or the horned toad, Phrynosoma.

Lizards with large accessory olfactory bulbs. GILA MONSTER (HELODERMA SUSPECTUM) AND VARANUS (VANARUS GRISEUS). In the Gila monster the cephalic end of the olfactory bulb (fig. 1 C) shows a typical olfactory formation for, beginning peripherally, there are, successively, a layer of olfactory nerve fibers, a glomerular layer, traces of an outer granular layer, an outer molecular or plexiform layer (in which are occasional out-wandered mital cells), a mitral cell layer composed of linearly arranged groups of mitral cells, an inner molecular or plexiform layer with some scattered neurons of granule type, and an inner granular layer with densely stained granule cells. These general relations are maintained for a short distance caudal to the tip of the olfactory ventricle (fig. 1 C). Soon, however, the wall thins down to a very narrow band, in which an occasional neuron may be seen except on the dorsal side, especially toward the dorsomedial angle of the bulb.

Here the typical bulbar formation is replaced by an enormous accessory olfactory bulb (fig. 1 D), having the usual layers but so large that it bulges into the ventricle, altering the ventricular outline to that of a modified crescent shape. This accessory bulb is bi- or trilobate or kidney-shaped, the marked hilus on the dorsomedial border being the place of entrance of the vomeronasal or Jacobson's nerve, the fibers of which break up in the relatively wide glomerular layer. Figure 1 D, illustrating the layers of the accessory bulb of Gila monster, shows that the mitral cell layer consists of a wide band of scattered groups of neurons and that the internal molecular layer is relatively very broad, the inner granular layer being represented chiefly by the closely packed, periventricularly placed cell bodies of granule cells bordered by more scattered cells of the type extending into the inner molecular or plexiform layer. Caudal to the accessory bulb the olfactory crus contains the anterior continuation of the anterior olfactory nucleus, and here the ventricle returns to a round or oval outline.

The toluidin blue material available of Varanus does not show the most cephalic tip of the olfactory bulb, the series beginning at planes where the accessory olfactory bulb has already invaginated the ventricle. The available silver material suggests that the relations at the anterior end of the bulb are comparable to those described for Gila monster. In planes through the accessory bulb of Varanus the relations are essentially the same as in Gila monster except that this formation is smaller, is on the medial side of the bulb (see also p. 130) with its hilus directed somewhat dorsally, and is not lobed. The outer wall of the olfactory bulb is still thinner than in Gila monster. Loewenthal (1894) gave a description of certain of the layers of the olfactory bulb in the lizard and illustrated from silver material the glomeruli and the characteristic neurons of this structure. Unger ('06) briefly described and presented figures of the olfactory formation in the Gecko. The relations of the accessory olfactory bulb were figured by Goldby ('34) in Lacerta viridis but no detailed account of this structure was given. The conditions indicated here correspond to those found in Tupinambis by Curwen ('37). However, she has regarded the portion here allocated to the accessory olfactory bulb as belonging to the olfactory formation.

The olfactory and accessory olfactory bulbs in snakes. COPPERHEAD (AGKISTRODON MOKASEN). In the copperhead (fig. 2, A and B), which will be described as representative of the snakes studied, the olfactory bulb is an elongated structure narrowing down at its point of union with the hemisphere proper. Rostral to the accessory olfactory bulb (fig. 2 A) is a typical but not highly developed olfactory formation, which shows, beginning at the periphery: a relatively few nerve fibers; a glomerular layer with periglomerular cells; an external molecular layer containing an occasional neuron, among which are displaced mitral cells; a mitral cell layer, represented by groups of very scattered neurons; an internal molecular layer and then a mass of central gray, the internal granular layer, in which the irregularly elongated ventricle appears. Behind the rostral tip of the ventricle the lateral walls become thinner and the typical arrangement of the olfactory formation (fig. 2 B) diffuse, but traces of this formation remain until, in the crus region, the anterior olfactory nucleus appears in the lateral wall. As the lateral wall thins out, the medial wall, formed by the accessory olfactory bulb, increases in size, bulging into the crescent-shaped ventricle and showing a deep hilus in which lie entering vomeronasal fascicles. This accessory olfactory bulb shows the usual arrangement, the various layers characteristic of bulbar formation being present as shown in figure 2 B. It extends caudalward into the crus region where it, too, is replaced by an anterior continuation of the nucleus olfactorius anterior.

WATER MOCCASIN (NATRIX) In the water moccasin (bulb not illustrated), in which the conditions described for the copperhead are accentuated, the olfactory and accessory olfactory formations form together a club-shaped structure. Rostrally, where only the olfactory formation is present, the

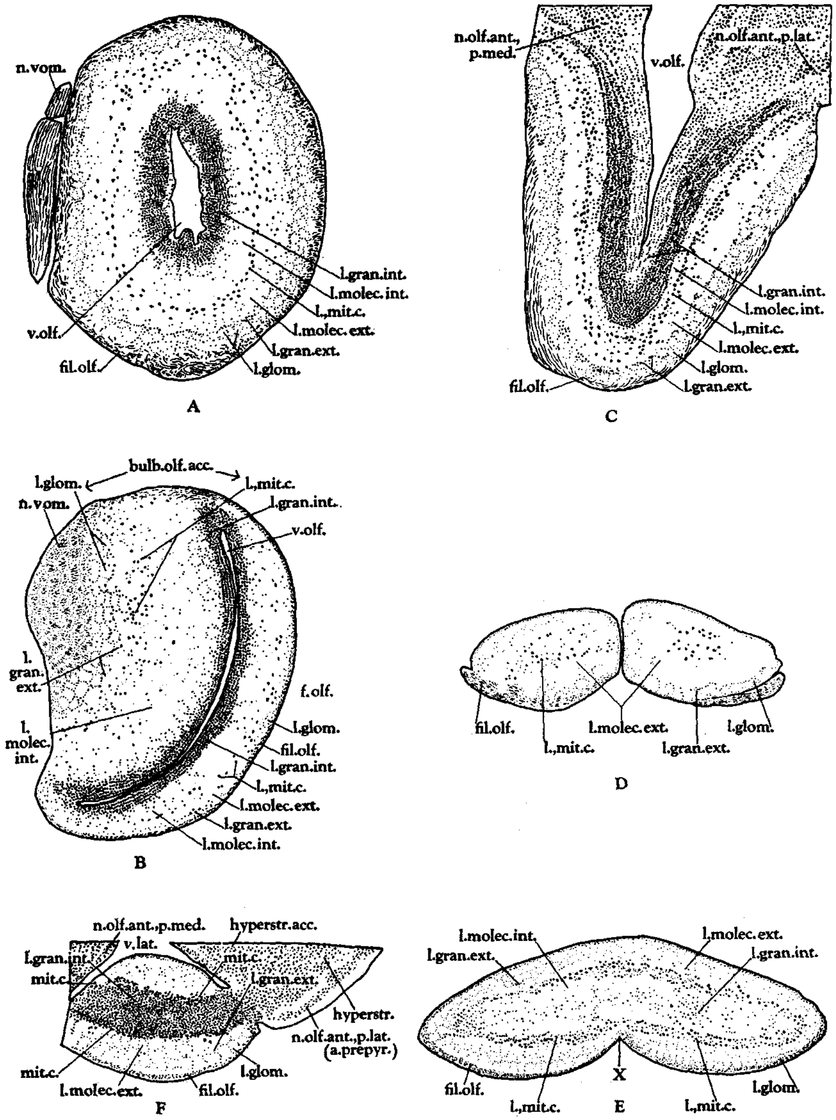

Fig. 2 A and B are drawings of transverse sections through the rostral end of the olfactory bulb (A) and through the accessory olfactory formation (B) of the copperhead, Agkistrodon mokasen. C to E are drawings of transverse sections through the right olfactory bulb (C) of the dove, Columba livia, the paired olfactory bulbs (D) and the single bulb, produced by fusion (E), of the crow, Corvus brachyrhynchos, and the single fused bulb of the adult sparrow, Passer domesticus (F), respectively. Toluidin blue preparations. × 25.

wall is relatively thin, the entering olfactory fibers are few, the glomerular layer is small with but few periglomerular neurons, the mitral cells are not organized into a definite layer but are somewhat scattered, and the inner granular layer is much decreased. Caudalward, as the frontal tip of the ventricle is reached, the olfactory formation becomes greatly reduced, being represented largely by scattered neurons which form the thin lateral, dorsolateral, and ventrolateral walls of the bulb. The greatly thickened, infolded medial side, which invaginates the crescentic ventricle, is occupied by the accessory olfactory formation, through the hilus of which enter the very numerous vomeronasal nerve fibers. In this accessory bulb (which is not figured) the granular layer is larger than in the main bulbar formation but still not highly developed, irregularly arranged mitral cells form a wide band several cells thick, the glomerular layer is broad with many associated periglomerular cells, and the entering fiber layer is relatively large.

Near the crus region, the olfactory formation is succeeded by an almost cell-free area except for a fairly wide layer of undifferentiated gray surrounding the ventricle. Although a few cells extend toward the periphery in the lateral part of the wall, there is much sharper separation between the bulbar formation and the anterior continuation of the nucleus olfactorius anterior than in most reptiles.

GARTER SNAKE (THAMNOPHIS SIRTALIS). In the garter snake (bulb not illustrated) a still further variant of the snake pattern of olfactory bulb is found. In planes through the ventricle, the wall, except dorsomedially where the accessory olfactory bulb lies, becomes exceedingly thin, carrying only a few loosely arranged cells of the olfactory formation. The accessory olfactory formation shows a wide layer of entering vomeronasal nerve fibers, a glomerular layer with periglomerular neurons, a mitral cell layer in the form of a band several cells thick from which neurons have wandered into the external molecular or plexiform layer, an internal molecular or plexiform layer containing occasional granule cells, and an internal granular layer apparently less sharply differentiated than in the other snakes studied, since, although its outer portion is made up of scattered neurons, its inner more dense band of gray contains cell bodies of both neuronic and supporting elements, which surround the ependymal wall of the ventricle. Secondary centers appear on the lateral side of the bulb in planes still cutting, on the medial side, the accessory olfactory formation.

THE AVIAN OLFACTORY BULBS

General considerations

The avian olfactory bulbs, which may be represented by a single structure or by fused or paired formations, and which show a wide range of development, have been described by various workers, among whom may be mentioned Bumm (1883), Turner (1891), Edinger, Wallenberg, and Holmes ('03), Edinger ('08), Strong ('10), Hunter ('23), Craigie ('28, '30, '32), Huber and Crosby ('29), Durward ('32), Crosby and Humphrey ('39), and many others. Descriptions of the olfactory formation in all the available series (p. 122) except that of the crow brain are to be found in the literature (Huber and Crosby, '29). As yet no accessory olfactory formation has been seen in any of our material or described in the literature for any avian form. In order to show the range of development, in the olfactory bulbs of birds, those of the dove (fig. 2 C) and the sparrow (fig. 2 F) have been refigured, but will not be further described.

Microscopic structure in birds

CROW (CORVUS BRACHYRHYNCHOS; figs. 2 D, 2 E, and 13 A). In this bird a somewhat unusual condition, intermediate between that seen in the paired olfactory bulbs of the dove and the single olfactory bulb of the sparrow (which, however, connects at each lateral border with a hemisphere) is found, for the crow has two bulbs rostralward (fig. 2 D) which unite to form a single bulbar formation (fig. 2 E) and this in turn redivides into two bulbs (fig. 13 A) just before joining each hemisphere by a short stalk, thus resembling the bulbs of the dove rostrally and caudally and that of the sparrow in its fused portion. A fusion of the two olfactory bulbs into a single enlargement has been described and figured from gross dissections (but without microscopic studies) by Strong ('10) for the white wagtail (Motacilla alba) and the serpent eagle (Cercaëtes gallicus). A very interesting condition was found by Craigie ('32) in the humming bird. Two of the series available for study showed the olfactory bulbs clearly separated; in one series they were fused. Under his account of the raven (Corvus corax), which belongs to the same family as the crow, Strong ('10) stated that "Although the crows and ravens have often been credited with a keen sense of smell, the olfactory lobes and nerves of the specimens examined were found to be surprisingly minute," and further that "In all of the Corvidae material studied, this condition prevails." Rostralward the olfactory fila enter the tip of the olfactory bulb of the crow to synapse with the relatively numerous, medium sized, triangularly shaped mitral cells, among which are interspersed a few, small granule cells. Gradually these mitral cells begin to extend medialward and, after the bulbs are fused, form a single flattened ellipse (fig. 2 E) within the single bulb (which itself shows an indentation, X, at its midline ventralward). The walls of this ellipse are formed by a rather wide band of scattered mitral cells and granule cells. Within the ellipse there are dispersed, larger and smaller granule cells, but these are few in number compared with the granule cells found in the bulbs of the other birds studied. In the crow bulb then a reverse condition to that seen in the sparrow (fig. 2 F; also Huber and Crosby, '29) is found, for in the crow a considerable number of granule cells appear to have migrated out and, by supplementing it, formed a relatively large mitral cell layer, thereby reducing the internal granular layer. In the sparrow the mitral cell layer is lacking but the granular layer is supplemented by intermingled, large mitral cells near its periphery.

In the crow, as the caudal end of the bulb is reached, a dorsal and a ventral band of mitral cells are seen rather than an ellipse, the nucleus olfactorius anterior replacing the mitral cells on each lateral border, beginning dorsalward. There is a progressive decrease of the mitral cells caudalward and, as the caudal end of the olfactory formation is approached, the dorsal and ventral bands join at the midline forming two crescent-shaped groups opening lateralward (fig. 13 A). Then the two groups separate and, with the separation, the fused mass divides into right and left portions so that, at the caudal end, for a short distance there are again two olfactory bulbs. The medial part of each bulb is occupied by olfactory formation and the lateral part by the nucleus olfactorius anterior. Almost immediately the olfactory formation disappears and the olfactory crus on each side extends back into the hemisphere carrying within it the nucleus olfactorius anterior.

THE MAMMALIAN OLFACTORY AND ACCESSORY OLFACTORY BULBS

General considerations

The mammalian, like the reptilian, olfactory and accessory olfactory bulbs show a wide range of development. Some forms—the bat, the macaque (p. 155), and man—have no accessory olfactory bulbs. In most mammals such accessory bulbs are present, although they vary in size, being tiny in the shrew, small in proportion to the olfactory formation in the pig, of moderate size in the carnivores and the opossum, and proportionately very well developed in many of the rodents.

Microscopic structure in marsupials

VIRGINIA OPOSSUM (DIDELPHIS VIRGINIANA). Among earlier observers who considered the olfactory bulbs of the opossum may be listed C. L. Herrick (1892), Ziehen (1897), Retzius (1898), Manoúelian (1899), Livini ('08), Röthig ('09), Jacob and Onelli ('11), and Johnston ('13). Gross figures of the olfactory bulbs of the Virginia opossum are to be found in various contributions to the literature, among which may be mentioned the papers of Retzius (1898), Johnston ('13), Gray ('24), and Ariëns Kappers, Huber, and Crosby ('36). The earliest account (with which the writers are familiar) of the microscopic structure of the bulb in these animals is that of C. L. Herrick (1892). This is an excellent description of the olfactory formation considering the time at which it was written. In his consideration of the olfactory bulb region of Didelphys, Ziehen drew attention to the limiting fissura rhinalis medialis (sulcus arcuatus rhinalis of Retzius, 1898). Considerably later, the microscopic structure of the olfactory formation and the accessory olfactory formation were figured for the Virginia opossum by McCotter ('12), Gray ('24), and C. Judson Herrick ('24). Gross relations of the olfactory bulb in certain South American marsupials (Didelphis azarae and Didelphis crassicaudata) are available in the atlases of Jacob and Onelli ('11, vol. 1, according to Gray, '24). Apparently, photographs of the brain, probably including the olfactory region, are to be found in volume 2 of this work by Jacob and Onelli but this volume is not available for examination. The general gross appearance of the olfactory bulb and a reference to the layers as figured for the American opossum by McCotter ('12), together with a description of the microscopic structure of the accessory olfactory formation, are to be found in the 1925 paper of Obenchain on the South American marsupial Caenolestes. The accessory olfactory bulb has been mentioned by Hines ('29), as well as Elliot Smith (1895), for Ornithorhynchus and these observers have described the olfactory bulb for this form. An early description of the Jacobson's organ in monotremes is to be found in the papers by Symington (1891) and Broom (1895). In the American opossum (figured by McCotter, '12, and Herrick, '24, and so needing no further illustration, but not described) the olfactory bulbs, which are relatively very large, are characterized, in front of the ventricle, by the following layers beginning at the periphery: a very large layer of incoming olfactory fibers; a broad glomerular layer showing both peri- and intraglomerular cells; an outer granular layer consisting of a dense accumulation of cells of the periglomerular type internal to the glomerular layers; an outer molecular or plexiform layer containing a few granule and many outwandered mitral cells, particularly toward the tip of the bulb, the major number of these latter lying near the outer granular layer; a mitral cell layer composed of some large mitral cells intermingled with many small granule cells, the mitral cells being arranged either singly or in clumps; an inner molecular or plexiform layer containing an unusually large number of granule cells, some of which are linearly arranged suggesting the lamination of the next deeper layer; and a wide inner granular layer made up of groups of granule cells, sometimes six or more neurons thick and concentrically arranged, with the inner part of the layer showing fewer cells, smaller, more rounded masses, and less evident lamination. In transverse planes through the ventricle, the layers remain the same except that a periventricular region almost free of granule cells, the internal medullary lamina, appears. On all sides of the bulb there are a great number of entering olfactory fila. Overriding these on the medial surface of the bulb is the vomeronasal nerve, which enters the accessory olfactory bulb on its dorsomedial angle and swings lateralward to reach the glomerular layer. Toward the caudal end of the bulb, fibers of the lateral olfactory tract encroach on the internal granular layer so that its fascicles are outlined by the granule cells. The pars lateralis of the nucleus olfactorius anterior then appears on the medial border of this tract, between it and the main mass of the internal medullary lamina. As the lateral olfactory tract shifts still farther toward the lateral surface of the bulb, all the outer layers disappear except the inner granular layer which now lies medial to the lateral olfactory tract, and, for a time, lateral to and somewhat intermingled with the pars lateralis of the nucleus olfactorius anterior. Behind this level the internal granular layer gradually disappears, its ventral tip being the last portion present. The olfactory formation later disappears from the lateral and dorsal, and then from the medial and ventral surfaces of the olfactory bulb, its caudal extent being greatest on the ventral surface. There it is still found in planes in which the nucleus olfactorius anterior completely encircles the olfactory ventricle, although it disappears at levels in which this ring formation is still present.

The accessory olfactory formation forms a slight eminence on the dorsomedial surface of the olfactory bulb, caudal to the olfactory formation in this region. This accessory olfactory formation, although relatively very small compared to the size of the bulb, is typical in structure but, on the whole, its layers are less well developed, particularly since its mitral cell layer encroaches on the laminae on either side, thus markedly reducing their size.

Microscopic structure in rodents

The olfactory and the accessory olfactory formations have been described in the rabbit by von Kölliker (1896), Winkler and Potter ('11), Ramón y Cajal ('11), and Young ('36); in the rat by van Gehuchten and Martin (1891), Gurdjian ('25), and Craigie ('25); in the mouse by Ramón y Cajal ('11, see fig. 428); and in the guinea pig by Ramón y Cajal ('11, see fig. 429) and by Young ('36, see fig. 18). The relative numbers of mitral and granule cells in Norway and albino rats have been studied by Leslie Smith ('28), who found that the latter animals had more mitral cells and less granule cells than did the former. A comparison of previous descriptions with our own material indicates that the accessory olfactory bulb varies from a slightly dorsomedial position in the rabbit to a distinctly laterodorsal one in the guinea pig, with the accessory bulbs in the mouse and the squirrel intermediate in position.

RED SQUIRREL (SCIURUS HUDSONICUS). The olfactory bulb of the red squirrel (fig. 3, B and C) is large and the olfactory formation relatively well developed (fig. 3, B and C, also fig. 14, A, B, C and D), with the usual layers present. The numerous olfactory fila enter as a ventromedial and a lateral division (fig. 3 B), of which the former has the greater caudal extent, reaching the end of the olfactory formation. The glomeruli are in a single layer except at the regions of entrance of the fila (fig. 3 B). Peri- and some intraglomerular cells are present and a well-developed external granular layer extends along the inner border of the glomerular layer and outward between the individual glomeruli. Among the numerous processes of the mitral and granule cells of the wide external plexiform layer there are, in addition to occasional neurogliar elements, a few granule cells and outwandered mitral cells. The latter vary from a few to a considerable number, being most numerous in planes through the accessory olfactory bulb, where they are arranged in groups (which almost form a layer) about halfway between the mitral cell layer and the external granular layer. The mitral cell layer is made up of the cell bodies of very large mitral cells (fig. 7 F), situated at its outer border, and of numerous granule cells with, of course, some supporting elements intermingled. Internal to a narrow plexiform layer is the internal granular layer which shows grouping of medium-sized and small granule cells exhibiting a somewhat imperfect concentric lamination. Between these groups are scattered granule cells, chiefly of the smaller type, and neurogliar elements are interspersed throughout the layer. Mitral cells are found occasionally in the outer border of the internal granular layer and, rarely, in its deeper portions. Their position in this layer, and sometimes in the internal molecular layer, is indicative of the trend of development, for they are specialized cells, differentiated from primitive periventricular gray, which secondarily wander out toward the source of their stimuli, the incoming olfactory fibers. The stratum album, a region of passage of the bulbo-fugal fibers, separates from the main mass of the internal granular layer, a layer of undifferentiated periventricular gray, representing a primordial portion of this lamina, which has, as yet, not migrated out to join the more differentiated portion of the internal granular layer. In this periventricular gray are neuronic and supporting elements and possibly elements which have not differentiated as yet into either cell type. The olfactory formation is replaced first dorsally by the accessory olfactory bulb (fig. 3 C), but later becomes confined to the ventromedial (fig. 14 C) and finally to the ventral part (fig. 14 D) of the bulb, in which region it extends caudalward to the main hemisphere wall.

The accessory olfactory bulb (figs. 3 C, 14 A and 14 B) in the red squirrel is proportionately not quite so large as in some of the other rodents (Crosby and Humphrey, '39; see also p. 142) although typical in structure and location. It is infolded into the olfactory formation (fig. 3 C) rather than forming a bulge on the surface, so that the layers show a concavity dorsalward. The external granular layer is somewhat less well developed than in the olfactory formation. The mitral cell layer is represented by a crescent-shaped clump of intermingled mitral and granule cells, the former resembling those of medium size in the olfactory formation, but more closely arranged and less deeply stained. The internal granular layer forms a calyx-like structure inclosing within it the other layers of the accessory olfactory bulb and, at its deepest point, extending down to the ependyma of the wide open ventricle (fig. 3 C). Only peripherally do its neurons show the clumping characteristic of this layer in the olfactory formation. The constituent elements are granule cells with a slight preponderance toward the larger type. With the appearance of the dorsal limb of the pars externa of the nucleus olfactorius anterior, the internal granular layer lies adjacent to it medialward (figs. 14 A and 14 B), a relationship which is maintained throughout the extent of this layer.

MOUSE (MUS —; see footnote, p. 122). A study of the mouse olfactory bulb (fig. 14 E) reveals many likenesses and certain differences from that of the red squirrel. On the whole the mouse bulb is relatively larger and more characteristically differentiated and usually lacks a patent ventricle in the adult, although occasionally ependymal bands or rings may be seen as in some other mammals (see pp. 151, 155). The follow-

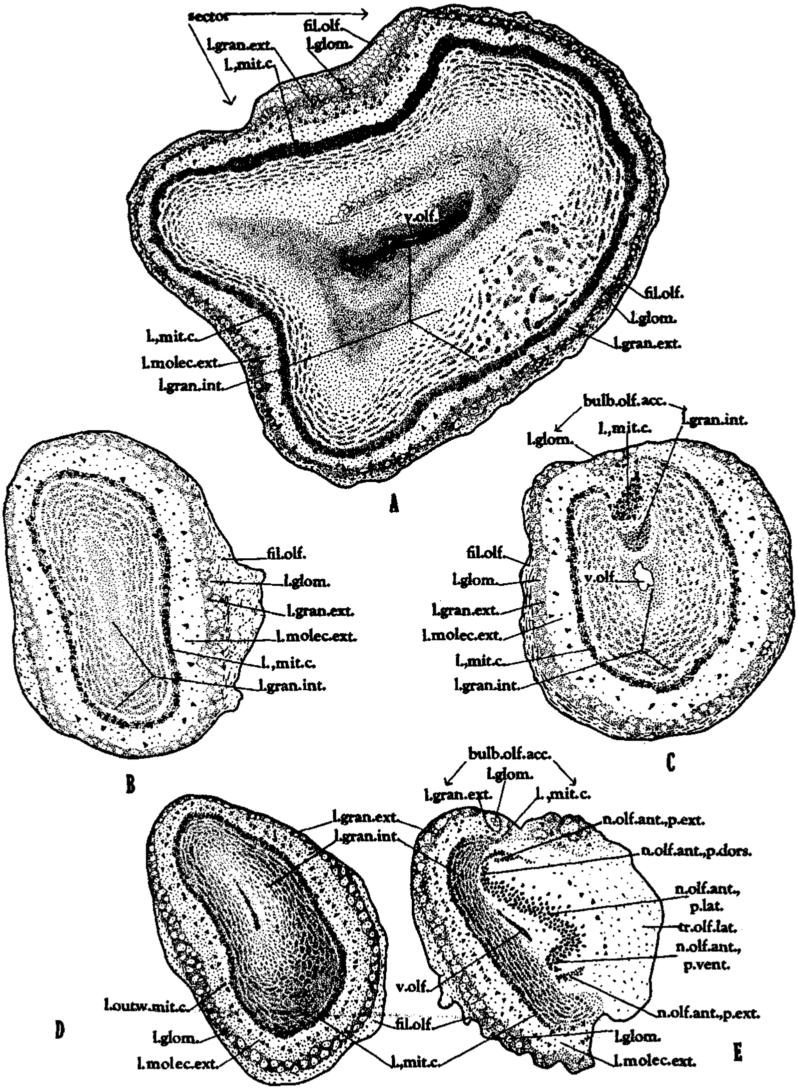

Fig. 3 Drawings of transverse sections through the olfactory formation (A) of the pig, Sus scrofa, and through the rostral end of the olfactory bulb (B) and the accessory olfactory formation (C) of the red squirrel, Sciurus hudsonicus, and illustrations of the olfactory bulb (D and E) of the short tailed shrew, Blarina brevicauda, with D drawn from sections through the rostral end of the bulb and E through the accessory olfactory formation. Toluidin blue preparations. × 12.5.

ing brief summary is intended to stress primarily those points of marked difference between these rodent bulbs. No further account is necessary since this region has been described and figured for the mouse by Ramon y Cajal ('11, see figs. 426 and 428).

In the mouse the lateral and medial (or ventromedial) divisions of the olfactory fila meet rostrally on the dorsal and ventral surfaces of the bulb, but, with the decrease in the lateral division, the medial division supplies the entire dorsal, ventral, and medial regions. In front of the plane of the accessory olfactory bulb the lateral surface becomes denuded of olfactory formation. There are many outwandered mitral cells which intermingle with the cells of the external granular layer and tend to form an outwandered mitral cell layer in many regions. This lamina in the mouse is characterized by the fairly large number of mitral cells, often in marked groups and two or even more cells thick as compared to the relatively scattered, but noticeably larger mitral cells in the squirrel. The internal granular layer shows better differentiation than in the squirrel, its periventricular, undifferentiated portion being rather small. Moreover its cells are of more uniform size and staining, and are arranged in larger and more definite clumps with a more marked concentric lamination than in the squirrel. The olfactory formation disappears first on the dorsolateral and lateral surfaces, and persists farther caudalward on the medial side of the bulb (fig. 14 E), being found at levels in which the nucleus olfactorius anterior forms a ring around the ventricle.

Although the accessory olfactory bulb of the mouse is infolded toward the ventricle as in the red squirrel, it forms an eminence on the surface for a greater portion of its extent. However, its rostral tip is more deeply implanted, being surrounded on all sides by the olfactory formation. The external granular layer is better developed than in the squirrel and the slightly less numerous mitral cells are of a similar size and type but grouped. The internal granular layer of the mouse is well developed, projecting frontally beyond the other layers of the bulb.

Microscopic structure in carnivores

Various earlier observers have reported upon the olfactory formation in carnivores; among them may be mentioned Golgi (1875), van Gehuchten and Martin (1891), Ramón y Cajal ('11), and Winkler and Potter ('14). According to Addison ('15) and others the Pinnepedia are microsmatic. A description of the olfactory and accessory olfactory bulbs of the cat is being presented by Fox ('38) in his study of the carnivore telencephalon and those interested are particularly referred to his account. Because of this recent study, only very brief consideration will be given here to these regions in the weasel.

WEASEL (MUSTELA NOVEBORACENSIS). In general the olfactory formation (fig. 4 B) of the weasel has an arrangement comparable to that described for other carnivores. There is a tendency toward sector formation similar to that mentioned for the pig (see p. 144) and dependent upon the grouping of the olfactory glomeruli around the regions of entrance of the fila olfactoria. The mitral cells are large and many of them have wandered out into the external plexiform layer, being scattered throughout its outer half particularly. In planes through the middle portion of the bulb the number of outwandered mitral cells about equals that of those remaining in the mitral cell layer, in which there are large numbers of granule cells.

In the weasel the accessory olfactory bulb forms a marked eminence on the dorsal surface of the olfactory formation and, on the whole, is poorly delimited from that formation. It has the usual arrangement of layers which are illustrated in figure 4 C.

Microscopic structure in ungulates

In his early report on the structure of the olfactory bulb as revealed by his special technique, Golgi stated that he had ungulate material but did not describe this material specifically or figure it. The gross relations of the olfactory bulb in the sheep are to be seen in the small book by Burkholder ('12), in the laboratory outline by Herrick and Crosby ('18) and in the Edinger ('08) and Ranson ('32, fig. 197) texts.

PIG (SUS SCROFA). The olfactory bulb in the newborn pig is connected with the hemisphere by a stalk and contains a patent ventricle. The olfactory formation (figs. 3 A, 4 A, 16 A and B) is very highly developed. One of the most interesting things about this bulb is the arrangement of this formation into four sectors into the middle of each of which bundles of olfactory fila enter to distribute peripherally toward the limits of the sector in diminishing amounts, so that the glomerular layer is thickened in the middle of such a subdivision and thinned out at the periphery. Such a sector is illustrated in figure 3A. Associated with this arrangement is the invagination of the mitral cell layer in the middle of each sector so that the layer takes on a crescentic shape. Such crescent-shaped invaginations are present in the dorsal and medial sectors at appropriate levels and are in the form of a deeply infolded pocket on the ventral sector (fig. 3 A) but are inevident in the lateral sector. These mitral cell invaginations are accompanied by corresponding infoldings of the internal granular layer. The olfactory fila enter at the middle of the sectors and so are particularly large ventrally and are successively less prominent dorsally and medially. The individual glomeruli, although small, are numerous and have peri- and intraglomerular cells. The neurons constituting the well-developed external granular layer border the glomeruli and extend between them. In addition to cell processes, the external molecular layer contains the cell bodies of granule cells and elongated groups of, on the whole, smaller mitral cells (fig. 7 E), which latter are particularly increased in number in the middle of each sector (fig. 3 A). The mitral cell layer is characterized by the relatively large number and the great size of many of its neurons (fig. 7 E), which, however, are variable both in shape and diameter. Such mitral elements are numerous, often arranged in groups more than one cell thick, and are interspersed with granule

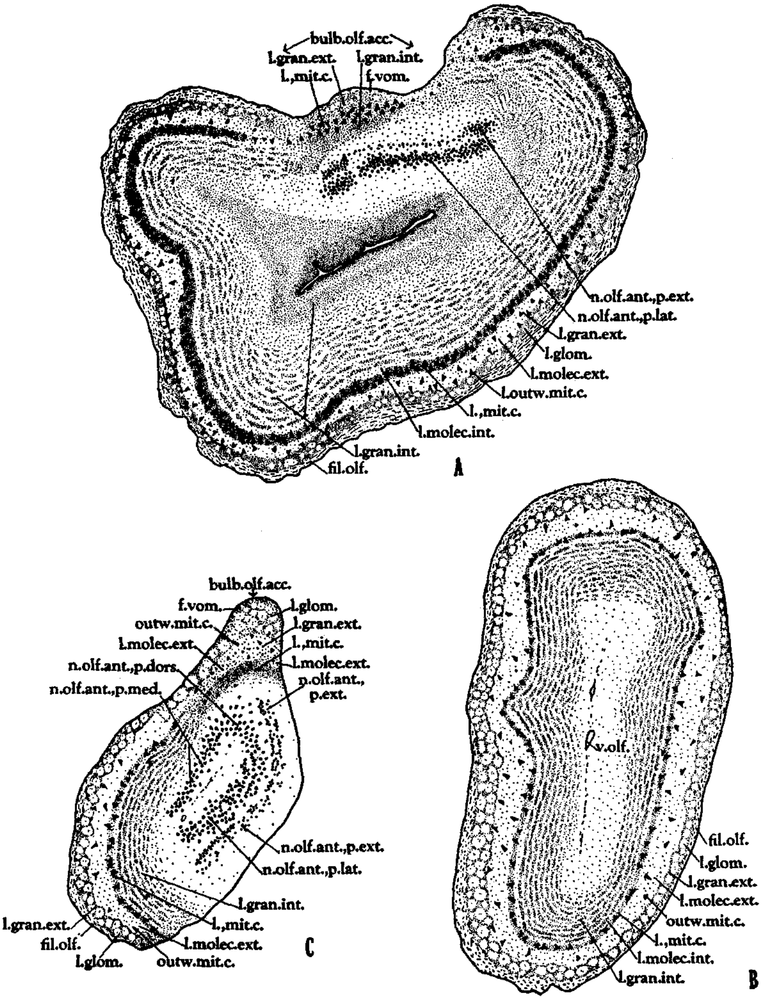

Fig. 4 Drawings of transverse sections through the olfactory bulbs of the pig, Sus scrofa (A), and of the weasel, Mustela noveboracensis (B and C). The plane of A is caudal to that of figure 3 A and B is rostral to C. Note the accessory olfactory formation and the pars lateralis and pars externa of the nucleus olfactorius anterior of the pig. These and other typical subdivisions of this nuclear complex are shown in C, in which the nucleus olfactorius anterior has almost formed a gray ring about the ventricle. Toluidin blue preparations. × 12.5

cells. The internal molecular layer is narrow. The internal granular layer is exceedingly large and shows two divisions separated by the bulbo-fugal fibers of the white layer. The outer, more differentiated portion of the internal granular layer is characterized by clumps of medium-sized granule cells (fig. 7 E) arranged in concentric rows with the cell masses toward the outside larger than in any of the other mammals studied. Among such clumps there are scattered granule cells of medium and small size. As the white layer is approached, the cell groups disappear, leaving only a continuous mass of granule cells. Through the extent of the white layer, scattered granule cells are found, and, between it and the ventricle is a mass of less differentiated, periventricular gray, varying in the density of its neurons, which represents the deeper portion of the internal granular layer. The staining of the Nissl granules in this material makes easy, even under medium power, the differentiation between the neurons and the supporting elements, which latter are found throughout the layers. The olfactory formation disappears first on the dorsal surface (fig. 4 A) and, in the denuded area thus formed, the accessory olfactory bulb makes its appearance although it never quite covers the entire area. For a considerable distance behind the accessory bulb the olfactory formation is found on the other three surfaces (fig. 16), gradually decreasing in size with the decrease in the bulb until it terminates at the caudal tip as the bulb goes over into the crus.

The accessory olfactory bulb (fig. 4 A) appears in the middle of an area denuded of olfactory formation on the dorsal side of the bulb and later shifts to a dorsomedial position contiguous with the medial olfactory formation. Although occupying a considerable frontocaudal extent, it never entirely fills this denuded area and disappears long before the crus is reached, so that in the newborn pig at least it is small in proportion to the development of the olfactory formation. It shows no tendency toward infolding but forms a slight elevation on the surface at some levels (fig. 4 A).

The vomeronasal nerve, which enters toward its caudal end, reaches it after a course along the medial and dorsomedial sides of the bulb. Such vomeronasal fibers form small but numerous glomeruli which are not well defined since the external granular layer is relatively poorly developed in the accessory bulb. The mitral cells are arranged in a band approximately parallel to the surface and, at some levels, separated from the mitral cells of the medial region of the olfactory bulb by scattered neurons. These mitral cells of the accessory formation are of the smaller and medium-sized type and are slightly less deeply stained than those of the remainder of the bulb. The band formed by them and by the few intermingled granule cells is quite wide but poorly defined, since the constituent neurons are found in the outer part of the internal granular layer. This latter layer shows none of the concentric clumping characteristic of certain portions of that lamina in the olfactory formation, but is merely a uniformly dense mass of small- and medium-sized granule cells, continuous with the homologous region of the remainder of the bulb.

Microscopic structure in insectivores

Studies of the olfactory bulbs of the mole have been made by Ganser (1882) and several observers (among whom may be mentioned Le Gros Clark, '24, '26 and '28) have illustrated the gross structure of the olfactory bulbs in Insectivora. No detailed description of the microscopic structure of the olfactory and accessory olfactory formations in the shrew has been found in the literature.

SHORT-TAILED SHREW (BLARINA BREVICAUDA). The olfactory bulb of the short-tailed shrew (figs. 3 D and E, and 17) is very similar in general type to that of the mouse. In the olfactory formation all the typical layers are present. The fila olfactoria apparently come in on all sides of the bulb, but predominantly on the medial, lateral, and ventral surfaces (fig. 3 D), where the glomeruli are often more than one layer thick. A few intra- and many periglomerular cells are present, the latter passing over into a densely packed external granular layer. The outer molecular or plexiform layer can be subdivided into external and internal portions (fig. 3D and E). The internal portion has fiber fascicles but only an occasional neuron. The external portion has, along its inner border, groups of mitral cells which form a band, wider in the region of entrance of large olfactory fila and there practically constituting an outwandered mitral cell layer (fig. 3 D and E). External to these mitral cells, and somewhat mingled with them, are granule cells which pass over into the outer granular layer. The mitral cell layer has a distinct, one-celled row of mitral cells and occasional granule cells, which latter are found also in the narrow internal molecular or plexiform layer. The internal granular layer, which consists of densely packed neurons rostrally, farther caudally shows conspicuous neuron groups with a concentric arrangement more marked peripherally than centrally, the cell groups in the latter region being smaller and the fiber bundles forming the internal white layer. As this white layer increases caudally, particularly on the lateral side, the rostral tip of the pars lateralis of the nucleus olfactorius anterior passes in front of the accessory olfactory bulb. At such levels the ventrolateral portion of the lateral olfactory tract streams out through the internal granular layer toward the ventrolateral region of the bulb and here the concentric lamination of the internal granular layer becomes less evident. After the dorsal limb of the pars externa (see p. 198) has appeared, the internal granular layer is separated from it by the pars dorsalis of the lateral olfactory tract, which tract becomes extremely large in this region. This bundle continues its encroachment on the internal granular layer until this layer disappears, at which level a few mitral cells are still found in the field (fig. 3 E). These, too, ultimately disappear and the enormously large lateral olfactory tract lies along the ventrolateral side of the bulb. The characteristic shapes and sizes of the mitral cells, the outwandered mitral cells, and the granule cells of the shrew are illustrated in figure 7 D. The olfactory formation of the dorsolateral wall, between the lateral olfactory tract and the accessory bulb, still shows olfactory glomeruli near the caudal end of the accessory bulb (fig. 3 E). The olfactory formation on the dorsomedial, medial, and ventromedial borders of the bulb remains highly developed (fig. 3 E), there being a clearly evident outwandered mitral cell layer as well as the true mitral cell layer. Followed caudalward, the olfactory formation disappears dorsally and ventrally, but persists along the medial wall of the hemisphere, until planes through the highly differentiated tuberculum olfactorium are reached (fig. 17). The so-called interbulbar component of the anterior commissure takes in general the same position and shape as in the mouse.

The accessory olfactory formation (fig. 3 E), which in the short-tailed shrew is situated along the dorsolateral surface of the olfactory bulb near its caudal end, is extremely minute (Crosby and Humphrey, '39). The entering nerve fibers form a bundle invaded at certain levels by granule cells so that the ending is in the form of one or two glomeruli in relation with which are periglomerular cells and granule cells of the external granular layer. Beneath these are scattered mitral cells intermingled with fibers, the outer part of this area probably being comparable to an invaded outer molecular layer. Internal to the mitral cells is an inner molecular layer made up of fibers contributing to the pars dorsolateralis of the lateral olfactory tract, which are joined on the ventral side by fascicles from the more medial olfactory formation. The internal granular layer is represented only by scattered granule cells. In front of this plane they increase slightly in amount, so that here, as in the mouse, the largest number of cells of the internal granular is to be found at the rostral tip of the accessory bulb. In other words, there is here a reproduction, in miniature, of the accessory olfactory bulb of the mouse. It is especially to be noted that the accessory olfactory formation in this insectivore, as in the mouse, has developed inside of the olfactory bulb rather than as an accessory lobe on its surface.

MOLE (SCALOPUS AQUATICUS). An excellent early account of the olfactory bulb of the mole (species not given) is to be found in the 1882 paper of Ganser. In this report he described the structure of both the olfactory and the accessory olfactory bulbs, calling attention to the layer arrangement and the general appearance of the constituent neurons. The material available for study documents Ganser's account. No further description is necessary here except to stress certain likenesses and differences as compared with the other insectivores considered. The mole bulb is illustrated in figure 5 A and B, and these illustrations should be compared with figures 3 D, 3 E, and 17 which picture the olfactory bulb of the shrew.

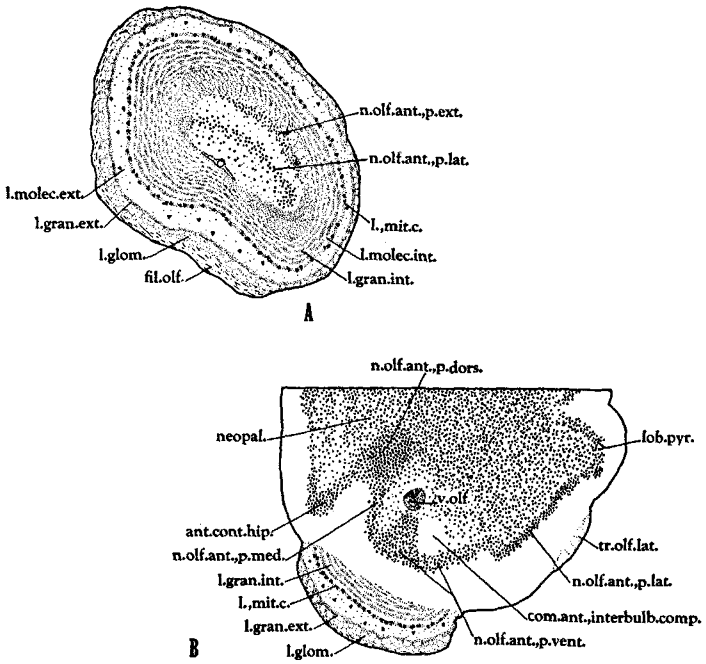

Fig. 5 Drawings of transverse sections through the more rostral (A) and the caudal (B) portions of the olfactory formation of the mole, Scalopus aquaticus. In A, intrabulbar portions, pars lateralis and pars externa, of the nucleus olfactorius anterior are clearly seen; B shows particularly the extension of pars lateralis into relation with the pyriform lobe cortex and the pars ventralis of the nucleus olfactorius anterior. Toluidin blue preparations. × 12.5.

In general the olfactory formations of the shrew and the mole bear a great resemblance to each other, both in their general shape and in their caudal extent, also in the relatively great development of the glomerular and internal and external granular layers, and in the presence of a layer of conspicuously large mitral cells. However, the outwandered mitral cells, which in the shrew are arranged in a peripheral layer, in the mole are scattered throughout the external molecular layer as far out as the external granular layer, with which some of them are intermingled without showing definite lamination. The internal molecular layer is greatly reduced in both the shrew and the mole, the mitral cell layer being developed practically within the outer border of the internal granular layer. No stratum album is present in the mole, the caudally running fibers being scattered through the internal granular layer, as Ganser found also. The olfactory ventricle is patent in the mole and contains traces of a chorioid plexus through the forward extension of the lateral ventricle.

The accessory olfactory bulb is minute in the mole, as it is in the shrew, and even less discrete. It shows even fewer mitral cells, this layer being represented by only an occasional neuron. It appears dorsally in the same position as it does in the shrew, occupying, but not completely filling, the dorsal area which has been denuded rostrally of olfactory formation.

Microscopic structure in chiropteres

FREE-TAILED BAT (TADARIDA MEXICANA). The olfactory bulb of the free-tailed bat, which has been described by Humphrey ('36) and is illustrated in figure 6 A and certain of its cellular constituents in figure 7 C, resembles that of the mouse and the shrew, in arrangement of the olfactory formation itself and in the lack of a patent olfactory ventricle, but is actually and relatively much smaller. In the ventrolateral portion of the bulb, at some levels there is a suggestion of an outwandered mitral cell layer, but the cells are less numerous and the band is not so well developed as in the shrew. There is no accessory olfactory formation in the bat, but its position is suggested by an area denuded of olfactory formation (Y on fig. 6 A) found in the dorsal region of the bulb, toward its caudal end.

Microscopic structure in primates

In general, in the primates available for study, the olfactory formation is less well developed than in many subprimates and the accessory olfactory bulb is absent or exceedingly small. No embryonic material has been available for study. Any text in neuroanatomy or gross anatomy shows the relations in human material and various special papers, even, in some cases, those dealing primarily with other brain regions, show the size, position, and shape of the bulb in a fairly wide range of primates (for example, see Woollard, '24; Le Gros Clark, '31 and elsewhere, and Ariëns Kappers, Huber and Crosby, '36). The microscopic structure of the bulb has been figured for Microcebus by Le Gros Clark ('31). The minute structure of the bulb in other primates has also received consideration by various observers (Le Gros Clark, '31, for Microcebus; Crosby and Humphrey, '39, for the macaque; Humphrey and Crosby, '38, for man; and others).

MACAQUE (MACACA MULATTA). The macaque olfactory bulb is small, club-shaped, with a fairly long stalk. Microscopic examination shows that the olfactory fibers enter around its tip and then separate into two major subdivisions, a ventromedial and a lateral, with the ventromedial distributing to the whole medial surface. Rostralward, the olfactory formation may be divided into medial and lateral subdivisions with the greater distribution of fibers in the middle of each sector and a thinning out at the ventral and dorsal (fig. 6 B) surfaces of the bulb. Slightly more caudalward the ventromedial and lateral subdivisions fail to meet dorsally and an area denuded of olfactory formation appears in this region and steadily increases in its extent on the dorsomedial surface. As this denuded area (Y of figure 6 C) appears, it apparently usually contains no indication of an accessory olfactory for-

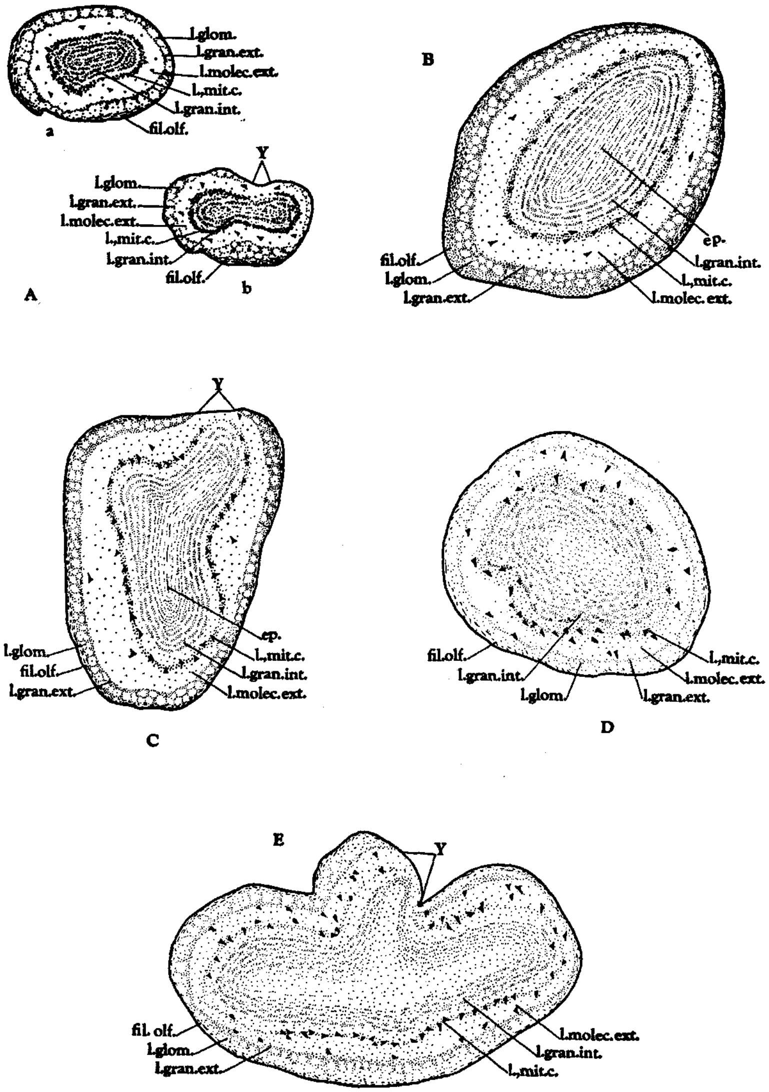

Fig. 6 Drawings of transverse sections through the right olfactory bulbs of the bat, Tadarida mexicana (A), the macaque, Macaca mulatta (B and C), and adult man (D and E). In each form the more rostral regions of the bulb (Aa, B, and D) and more caudal levels (Ab, C, and D), through the area (Y) first denuded of olfactory formation, are illustrated. Occasionally a minute accessory olfactory bulb makes its appearance within the denuded area of the macaque. Such a condition is illustrated in figure 18 A, with which C should be compared. Toluidin blue preparations. × 12.5.

mation such as was found in a comparable region in the pig, but may have a vestigial accessory olfactory bulb (see p. 155). As the crus is approached an eminence containing olfactory tract fibers and cells of the nucleus olfactorius anterior is found on the dorsomedial surface. Shortly after the appearance of this denuded area, the olfactory formation on the medial surface of the bulb shows two sectors with special olfactory bundles from the ventromedial division entering each portion, although on the lateral surface a single sector remains (fig. 6 C). These sectors are retained for a considerable distance and then the more dorsomedial one disappears. At about the same time the dorsal part of the lateral field begins to lose its olfactory glomeruli (fig. 6 C). Caudal to this level there is a gradual diminution of olfactory fibers and glomeruli, particularly along the lateral border of the bulb (fig. 18 A), and, as the crus is approached, they disappear first on the lateral and then on the ventral side, persisting on the ventromedial surface (fig. 18 B) to the caudal pole of the bulb. The glomeruli vary from small to medium size and tend to be more than one layer thick in the middle of the sectors and to thin out to one layer at the extremes. Certain characteristic features of the macaque bulb will be mentioned. Occasional intra- and periglomerular cells are seen and a not very highly developed external granular layer, with granule cells and a rare outwandered mitral cell, borders the glomeruli. The outer molecular layer contains some granule cells and either single outwandered mitral cells or, rarely, clusters of these but never enough to suggest an outwandered mitral cell layer (see pp. 142, 148). The mitral cell layer consists of groups of cell bodies of relatively large mitral neurons (fig. 7 B) interspersed with the smaller cell bodies of granule cells, the two together forming a row parallel to the glomerular layer, so that where the sectors are most prominent, the layer is crescent-shaped with the concavity toward the entering nerve fibers. The internal granular layer consists of rows of neurons, concentrically arranged and frequently only one cell thick, which are separated from each other by almost cell-free areas. These encircle a relatively acellular region in which the fibers collect about the ependymal vestiges of the ventricle.

In one of the young macaque brains available, the left olfactory bulb shows, in the dorsolateral part of the area first denuded of olfactory formation, a miniature accessory olfac-

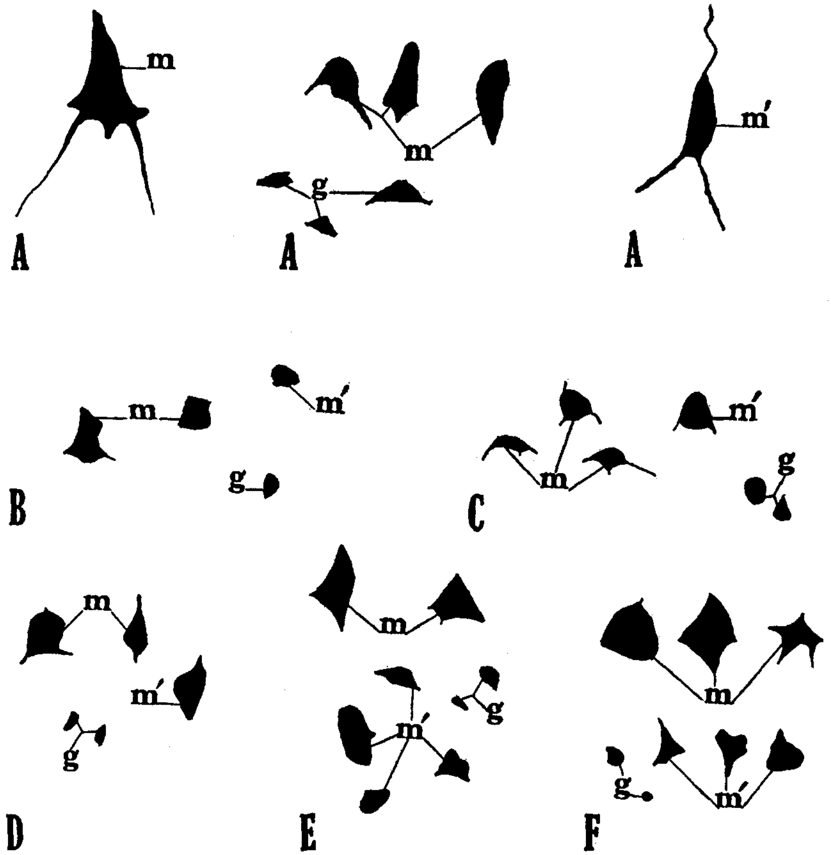

Fig. 7 Camera lucida drawings of the mitral cells from the mitral cell layer (m), outwandered mitral cells (m′) and granule cells (g) from the internal granular layer of human (A), macaque (B), free-tailed bat (C), short-tailed shrew (D), pig (E), and red squirrel (F), olfactory bulbs. In all these bulbs differences in the planes in which the individual neurons are cut and variations in size make the range in diameter and shape rather great. Toluidin blue preparations. × 335.

tory bulb (fig. 18 A). This accessory olfactory formation is still smaller than that described for the shrew but forms a tiny eminence on the surface of the olfactory bulb instead of being folded into the underlying area. In a plane through its best developed portion, the macaque accessory bulb has two or three glomeruli, fairly numerous external granule cells, three or four small mitral cells, and an internal granular layer connected by scattered neurons with the corresponding layer of the olfactory formation. Neither the right olfactory bulb of the same macaque nor either bulb of the other macaque brains studied showed this accessory olfactory formation. Not enough macaque material has as yet been prepared to permit any estimate of the frequency with which such an accessory olfactory bulb is present. It is our opinion that such a structure is infrequent, and is possibly more often present in younger than older animals, but these statements need further documentation. It is of interest that in man Jacobson's organ and a vomeronasal nerve have been found in the embryo (McCotter, '15) and not in the adult. It would seem that accessory olfactory bulbs are going out of fashion in primates.

MAN (HOMO SAPIENS). The human olfactory bulb has been described in a recent paper by the present authors (Humphrey and Crosby, '38), and the description will not be repeated. Certain points in that description which are of value for the general discussion will be enumerated here. The olfactory formation is poorly developed in man, the number of entering olfactory fibers being small (consequently the glomeruli being relatively reduced) and the cellular elements within the bulb comparatively less in number than those found in the macaque (compare figures 6 B and C, and 18 A and B, of the macaque bulb with figures 6 D and E, of the human bulb). Nevertheless, all the layers typical of the olfactory bulb of mammals are represented in man (see above quoted figures) and the fewness in number of the mitral cells is compensated for in part by their unusually great size (fig. 7 A) and in part by the exceptional number of outwandered mitral cells. The internal granular layer is reduced and, on the whole, not very well differentiated. Its granule cells are shown, drawn to scale, in figure 7 A. In the position on figure 6 E at 'Y,' an area denuded of olfactory formation is found in the region in which the accessory olfactory bulb makes its appearance in forms such as the pig, and rarely in the macaque (see p. 155), but no accessory olfactory bulb has been found in our adult human material (see p. 156). The presence of a vomeronasal nerve in a 6-months human embryo (McCotter, '15) and occasional vestiges of the vomeronasal in the adult (Piersol, '30) suggest the presence of such an accessory olfactory bulb in man during embryonic life, a point which needs substantiation.

THE REPTILIAN NUCLEUS OLFACTORIUS ANTERIOR

General considerations

The nucleus olfactorius anterior has representation, but shows a wide range in degree of differentiation, in all of the reptilian brains thus far considered. Various descriptions of portions of this nucleus are to be found in the literature based on various reptilian forms, but most of them have included only a portion of the gray of the crus under this term. To this statement the brief description of Goldby ('34) is an exception (see p. 164). In the following account this more or less undifferentiated gray has been studied in the light of its mammalian homologies and a terminology employed directly comparable to that used by students of the mammalian nucleus olfactorius anterior.

Microscopic structure in turtles

Although in all the turtles available for study the nucleus olfactorius anterior exhibits a more or less common pattern, there are sufficient variations to necessitate a description of this nucleus in more than one form.

The pond and land turtles (*Testudinidae*). EMYS MELAGERIS. In Emys melageris the mitral cell layer of the olfactory formation disappears first in the ventral half of the bulb, the thinning out occurring gradually and the region being replaced by scattered cells, particularly ventromedially. This diminution of the mitral cell layer is accompanied by a corresponding disappearance of the typical arrangement in the granular layer, which is replaced by the scattered undifferentiated gray of the crural portion of the nucleus olfactorius anterior, which can be separated into various parts only on the basis of positional relationships. In planes through the accessory olfactory formation (fig. 8 A) the granule cells have disappeared except at the dorsal pole of the ventricle. At these levels a heavily stained and closely packed group of cells appears ventrolaterally at the border of the undifferentiated nucleus olfactorius anterior to form a differentiated pars lateralis of this nucleus (fig. 8 A). The only indication of a pars externa is furnished by some scattered cells occasionally found lateral to the pars lateralis. Behind the accessory olfactory bulb the nucleus olfactorius anterior forms a ring around the ventricle. Then the differentiated pars lateralis becomes continuous caudalward with the pyriform lobe formation; a pars dorsalis differentiates in the dorsal portion of the nucleus olfactorius anterior but is soon replaced by the anterior continuation of the general cortex; the medial undifferentiated portion, which consists of scattered cells, disappears to give way to the anterior continuation of the hippocampus dorsally and the septal region ventrally; and the ventral undifferentiated gray of the nucleus olfactorius anterior is substituted for by the paleostriatum dorsally and then the tuberculum olfactorium ventrally.

Likeness in relations permits the homologizing of the pars lateralis of the reptilian nucleus olfactorius anterior with the similarly termed region in mammals. However, this pars lateralis (fig. 8, A and B) is often spoken of in the reptilian brain as the anterior continuation of the pyriform lobe (in mammals as the prepyriform area), and this designation actually gives its relations in these forms, for it passes over gradually into the wider, less closely packed band of gray generally recognized as the pyriform lobe cortex (fig. 8 B). Such transition has begun to take place in front of the tuberculum olfactorium and the pars lateralis has disappeared

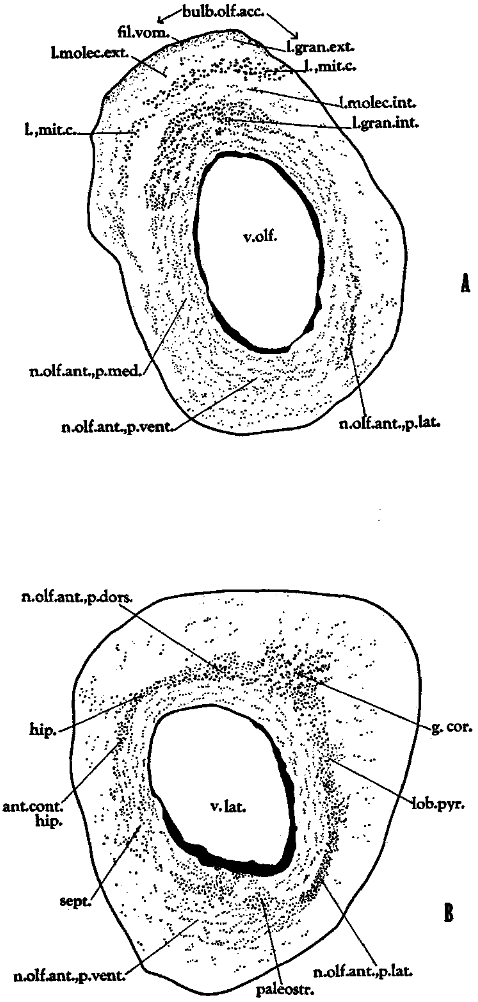

Fig. 8 Drawings of transverse sections of the brain of the turtle, Emys melageris, through the accessory olfactory formation and the rostral portions of the nucleus olfactorius anterior (A), and through the frontal end of the hemisphere caudal to the attachment of the olfactory bulb (B). Both figures illustrate particularly the positions and relations of the nucleus olfactorius anterior. Toluidin blue preparations. × 25.

before the caudal border of the tuberculum is reached. Among the neurons of the pars lateralis are occasional pyramidal cells.

The pars dorsalis (fig. 8 B) consists of a band of gray dorsal to the ventricle and continuous on either side with the pars medialis and the pars lateralis respectively. This area extends for a short distance in the crus as the dorsal part of the undifferentiated nucleus olfactorius anterior and back into the hemisphere but is replaced rather quickly by the general cortex (fig. 8 B).

The pars medialis (fig. 8 A) of the nucleus olfactorius anterior is replaced dorsally by the anterior end of the hippocampus, and, below the hippocampus, by the nucleus septohippocampalis (Ariëns Kappers, Huber and Crosby, '36; Young, '36) and the septal region proper. This replacement has taken place near the cephalic tip of the tuberculum olfactorium.

The nucleus olfactorius anterior pars ventralis (fig. 8, A and B), which is better developed in the crus region than is either the pars medialis or the pars dorsalis, is gradually replaced by the deep layer of the tuberculum olfactorium at levels in which the hemisphere begins to widen out. The transition is indicated by the grouping of cells into nests of deeper staining neurons and by the gradual appearance of an outer cortical layer. The more periventricular portion of this pars ventralis, especially laterally, is directly continuous with the rostral tip of the paleostriatum, which begins to form a slight indentation in the ventral ventricular floor in planes near the cephalic pole of the tuberculum olfactorium (fig. 8 B).

PSEUDEMYS ELEGANS. In Pseudemys elegans the relations of the various portions of the nucleus olfactorius anterior are essentially the same as those described for this gray mass in Emys melageris. Consequently only certain differences need be considered here, first among which is the greater size of the pars lateralis of the nucleus olfactorius anterior in Pseudemys, in which it forms a wider, longer band encircling almost a quarter of the bulb laterally at some levels and continues caudalward into the pyriform lobe cortex proper through a narrowed transitional zone of faintly staining cells. The pars dorsalis (fig. 1 B) and the pars medialis show essentially the same relations in Pseudemys as in Emys. The pars ventralis (fig. 1 B) is replaced far forward in the former reptile by the tuberculum olfactorium, the cortical layer of which appears in planes through the accessory olfactory bulb and the anterior part of the pars lateralis, and before the inner portion of the tuberculum olfactorium, with which the nucleus olfactorius anterior pars ventralis is continuous, can be definitely separated from the paleostriatal area.

GRAPTEMYS PSEUDOGEOGRAPHICA (THE FALSE MAP TURTLE). In this turtle the nucleus olfactorius anterior shows the same subdivisions and the same essential relations as those seen in Pseudemys elegans. The nuclei are so alike in these two turtles that no further description or illustrations need be given.

CHRYSEMYS MARGINATA. The relations in Chrysemys are again essentially the same as those in Emys. The olfactory bulb is larger in the former turtle, but, in the material available, the pars lateralis is less easily differentiated, since its cells are neither quite so closely packed nor so deeply stained. Consequently it is even more difficult to delimit distinctly the caudal border of the pars ventralis since this portion grades over directly into the rostral end of the paleostriatum and the deeper portion of the tuberculum olfactorium. In better stained material it might be possible to delimit the nucleus olfactorius anterior more sharply, but the preparations available are sufficiently good to indicate that the pattern is that common to the family Testudinidae, of which Chrysemys is a member.

The snapping turtles (*Chelydridae*). CHELYDRA SERPENTINA. In the common snapping turtle, Chelydra, essentially the same relations as those described for the Testudinidae can be demonstrated.

Box turtles (*Kinosternidae*). STERNOTHERUS ODORATUS. In one of the box turtles, the musk turtle, Sternotherus odoratus, the pattern common to the other turtles studied is repeated but with certain slight variations, which are of some interest. In this animal the pars lateralis of the nucleus olfactorius anterior is, in every sense, an anterior continuation of the pyriform lobe cortex, distinguishable from this cortex only by the darker staining and slightly more dense arrangement of its cells. The tuberculum olfactorium extends slightly farther forward than in Emys as does the rostral tip of the paleostriatum. In other words, the differentiation has proceeded slightly farther in Sternotherus than in Emys. The pyriform lobe cortex proper, which appears at the dorsal tip of the pars lateralis, and the anterior end of the general cortex, which replaces the nucleus olfactorius anterior pars dorsalis, are found at about the same level as is the rostral tip of the tuberculum olfactorium. At this level larger cells infiltrated among the characteristic neurons of the dorsal part of the nucleus olfactorius anterior pars medialis mark the cephalic end of the hippocampus. Ventral to the hippocampus is a mass of scattered neurons which represents the replacement of a part of the nucleus olfactorius anterior pars medialis by the cephalic end of the septum, the septo-hippocampal nucleus. As in all the other turtles studied, the nucleus olfactorius anterior completely encircles the ventricle in the crus region.

Microscopic structure in the alligator

As the olfactory formation disappears in the bulb of the alligator, Alligator mississippiensis, in the dorsolateral and dorsomedial walls the cortex-like bands of the anterior end of the hippocampal and pyriform lobe cortex are seen. These consist of closely arranged dark staining neurons, the hippocampal portion representing the anterior continuation of the pars dorsomedialis hippocampi and the lateral portion representing the anterior continuation of the pyriform lobe cortex. From its position this latter corresponds to the pars lateralis of the nucleus olfactorius anterior in the crus region and the ventromedial portion of the olfactory lobe, but shows a greater resemblance to the pyriform lobe cortex than in some of the other reptiles studied. Ventral to the anterior continuation of the hippocampus, in the medial wall of the hemisphere, is the small patch of undifferentiated gray which almost immediately goes over into the nucleus septohippocampalis (or primordium hippocampi of Johnston, '13, and Crosby, '17). Aside from this there is no gray which could be called undifferentiated gray in the dorsal part of the crus in this form. As the olfactory formation disappears from the ventral half of the crus it is replaced by the pars ventralis of the nucleus olfactorius anterior to which earlier observers (Herrick, '10; Crosby, '17, and others) have restricted the name of nucleus olfactorius anterior. This pars ventralis can be followed caudalward into the olfactory lobe where it lies in intimate relation with the paleostriatum and becomes continuous with the deep portion of the tuberculum olfactorium. It is evident that differentiation has progressed farther forward in the alligator than in many reptiles into the region usually occupied by the dorsomedial and dorsolateral portions of the nucleus olfactorius anterior. The relations described here are essentially those given by Crosby ('17, figs. 3, 4, and 5, and Ariëns Kappers, Huber, and Crosby, '36, fig. 573 A) for this reptile and so are not illustrated again but are summarized as a basis for a comparison with other reptilian forms.

In Sphenodon (Cairney, '26) a relation resembling in certain respects that found in the alligator appears to exist, since it has been found that the hippocampal cortex extends forward to the base of the peduncle but that the rostral pyriform gray and the cephalic end of the striatal complex grade over into the undifferentiated gray at the base of the peduncle which corresponds to the nucleus olfactorius anterior of the earlier accounts of the alligator brain. This nucleus does not appear to have been studied either by Hines ('23) or by Durward ('30), unless it is included in the cephalic end of Durward's olfacto-striatum, of which homology there is some uncertainty.

Microscopic structure in lizards

Kuhlenbeck's ('24) area ventralis anterior (as seen for example in his figure 18 of Lacerta) appears to include both the tuberculum olfactorium and the nucleus olfactorius anterior of most workers on reptilian brains. (For his views on the homologies in birds see p. 183). A very interesting but brief account of the nucleus olfactorius anterior is that of Goldby ('34), who found in the lizard, Lacerta viridis, relations of this gray comparable to those given by Herrick ('24) for the marsupial on the one hand and by Crosby ('17) for the alligator on the other, but with such variations as were to be expected from the forms considered. He stated with regard to this nucleus in the alligator that "it is possible that here is a nucleus olfactorius anterior which differs from that in Lacerta only in its degree of differentiation" and this expresses the opinions of the present writers very well. Goldby stressed that in Lacerta this gray formed a characteristic ring around the ventricle, was easily separable from the anterior extension of the hippocampus and was not sharply separable from the forward continuation of the pyriform lobe.

An anterior olfactory nucleus has been labelled in only a single figure (fig. 1) of Shanklin's paper ('30) on Chameleon vulgaris. No description is given other than to state it "is found in its usual place at the rostral end of the hemisphere."

For purposes of comparison the lizard material may be divided here into the same groups used in the description of the olfactory bulb, that is, into lizards having no accessory olfactory formation and those having large accessory olfactory bulbs. As characteristic of the first group the nucleus olfactorius anterior of Anolis and of the horned toad, Phrynosoma, will be described, and for the second group that of the Gila monster and Varanus.

Lizards with no accessory olfactory bulbs. AMERICAN CHAMELEON (ANOLIS CAROLINENSIS). In Anolis, surrounding the very minute olfactory crus in the region behind the bulbar formation, are scattered cells which represent the anterior portion of the nucleus olfactorius anterior. These cells are not sharply separated either as to type or as to subdivisions from the granular layer of the bulb, but in the crus represent a very poorly developed nucleus olfactorius anterior which characteristically encircles the ventricle (fig. 9 A). In the region where the crus joins the base of the hemisphere, a pars ventralis of the nucleus olfactorius anterior (fig. 9 B) appears ventromedially. This pars ventralis lies in relation dorsally with the ventral portion of the paleostriatum, although more sharply separated from it in cell character than is usual in many reptilian forms, the neurons of the pars ventralis being slightly smaller and more closely packed than those of the paleostriatum (fig. 9 B). This pars ventralis is bounded caudally by scattered neurons of the rostral part of the very poorly developed tuberculum olfactorium (fig. 9 C). In spite of differences in degree of development of this nucleus and its associated structures the relations follow the pattern common to reptiles. On the lateral border of the pars ventralis, essentially continuous with it, is a band of cells, relatively wide in some regions and showing a minimal appearance of cortex-like pattern, which corresponds to the pars lateralis of the nucleus olfactorius anterior (fig. 9, A to E). It extends for a considerable distance along the ventrolateral surface of the hemisphere coming into relationship with the region usually occupied by the pyriform lobe. The dorsal part of pars medialis of the nucleus olfactorius anterior is continuous with the anterior continuation of the hippocampus (fig. 9, A to C) and its more ventral portion is replaced by the septum. The scattered cells of the pars dorsalis (fig. 9 B) swing dorsalward and frontalward and border by occasional cells on the general cortex and the hypopallium but show no particular relation to them in the material available. Shanklin ('30) labeled an area as nucleus olfactorius anterior in his study of Chameleon vulgaris. However, he has given no account of this nuclear mass.

HORNED TOAD (PHRYNOSOMA CORNUTUM). In the horned toad the relations described for Anolis are repeated with certain additions and modifications. Primarily evident among such modifications is the presence of a somewhat better developed cephalic portion of the tuberculum olfactorium (fig. 9 F), the deep layer of which is directly continuous forward with the pars ventralis of the nucleus olfactorius anterior. This pars ventralis, which begins in the crus as scattered cells and increases in size when the lobar portions of the hemisphere are reached, lies ventral to, and at all levels not sharply delimited from, the ventral portion of the paleostriatum and the nucleus accumbens. It must be emphasized that there is less cellular differentiation from the surrounding region and the boundary of the nucleus is less clear than in Anolis. The pars lateralis (fig. 9 F) extends forward into the crus region of the olfactory bulb, beginning as scattered cells which form a rather more distinctly cortex-like band than in Anolis but lie in the same relation, occupying a peripheral position along the ventrolateral surface of the hemisphere at levels behind the bulb (fig. 9 F) and continuous dorsolaterally with the pyriform cortex, of which they may be considered an anterior continuation. The pars medialis, which is also slightly better developed than in Anolis, is continuous caudally with the septal region (fig. 9 F) and dorsomedially with the hippocampus. The pars dorsalis is better developed, or at least more easily delimited in the material of horned toad, than in that of Anolis, and extends caudally and dorsally ultimately to be replaced by the general cortex as it is in turtles. In general the nucleus olfactorius anterior is somewhat better developed in the horned toad than in Anolis, and this is evident even in the bulb in which the number of cells is slightly increased and the ring around the ventricle consequently more evident. Even so, such bulbar representation is extremely small.

Lizards with large accessory olfactory bulbs. GILA MONSTER (HELODERMA SUSPECTUM). Conditions quite different from those described in Anolis are found in Gila monster, in which an enormous accessory olfactory bulb greatly distorts the pattern. At levels through the middle of this accessory formation, the nucleus olfactorius anterior already has representation in an exceedingly few, scattered cells in the thinwalled medial portion of the bulb. These cells are slightly more numerous dorsally and ventrally, in which regions they lie in relation with the accessory olfactory bulb. Behind the accessory bulb, the cells in the medial and ventromedial areas have increased and the portions of the nucleus olfactorius anterior lateral and dorsolateral to the ventricle begin to make their appearance.

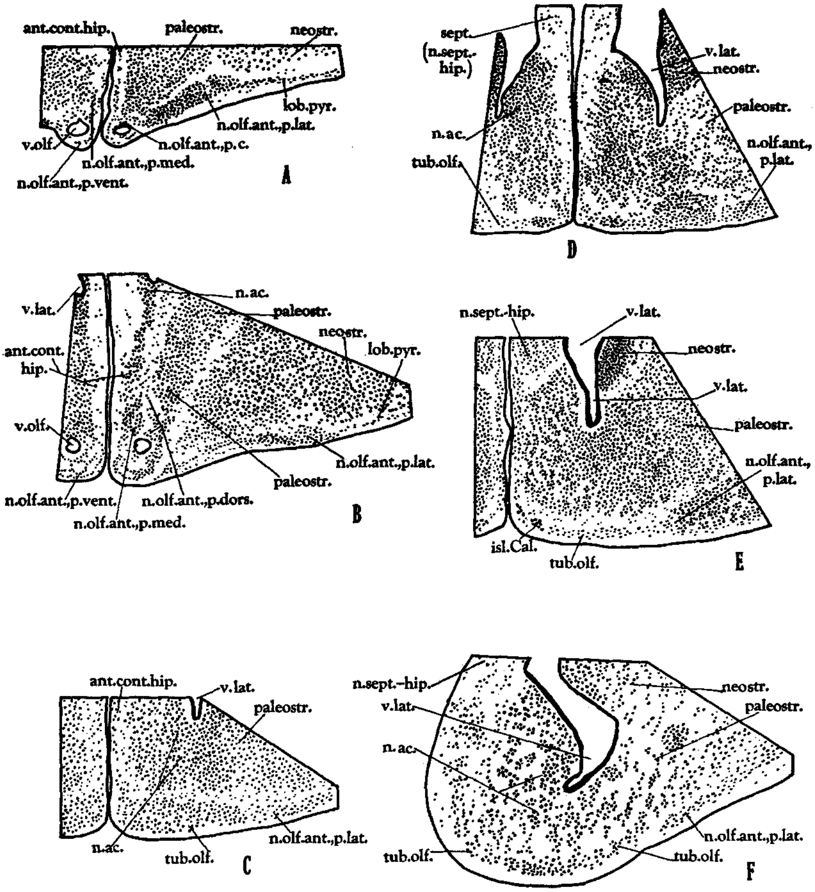

Fig. 9 Drawings of a series of transverse sections (A to E) of the brain of the American chameleon, Anolis carolinensis, arranged in rostro-caudal order to illustrate the relative positions and development of various portions of the nucleus olfactorius anterior with reference to other areas of the hemisphere. F is a drawing of a transverse section through the cerebral hemisphere of the horned toad introduced for comparison with E. Toluidin blue preparations. × 25.

In the dorsolateral wall a V-shaped mass (fig. 10, A and B) appears with the apex of the V directed dorsolateralward. This apex, which soon becomes composed of deeply staining cells, as does the rest of the V, together with the immediately joining arms of the V shows a somewhat looser arrangement of its cells farther caudalward and becomes continuous caudally through the hypopallium with the general cortex. This is representative then of the more differentiated pars dorsalis (fig. 10, A and B) of the nucleus olfactorius anterior as described in the preceding pages. Pars dorsalis is repre-ented in a less differentiated form in the underlying periventricular gray which is connected with it by scattered cells and which continues caudally, behind the transition of the differentiated pars dorsalis into hypopallial areas. Ultimately this undifferentiated portion of the periventricular gray becomes continuous with the neostriatum.

The lower part of the lateral limb of the V continues directly caudalward, to come into relation with the pyriform lobe cortex, and, at its ventral tip, with the tuberculum olfactorium, thus constituting a more differentiated pars lateralis (fig. 10) of the nucleus olfactorius anterior. Deep to it is undifferentiated periventricular gray of potentially the same character which disappears largely before the plane of figure 10 C. The medial extremity of the V extends caudalward, dorsally and dorsomedially, and becomes continuous with the anterior end of the hippocampus (pars dorsomedialis). The intermediate portion of the nucleus olfactorius anterior pars medialis, as represented medial to the ventricle by the scattered neurons of the crus region (slightly caudal to the plane of fig. 10), is replaced ventral to the hippocampus by the nucleus septo-hippocampalis.

The remainder of the nucleus olfactorius anterior may be divided into two portions on the basis of a comparison of their relations with those of other forms—a pars ventralis subventricularis and a pars ventralis supraventricularis. The slit-like olfactory ventricle in the Gila monster is tilted with the lower end ventrolateral instead of ventral in position

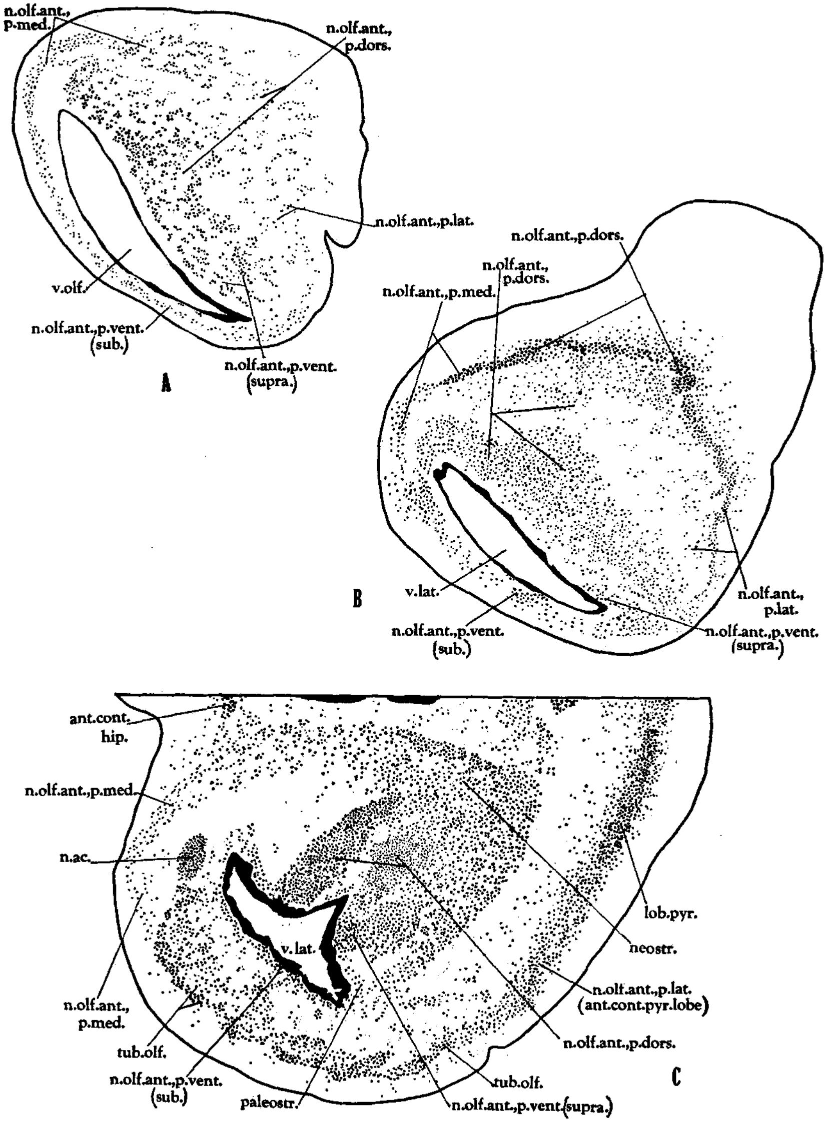

Fig. 10 Drawings to illustrate three levels through the forebrain of the Gila monster (Heloderma suspectum). A is through the olfactory crus, B near the attachment of the crus to the hemisphere, and C through the hemisphere behind the attachment of the crus. The figure is intended to show the positions and relations of the various portions of the nucleus olfactorius anterior. Toluidin blue preparations. × 25.

(fig. 10). This change affects the location of the pars ventralis (fig. 10) of the nucleus olfactorius anterior which in many reptiles is the gray surrounding the lower end of the ventricle medially, ventrally, and laterally. With the relative change in tilt of the ventricle in Gila monster that portion of the pars ventralis which was lateral in many other reptiles becomes dorsolateral and the part which was medial becomes ventromedial, the two being joined under the ventricle merely by scattered cells. In this way the lateral portion of the pars ventralis becomes supraventricular and the medial part subventricular in position. In regions immediately behind the accessory olfactory bulb the subventricular portion is quite well developed (fig. 10, A and B) but the cortical layer of the tuberculum olfactorium soon appears, crowding this subventricular part away from the surface so that it becomes continuous, medial to the ventricle, with the deep layer of the tuberculum (fig. 10 C). The scattered cells at the tip of the ventricle, connecting the supra- and subventricular portions, are continuous with the deep part of the tuberculum throughout its subventricular and lateral portions, disappearing in front of the paleostriatum as it swings beneath the ventricle. The supraventricular portion of the pars ventralis is that part of the undifferentiated periventricular gray situated ventrolaterally above the ventricle (below the neopaleostriatal sulcus) in levels immediately caudal to the accessory bulb and extending backward. It is not separable from the remainder of the supraventricular portion of the nucleus olfactorius anterior. It continues directly caudalward, to be replaced by the paleostriatum, the basis for regarding it as a pars ventralis of the nucleus olfactorius anterior. In this connection it should be stated, however, that it is not purely pars ventralis since strings of cells extend from it into neostriatal regions and it is probable that it contributes to both paleostriatal and neostriatal areas during development. It is evident that in Gila monster the portions of the nucleus olfactorius anterior characteristic for various higher vertebrate forms can be demonstrated but that these specialized portions are supplemented by a considerable amount of undifferentiated gray of similar character which retains substantially a primitive periventricular position—a position, it may be said in passing, which is that of the later differentiated portions early in their development.

Varanus (Varanus griseus). The development of the nucleus olfactorius anterior of Varanus is influenced by the presence in this reptile of an enormously large accessory olfactory bulb and an olfactory formation which is reduced to a minimum. In sections through the accessory olfactory bulb, behind the remnants of the olfactory formation, the lateral wall is a thin sheet carrying fiber bundles in the course of which is an occasional intercalated neuron. Dorsally and ventrally in the region of transition into the accessory olfactory formation, the neurons, although still intermingled with fiber bundles, are somewhat increased. These represent the bulbar portion of the secondary olfactory center. The internal granular layer of the accessory olfactory formation (like that of the olfactory formation) is composed of periventricular gray, which, as the caudal tip of the mitral layer is reached, begins to thicken up dorsally and ventrally. Behind the accessory bulb a continuous band of periventricular gray surrounds the ventricle, although represented by only a very few cells ventrolaterally. This gray is similar in appearance to that of the granular layer, but is a secondary olfactory nucleus, that is a nucleus olfactorius anterior, since it is overlaid by no mitral or glomerular layer. This layer of periventricular gray (fig. 11 A) is of a primitively undifferentiated type, its neurons being large, globular and in very intimate relation with the underlying ependyma. It does not have the appearance of a well-differentiated correlation center. Before it has formed a complete ring around the ventricle, a few, scattered, light staining, fairly large cells appear in the dorsolateral portion of the crus. These represent neurons migrating peripherally from the undifferentiated periventricular gray to form a trace of a nucleus olfactorius anterior pars dorsalis, further representation of which must be sought in the undifferentiated periventricular gray. Such cells increase in number caudalward and appear to pass over without break into the hypopallium (primordium neopallii etc., see fig. 11 B) and the anterior portion of the neostriatum. A very large part of the crus is occupied by fiber bundles which form an enormous C-shaped mass dorsomedial to the ventricle.

Behind this level there is an accumulation of scattered cells in the lateral part of the field again migrated outward from the periventricular gray, and representing (with the lateral periventricular gray) the cephalic tip of a pars lateralis of the nucleus olfactorius anterior. These increase in number gradually and form ultimately a rather deeply stained and fairly closely arranged band of neurons, which extends back along the ventrolateral region of the hemisphere to become continuous dorsally with the pyriform lobe, of which it is regarded as the anterior continuation or as a pars lateralis (fig. 11) of the nucleus olfactorius anterior. Ventrally this cell band lies in relation with the most dorsolateral portion of the cortical region of the tuberculum olfactorium. It is to be noted that this pars lateralis of the nucleus olfactorius anterior shows better nuclear differentiation than does the pyriform lobe proper.

At about the same level at which the scattered cells mark the rostral tip of the pars lateralis, dispersed neurons make their appearance along the ventromedial border of the crus region, to form the subventricular portion of the pars ventralis (fig. 11 A) as described for Gila monster (see p. 168). They are extremely few in number and are continuous with the deep portion of the tuberculum olfactorium (fig. 11 B) which is very poorly developed in this form. The supraventricular portion of the pars ventralis of the nucleus olfactorius anterior of Gila monster is represented (fig. 11 B) by the periventricular gray lying dorsolateral, and, farther caudalward, dorsal to the ventricle in Varanus. It diminishes as the crus region broadens out, certain of the cells of the periventricular gray migrating dorsally to contribute to the paleostriatum, as it makes its appearance. Thus, as in the Gila monster, this supraventricular portion of the pars ventralis is directly related to the rostral end of the paleostriatum. A few cells of this supraventricular gray have migrated out into the lateral portion of the tuberculum olfactorium thus repeating the usual relations.

Except for undifferentiated periventricular gray and for very rare neurons (fig. 11 A) there is no representation of a pars medialis (fig. 11 B) of the nucleus olfactorius anterior until the crus begins to broaden out into the hemisphere. There it appears in the form of diffusely arranged gray along the medial wall, dorsal to the pars ventralis and the tuberculum olfactorium. It never reaches any degree of differentiation and is replaced by the poorly developed anterior end of the hippocampus and by the septum.

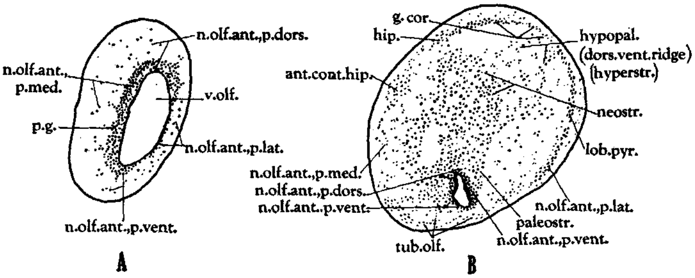

Fig. 11 Drawings of transverse sections of the brain of Varanus, selected in planes through the right olfactory crus and through the hemisphere somewhat caudal to the crus. The figures illustrate various portions of the nucleus olfactorius anterior. Toluidin blue preparations. × 25.

Microscopic structure in snakes

Garter snake (Thamnophis sirtalis). In the brain of this snake, slightly caudal to the rostral tip of the olfactory ventricle, in planes in which the olfactory formation has practically disappeared on the lateral wall of the bulb and midsections of the accessory olfactory bulb are seen, there appears in the lateral wall a band of deeply staining, closely packed cells, constituting the pars lateralis (fig. 12) of the nucleus olfactorius anterior. This band can be traced directly caudalward into the pyriform lobe formation, from which it is distinguished by the closer arrangement of its neurons. A fiber tract in intimate relation with it, arising from the accessory olfactory bulb and forming a dorsolateral component for the lateral olfactory tract, is visible even in the cell material where it can be traced caudalward with the pars lateralis.

At rostral levels of the pars lateralis scattered cells lie dorsal to it representing a pars dorsalis (fig. 12) of the nucleus olfactorius anterior. Traced caudalward these are replaced by the general cortex.

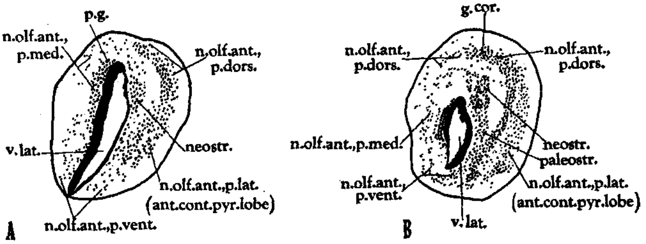

Fig. 12 Drawings of two sections of the brain of the garter snake (Thamnophis sirtalis) chosen through the hemisphere wall caudal to the right, transversely cut olfactory bulb. A is rostral to B. Both illustrations are designed to show the relations of the parts of the nucleus olfactorius anterior to other centers of the hemisphere. Toluidin blue preparations. × 25.

Slightly caudal to the beginning of the pars dorsalis, a few cells group to form the pars ventralis (fig. 12) which is ventrolateral and also ventromedial to the ventricle. They then form a crescent-shaped mass ventral to the ventricle, which is replaced caudally by the deep layers of the tuberculum olfactorium, there being no sharp line between the two areas. The neostriatum projects into the crus region of the olfactory bulb separating the pars lateralis (p. 173) from the ventricle. At such levels the accessory bulb is still present on the medial surface, and consequently the typical, ring-shaped pattern of the nucleus olfactorius anterior, characteristic of the crus region of turtles and various other reptiles, is represented in the garter snake by a C-shaped arrangement of the nucleus olfactorius anterior with the ends of the C separated by the accessory bulb, or immediately caudalward, by an almost cell-free area, and with the C enclosing laterally, between itself and the ventricle, the tip of the neostriatum (fig. 12 A). It should be strongly emphasized that tracts passing back from the olfactory bulb, in a form such as the garter snake, must of necessity carry connections related to the accessory olfactory bulb, since the olfactory formation is reduced while the accessory bulb is enormously large.

At the extremities of the ventricle the granular layer of the accessory olfactory bulb is continuous with a periventricular band of gray which swings over onto the lateral surface for a short distance and occasional clumps of periventricular gray are easily observed along the outer border of the ventricle, indicating that this region is not highly specialized and tends to retain traces of an embryonic condition. Likewise on the medial surface, behind the accessory olfactory bulb, a considerable part of the gray maintains a periventricular position (fig. 12) so that much of the medial portion of the pars ventralis remains extraependymal (in comparison with the Gila monster, supraventricular; see p. 168) in position.

In the crus behind the accessory olfactory bulb there is an enormous amount of periventricular gray and the nucleus olfactorius anterior pars medialis is represented largely by such gray and, to a small extent, by peripherally distributed neurons (fig. 12). Gradually the number of such peripheral neurons increases and the dorsal part is replaced by the hippocampus, of which it may be regarded as an anterior extension. The intermediate zone, at levels through the cephalic end of the hippocampus, shows indication of migration from the periventricular gray and this area becomes the nucleus septohippocampalis. Ventralward the cells on the medial side, which belong to the pars ventralis, are very greatly decreased in number, but continue back into the poorly developed tuberculum olfactorium.

PYTHON (PYTHON MOLURUS) AND COPPERHEAD (AGKISTRODON MOKASEN). The series available for python and copperhead are not sufficiently well stained to warrant a detailed description. They do indicate that the pattern of the nucleus olfactorius anterior described for the garter snake is repeated in essentials in these forms.

WATER MOCCASIN (NATRIX). This form is not illustrated since the relations in general are those typical of snakes. Behind the main mass of the olfactory formation of Natrix, the lateral wall of the bulb is reduced to an extremely thin sheet with only an occasional neuron. Dorsally and ventrally, at the line of transition into the very large, inbulging accessory olfactory bulb, the wall is a little thicker and here the granular layer becomes continuous with a band of periventricular gray which extends over the end of the ventricle and around into the lateral wall. With this become associated a few outwandered secondary neurons, the first representatives of the nucleus olfactorius anterior. The more dorsally placed of these scattered cells constitute the cephalic tip of the pars dorsalis of the nucleus olfactorius anterior. This pars dorsalis, as followed caudally in the series, increases slightly in cell content, but never becomes a differentiated nuclear mass. It is continuous with the general cortex through the neostriatum.

As the lateral wall begins to thicken, traces of periventricular gray form a discontinuous band along the ventricle. This band represents a primordial pars lateralis, its low degree of development being characteristic of that of the secondary centers in this region. The neurons of pars lateralis increase in number but are still scattered for a considerable distance. Gradually, however, in the midlateral region a more discrete pars lateralis of the nucleus olfactorius anterior appears, but, in the material available, never becomes so compact or so deeply stained as does the comparable cell mass in some of the other reptile material studied. However, it can be followed directly caudalward into relationship with the pyriform lobe cortex and ventrally overlies the tuberculum olfactorium.

Behind the accessory olfactory bulb, on the medial wall of the crus, the major number of neurons is arranged as periventricular gray bordered externally by a very few scattered cells. As the sections are followed caudalward the crus narrows down and the diffusely arranged neurons of the pars medialis are gradually replaced dorsally by the hippocampus, an area which is poorly developed here. Ventral to the hippocampus the slight concentration of neurons representing the cephalic tip of the septum is connected by scattered gray with the periventricular and other surrounding areas. This region represents the acme of failure of differentiation as seen in the reptiles studied.

The pars ventralis, which begins, in planes through the accessory olfactory bulb, as widely dispersed cells, gradually thickens into a fair sized nucleus with an associated decrease in the related periventricular gray. This nucleus continues back to the rostral pole of the tuberculum olfactorium, with the deep layer of which it is continuous, being gradually replaced from the lateral surface by the incoming outer layer of the tuberculum which appears first on the lateral side. Dorsolaterally the pars ventralis is in relation with the paleostriatum, which swings down behind it to form the nucleus accumbens.

THE AVIAN NUCLEUS OLFACTORIUS ANTERIOR

General considerations

The area at the base of the avian cerebral hemisphere which corresponds to the various portions of the nucleus olfactorius anterior and the tuberculum olfactorium of reptiles and mammals is, on the whole, much less differentiated in birds. However, within the avian class there are considerable differences in the degree of specialization in this region, depending upon the extent of the olfactory formation, and possibly other factors, the more direct relationship beween this formation and the other olfactory centers being through the various portions of the nucleus olfactorius anterior. The following account is based on series of sparrow, dove, and crow brains. The other bird material available for study shows variations of the pattern seen in the forms described, the whole complex being exceedingly poorly developed in the parakeet and relatively fairly well differentiated in the chicken and the dove.

Microscopic structure in birds

ENGLISH SPARROW (PASSER DOMESTICUS). In their account of the sparrow forebrain, Huber and Crosby ('29) divided the area at the base of the olfactory bulb into three major portions—a nucleus olfactorius anterior, an area prepyriformis of Rose, and, behind this latter area, a mass of undifferentiated gray to which no specific name was attached. The nucleus olfactorius anterior of the sparrow, dove, and certain other birds (as described by Huber and Crosby), and also that of the humming bird (according to the 1932 account of Craigie), consists of gray extending dorsally from the base of the olfactory bulb into relation with the anterior continuation of the hippocampus in planes through the bulb and immediately caudal to it. For a detailed account of this nuclear mass the earlier descriptions and figures should be consulted, and figures 2 F and 13 C of the present paper, which illustrate it. In general it is, where well developed, a triangular, planoconvex mass of medium-sized neurons which, in addition to its relation to the anterior continuation of the hippocampus, is not sharply separable from the hyperstriatum accessorium rostralward and abuts against the cephalic pole of the septal area which replaces it. Frontally it is separated from the hyperstriatum dorsale by the lamina frontalis suprema (fig. 13 C) but farther caudally it lies against the paleostriatum primitivum and the anterior part of the nucleus accumbens. It is obvious from its position with regard to that of the anterior continuation of the hippocampus and the cephalic pole of the septal area (which are shown in the 1929 paper of Huber and Crosby) that this nucleus olfactorius anterior has the characteristic relations of the pars medialis of reptilian and mammalian forms. Its close association with the hyperstriatum accessorium, which, according to one's interpretation, is either cortex or vicarious cortex, suggests that this portion of the nucleus has also the characteristics of the pars dorsalis of other forms, particularly its more frontal portions. (Possibly its most ventral part should be considered as forming a small portion of the pars ventralis). The area prepyriformis of Rose ('14) extends lateralward into relationship with the poorly differentiated pyriform lobe cortex in planes through the olfactory bulb (fig. 2 F) and, caudal to the bulb, swings around the medial angle of the hemisphere. In so doing, it partly replaces and partly overrides an undifferentiated mass of gray lying between the area prepyriformis of Rose and the nucleus olfactorius anterior pars medialis at planes where the olfactory bulb attaches to the hemisphere and immediately behind them. This undifferentiated gray, the pars ventralis of the nucleus olfactorius anterior (fig. 13 C), which is partly replaced by the paleostriatum primitivum and partly continuous with the inner scattered gray of the pars medialis of the area prepyriformis of Rose (or rostral tip of the tuberculum olfactorium), has undoubtedly been placed by most observers, including Huber and Crosby, with the area prepyriformis. The frontal and lateral portion of this area prepyriformis of Rose corresponds to the nucleus olfactorius anterior pars lateralis of reptiles (or the anterior continuation of the pyriform lobe of these and mammalian forms, or the prepyriform area of mammals). The medial part, comparable perhaps to the medial part of the area prepyriformis of Rose as seen in the kiwi (Durward, '32), in our opinion, could not correspond to the pars lateralis of the nucleus olfactorius anterior either from its position or relations. This portion of the prepyriform area extending medialward to the angle of the hemisphere and then slightly dorsalward and so replacing the pars ventralis may be regarded either as a differentiated caudal tip of the pars ventralis of the nucleus olfactorius anterior or as a differentiated rostral pole of the tuberculum olfactorium. The present writers are inclined to the latter view in the case of the sparrow brain but regard the question as more of academic than of practical significance since the

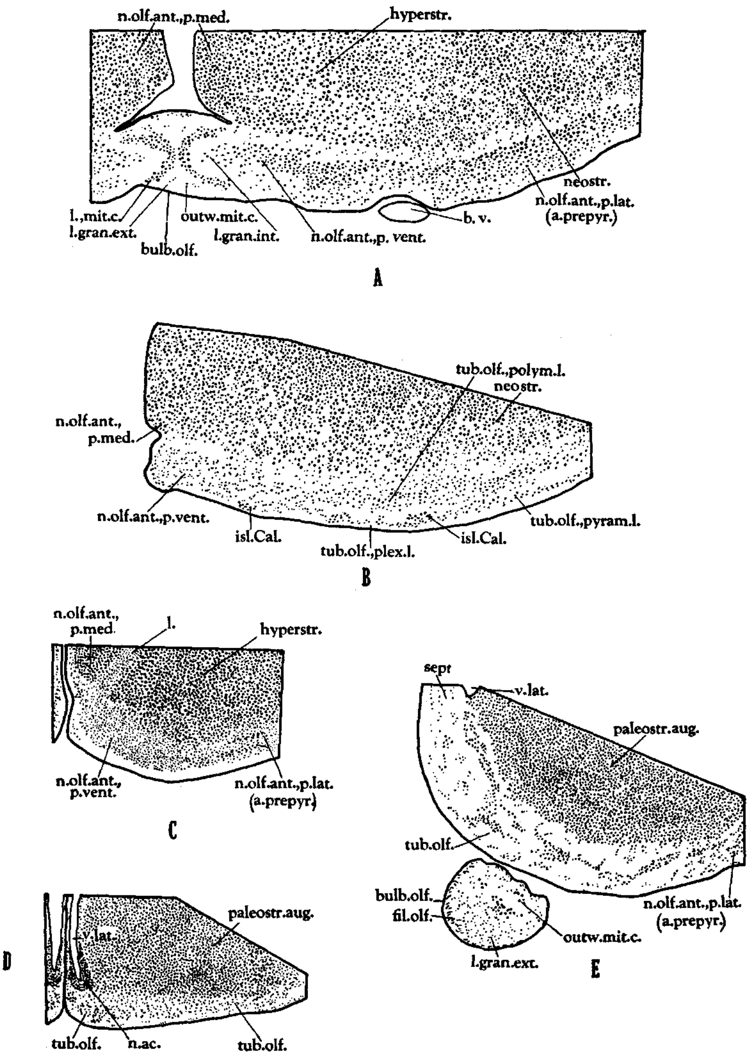

Fig. 13 A series of figures to illustrate the relations of various portions of the nucleus olfactorius anterior in the brain of the crow, Corvus brachyrhynchos (A and B), the sparrow, Passer domesticus (C and D), and the dove, Columba livia (E). A and C are drawn from planes rostral respectively to those of B and D. Toluidin blue preparation. × 25.

tuberculum differentiates from the less specialized pars ventralis phylogenetically. Behind the differentiated band constituting the prepyriform area of Rose is a region of scattered neurons showing no particular specialization, and corresponding to the undifferentiated gray mentioned earlier by Huber and Crosby as present in these levels. This poorly developed area extends caudalward to the diagonal band of Broca and forms the main extent of the tuberculum olfactorium (fig. 13 D). In general one may say, then, that in the sparrow the nucleus olfactorius anterior of earlier observers has within it the pars dorsalis and the pars medialis of that complex as it has been described by Herrick and others for mammals. (It may make, caudoventrally, some slight contribution to the pars ventralis.) The pars ventralis of the nucleus olfactorius anterior has representation primarily in the sparrow in undifferentiated gray at the base of the hemisphere. The pars lateralis finds its counterpart in the lateral and frontal portions of the area prepyriformis of Rose. The caudomedial portion of the area prepyriformis of Rose lies at the transition between the pars ventralis of the nucleus olfactorius anterior and the tuberculum olfactorium and may be allocated to either area. The main extent of the tuberculum olfactorium is represented by the unspecialized gray extending caudalward to the diagonal band of Broca.

DOVE (COLUMBA LIVIA). In its specialization the gray complex representing the dove nucleus olfactorius anterior approaches more nearly that of the homologous area in reptiles and mammals than does the same region in the sparrow. A patch of undifferentiated gray extends dorsal, medial, and ventral to the dove olfactory ventricle and continues caudalward on the medial side of the ventricular space, to come into relationship dorsally with the overlying band-like neocortex found in this bird and with the hyperstriatum accessorium. Medially to the ventricle this gray is replaced by the anterior continuation of the hippocampus and by the septal areas and, ventrally to the ventricle, by the deeper portion of the very poorly developed tuberculum olfactorium and by the nucleus accumbens. Thus in the dove a pars dorsalis, a pars medialis (fig. 2 C), and a pars ventralis of the nucleus olfactorius anterior are distinguishable. At about the place of attachment of the olfactory bulb to the main mass of the hemisphere, the undifferentiated gray is found lateral to the ventricle, so that a complete ring of gray of the grade of nucleus olfactorius anterior surrounds the ventricle although the whole ring is not demonstrable in a single plane of the series studied. The undifferentiated gray is continuous laterally with a deeply staining band, bordered internally by more scattered cells, which extends out toward the pyriform lobe cortex. This band of gray corresponds to the area prepyriformis (or 51 of Rose); the lateral part of this area as described for the kiwi by Durward ('32) is, at this level, a relatively well-differentiated pars lateralis of the nucleus olfactorius anterior (or anterior continuation of the pyriform lobe complex or area prepyriformis of mammals; see fig. 2 C). Behind the attachment of the olfactory bulb the area prepyriformis of Rose swings medialward (forming a pars medialis, see Durward, '32, for the kiwi) to replace the undifferentiated gray of the pars ventralis. At such levels the lateral part of this area prepyriformis of Rose represents the caudal end of the pars lateralis of the nucleus olfactorius anterior (fig. 13 E) but the medial part of the band, which has a very slightly different appearance, must be regarded either as the most rostral tip of the tuberculum olfactorium or as a caudal differentiated portion of the pars ventralis of the nucleus olfactorius anterior (see the account of this nucleus in the sparrow). Actually it is in the transition region between the two areas and might be allocated to either. Personally we should be inclined to regard it as the most rostral portion of the tuberculum olfactorium, an interpretation with which the 1938 account of Kuhlenbeck is not in accord. However this differentiated medial portion may be interpreted, both it and the rest of the prepyriform area of Rose are soon replaced by a peripheral band of very poorly developed gray, which undoubtedly represents the main part of the tuberculum olfactorium (fig. 13 E). In this poorly differentiated tuberculum occasional groups of cells suggest primordial islands of Calleja. It is obvious that the relations here are similar to those in the sparrow but that in the dove, as might be expected in a form with better developed olfactory nerves and larger olfactory bulbs, the various parts of the nucleus olfactorius anterior are more highly differentiated.

Before closing this account attention must be called to the work of Kuhlenbeck and others on this region of the hemisphere. Kuhlenbeck ('24, '27, '29, and elsewhere) termed the ventrolateral portion of this region the area ventrolateralis anterior or basal olfactory cortex of the tuberculum olfactorium, and apparently included therein everything from the base of the bulb to or through the nucleus of the diagonal band and the diagonal band of Broca. Huber and Crosby ('29) and Ariëns Kappers, Huber, and Crosby ('36) stated that this same area was "probably homologous in part with the tuberculum olfactorium described for reptiles" but that they were not sure how much of this area was to be homologized with the reptilian tuberculum olfactorium. In his recent paper, Kuhlenbeck ('38) states that this area "is therefore homologous to the rostroventral part of the lateral cortex of reptiles and to the rostroventral part of the prepyriform area of mammals, not to the tuberculum olfactorium."

CROW (CORVUS BRACHYRHYNCHOS). In many interesting respects, areas here under discussion in the crow brain show marked resemblance to the homologous regions in the sparrow brain, a fact of considerable interest since in both these forms there is a fusion of the olfactory formation to form wholly or partly a single bulb (see p. 133 and figs. 2 D, 2 E and 13 A). The medial portion (fig. 13 A and B) of the nucleus olfactorius anterior is the usual slightly triangular shaped, undifferentiated mass of gray, at the base of the hemisphere dorsal to the olfactory bulb, which extends caudalward to be replaced by the septal region (the pars medialis). It passes over dorsally into association with hyperstriatal areas, indicating the relations of a pars dorsalis. Although relatively clearly delimited, nowhere throughout its extent does it show any differentiation. The ventral and the ventromedial superficial areas of the hemisphere, dorsal and dorsolateral to the olfactory bulb, are occupied by a band of gray consisting of a few darkly staining neurons intermingled with smaller cells. This band corresponds to the rostral part of the area prepyriformis of the sparrow or to the pars lateralis (fig. 13 A) laterally and to the pars ventralis (fig. 13, A and B) of the nucleus olfactorius anterior medially. Behind the bulb this band of gray fades out into a region occupied by a few scattered cells with rare but conspicuous clumps of medium sized, deeper staining neurons suggesting primitive islands of Calleja (fig. 13 B). This area extends back toward the preoptic region and represents all that this bird has of a tuberculum olfactorium (fig. 13 B), in which the plexiform, pyramidal, and polymorph layers are distinguishable although not highly developed.

THE MAMMALIAN NUCLEUS OLFACTORIUS ANTERIOR

General considerations

In mammals in general the nucleus olfactorius anterior shows subdivisions comparable to those seen in reptiles. However, descriptions in the literature and our own material indicate that it has a very considerable range of variation in the details and in the degree of its development in the various forms. Outstanding among such differences is the appearance of a clear-cut pars externa in all mammals except primates, in which it is indefinite.

Microscopic structure in marsupials

VIRGINIA OPOSSUM (DIDELPHIS VIRGINIANA). The nucleus olfactorius anterior has been described in detail for the opossum by Herrick ('24). The material available for study here for the most part merely documents his findings and the description need not be repeated. Attention, however, is called to the fact that in planes through the anterior continuation of the hippocampus some scattered neurons of slightly larger size appear at the upper tip of the pars ventralis below the ventricle and similar cells appear medial to the ventricle. Slightly farther caudalward these scattered cells form a loose gray band, which extends dorsal to the deep portion of the tuberculum as this latter area appears. Probably this band is comparable to a pars posterior of the nucleus olfactorius anterior as described for other forms but it is very small, being found only for a short distance and disappearing in front of the head of the caudate nucleus.

Microscopic structure in rodents

The nucleus olfactorius anterior has been described in the rat by Gurdjian ('25) and in the rabbit by Young ('36). Their results in essentials correspond to those given in the following description of this nuclear complex in the squirrel and the mouse. The terminology employed by Gurdjian is that in accord with the earlier descriptions in the literature. The nomenclature of Young, like that of the present account, is based on that of Herrick ('24) and Obenchain ('25) for mammals but the patterns are essentially the same for all these rodents. In Young's account the various subdivisions of the main nucleus olfactorius anterior have been recognized and the ring formation around the ventricle emphasized. Likewise a pars externa has been described and its ventral and dorsal limbs (or tail pieces) traced. Apparently these two portions do not unite and in the rabbit, as in the mouse, the pars externa does not form a gray ring around the ventricle as does the homologous nuclear mass in the squirrel (see p. 188).

No edentate material has been available for study. However, a very good description of the nucleus olfactorius anterior of Orycteropus is to be found in the 1925 paper of Sonntag and Woollard.

RED SQUIRREL (SCIURUS HUDSONICUS). The most rostral part of the nucleus olfactorius anterior of the squirrel is the more dorsal portion of the pars lateralis, which appears as a rounded mass of fairly large neurons in planes through the caudal half of the accessory olfactory bulb, just ventrolateral to this structure. It is bordered dorsomedially by the internal granular layer of the accessory bulb, with which layer at these levels it is practically continuous, but is separated from the internal granular layer of the olfactory formation and the periventricular undifferentiated gray by an almost cell-free zone.

As the olfactory formation gradually disappears lateral to the accessory olfactory bulb, leaving a denuded area, the cephalic tip of the pars externa begins to make its appearance dorsal to the pars lateralis (fig. 14 A). This pars externa is not sharply separable from the internal granular layer of the accessory bulb, since it begins as an infiltration of the lateralmost portion of this layer with small groups of larger (though still medium sized), more deeply staining cells to form a narrow pars externa which is continuous medially with the internal granular layer. Followed caudalward, the pars lateralis widens out in the area of the mass of gray (in the shape of an inverted U) formed by the pars externa dorsolaterally and the internal granular layer of the accessory bulb dorsomedially. With the gradual disappearance of the accessory olfactory formation, the pars externa encroaches upon the position occupied by the internal granular layer and takes on a U-shaped outline also (fig. 14 B), and, in the same plane, the pars lateralis begins to extend both ventromedialward and ventrolateralward. Its ventromedial limb forms, from the apex ventralward, the homologue of the pars dorsalis and the pars medialis of the nucleus olfactorius anterior respectively. The lateral limb, with the dorsally lying apex of the U, is homologous with the pars lateralis of the nucleus olfactorius anterior of other mammals. The whole U-shaped mass is a broad, homogeneous band of fairly large neurons. At such planes, then, there are two similarly shaped gray masses belonging to the nucleus olfactorius anterior (fig. 14 B)—a narrow, deeply stained, small celled, overlying pars externa and a broader, less deeply stained, wider band con-

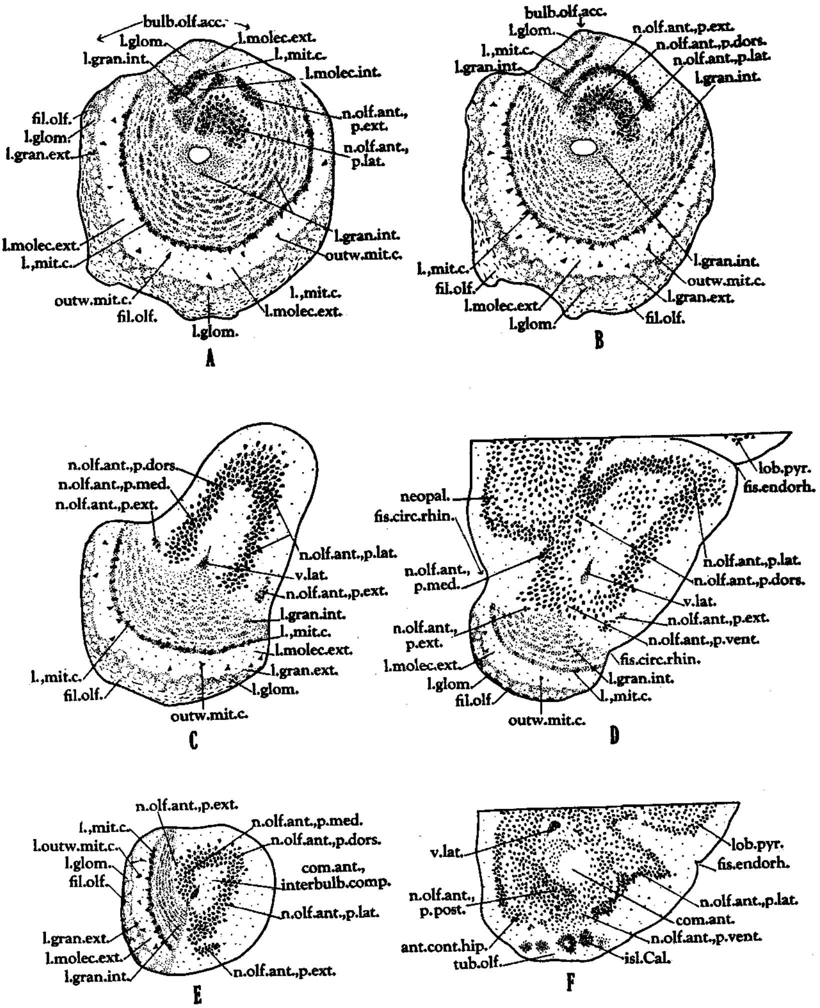

Fig. 14 Illustrations, arranged in rostrocaudal order, of selected transverse sections through the nucleus olfactorius anterior of the red squirrel, Sciurus hudsonicus (A to D) and the mouse (E and F). Attention is called particularly to the manner in which the caudal tips of the pars externa approach each other (C, D, and E) and also to the gray periventricular ring (D and E) formed by the main mass of the nucleus olfactorius anterior. Toluidin blue preparations. × 12.5.

stituting the pars lateralis, pars dorsalis, and pars medialis of this nuclear complex. Soon the apex of the outermost U-shaped mass, the pars externa, disappears leaving medial and lateral limbs of this nucleus which gradually become reduced to small patches of gray on the ventromedial and ventrolateral sides of the bulb respectively (fig. 14 C). These patches of gray extend caudalward, and, as the caudal end of the bulb is reached, tend to approach each other ventromedialward. The lateral cell group can be traced past the midline of the bulb on the ventral surface. The medial limb is somewhat discontinuous caudally, there being sections in which only one or two neurons, and in some cases no neurons, of this gray can be seen, although small patches of this medial limb again appear in more caudal sections. Ultimately it is continuous by means of three or four cells with the lateral limb of the nucleus. Obviously the pars externa forms an almost complete ring around the crus, but with the dorsal part of the ring rostral to the ventral part.

In planes in which only the medial and lateral limbs of the pars externa can be distinguished, the main part of the nucleus olfactorius anterior elongates at the apex of the U-shaped mass formed by it, and extends dorsalward between the two limbs of the pars externa, becoming much elongated (fig. 14 D). Its dorsal tip extends back to become continuous with the pyriform lobe cortex, so that the apical region and lateral portion are comparable to the pars lateralis (fig. 14 D) of the nucleus olfactorius anterior of other mammals. The part immediately ventromedial to the apex, which constitutes a pars dorsalis (fig. 14 C and D), comes into relationship with the neopallial cortex which replaces it. The ventral part of the medial limb of the U-shaped mass forms a pars medialis (fig. 14 D) and becomes continuous with the rostroventral portion of the anterior continuation of the hippocampus. The nucleus olfactorius anterior is converted into a ring of gray around the ventricle (just frontal to fig. 14 D) by the appearance of a pars ventralis, found at caudal levels of the bulb in which the olfactory formation still persists ventromedially. Behind the olfactory formation this pars ventralis extends caudalward along the ventromedial surface of the hemisphere in relation with the head of the caudate, from which it is not sharply delimited rostrally although more readily differentiated than in some other forms. Caudalward the pars ventralis grades over into the deep portion of the tuberculum olfactorium.

Between the pars ventralis and the ventricle, in planes behind the pars medialis, a small, somewhat more deeply stained cell mass, the pars posterior of the nucleus olfactorius anterior, appears between the pars ventralis and the ventricle, without evident relation to the pars medialis. It extends caudalward, intervening between the caudate nucleus and the polymorph layer of the tuberculum, but has less mediolateral extent in the squirrel than in the mouse and on the whole is smaller and much less conspicuous than in this latter rodent (see p. 192), actually resembling more nearly the homologous nucleus of the cat (Fox, '38) and of the weasel (see p. 194). It lies entirely behind the plane of the figures.

MOUSE (MUS —; see footnote, p. 122). In the mouse, in planes immediately caudal to the rostral end of the accessory olfactory bulb, the most medial portion of the granular layer of its lateral wall is replaced by an elongated band of larger neurons constituting the nucleus olfactorius anterior pars lateralis. Slightly caudal to this, in planes marking the first appearance of mitral cells in the accessory olfactory bulb, a second group of smaller, more deeply staining neurons, the pars externa of the nucleus olfactorius anterior, appears lateral to its pars lateralis, again supplanting the granule cells of the olfactory formation and becoming intermingled with the cells of the granular layer. As the series is followed caudalward, the olfactory formation gradually disappears in the lateral wall and its granular layer is partially substituted for by the enlarging pars lateralis and the pars externa. With the further development of the accessory olfactory bulb, the lower border of the granular layer belonging to it lies farther from the ventricle, due to the fact that the accessory bulb is less submerged in this region and that its granular layer has decreased in size. At these levels the pars externa, at its dorsal extremity, projects medialward and this dorsomedial projection, together with that portion of the pars externa which has appeared frontalward, constitutes in the terminology of Herrick ('24) the dorsal limb. The dorsal limb can be followed caudalward until substantially the plane of disappearance of the mitral cells of the accessory olfactory bulb, suggesting a functional relationship between the two structures. Not only does the pars externa grow dorsalward but gradually, behind its cephalic tip, extends ventrally and ventromedially, thus forming a ventral limb. This limb continues caudalward slightly beyond the limit of the accessory olfactory bulb, so that it does not have the precise relations in plane to the accessory bulb that are seen with the dorsal limb.

In planes through the cephalic tip of the dorsomedial and ventromedial extensions of the pars externa, the main portion of the nucleus olfactorius anterior becomes comma-shaped, with the concave side toward the ventricle, the upper part constituting the pars dorsalis. This upper part increases steadily in size with the decrease in the granular layer of the accessory olfactory bulb and, in planes through caudal levels of this bulb, has swung medialward to form the dorsal part of a pars medialis. Behind the accessory bulb the olfactory formation on the medial wall disappears, but even earlier the nucleus olfactorius anterior completely surrounds the olfactory ventricle, taking on here the outline of a triangle with the apex ventromedialward (fig. 14 E). Topographically this nucleus may be considered to have dorsal, medial, ventral, and lateral portions, all of which are of a similar cell character, but there are differences in arrangement which are particularly marked in the looser spacing of the neurons in the middle part of the pars medialis. In surrounding the ventricle the portion on the medial side lies close to this cavity but the remainder of the cell band is separated by the large tractus olfactorius intermedius or interbulbar component of the anterior commissure (fig. 14 E).

Shortly after the periventricular gray is formed, there is an accumulation, ventromedially, of neurones of a small pyramidal type which form the anterior continuation of the hippocampus, from which more scattered and smaller cells extend up toward the ventricle. Slightly caudal to this plane the pars dorsalis of the nucleus olfactorius anterior is continuous with the neocortex through its outermost cell layers, and, at the same level, the deeper, larger cells of the neocortex make their appearance within the crus. The connection with the neocortex gradually widens out and the pars lateralis of the nucleus olfactorius anterior (fig. 14 F) becomes continuous, around the endorhinal fissure, with the pyriform lobe cortex. At such levels the interbulbar component of the anterior commissure (fig. 14 F) is seen as a prominent fiber mass ventrolateral to the ventricle and, near the surface of the crus, the first islands of Calleja make their appearance.

The anterior continuation of the hippocampus is relatively very large in the mouse, forming an eminence on the ventral surface of the brain in front of the tuberculum olfactorium (fig. 14 F). In cross sections this anterior continuation appears as a band of cells differentiating in relation with the nucleus olfactorius anterior pars medialis but ventromedial and medial to it. In such planes it swings around the ventral angle of the crus. In sagittal sections this anterior continuation can be traced with great ease back to the hippocampal gray overlying the corpus callosum. The undifferentiated portion of the nucleus olfactorius anterior pars medialis extends through the crus region into the hemisphere as a small-celled mass of gray near the ventricle, which mass gradually disappears.

Lateral to the anterior continuation of the hippocampus, and replacing caudally the pars medialis of the nucleus olfactorius anterior, is a band of neurons, larger and more deeply stained than those of the pars medialis, which constitutes the pars posterior of the nucleus olfactorius anterior (fig. 14 F) as described by Obenchain ('25) for Caenolestes and Fox ('38) for carnivores. Apparently it is not that identified by Le Gros Clark ('28) for Macroscelididae. This band increases in size, replacing also the pars ventralis of the nucleus olfactorius anterior, and forms an obvious, crescent-shaped gray mass between the nucleus accumbens and the caudate nucleus on the one hand and the polymorph layer of the tuberculum olfactorium on the other hand, throughout the mediolateral limits of the tuberculum. It persists for a short distance and then disappears from the field. Behind it the caudate complex overlies the deep layer of the tuberculum.

Microscopic structure in carnivores

The study of the carnivore forebrain (cat) recently completed by Fox ('38) shows an anatomical pattern for the nucleus olfactorius anterior which is in line with that found in the series presented here. For the present paper the relations in this area, as seen in the weasel, will be described.

WEASEL (MUSTELA NOVEBORACENSIS). The nucleus olfactorius anterior appears rostrally in the weasel olfactory bulb as a small group of cells dorsolateral to the ventricle and in the region where the olfactory formation thins out. This nucleus rapidly extends dorsoventrally, forming a band of cells medial to the area denuded of olfactory formation (fig. 4 C). About halfway between this nucleus and the surface there is a narrower band of deeply staining cells, the pars externa (fig. 4 C). The nucleus olfactorius anterior itself bends medialward, at its dorsal border, to form an inverted J-shaped mass and the pars externa lengthens out dorsoventrally. The extension of both nuclear groups continues, the main portion of the nucleus becoming horseshoe-shaped in planes through the accessory bulb (fig. 4 C) and the ventral tips later uniting to form a ring (see Fox, '38) around the obliterated ventricle. From their positions and caudal relations all four subdivisions of the nucleus olfactorius anterior can be recognized in this ring (fig. 15 A). Prior to this union the pars externa disappears in its midportions but the tips persist as the dorsal and ventral limbs of this nucleus. The dorsal limb is directed dorsomedially and then ventrally, and the ventral limb ventromedially thus approaching each other but disappearing from the field before they meet, so that the pars externa in the weasel, as in the cat (Fox, '38), does not completely encircle the bulb. The crus is relatively long in this carnivore and for many sections there is no great change in the gray ring (fig. 15 A) surrounding the ventricle. Then, as the hemisphere is approached, the pars dorsalis becomes continuous with the neopallial cortex (fig. 15 B). In the ventral part of the field is the pars medialis (fig. 15 B) which shows on its medial border a group of cells passing

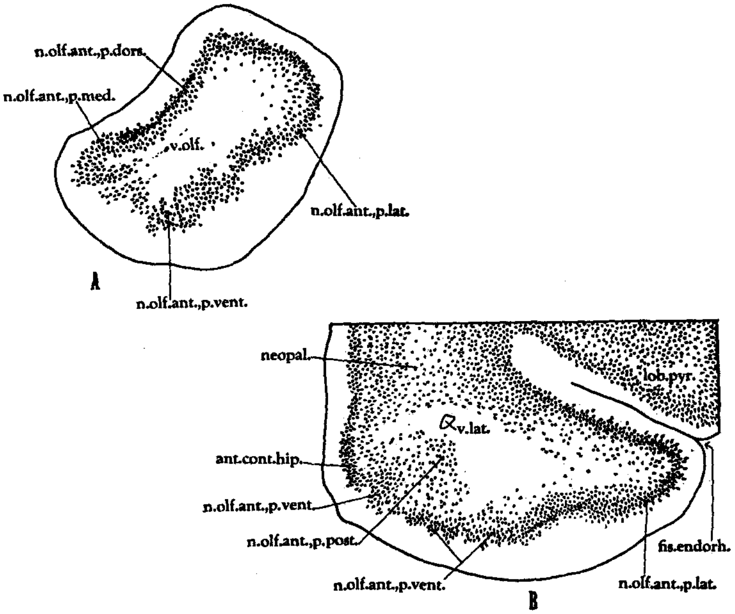

Fig. 15 Drawings of transverse sections of the weasel brain, selected from planes through the right olfactory crus (A) and through the hemisphere caudal to the attachment of the crus (B). These figures show the ring of gray around the ventricle formed by the nucleus olfactorius anterior and the relations of the various parts of the nucleus to other centers of the hemisphere wall. Toluidin blue preparations. × 12.5.

over into the anterior continuation of the hippocampus, so that this continuation may be said to extend directly into the crus in the weasel. The pars lateralis (fig. 16 B), which lies lateral to the pars dorsalis, has the usual relations, being continuous around the endorhinal fissure with the pyriform lobe cortex. The large pars ventralis (fig. 16 B) has a tendency to be folded and to show a concentration of cells at its outer border with more scattered neurons inside, suggesting a differentiation toward the caudally lying tuberculum with the polymorph layer of which it is continuous behind the plane of the above mentioned figure.

Between the pars ventralis and the ventricle appears the pars posterior that resembles in cell character the deeper part of the pars ventralis with which it is continuous by scattered cells (fig. 15 B). The pars posterior extends caudalward to planes in which it is wedged between the caudate nucleus and the ventricle dorsally, the interbulbar component of the anterior commissure laterally and the polymorph layer of the tuberculum ventrally. This pars posterior shows relations comparable to those described for the cat by Fox ('38) and for the squirrel on page 189 of the present paper.

Microscopic structure in ungulates

PIG (SUS SCROFA). The ungulate nucleus olfactorius anterior, of which there is no description in the literature, appears as a long band of cells, in the midst of the intermediate portion of the internal granular layer on the dorsal side of the ventricle, in planes in which the olfactory formation surrounds the bulb but begins to thin down dorsally. This gray mass (fig. 4 A), which consists of medium sized, darker staining and intermingled darker neurons, elongates relatively rapidly, having a slightly oblique dorsolateral-ventromedial orientation, and soon develops into a wide spread V with the apex and the dorsolateral limb representative of the pars lateralis of the nucleus olfactorius anterior and the dorsomedial limb representative of the pars dorsalis and the more medially placed pars medialis, there being at this level no differentiation between these two portions. As the nuclear mass is followed caudalward, although this V-shaped arrangement is maintained for many sections, differences in cell staining and thickness of the various portions become evident. The pars lateralis is composed of more deeply stained, more closely packed neurons, the pars dorsalis is a less dense, less deeply stained band, and the pars medialis is the very slightly widened out and a little more loosely arranged medial tip of the pars dorsalis which varies in the ease with which it can be differentiated from level to level. The pars lateralis (fig. 16) extends back to the crus in relation with the pyriform lobe cortex in a fashion comparable to that found in other mammals. The pars dorsalis passes over into the neopallial cortex, the connection here being relatively very broad. As the crus region is approached the pars medialis (fig. 16 A) becomes more condensed and deeper staining, and continues into an enlargement of gray on the medial surface, immediately behind the bulb and adjacent to the pars ventralis, the pars posterior of the nucleus olfactorius anterior (fig. 16 B), and, through this latter, becomes continuous with the hippocampal cortex. The pars ventralis lies in the ventromedial portion of the crus immediately behind the olfactory formation and the region of union of the two limbs of the pars externa. Its outer part passes caudalward into the deep layer of the tuberculum and its deeper portion continues directly caudalward as a pars posterior of the nucleus olfactorius anterior. This pars posterior lies at first between the ventricle dorsally, the anterior continuation of the hippocampus medially, the polymorph layer of the tuberculum ventrally and the interbulbar component of the anterior commissure laterally, and is differentiable by the slightly closer arrangement of its cells from the deep part of the tuberculum olfactorium. Caudally the caudate nucleus swings ventrally and the pars posterior intervenes for a time between this area and the polymorph layer of the tuberculum and then disappears. The relations of the pars posterior of the pig are comparable to those in the weasel, but the gray is larger in amount and somewhat better differentiated in the former animal.

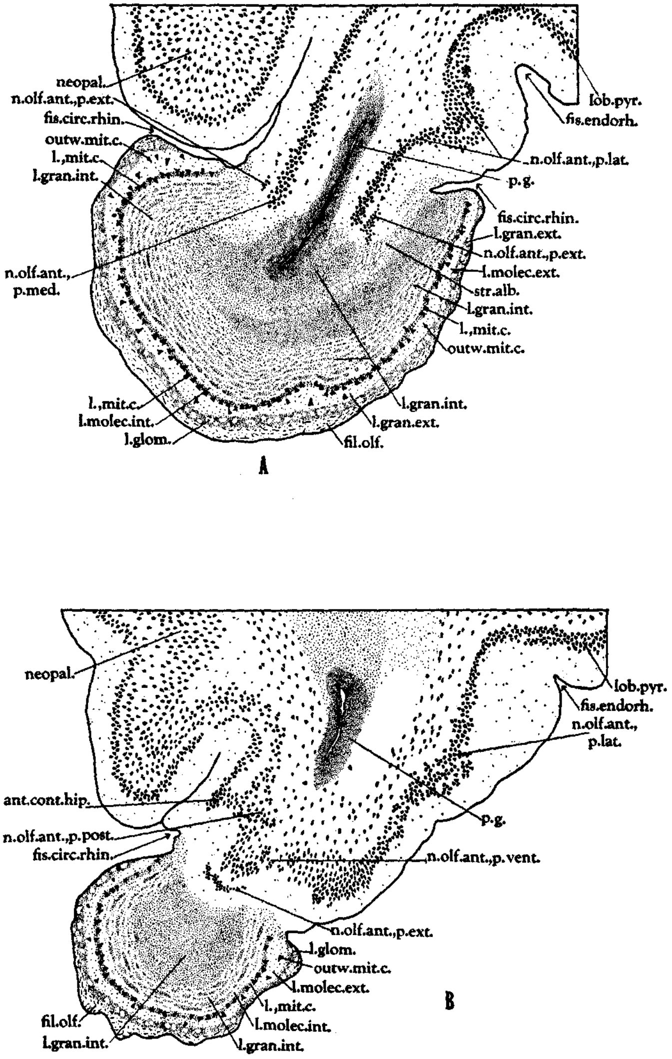

Fig. 16 Drawings of sections from transversely cut series of the pig brain in planes through the attachment of the right olfactory bulb to illustrate the various porions of the nucleus olfactorius anterior. Attention is called particularly to the relations of the pars externa and the presence of a pars posterior of the nucleus olfactorius anterior. Toluidin blue preparations. × 12.5.

The pars externa appears in planes immediately caudal to the rostral tip of the main mass of the nucleus olfactorius anterior. This pars externa (fig. 4 A) consists of a narrow layer of deeply staining neurons, which soon thin out in its midportion leaving the two ends. One of these ends is ventral to the accessory olfactory bulb and, from this relation, comparable to the dorsal limb in the other mammals described but in the pig is medial in position. The outer end of this nucleus, which presumably then would be the ventral limb of other mammals, is lateral in the pig. Both of these extensions (fig. 16 A), which vary greatly in the number of their constituent neurons and in their conspicuousness at different levels, turn ventrocaudalward to meet (fig. 16 B) ultimately in planes through the beginning of the olfactory crus and so to form an encircling mass of gray of the pars externa around the ventricle.

Microscopic structure in insectivores

The brains of two insectivores—the shrew and the mole—have been available for this study. The brain of the mole has been described by Ganser (1882) but no mention was made of the nucleus olfactorius anterior. Only gross descriptions are given of these regions of the brains of the numerous insectivores studied by Le Gros Clark ('24 and '26) but the nucleus olfactorius anterior is described in his 1928 paper. The structure and relations of this nucleus will be described first in the shrew and then the homologous region in the mole compared with it.

SHORT-TAILED SHREW (BLARINA BREVICAUDA). The pars lateralis of the nucleus olfactorius anterior of the shrew begins rostrally as an oval mass of rather closely arranged cells replacing the inner portion of the internal granular layer. It lies between the ependyma of the obliterated olfactory ventricle and the lateral part of the internal granular layer but is separated from each by a cell free zone in which are fiber bundles. This oval cell mass rapidly enlarges and soon shows evidences of being more loosely arranged on its lateral border. As this arrangement becomes more marked, the pars lateralis is separated from the outer part of the internal granular layer by the pars externa and by a fiber mass in which there are scattered neurons. This relation is similar to that illustrated for the mole in figure 5 A. Farther caudalward, after the middle portion of the pars externa has disappeared (fig. 3 E), the pars lateralis begins to alter in shape, its lower border swinging ventromedialward; gradually it assumes a C-shape with the concave part of the C directed medialward and the upper and lower tips extending dorsomedialward and ventromedialward respectively. At such planes only the dorsal and the ventral limbs of the pars externa remain; along the medial half of the bulb the bulbar formation itself is still highly developed. Caudal to this level, at planes through the rostral end of the pyriform lobe, the tips of the C-shaped anterior olfactory nucleus begin to turn toward each other, looking forward to the completion of the ring around the ventricle. The portion which swings dorsalward from the ventral tip shows a more dense arrangement of cells and is thinner than the rest of the layers, this difference being evident after the ring is formed.

The pars externa of the nucleus olfactorius anterior is seen well forward in the olfactory bulb, lateral to the rostral portion of the pars lateralis and separated from it by fiber bundles. In this region the pars externa forms a crescent of small, closely packed, deeply stained neurons which are medial to the lateral part of the internal granular layer. With the disappearance of this granular layer the middle portion of the pars externa thins down and likewise disappears from the field, leaving only the dorsal and ventral limbs. These latter extend caudalward within the crus region, swinging respectively dorsomedialward and ventromedialward and then, as small masses of gray (fig. 3 E), turn toward each other on the medial border and ultimately unite, after which they immediately disappear. Thus it is evident that the pars externa in the shrew forms a ring around the nucleus olfactorius anterior proper, which in turn forms a ring around the ependyma marking the position of the obliterated ventricle. Both limbs of the pars externa, but particularly the dorsal one, are very tiny caudalward. The pars externa apparently differs in Blarina and Macroscelidae in the fact that it forms a periventricular ring in the former but not in the latter shrew.

Just before the nucleus olfactorius anterior proper forms this ring around the ventricle, the rostral tip of the pyriform cortex appears as a band of closely arranged, darkly staining cells at the lateral border of the pars lateralis and fused with it, although clearly differentiable on the basis of cell character. This band increases in size and continues directly caudalward into the main mass of the pyriform cortex (fig. 17). With the gradual development of the pyriform lobe cortex the pars lateralis of the nucleus olfactorius anterior disappears. The pars lateralis of Blarina resembles that of Macroscelidae (Le Gros Clark, '28).

In planes through the caudal end of the olfactory formation the pars dorsalis of the nucleus olfactorius anterior is replaced, beginning lateralward, by the neopallial cortex. Figure 17 shows a plane in which the more medial portion of the pars dorsalis is passing over into the outer layer of the neopallium, the two together forming a continuous loop-shaped band, with the pars dorsalis the wider, less densely arranged portion of the loop. At this level the dorsomedial end of the loop shows a small mass of especially deeply stained neurons which constitutes the frontal pole of the anterior continuation of the hippocampus. As the sections are followed caudalward and further replacement of the pars dorsalis by the deeper part of the neopallium occurs, the loop (except the dorsomedial tip constituted by the anterior continuation of the hippocampus) becomes a circle and then an ovoid mass of cells, predominantly though not exclusively of the character of a pars dorsalis, after which this portion of the nucleus olfactorius anterior disappears. This caudalmost tip of the pars dorsalis has an appearance similar to that figured for the homologous region in the mole (fig. 5 B). After the ends of the loop have joined, the anterior continuation of the hippocampus lies in close approximation to the medial side of the loop and then extends ventralward into relation with the pars medialis of the nucleus olfactorius anterior. The lower portion of the pars medialis of the nucleus olfactorius anterior is gradually replaced by the cephalic end of the septal area, the septo-hippocampal nucleus (Ariëns Kappers, Huber, and Crosby, '36; Young, '36; or primordium hippocampi of Johnston, '15) and by the nucleus accumbens. The relations of the pars dorsalis and pars medialis are essentially those described by Le Gros Clark ('28) for Macroscelididae except that, as is evident from figure 17, there is a direct continuity between the pars dorsalis and neopallial cortex in Blarina, although none was found by Le Gros Clark in the shrew studied by him.

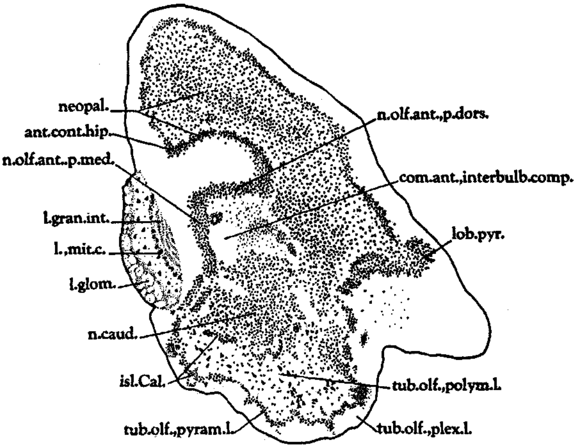

Fig. 17 Drawing of a transverse section through the caudal pole of the olfactory formation and the very large tuberculum olfactorium of the short-tailed shrew (Blarina brevicauda) to show certain relations of the olfactory bulb and the subdivisions of the nucleus olfactorius anterior. Toluidin blue preparations. × 12.5.

The pars ventralis of the anterior olfactory nucleus (fig. 3) of Blarina is characterized by a cellular appearance essentially similar to that of other portions of the nucleus olfactorius anterior but sufficiently different from that of the head of the caudate so that its gradual replacement by the caudate is clearly evident. At this level of replacement the pars ventralis lies dorsal to the tuberculum olfactorium. Between the head of the caudate and the cortical layer of the tuberculum olfactorium are patches of large, multipolar neurons some of which extend out into the folds of the cortical layer and throughout the extent of the tuberculum and so are replaced by the diagonal band of Broca caudalward. These large cells apparently represent the pars posterior of the nucleus olfactorius anterior in Macroscelididae as described by Le Gros Clark ('28), according to whom they extend caudalward between dorsal and ventral laminae of the tuberculum olfactorium, but have, from his figures and his descriptions, a less rostrocaudal extent than in Blarina brevicauda. The present writers regard these cell groups as constituents of the polymorph layer of the tuberculum olfactorium, a statement which they consider to be in entire agreement with Obenchain ('25; compare fig. 17 of the present paper with her illustration of the tuberculum). No nuclear gray homologous to the pars posterior as described for other mammals has been recognized in Blarina.

MOLE (SCALOPUS AQUATICUS). The relations of the nucleus olfactorius anterior of the mole resemble in most essentials those described for the shrew and so need be only briefly summarized here. The main mass of the nucleus olfactorius anterior appears within the olfactory bulb, slightly dorsolateral to the ventricular ependyma and deep to the internal granular layer but separated from both by a relatively cell-free zone. From a small mass of cells it rapidly elongates into a crescent-shaped area (fig. 5 A) and then there appears, lateral to it, the elongated, narrow band of the pars externa, which at first is intermingled with the deeper portions of the internal granular layer but later is clearly separated from this layer by a fiber bundle. Very soon, as the sections are followed caudalward, the middle portion of the pars externa disappears leaving, dorsally and ventrally, small patches of gray which constitute respectively the dorsal and ventral limbs. These dorsal and ventral limbs extend caudally for some distance turning toward each other at their medial tips but never uniting to form a ring as in the shrew. Otherwise the relations are so nearly the same that they are not illustrated. Of the two limbs the ventral is the better developed.

As the midportion of the pars externa disappears the remainder of the nucleus olfactorius anterior increases in size and forms a C-shaped mass which later on is converted into a ring of gray around the olfactory ventricle. The lateral part of this ring, which is continuous with the pyriform lobe cortex around the endorhinal fissure, constitutes the pars lateralis of the nucleus olfactorius anterior (fig. 5 B).

The dorsal and dorsomedial portions of the gray ring, which together form a pars dorsalis (fig. 5 B), lie in broad continuity around the circular fissure with the neopallial cortex which gradually replaces them within the hemisphere. The deep infolding of cortical gray characteristic of this region in the shrew (fig. 17) does not appear in the mole.

The ventromedial portion of the ring in this latter insectivore is continuous with the anterior continuation of the hippocampus which extends down to it along the medial side of the neopallial cortex, disappearing soon after this continuity has been established. This medial portion (fig. 5 B) is sharply differentiable from the anterior continuation of the hippocampus, being obviously of the basal type of gray. The pars medialis is replaced caudally by the pars posterior of the nucleus olfactorius anterior.

The ventral part of the gray ring formed in the crus by the nucleus olfactorius anterior at first lies dorsal to the olfactory formation (fig. 5 B) and, behind this formation, is internal to the highly developed rostral continuation of the cortical layer of the tuberculum and to the gray of the ventral part of the head of the caudate, from neither of which areas is it sharply delimited.

The pars posterior in the mole is the caudal continuation of the pars ventralis of the nucleus olfactorius anterior. It extends caudalward for some distance between the head of the caudate nucleus and the polymorph layer of the tuberculum and is homologous with the similarly designated area of Obenchain ('25) and of Fox ('38) and with the region described under that name elsewhere in this paper, but appears to have no representation in Blarina (see p. 201).

Microscopic structure in chiropteres

FREE-TAILED BAT (TADARIDA MEXICANA). A detailed description of the nucleus olfactorius anterior is to be found in the paper on the bat forebrain by Humphrey ('36) and no further account is necessary. It may be said that, in general, in the bat the nucleus is relatively small and less well differentiated than in most of the mammals thus far considered but better developed than in primates. Although a small pars externa was described no pars posterior was identified. For further details the original paper should be consulted.

Microscopic structure in primates

As far as is known there is no description of the nucleus olfactorius anterior in the primate except for the brief mention made by Tilney and Riley ('21, p. 661) to gray (apparently the pars dorsalis of the nucleus olfactorius anterior) associated with the olfactory tracts in the crus region. The present writers have in course of preparation a paper on certain tertiary olfactory centers of adult man which includes a description of the nucleus olfactorius anterior. Figures of Microcebus by Le Gros Clark ('31), illustrating the relations in this region, show beautifully certain portions of this complex, but these are neither labelled nor described.

MACAQUE (MACACA MULATTA). The nucleus olfactorius anterior of the macaque makes its appearance as the olfactory bulb begins to narrow down toward the crus and in regions in which there is still olfactory formation except for the denuded area on the dorsal surface. In that olfactory bulb which shows an accessory olfactory formation (see p. 155) the nucleus olfactorius anterior was seen approximately at the caudal tip of this formation (just behind the plane of fig. 18 A) and just internal to it. The nucleus soon occupies a position dorsal to the line of the obliterated ventricle (fig. 18 B) and extends from this point caudalward to the place where the crus joins the hemisphere. Throughout this relatively great extent the mass varies slightly in cellular content from level to level, consisting at first of a group of a dozen or so cells forming a rounded mass in the depth of the crus, but, toward the caudal end, where the crus is reduced in size, the nucleus elongates into a considerable band of neurons dorsal to the obliterated ventricle (fig. 18 C). In addition to this main mass of the nucleus olfactorius anterior occasionally scattered neurons of a similar, medium sized, multipolar type occur ventral to the ventricle (fig. 18 B and C) and particularly at the lateral border of the crus, in which region they are most evident although they do not form a continuous mass through out its extent. As the caudal end of the crus is approached the nucleus tends to swing lateralward (fig. 18 D and E) and medialward (fig. 18 D and E) around the angles of the ventricle but does not form a complete periventricular ring in this region. After the crus joins the hemisphere, the ventrally placed, scattered cells increase in number forming a better developed pars ventralis (fig. 18 F and G), that (with the rostral end of the tuberculum olfactorium, from which it is not delimitable in the available material) tends to complete the gray ring around the obliterated ventricle (fig. 18 G).

As the crus passes into the hemisphere the typical subdivisions of the lobar portion of the nucleus olfactorius anterior become evident from their relations to the centers of the hemisphere. The most dorsal portion, constituting a pars dorsalis (fig. 18 E) of the nucleus in question, immediately passes over into the neopallial cortex, leaving a pars medialis, a pars lateralis, and a pars ventralis represented by a few scattered cells (fig. 18 F). The pars medialis (fig. 18 E, F and G), a deeply staining mass of gray, extends directly caudalward for a considerable distance and comes into immediate relation with the anterior continuation of the hippocampus, which forms a deep curve in these forms, following the line of the caudal border of the frontal cortex. This

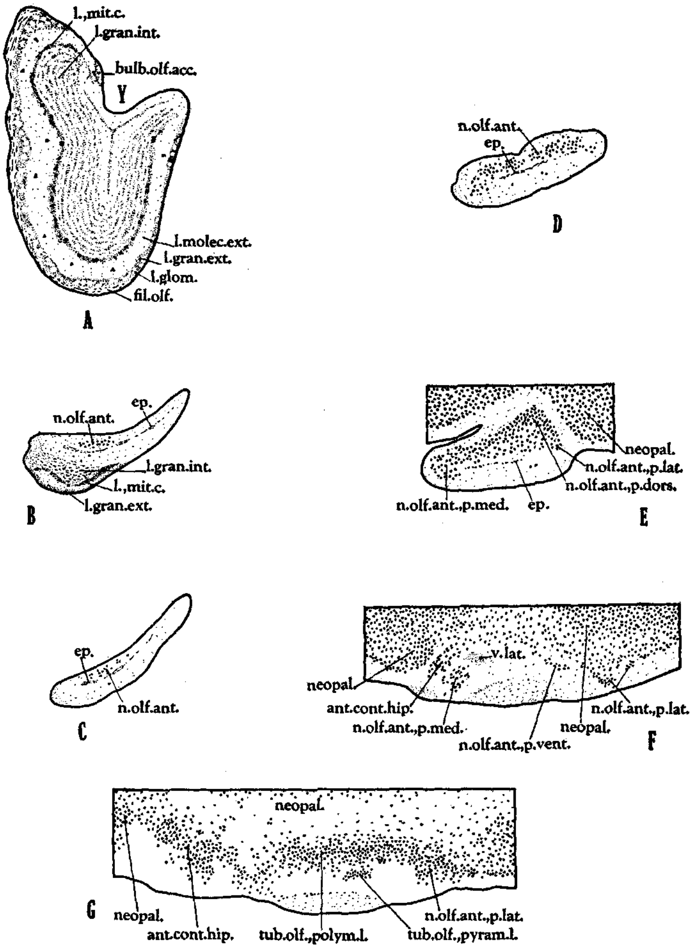

Fig. 18 A group of drawings of Macaca mulatta, showing rostrocaudally from A to G the tiny accessory olfactory formation (A) identified in the one bulb here figured and the greatly drawn out nucleus olfactorius anterior through the crus region (B to E) together with its relations behind the crus to other centers at the base of the hemisphere (F and G). Toluidin blue preparations. × 12.5.

pars medialis is better developed in the monkey than in man (see p. 203). The pars lateralis (fig. 18 E, F and G) is small in the monkey but can be traced along the laterally running lateral olfactory tract into continuity with the pyriform lobe cortex. It consists of small patches of deeply staining cells connected by scattered neurons. The pars ventralis (fig. 18 F), represented, except for an occasional neuron, only within the lobar portion of the nucleus olfactorius anterior, consists of a small group of neurons showing no specific arrangement, which passes by imperceptible transition into the anterior end of the polymorph layer of the tuberculum olfactorium. No pars externa and no pars posterior have been identified in the macaque material studied.

DISCUSSION

The foregoing account shows clearly that a common pattern underlies the morphology of the olfactory bulb in the various reptiles, birds, and mammals, although there are great differences in the proportionate size of the bulb and in the degree of development and clearness in differentiation of the several laminae, depending upon the relative importance of the olfactory system in the form under consideration. A wide range in both the number of peripheral olfactory fibers and the size of the olfactory formation is found not only in mammals but also in reptiles and in birds. Thus the olfactory formation is well developed in turtles and alligators among the reptiles, in such birds as the duck, the chicken, and the dove, and, among the mammals studied, in the opossum, the squirrel, the mouse, the bat, the shrew, the weasel, and the pig. It is smaller but still of typical structure in the macaque and man. The olfactory formation is also reduced in the crow, in which the bulbs are partly fused, in the single bulb of the sparrow, through the larger part of the olfactory bulbs of such lizards as Gila monster and Varanus, and in the snakes studied, and it is rudimentary in the tiny bulbs of the American chameleon, Anolis, and in the horned toad.

It is of interest that a decrease in the number of mitral cells in some of these forms which show a reduction in the olfactory formation—and most particularly in primates—is compensated for to some extent by an increase in size of the individual elements. Outwandered mitral cells are present in certain reptiles and birds, as well as in mammals, but are most numerous in mammals, in which they are found either as supplementary to a highly developed mitral cell layer, in forms in which the olfactory fibers are numerous (as in the shrew or the weasel), or as compensatory in forms such as primates, which show a marked diminution of the mitral cell layer itself.

The accessory olfactory formation reaches its highest peak of development, as indicated by the forms observed thus far, in such lizards as the Gila monster and Varanus, and in the snakes. Among the other reptiles considered, it is well developed in all the turtles but absent in the alligator and in such lizards as the American chameleon (Anolis) and the horned toad. It is likewise absent in all the birds studied. Among mammals a well-developed accessory olfactory bulb appears in the opossum, in all the rodent material available, in the weasel, and in the pig. A small accessory bulb is identifiable in the mole, an even tinier one in the shew, and, in one case, a vestigial accessory formation is demonstrable on the left olfactory bulb of a young macaque, although a comparable structure is lacking on the right bulb of the same animal and in all other available macaque material. No accessary olfactory bulb is evident in the brains of the adult bat or adult man examined. Its possible function in the reception of contact stimuli and its use in following trails, as shown by the recent experimental work of Kahmann ('32), Noble and Clausen ('36), Noble and Kumpf ('36), Wilde ('38) and others, are discussed in the 1939 paper of Crosby and Humphrey.

The fundamental pattern established for the nucleus olfactorius anterior in marsupials by Herrick ('24) and Obenchain ('25) and described for the edentate brain by Sonntag and

Woollard ('25), for the rabbit brain by Young ('36), and for the cat brain by Fox ('38), has been documented for a considerable number of mammalian brains in which this nuclear group either has not been identified or has not been described in detail hitherto. Furthermore, it has been possible to show that this mammalian pattern is definitely foreshadowed in the structure and relations of the homologous gray *in the reptilian and* avian brains.

In 1924 Herrick defined the nucleus olfactorius anterior as unspecialized gray at the base of the hemisphere intervening between the olfactory formation frontally and various centers of the hemisphere caudally. The series studied here show that there is a wide range in the amount of its specialization depending on the form examined and that there may be considerable differentiation of its various parts as Sonntag and Woollard ('25) also found to be the case in Orycteropus. Examples of this are seen not only in the degree of specialization of the various parts but also in the presence only in mammals of a clear-cut pars externa, which is well developed in those forms with accessory olfactory bulbs, and a pars posterior. Nevertheless in principle Herrick's interpretation seems to the present writers to stress the real significance of this nuclear complex, for the pars dorsalis of the nucleus olfactorius anterior grades over into the neocortex (or its equivalent, the vicarious cortex or hyperstriatal complex of birds and the general cortex of reptiles), its pars lateralis is replaced caudally by the pyriform lobe cortex, its pars medialis is in relation with the septal areas and the anterior continuation of the hippocampus, and its pars ventralis with the deep portion of the tuberculum olfactorium and the ventrofrontal areas of the striatal complex. These relations remain constant throughout the series, and are indications of the common pattern for reptiles, birds, and mammals. In all these forms the various portions of the nucleus olfactorius anterior are in greater or less degree in the process of specialization, each portion in the direction of the hemisphere center with which it is related. The amount and differentiation of this complex (and of its individual portions) will depend in any of these forms primarily on two factors. One of these is the extent of olfactory and accessory olfactory formations—that is, the size and the degree of specialization of the bulbar centers. The other factor is the proportionate forward differentiation of the various areas of the hemisphere, of which the neopallium is the most influential in higher mammals. In general the nucleus olfactorius anterior will be large in direct proportion to the degree of development of the bulbar centers and in inverse proportion to the amount of forward specialization of the hemisphere and particularly the cortical regions behind the bulb.

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