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THE BRAINS OF THE SOUTH AMERICAN  
MARSUPIALS CAENOOLESTES  
AND OROOLESTES

BY

JEANNETTE BROWN OBENCHAIN

Hull Laboratory of Anatomy, University of Chicago

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WILFRED H. OSGOOD  
Curator, Department of Zoology

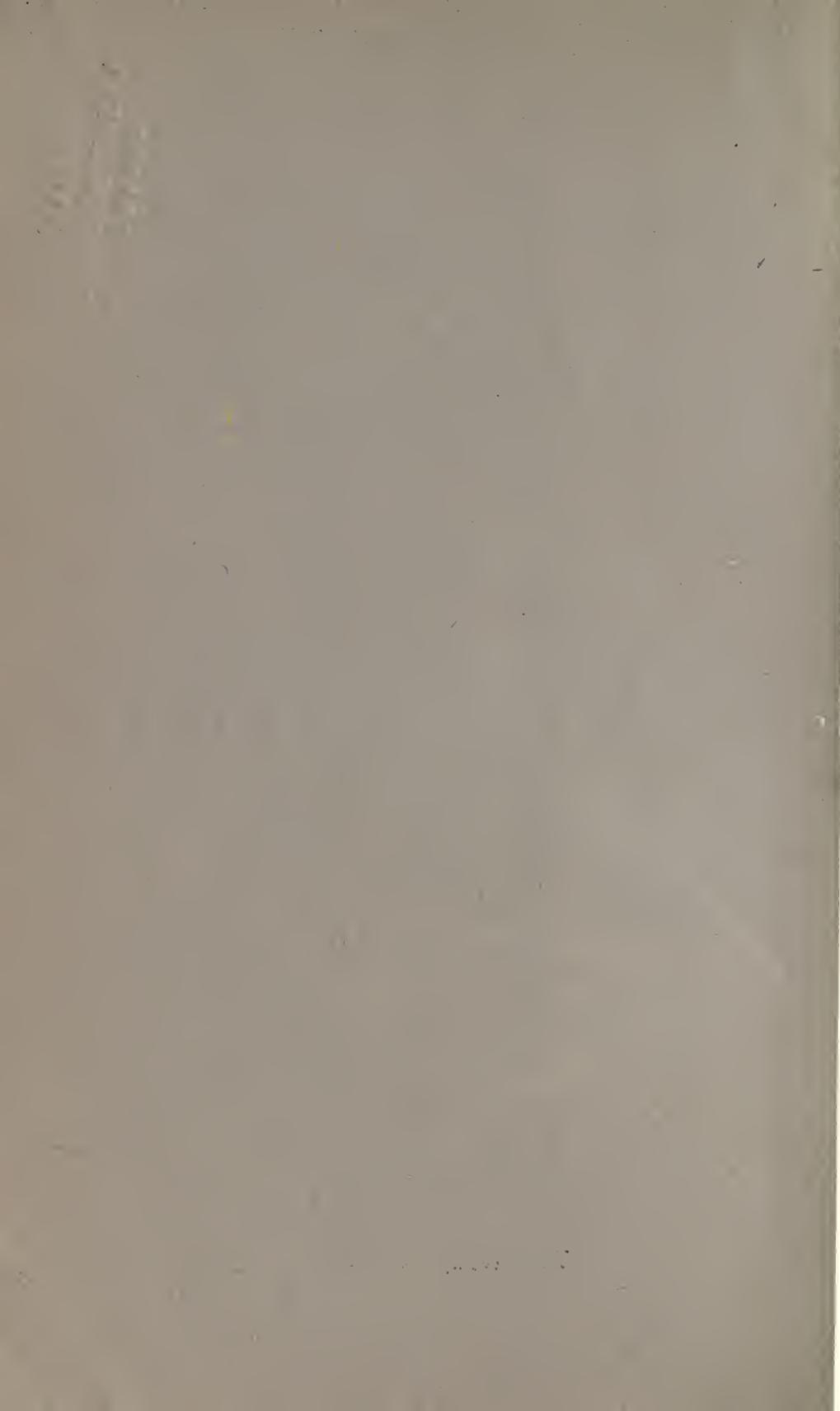


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# THE BRAINS OF THE SOUTH AMERICAN MARSUPIALS CAENOLESTES AND OROLESTES

BY JEANNETTE BROWN OBENCHAIN

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## INTRODUCTION

*Caenolestes* and *Orolestes* are tiny shrewlike marsupials five inches in length of head and body exclusive of the slender tail. They are natives of high Andean forests from Venezuela southward into Peru, and although discovered in 1863, have not been known to science, except by imperfect material, until recent years. Their peculiar dentition has made their assignment to one or the other of the marsupial suborders (*Diprotodontia* and *Polyprotodontia*) a matter of much uncertainty. This question remains even yet, perhaps, in suspense, since the one brain character of evidential value seems to reverse the latest conclusion, based on careful sifting of all non-nervous characters (Osgood, 1921; Obenchain, 1923).

Aside from its bearing upon classification, the study of the brains of these species is warranted by many other considerations. These small marsupials, surviving members of an ancient American group, are characterized by the retention of many primitive features, by the absence of any great degree of specialization, by few non-marsupial characters, by numerous resemblances to the modern peramelids (Australian polyprotodonts), and by lack of affinity to the other living American marsupials, the polyprotodont *Didelphiidae* (Osgood, 1921, pp. 150-151).

*Material.*—The material which forms the basis of the present study consists of the brains of three female specimens, one of *Caenolestes obscurus* and two of *Orolestes inca*. The first brain came from an adult female of *Caenolestes* collected in 1911 in the Colombia-Venezuela boundary region by Dr. Wilfred H. Osgood of the Field Museum of Natural History; it was examined by Dr. C. Judson Herrick, who described and figured its external surface in a short paper (1921, *antea*, pp. 157-162, 3 figures) appended to Dr. Osgood's long monograph on the anatomy and zoological position of *Caenolestes*. Dr. Herrick later offered me the opportunity of studying this brain, if I could convert it into serial sections. The other two brains, from adult females of *Orolestes inca*, were collected by Mr. E. Heller of the Yale National Geographic Society Peruvian Expedition of 1914-15, and were loaned by the U. S. National Museum to the Field Museum to be transferred to me for the purpose of this study. The first specimen alone (*Caenolestes*) has been sectioned and stained. The description of the internal anatomy is therefore based entirely on this one transverse series, which, although somewhat imperfect because of incomplete fixation within the unopened skull, has stained with unexpected brilliancy by the iron-haematoxylin method. This series, owing to the fact that both cells and fibers have been stained, serves remarkably well, all things considered, for the study here undertaken. Since the brain was sectioned whole, its medial surface is known only by means of wax and linear reconstructions made from the sections. These are believed to be reasonably trustworthy, but since they are made from an imperfect series, additional corroboration was greatly to be desired. Therefore the two brains of *Orolestes* were especially welcome. I take this opportunity to thank Mr. W. J. Owen of the Anatomical Institute of Melbourne, Australia, for his kind assistance in the attempt to remove them as nearly intact as possible from the skulls. The smaller of the two brains (No. 194948) was divided by a sagittal cut, the right hemisphere was detached from the brain stem, and drawings

of the medial surface of both the whole brain and the detached hemisphere were made by Mr. Kenji Toda, of the University of Chicago, to whom I am indebted for the five beautiful and accurate air brush pictures of the brain of *Orolestes* (Figs. 1-5). The larger brain (No. 194921) was used for the external views, with correction and supplement from the other where necessary, as in the case of the parafloccular lobes, which the larger brain had lost. The business of clearing these small and fragile brains from membranes and coagulated cerebro-spinal fluid was both tedious and difficult, but fairly successful in the end, and the figures are offered as faithful representations of the actual specimens.

Three air brush drawings of the brain of *Caenolestes* by Mr. A. B. Streedain, formerly of the Department of Anatomy, also may be consulted (Herrick, *antea*, pls. XXI-XXII). This brain, owing to the difficulty of removing membranes and débris, was in somewhat less favorable condition for drawing than were the other two. This applies particularly to the ventral surface, which was further marred by a considerable hole due to faulty fixation.

All three specimens were originally preserved whole, with only a ventral longitudinal opening of the body, in 10% formalin, and subsequently transferred to alcohol. In the case of *Caenolestes*, the brain, when freed from the skull, ballooned out with a glistening white surface, but later shrunk and darkened. The other two brains (*Orolestes*) were quite rigid when uncovered, and presented a dull, light brown surface. All three completely filled the skull. It is hoped that the two brains of *Orolestes* may be successfully converted into sagittal and horizontal series.

*Method.*—The brain of *Caenolestes*, infiltrated in 42 degrees paraffine and blocked in 56 degree paraffine (to minimize brittleness), was cut 10 micra anteriorly and 15 micra farther back, and made about 1200 sections. About 850 sections were drawn at a magnification of 25 diameters with the aid of the Edinger projection apparatus. These have proved a very useful close series for annotation. A wax model made from these drawings, while somewhat disappointing, especially in the midregion, owing to the emptiness of the greatly expanded ventricles (the fragility of the specimen precluded aspiration) and consequent wrinkling and uneven spreading of the thinner portions of the walls, has been an invaluable aid to study. Linear reconstructions drawn to scale have also proved indispensable. An additional series of 31 Edinger drawings with a magnification 85 was made from the precommisural hippocampal region.

## EXTERNAL ANATOMY

Dr. Herrick, in the first account ever given of the brain of *Caenolestes* (or of any caenolestid brain), emphasized its extreme simplicity, the enormous development of its rhinencephalon, the smoothness and limited extent of its neopallium, and called attention to the fact that it most closely resembles the brains of the lowly Australian polyprotodonts, *Notoryctes* and *Perameles*. To this it will be necessary to add the description of the median section of the whole brain and median surface of the hemisphere, as well as a discussion of the other surfaces in the light of knowledge of the internal structure of *Caenolestes*, with reference to changes of nomenclature, or in comparison with the brain of *Orolestes*. This will of course involve some unavoidable repetition.

The two types, *Caenolestes* and *Orolestes*, exhibit only minor differences in external anatomy. Although all three brains are supposed to have come from adult female specimens, they differ somewhat in size and proportions, as may be observed in the table of measurements. *Caenolestes* is the smallest of all, but it has the longest hemisphere. Its cerebellum is smaller and less plump than the other two, and exhibits an extra furrow and convolution—not a matter of great importance, as will be seen below under the description of the cerebellum. It is, however, to be remembered that the three brains represent two genera of caenolestids.

The *olfactory bulbs* are truly enormous, almost half the total length of the hemisphere at the medio-ventral angle. They are of the "sessile" type, with no visible olfactory peduncle in the intact brain. Following Livini (1908), we have called the deep constricting sulcus which marks the posterior border of the olfactory formation, the *fissura circularis* (*fs.circ.*, Figs. 6, 12, 15, 25-28; unlabelled, Fig. 1-5). The circular fissure is a compound structure whose component parts are homologous to portions of fissures described in the brains of other animals. Medially it represents the anterior portion of the *fissura prima* of His, above the antero-medial tip of the rhinal arcuate fissure (*fs.rh.acr.*, Figs. 12, 28); dorsally, after meeting the medial prolongation of the rhinal fissure (*fs.rh.a.*, Figs. 15, 25) at its medial end, it diverges from the latter to leave the interval for an exposed triangle of dorsal olfactory peduncle, and then meets the rhinal fissure again as the latter turns caudad on the lateral surface of the brain (Fig. 14); meets also the anterior end of the endorhinal fissure (*fs.erh.*, Fig. 13) just below, and then drops downward across the wide lateral olfactory tract (*tr.*

*ol.l.*, Fig. 13) overlying the pyriform lobe, to continue as a deep constriction across the base of the brain between the olfactory bulb (*b.ol.* and the olfactory tubercle (*t.ol.*, Fig. 15), finally joining the anterior end of the medial portion of the rhinal arcuate fissure (Fig. 15), and thus completely defining the caudal border of the olfactory formation. Dorsally the olfactory bulb is overhung by the projecting frontal pole of the hemisphere, which conceals the exposed olfactory peduncle from view. The rest of the olfactory peduncle (see *anterior olfactory nucleus*, page 191) is thrust deep into the heart of the olfactory bulb, as recognized long ago in this type of brain by Elliott Smith and others. This condition is partly the result of the great caudal extension of the olfactory bulb itself, partly one of the numerous expressions of the very considerable fore-and-aft "telescoping" characteristic of this brain, which puts it in rather marked contrast to more elongated brains like that of the Virginia opossum (*Didelphis virginiana*), for example. *Didelphis marsupialis*, however, resembles the caenolestid brain in this respect (Beccari, 1910, Fig. 18).

The great hemispherical mass of the tuberculum olfactorium (*t.ol.*) is also delimited by an encircling sulcus, the *fissura rhinalis arcuata* (*fs.rh.arc.*, an adaptation of one of Retzius' names; see Herrick, 1924a). Medially the fissure is homologous to the caudal portion of the *fissura prima* of His. Its posterior more transverse portion has been called the *fissura diagonalis* by Beccari (1910), but his median continuation of it upward in the septum is not followed here (see *tuberculum olfactorium*, page 196). Laterally the rhinal arcuate fissure is usually taken to be homologous to the endorhinal fissure, but this is not strictly accurate, since the endorhinal fissure lies wholly within the pyriform lobe and therefore above the tuberculum, as has been noted in other forms by Smith, Johnson and others. The endorhinal fissure really marks the dorsal border of the massive part of the lateral olfactory tract, which is very wide rostrally, but rapidly diminishes caudally through the loss of fibers to the pyriform lobe and tuberculum olfactorium, so that in its caudo-ventral course it gradually approaches the rhinal arcuate fissure and finally meets it near the posterior limit of the tuberculum (Figs. 13, 15, 33-34). The greatly reduced massive part of the lateral olfactory tract lies at that level within the endorhinal fissure, where the latter fuses with the rhinal arcuate fissure and so comes to an end. In its caudo-ventral course the lateral olfactory tract leaves a thin film of fibers (*tr.ol.l.d.*, Figs. 25-33) covering the pyriform cortex almost to the height of the rhinal fissure and far toward the caudal pole of the pyriform lobe.

Another important fissure visible on the lateral surface of the hemisphere of these brains is the *rhinal fissure* (*fs.rh.*, to be seen in the majority of the figures), which separates the dorsal or neopallial convexity from the latero-ventral pyriform lobe. It traces an almost exactly horizontal course backward over the lateral surface of the brain at the very high level characteristic of the lowly marsupials *Notoryctes* (where it is internal only) and *Perameles* and the insectivore *Erinaceus*, forms whose neopallial development is the least extensive among mammals. Anteriorly the rhinal fissure is a continuation of the deep groove between the projecting frontal pole of the neopallium and the exposed dorsal part of the olfactory peduncle (*fissura rhinalis medialis* of some writers, but here called the *fissura rhinalis anterior*, *fs.rh.a.*, Figs. 12-15), which bends sharply on to the lateral surface of the hemisphere just above the rostral end of the endorhinal fissure and runs horizontally backward at this high level to round the caudal pole of the hemisphere, where it appears upon the median surface as the median rhinal fissure running obscurely forward into the subicular border of the hippocampus (*fs.rh.m.*, Figs. 6, 12, 42-43; *rh.*, Fig. 5, where it probably coincides only caudally with the diagonal groove shown—there has been no control with sections in *Orolestes* so far). Even where imperfectly developed externally the position of the *fissura rhinalis* is unmistakably discernible throughout, and internally it is in *Caenolestes* always clearly defined.

The dorsal convexity or *neopallium* contains only one other externally visible fissure. In *Caenolestes*, "about one-fifth of the distance from the frontal to the posterior pole of the hemisphere there is a distinct, though shallow, transverse sulcus which probably represents the *sulcus orbitalis* of Elliot Smith's descriptions (Herrick, 1921, *antea*, p. 158). Ventrally the orbital fissure is "obscurely confluent" with the rhinal fissure. In the smaller of the two brains of *Orolestes* this fissure seems to be absent as an external groove, but its position is apparently marked by blood vessels. In the reconstructions of *Caenolestes* also it does not show up, and a cursory examination of the sections has failed to reveal it. A more careful study might disclose its position.

The *pyriform lobe* comprises the larger part of the lateral and ventral aspects of the hemisphere. Its dorsal boundary is the rhinal fissure, which is at the same time the latero-ventral boundary of the neopallium. Antero-laterally the pyriform lobe contains the very sharp endorhinal fissure (as explained above, page 179) and below this fissure its antero-lateral boundary is the lateral portion of the rhinal

arcuate fissure (sharply incised in *Orolestes* but not depressed at all in *Caenolestes*), a fissure marking the ventral border of the massive portion of the lateral olfactory tract, as the boundary of the tuberculum, since the latter appears just ventral to this line.

The greatly widened caudal portion of the pyriform lobe is divided into two distinct parts by a very important fissure so faintly indicated externally that its existence was unsuspected before the brain was sectioned. This is the *fissura amygdaloidea* (1913, 1923) of Johnston (*fs.amg.*, Figs 2, 3, 6, 12, 13, 15, 36-43). In the sections it branches quite clearly from the rhinal arcuate fissure a short distance in front of the caudal pole of the tuberculum (between Figs. 35 and 36), and very soon disappears as a recognizable fissure. Internally it is quite distinct throughout its course, marking the quasi-horizontal line of junction between the sharply defined ventral edge of the pyriform cortex and the lateral border of the amygdaloid complex which occupies practically the entire base of the hemisphere behind the tuberculum. The rather pronounced sculpturing of this region is due to the state of development of the different amygdaloid nuclei, which have been so thoroughly worked out in the Virginia opossum by Johnston (1923). These will be more fully described further on, in connection with the internal anatomy of this brain (page 201).

In *Caenolestes* a very salient caudo-ventro-lateral prominence corresponds to the "natiform eminence" of Elliot Smith (1895b) in *Notoryctes* (*em.nat.*, Figs. 37-41; unlabelled, Fig. 2, pl. XXI, *antea*, Herrick; cf. *Orolestes*, figure 3 here, which shows it much less distinctly). It is due both to an actual thickening of the lateral wall of the hemisphere in this region and, in greater degree perhaps, to the lateral cupping of the hemisphere to accommodate the wide midbrain. Elliot Smith thinks that the temporal bending of the hemisphere has been a main factor in the formation of this eminence. This is much more strongly suggested in *Notoryctes* than in *Caenolestes* (see page 213).

The median section of the brain of *Caenolestes* is known only in wax and linear reconstructions, but the smaller of the two brains of *Orolestes* was divided sagittally, and figures 4 and 5 show respectively the left median section of the whole brain and the median surface of the right hemisphere. Figure 6 is a linear reconstruction of the left hemisphere (reversed) of *Caenolestes*.

The third ventricle and external medial surface of the brain of *Orolestes* were so filled or coated with a hard coagulum of the same color as the tissue and so tightly adherent to it that it was not found

possible to remove it without some laceration of the tissue. Thus the edges of the massa intermedia (*m.i.*, Fig. 4) were somewhat frayed, the aqueduct was probably widened, and the epiphyseal attachments and choroid roof of the third ventricle were torn. But these defects, regrettable as they are, do not greatly impair the value of the section for present purposes. At least the sacrifice of the other brain with the prospect of no better success did not in the circumstances seem to be justified.

The large anterior or ventral commissure of *Orolestes* (*v.*, Figs. 4 and 5) is slightly oval and considerably darker than the rest of the surface, standing out sharply. That of *Caenolestes* (*v.*, Fig. 6) is similar in size, shape and position. The dorsal commissure (*d.*) of *Orolestes* appears as a moderately darker and distinctly bilaminar mass occupying the dorsal and posterior borders of this portion of the lamina terminalis (lamina supraneuroporica of Johnston), enclosing a small whitish triangular space which gives the impression of being without transverse fibers. The dorsal commissure of *Orolestes* (counting it only as the darkened bilaminar mass) thus exhibits macroscopically the typical marsupial form, while that of *Caenolestes* (*d.*, Fig. 6) as reconstructed from sections, shows only the merest hint of bilaminarity in the slightly reentering anterior angle and the dorso-caudal prolongation ("splenium"), suggesting an intermediate type between the solid rounded type of the monotremes and the bilaminar type of the marsupials. The reconstruction of *Caenolestes* was made from the exact midline of the sections, the outline enclosing only the area through which commissural fibers were coursing. These fibers are much less dense in the ventral than in the dorsal region of the commissure, owing to the intermingling of many cells (bed or nucleus of the dorsal commissure) with the fibers in its ventral region.

In *Orolestes* the third ventricle (Fig. 4), as seen from the median surface, has the form of a tall parallelogram tipped slightly backwards and downwards. Its walls are formed anteriorly by the lamina terminalis, whose upper half is greatly thickened by the two commissures, while the lower half remains very thin; posteriorly, by the almost vertical mammillary body and tuberculum posterius in line with the rostral opening of the aqueduct (*aq.*) and the thick anterior end of the tectum mesencephali (*tect.*); dorsally by the choroid roof and the epiphysis; ventrally by the thin floor plate containing the small chiasma (*ch.*) rostrally, and the infundibular lumen more caudally; laterally, by the median surfaces of the thalamis. The upper half of the third ventricle is almost filled by the enormous oval massa intermedia, which

so nearly approaches the neighboring walls as to leave on three sides of it only two very narrow passages leading into the aqueduct. The lower half of the ventricle is quite open, and the thalamic lateral wall displays a diagonal sulcus running backward and downward from the middle of the lower border of the massa intermedia to the posterior wall of the ventricle just above the floor. The ventricle is also deepened laterally just above the floor in two places—the preoptic recess and the mammillary recess. The interventricular foramen opens into the narrow canal between the dorsal commissure and the massa intermedia.

A very sharp midbrain flexure results in the formation of a deep and narrow vertical cleft across the base of the brain which folds a section of it between the pons and the mammillary region together like the pages of a book. The tectum mesencephali (*tect.*) is entirely concealed from above by overlying structures, the rostral three-quarters by the cerebral hemispheres and the caudal quarter by the anterior tip of the median lobe of the cerebellum. (Figure 4 shows a gap between the hemisphere and the cerebellum, due to a mass of coagulum afterwards cleared away; the relations in *Caenolestes* and *Orolestes* are the same.) "This is in contrast to the usual marsupial arrangement, for the corpora quadrigemina are in most cases well exposed dorsally. (*Petaurus* is another exception; see Elliott Smith, 1895, p. 188)" (Herrick, 1921, *antea*, page 158). The condition in *Orolestes* and *Caenolestes* is apparently one of the many expressions of the fore-and-aft compression already mentioned. Partly in response to the crumpling of the brain base as described above, the tectum displays a marked caudal prolongation, emphasized by its recurved keel, as indicated by the forward point of attachment of the anterior medullary velum (*v.m.a.*, Fig. 10). Laterally the posterior colliculus is even more caudally extended (*col. p.*, Figs. 7, 8, 10). The cerebellum, which will be described below, fits snugly into and around these structures, behind an almost perpendicular anterior medullary velum, and below, behind and above the tectum.

The median surface of the cerebral hemisphere of *Orolestes* (Fig. 5) and of *Caenolestes* (Fig. 6) exhibits a flattened surface anteriorly, in close apposition with its fellow, and a deeply concave postero-median surface, hollowed out to accommodate the bulky midbrain. It is traversed by four prominent arcuate fissures, concentrically arranged and different in extent and curvature. These are, in order from without in, the hippocampal, fimbrio-dentate, fimbrio-alvear (to coin a term), and choroid fissures.

The outermost or *hippocampal fissure* (*fs.hip.*, Figs. 5 and 6) apparently describes almost three-quarters of a circle in *Orolestes* (Fig. 5), stretching from the *fissura circularis* (*fs. circ.*) upward, backward, downward and forward nearly to the posterior end of the *tuberculum olfactorium*. The same fissure in the reconstruction of *Caenolestes* (*fs.hip.*, Fig. 6) falls short of this at both ends. It does not reach the *fissura circularis* rostrally and it ends more briefly caudally near the medial prolongation of the *fissura amygdaloidea*, as the latter goes forward towards the posterior end of the *choroid fissure*. Perhaps also in *Orolestes* what appears to be the strongly recurved temporal end of the hippocampal fissure is really the *fissura amygdaloidea medialis*. Indeed this interpretation is suggested by the sudden pronounced shallowing and narrowing of the fissure at the exact point where a slight diagonal fissure runs into it from behind. The posterior end of the diagonal fissure coincides with the apparent level of the caudal end of the amygdaloid fissure on the lateral surface, which on the figured lateral view of the left hemisphere (Fig. 3) is much less clearly indicated than on the right (Fig. 5). The sections of this particular right hemisphere will, when made, clear up this point, which now rests partly on the external configuration of the hemisphere of *Orolestes* and partly on the internal configuration of that of *Caenolestes*.

The second fissure, the *fimbrio-dentate fissure* (*fs.fim.d.*) extends also in *Orolestes* (Fig. 5) to the *fissura circularis*, just below the *fissura hippocampi*. In *Caenolestes*, however, it drops sharply downward away from the hippocampus entirely, and ends briefly just in front of the dorsal commissure (Fig. 6). This portion of the fissure seems to be purely a response to the pressure of a blood vessel which is lodged in the canal formed by the corresponding fissures of the two hemispheres (Figs. 6, 17b). The postcommissural and main portion of the fimbrio-dentate fissure separates the *gyrus dentatus* (*gy.dent.*) not from the massive *fimbria*, but from the extraventricular ammon's horn or inverted hippocampus, with its thin coating of subpial alveus fibers, and it is therefore really an *alveo-dentate fissure* in this region. Posteriorly it is both less extensive and less recurved than the hippocampal fissure.

The third fissure seems to have no name, but it is nevertheless quite distinct as the line of demarcation between the massive *fimbria* and the *alveus*-coated extraventricular hippocampus (ammon's horn), defining its rolled ventral limit. It might be designated as the *fimbrio-alvear fissure* (*fs.fim.al.*, Figs. 6, 17a; unlabelled, Figs. 5, 35-38). It begins rostrally just behind the dorsal commissure as an offshoot of

the fimbrio-dentate fissure, dropping rapidly away from the fimbrio-dentate fissure as the extraventricular hippocampus widens, and it runs out caudally as the massive fimbria tapers down to nothing at the posterior end of the choroid fissure (just in front of figure 39).

The innermost or *choroid fissure* (unlabelled, Fig. 5; *fs.ch.*, Figs. 6, 17a, 35-39; Fig. 39 is really just behind the caudal end of the choroid fissure) extends from the ventral tip of the dorsal commissure backwards and downwards in a smooth curve outlining the ventral border of the fimbria and the thalamo-hemispheric junction. In *Caenolestes*, as noted above, the internal medial prolongation of the fissura amygdaloidea can be quite clearly traced forward to the neighborhood of the caudal end of the choroid fissure.

Other features of the medial surface of the hemisphere are the *tuberculum olfactorium* in profile behind the olfactory bulb, followed immediately in *Oroestes* by the small ventro-median eminence (Fig. 5, unlabelled) which is probably due to the nucleus of the lateral olfactory tract (*nuc.tr.ol.l.*, Figs. 36-38). This small tubercle appears in *Notoryctes* (Elliot Smith, 1895b) and in a number of other marsupials and lowly eutherian mammals, but is apparently absent or not very prominent in *Caenolestes*, although the nucleus, as will appear below, is well developed. It is, however, partly covered by the *tuberculum olfactorium*, and this masks it to some extent. The *amygdaloid complex* (*amg.*, Fig. 6; unlabelled, Fig. 5) extends upward as high as the position of the medial portion of the amygdaloid fissure (*fs.amg.m.*) already described, and the posterior pyriform cortex (*cx.pir.p.*) curves around the caudal pole of the hemisphere to form the more temporal subicular border between the medial extensions of the rhinal and amygdaloid fissures, in the familiar mammalian pattern. From the postero-medial extension of the rhinal fissure (*fs.rh.m.*) forward to the antero-medial extension of the same fissure (*fs.rh.a.*) the space above the hippocampal fissure is occupied by neopallium. In front of the anterior rhinal fissure the hippocampal cortex is in cellular continuity with the dorso-medial portion of the anterior olfactory nucleus (*nuc. ol. ant.d.*, Fig. 26), the peduncular or postbulbar gray matter which laterally merges without interruption into the pyriform cortex (see page 192). Save for these rostral and caudal junctions the lateral and medial olfactory cortices are split apart dorsally by the wedge-like neopallial cap of the hemisphere.

The entire length of the *fissura prima* of His appears upon the median surface of the hemisphere as the visible portions of the *fissura circularis* rostrally and *fissura rhinalis arcuata* caudally (see page

178). Between it and the lamina terminalis lies the precommissural area (paraterminal body) of Elliot Smith, the parolfactory region of Johnston, the septum of most neurologists (*a. prcom.*, Fig. 6; unlabelled, Fig. 5). The nucleus parolfactorius medialis, the nucleus of the diagonal band of Broca, the precommissural fornix, olfacto-hippocampal fibers, and the medial forebrain bundle (*fasciculus medialis telencephali*), are the more superficial structures lying above the posterior part of the fissura prima (medial part of the fissura rhinalis arcuata). The sharply grooved dorso-medial margin of the hemisphere is the imprint of the longitudinal sinus, which is seen in position in figure 4.

The enormously expanded lateral ventricle of *Caenolestes* (*v.l.*, Figs. 28-42) is probably not pathological, but the result of defective fixation. As a cursory inspection of the more caudal sections will show, a recurved temporal horn has not even begun to form. The posterior horn, present in the Virginia opossum, is also absent in *Caenolestes*. In the lower rostral wall of the ventricle a flaring opening leads into a narrow crooked canal, which in turn expands into a widened terminal sac. These constitute the olfactory ventricle (*v.ol.*, Figs. 12-15, 17, 23-27).

*Cerebellum*.—(Figs. 1, 3, 4, 7-10, 10a and 10b, 41-44; also Herrick, 1921, ante, pl. XXI.) The cerebellum of *Caenolestes* and *Orolestes* (the two forms are practically identical in general structure) very neatly fills the gap between those of *Notoryctes* and *Perameles*, the two simplest mammalian cerebella hitherto described. (Elliot Smith, 1902b, 1903c, d, e). The cerebella of the insectivores *Macroscelides* and *Erinaceus* (also described by Elliott Smith, 1902c, 1903c) probably occupy the fourth and fifth places in the series. The cerebellum of the Virginia opossum is considerably more complex than any of those mentioned.

Of the three fundamental cerebellar lobes separated by the fissura prima (*fs.pr.*) and fissura secunda (*fs.s.*), the median and posterior lobes differ little in the first four forms named above. But the anterior lobe grades very clearly from the simple unfissured lobe of *Notoryctes* (10a), through *Caenolestes* (Figs. 4, 7-10) or *Orolestes*, with two lobules separated by the deep fissura preculminata (*fs.prcul.*), and a third well developed lobulus, the lingula (*lg.*), which is not separated from the rest by a fissure, to *Perameles* (Fig. 10b), with an anterior lobe crossed in the midline by four fissures of varying depth. The anterior lobe and the fissura prima are entirely concealed in the intact

brain. The visible portion of the cerebellum is formed by the exposed parts of the median and posterior lobes. It is crossed in the midline by a ventrally concave fissure, the fissura secunda (*fs.s.*), separating a small postero-medial convolution, the uvula (*uv.*) belonging to the posterior lobe, from the larger median lobe above. In *Caenoestes* but not in *Oroestes*, the secondary fissura suprapyramidalis (*fs.spyr.*), shallow but sharp, divides the median lobe into a large suprapyramidal region (*p.spyr.*) and a slender curved ventral convolution, the pyramis (*pyr.*), concentric with the uvula, which fills the ventral concavity of the fissura secunda. The other lobule of the posterior lobe, the nodulus (*nod.*), lies entirely hidden on the ventral surface of the cerebellum, being separated from the uvula by the concealed fissura postnodularis (*fs.pnod.*). The cerebellar ventricle (*v.cb.*) is seen between the nodulus and the lingula.

The large mushroom-shaped pedunculate lateral masses projecting beyond the lateral lobes (these indicated only by a very slight partial constriction) are the paraflocculi (*pfloc.*), the dorsal components of the floccular lobes. The ventral components are the tiny flaplike flocculi, concealed from view, being plastered against the medulla beneath the paraflocculi, from which they are separated by the fissura floccularis (*fs.floc.*). The fissura parafloccularis (*fs.pfloc.*), visible laterally, separates the paraflocculus from the median lobe. It cuts down to the floccular peduncle between these structures.

All the cerebellum save the floccular lobe and the lateral lobes (area pteroidea, *a.pt.*, in part) corresponds probably to the vermis of higher cerebella. The lateral lobes similarly are probably homologous with the cerebellar hemispheres.

The deep nuclei (*deep nuc.*) form a pair of large oval masses almost meeting in the midline, with a large area of their ventral surface exposed in the roof of the fourth ventricle. They exhibit the mammalian characteristic of complete separation from Deiters' nucleus, as van Höevell (1916) found in some other marsupials. There are only slight indications of differentiation into separate nuclei (dentate and roof nuclei).

Since the cerebellum of *Caenoestes* and *Oroestes* will form part of the next report on these brains, it need not be further discussed at this time. The intra- and extracerebellar relations will be partially clarified by the diagrammatic reconstructions, figures 7-10, together with the sections, figures 41-44. The nomenclature follows the usage of Elliot Smith.

*Measurements*.—The dimensions of these three brains as measured on the alcoholic specimens are as follows:

	<i>C. obs.</i> *	<i>O. inca</i>	
	18507 F.M.	194948 U.S.N.M.	194921 U.S.N.M.
1. Total length, tip of olfactory bulb to first spinal nerve .....	14.1 mm.	16.5 mm.	19.1 mm.
2. Length, tip of olfactory bulb to end of cerebral hemisphere .....	2.6	3.0	3.6
3. Length of cerebral hemisphere.....	10.0	9.3	8.8
4. Length of cerebellum on longitudinal axis of brain in median plane .....	3.0	5.0	6.2
5. Greatest width of olfactory bulbs.....	7.6	7.8	7.9
6. Greatest width of both cerebral hemispheres .....	11.8	11.8	12.6
7. Total width of cerebellum and floccular lobes .....	11.0	11.7	....
8. Width of cerebellum exclusive of floccular lobes .....	8.8	11.0	11.0
9. Maximum vertical height of cerebral hemispheres .....	...	7.9	8.9
10. Distance of orbital fissure behind rostral tip of hemisphere.....	(2.0)*	2.3*	2.4
11. Distance of rhinal fissure below vertex at orbital fissure .....	...	2.7*	4.2
12. Length, head and body .....	107.0	(89.0)	(102.0)
13. Length, tail .....	118.0	115.0	116.0
14. Length, total .....	225.0	204.0	218.0
15. Weight of brain, immediately out of 80% alcohol .....		760.9 mg.	961.0 mg.
* <i>C. obscurus</i> , measurements 1-11, from Herrick (1921); 12-14, from Dr. Osgood.			
* Position of orbital fissure in <i>C. obscurus</i> is "about one-fifth of the distance backward from the frontal to the posterior pole of the hemisphere".			
* Orbital fissure not very clear in <i>O. inca</i> , No. 194948.			
<i>O. inca</i> No. 194921 had probably all of cervical cord attached, but lost parafloccular lobes on removal from the skull.			
<i>O. inca</i> No. 194948 was broken off just behind cerebellum, in removing it from the skull.			

## INTERNAL ANATOMY

The twenty-two simplified cross sections from the hemisphere of *Caenolestes obscurus* (Figs. 23-44) and the linear reconstructions of the hemisphere or of parts of it (Figs. 12-15, 17a and b) may perhaps, with the aid of the figures and descriptions of the external surfaces, render a brief and incomplete account of the internal anatomy comprehensible. The following table of critical levels and their section numbers may also assist in the orientation of internal structures.

Sec. 1—Anterior tip of the olfactory bulb.

Sec. 225—Anterior tip of the frontal lobe of the neopallium (Fig. 23).

Sec. 400—Caudal (medio-ventral) limit of the olfactory bulb, adjoining the tuberculum olfactorium (Fig. 25).

Sec. 710—Caudal limit of the tuberculum, adjoining the amygdaloid complex (Fig. 36).

Sec. 935—Posterior tip of the cerebral hemisphere (Fig. 44).

## PRIMARY OLFACTORY AREA

The description of the histological pattern of the *bulbar formation*, both ordinary and accessory, may be dispensed with here, in view of its similarity to that of the Virginia opossum, already described in detail by McCotter (1912). Contrary to the condition in the opossum, however, the horizontal diameter of the olfactory bulb in *Caenolestes* is greater than the vertical diameter. The usual medial displacement of the olfactory ventricle is emphasized here by the considerable dorsoventral flattening of the olfactory bulb. This displacement may perhaps be a condition of interest in connection with the disposition of the olfactory tract fibers.

The well developed *accessory olfactory bulb* (*b.ol.ac.*, Figs. 12, 14, 23-24) is embedded in the postero-dorsal olfactory formation beneath the overhanging frontal pole of the neopallium. It is outlined by a slight fissure. Its peripheral nerve, the *vomeronasal nerve* (*n.vn.*, Figs. 12, 14, 23-24) is quite clear as it curves up over the medio-dorsal angle of the olfactory bulb and spreads out to cover the surface of the accessory bulb. The *secondary tract* of the accessory bulb passes laterally and superficially and helps to make up the *pars dorsalis* of the lateral olfactory tract (*tr.ol.l.d.*, Figs. 23 ff.). The olfactory tracts, which, as Cajal pointed out (1911), arise indiscriminately from all parts of the olfactory formation and are without specificity (save for the fibers from the accessory bulb), first condense in the center of the bulb some distance in front of the olfactory ventricle (*tr.ol.*, Figs. 12-15). Since they so quickly begin to distribute to the secondary olfactory areas and even in part (intermediate olfactory tract) to receive fibers from them, their description will be continued below under that head.

## SECONDARY OLFACTORY AREAS

The olfactory fibers spin a whorl around the olfactory ventricle, much thicker on the lateral side than elsewhere. A second independent half-whorl forms within the first, between its thick lateral portion and the ventricle. This mass of fibers, composed of secondary (direct) and tertiary olfactory fibers, soon rounds up in the lateral wall of the ventricle as the intermediate olfactory tract (*tr.ol.i.*, Figs. 23-28), largely forming the rostral limb of the anterior commissure (*c.a.*, Figs. 24-28). Meanwhile, between it and the lateral part of the first whorl (the massive portion of the lateral olfactory tract, *tr.ol.l.*) appear the most anterior cells of the peduncular grey or anterior olfactory nucleus, pars lateralis (*nuc.ol.ant.l.*, Figs. 12-15, 17, 23-25). This growing

cell mass rapidly increases the widening interval between the lateral part of the big whorl externally and the half-whorl internally, and immediately begins to contribute tertiary olfactory fibers to the inner half-whorl, the intermediate or commissural olfactory tract, which also continues to receive secondary olfactory fibers from all parts of the olfactory formation. Still farther back the tuberculum olfactorium (*t.ol.*, Figs. 13, 28) cuts the outer whorl into two parts, the *lateral olfactory tract*, much the largest of all the olfactory tracts, and the slender *medial olfactory tract* (*tr.ol.m.*, Fig. 28). The *intermediate tract*, which retains its subependymal position back to the point where the head of the caudate nucleus (*nuc. caud.*, Fig. 28) overlies it, soon contains perhaps more tertiary than secondary fibers, and is therefore labelled only anterior commissure (*c.a.*) from figure 24 back.

The *lateral olfactory tract*, the most widely distributed of the three, becomes superficial (*tr.ol.l.*, Figs. 3, 12, 25) behind the fissura circulalis, forming the medullated external fiber layer of the lateral surface of the hemisphere over most of its extent below the rhinal fissure. It may be divided into several parts: anteriorly, two peduncles, a subventricular ventral peduncle (*tr.ol.l.p.v.*, Figs. 24-27) a part of which caudally becomes independent and is then called the medial olfactory tract (*tr.ol.m.*, Fig. 28) as noted above, and a supraventricular dorsal peduncle (*tr.ol.l.p.d.*, Figs. 23-24) with two roots, a ventral root, below the accessory olfactory bulb, and a dorsal superficial root which is continued caudally as the pars dorsalis of the lateral olfactory tract (*tr.ol.l.d.*, Figs 25 ff.) ; a clubshaped massive portion (*tr.ol.l.*, Figs. 23-35) filling the interval between the endorhinal and the rhinal arcuate fissures, wide anteriorly but decreasing to the vanishing point as these fissures meet (*fs.erh.*, *fs.rh.arc.*, Figs. 13, 33); posteriorly a pars ventralis (*tr.ol.l.v.*, Figs. 29 ff.), distributing to the tuberculum, nucleus of the lateral olfactory tract (*nuc.tr.ol.l.*, Figs. 12, 36-38) and other amygdaloid nuclei, and perhaps also to the diagonal band nucleus (*nuc.d.b.*, Figs. 32-33). The small *medial olfactory tract* (*tr.ol.m.*, Fig. 28) can be seen turning sharply downward into the plexiform layer of the tuberculum at its medial border, where some observers (e.g., Livini, 1908) recognize a terminal nucleus of the median olfactory tract in a large median rolled portion of the tubercular formation. Such a structure is present here (*nuc.ol.m.*, Fig. 31). Beccari (1910) inclines to doubt the distribution of secondary olfactory fibers to any extent to the tuberculum, but such evidence as these sections give, while not at all conclusive, seems to point to it.

*Anterior olfactory nucleus.*—The less differentiated postbulbar gray matter of the rhinencephalon has been termed by Herrick (1910, pp. 191-2, Figs. 9 and 10) the anterior olfactory nucleus. In *Caenolestes* it is almost entirely intrabulbar and in direct continuity with the rest of the more ventral gray subjacent to the lateral olfactory tract. Rostrally therefore it completely surrounds the olfactory ventricle. It corresponds essentially to the peduncular gray of Cajal, and is not included in his pyriform lobe. It is here excluded from the pyriform lobe, though earlier, following Johnston's definition of the pyriform lobe as all the gray underlying the lateral olfactory tract, I counted it a part of the pyriform lobe (Obenchain, 1923). Since its lateral border is farthest advanced rostrally, this periventricular rhinencephalic ring appears incomplete in the more rostral sections (Figs. 23-26), and since the pyriform cortex is also advanced rostrally beyond some portions of the anterior olfactory nucleus, the whole of the latter is never seen in any transverse section. The anterior olfactory nucleus, on both topographical and histological grounds, may be subdivided into several parts, all in cellular continuity rostrally. I have, as far as seemed advisable, conformed to the terminology applied to the different parts of the anterior olfactory nucleus in the Virginia opossum (Herrick, 1924a). Divergences will be noted as they occur.

The *lateral part* (*nuc.ol.ant.l.*, Figs. 12-15, 17, 23-25), rostrally most advanced, passes caudally without interruption into true pyriform cortex, and therefore has no really definite posterior limit. The pars lateralis is extended medially above the olfactory ventricle as the pars dorsalis (*nuc.ol.ant.d.*, Figs. 12-15, 17, 25-26); it corresponds to Cajal's superior peduncular nucleus. Just in front of the antero-median extension of the rhinal fissure (*fs.rh.a.*) it comes to the surface, as noted above, and just behind it fuses with the cell mass of the overlying neopallial frontal pole. More caudally and below the ventricle the anterior olfactory nucleus is also prolonged medially by another hooklike extension, the *pars latero-ventralis* (*nuc.ol.ant.l.v.*, Figs. 12, 15, 17, 26), and beyond that the *pars posterior* (*nuc.ol.ant.p.*, Figs. 12, 15, 17, 27-29), which fills the wedgelike interval in front of the fusion of the head of the caudate nucleus and the tuberculum olfactorium. The pars posterior extends further back than other portion of the anterior olfactory nucleus, but it is neither in continuity with the caudate nucleus—forming the rostral portion of its head, as in the turtle, *Cistudo carolina* (Johnston, 1915)—nor with the deeper layer of the tuberculum, as in the alligator (Crosby, 1917). It stops bluntly just rostral to the fusion of the caudate head and the tuberculum. This part

of the anterior olfactory nucleus never shows any appreciable degree of differentiation, probably owing to the too purely olfactory character of its connections. The latero-ventral and posterior parts of the anterior olfactory nucleus as here described do not exactly coincide with the divisions in the Virginia opossum. More caudally the dorsal and posterior parts meet medially, thus completing the anterior periventricular rhinencephalic ring by means of a *pars medialis* (*nuc.ol.ant.m.*, Figs. 12, 15, 17, 26).

At the dorso-medio-rostral border of this ring there is a small superficial condensation of cells. This is the anterior tip of the *hippocampal formation* (*hip.a.*, Figs. 12, 17; *cx.hip.a.*, Fig. 26). It corresponds to a similar dorso-lateral *pyriform* condensation (*cx.pir.a.*, Fig. 25), which, although it appears in more rostral sections, does not quite reach the rostral border of the ring. The lateral and medial olfactory cortices (*pyriform* and *hippocampal*) are thus only *indirectly* continuous rostrally by a double bond (*supra-* and *infraventricular*) through the agency of the anterior olfactory nucleus, while, as we have seen, they are directly continuous caudally. There are thus two periventricular rhinencephalic rings, a smaller transverse and a larger horizontal one, which are partially fused anteriorly.

The medial part of the anterior olfactory nucleus soon passes obscurely backward into the lateral parolfactory nucleus (*nuc.pol.l.*, at a level between figures 26 and 27). The latero-ventral part, which is transitional between the lateral and posterior parts, continues backward into the ventral pyriform cortex underlying the massive portion of the lateral olfactory tract along the lateral border of the tuberculum (*pars ventralis, lobus piriformis*, Gray, 1924; *ex.pir.v.*, Figs. 27-33), and still more caudally perhaps into the diffuse region of the anterior perforated space (Johnston, 1923) (*l.perf.a.*, Figs. 35-38), along the anterior portion of the amygdaloid fissure (*fs.amg.*, Figs. 12, 15, 36-38).

One other—and the most interesting—part of the anterior olfactory nucleus remains to be described, the *pars externa* (*nuc.ol.ant.ex.*, Figs. 13, 15, 24-26). It is apparently the result of the doubling of the intrabulbar portion of the lateral part of the anterior olfactory nucleus, which is the only portion to exhibit this phenomenon. The external nucleus appears rostrally as a vertical plate of smaller cells between the *pars lateralis* and the massive lateral olfactory tract. It is separated from the subjacent *pars lateralis* by a wide plexiform layer narrowing ventrally to suggest cellular continuity between the two nuclei. Rosstrally a very narrow but definite external plexiform layer separates it

from the fibers of the lateral olfactory tract. Caudally the external nucleus, or external part of the lateral part of the anterior olfactory nucleus (to give it its full designation) slides downward along the internal surface of the lateral olfactory tract, gradually diminishing and rounding up into a small mass of cells which, as it slips medialward around the inside of the "elbow" of the lateral tract, becomes countersunk in a space due to the clearing away of some of the blue tract fibers. It is here opposite to the pars latero-ventralis, but its main bulk lies opposite the pars lateralis—there is no definite boundary between these two parts. The general form of the external nucleus is that of a long and slender pennant (Fig. 13) whose caudo-ventrally extended tail curves far medialward to end almost beneath the olfactory ventricle (Fig. 15). The external nucleus of *Caenolestes* is thus entirely intrabulbar, so that it faces the granular olfactory formation across the olfactory tract. Dr. Herrick finds that the Virginia opossum also possesses an essentially similar nucleus, save that it lacks an external plexiform layer, and is caudally unevenly swallow-tailed. In *Caenolestes* a small dorsal group of cells tends to be separated from the rest by the fibers of the ventral root of the dorsal peduncle of the lateral olfactory tract. Röthig (1910, Fig. 1) figures but does not name a small vertical cell plate in *Didelphis marsupialis*, which is plastered against the inner aspect of the dorsal thin part of the lateral olfactory tract *behind* the bulbar formation, a dorsal shift which would bring it nearer to the remaining bulbar formation at this level. The entire width of the plexiform layer separates it from the underlying pyriform cortex. As this is the most anterior section figured by Röthig, the more rostral extent and relations of this cell plate are unknown to me. Livini (1908, Fig. 2) shows in *Hypsiprymnus rufescens* a doubling of the intrabulbar portion of his anterior pyriform lobe (which corresponds to the lateral part of the anterior olfactory nucleus as described here) into two nearly equal vertical plates of cells only narrowly separated, the outer of which seems to be composed of somewhat smaller cells. In a Nissl series of a white rat brain I find the anterior olfactory nucleus also doubling laterally in the olfactory peduncle, in the gap between the dorsal and ventral edges of the bulbar formation, which in cross section has just broken in two—in other words, just behind the fissura circularis. The external portion is a more condensed vertical plate of cells, immediately beneath the massive lateral olfactory tract, bridging the gap in the olfactory formation and therefore in contact with it at its dorsal and ventral margins. More caudally, with the widening of the gap between the receding edges of the olfactory

formation, the external nucleus separates into two parts, dorsal and ventral, which diminish as they separate more and more, and finally end as tiny cell masses at the upper and lower borders of the bulbar formation near its caudal limits. Its general form is that of an evenly swallow-tailed pennant. The Winkler-Potter rabbit and cat atlases (1911, 1914) give no figures showing such a nucleus. Cajal (1911) neither mentions nor figures it, a circumstance which is perhaps to be ascribed to its failure to impregnate in his rich collection of Golgi series of the brain of the mouse. His only figure showing the lateral peduncular gray (1911, II, Fig. 431, p. 696, mouse, 5 days old, after Calleja) is apparently a horizontal section, which may miss the level of the external nucleus, if there be such a nucleus in the mouse. I have so far found no reference in the literature to this curious cell mass beyond the Röthig and Livini figures cited above, in which it was unlabelled.

The interpretation of this nucleus offers apparently no great difficulty. It is, probably, some sort of reenforcing or stepping-up device for olfactory stimuli, an *accessory olfactory nucleus*, discharging its afferent fibers into the subjacent lateral part of the anterior olfactory nucleus. It is a regulatory response probably provoked in part by the antero-posterior compression of this highly macrosmatic type of brain at the point where the neurobiotactic attraction of accumulated secondary fibers is strongest. Does this nucleus represent the morphological anterior end of the anterior olfactory nucleus, detached and carried back by the more anterior collaterals of the lateral olfactory tract, either actually or by being held fast by them during the progress of the compression which telescopes bulb and anterior end of the extrabulbar rhinencephalon? Or is it delaminated *in situ* from the subjacent cell mass, being composed of the cells which possess no basilar dendrites and are therefore unable to resist the unopposed neurobiotactic influence of the overlying fibers? It is not inconceivable that both delamination and dislocation may have operated in its formation. Although Cajal neither pictures nor describes the external nucleus, and gives but one copied figure of the lateral peduncular formation in connection with which it arises, his figure and description of the region immediately *behind* its due position furnish apparently unmistakable clues, in the light of Kappers' concept of neurobiotaxis, of the mode and causes of its formation further forward (1911, II., Fig. 433, p. 680, rabbit, aged 25 days). In the cortex of his "frontal lobe" (anterior area of pyriform cortex, Gray, 1924) the third layer (outer cell layer, superficial polymorphs or medium pyramids) contains cells without basilar den-

drites, all their dendrites being directed outward toward the fibrillar layer (lateral olfactory tract). These cells form, according to Cajal, a rather precise wavy band, not however separated off from the cells below, and they are extremely variable in form. The deeper pyramidal cells and the still deeper polymorphic cells are provided with both ascending and descending dendrites, and are therefore doubly anchored and not subject to extreme outward displacement by unbalanced olfactory stimuli of the lateral olfactory tract, as are the more superficial cells without descending dendrites. The balancing attraction resides, probably, in the heterolateral secondary and perhaps in the tertiary fibers in the rostral limb of the anterior commissure, which lies beneath the lateral portion of the anterior olfactory nucleus. Whether any other fibers reach it from this direction, as, for example, homolateral secondary fibers of the intermediate olfactory tract, I do not know. At any rate this external part of the anterior olfactory nucleus is slung like a hammock between two opposing neurobiotactic forces, and the doubling or splitting of the nucleus in this region expresses the resolution of the situation. The deep and main portion of the nucleus in this region lies in *Caenolestes* closer to the anterior commissure than to the lateral olfactory tract. Cajal (1911, II., p. 678) says that the cortex of the olfactory peduncle and of the "frontal lobe" (which lies next behind it) are essentially the same in structure. We should indeed expect to find the lateral peduncular gray less differentiated, with perhaps shorter axons and fewer descending dendrites, and with only a slight tendency toward cortical lamination. If the situation is as sketched we have a clear and exquisite illustration of the two-fold activity of neurobiotaxis at work. Since the lateral olfactory tract is always in macrosmatic animals an exceedingly heavy mass of fibers it is not improbable that the external olfactory nucleus is well developed in at least all those forms whose olfactory peduncle (anterior olfactory nucleus) is jammed forward and largely enclosed within the bulbar formation, as in the forms mentioned here. We should expect to find vestigial traces of it widespread among mammals in general, and it has most likely already found its way into the literature in some form or other.

*Tuberculum olfactorium*.—The enormous tuberculum olfactorium begins in these sections latero-ventrally (*t.ol. (i.C.)*, Figs. 2-5, 12, 13, 15, 28-36), instead of medio-ventrally as in the Virginia opossum. It rapidly expands medialward to occupy the entire width of the base of the brain, and caudally to a point beyond the middle of the hemisphere (section 710 in a hemisphere numbering 935 sections). Antero-medially it turns up on the medial surface for a short distance, where it is de-

limited by the medial portion of the fissura rhinalis arcuta (*fs.rh.arc.*), which does not as here described quite agree with Beccari's account (1910, Fig. 18); he extends the anterior and posterior parts of the encircling fissure of the tuberculum upward in the medial wall to meet at the ventral border of the hippocampal formation; but I have thought it simpler (and more in keeping with corresponding conditions of the lateral wall) to carry it across the base of Beccari's median triangle, in a fissure which is present and which delimits the *cellular* formation characteristic of this region, just as the arcuate fissure does laterally. In the more rostral sections it will be seen that the median part of the rhinal arcuate fissure is much shallower than the very sharp one lying immediately below it within the tuberculum. The two fissures define a rather prominent rolled portion of the tuberculum which is probably to be identified with the *nucleus of the medial olfactory tract* of Livini (1908) and others. Above the rhinal arcuate fissure the characteristic formation of the tuberculum falls away from the surface and runs up along the median border of the nucleus accumbens (*nuc. ac.*, Fig. 30), almost if not quite to the ventricular ependyma beneath the more rostral portion of the body of the anterior commissure, where the latter breaks across the ventricle to reach the septum. It thus intervenes between the sharply defined nucleus accumbens and the ventral portion of the precommissural body or septal formation. Its own medial boundary is also sharply defined from the septal formation. The tuberculum apparently receives secondary olfactory fibers from both the lateral and medial olfactory tracts (Fig. 28), whose fibers may be seen bending down into the plexiform layer of the tuberculum on its lateral and medial borders. Beccari (1910) questions this (see page 190 above), finding evidence of other sources of origin (the pyriform lobe in particular) for the fibers of the external plexiform layer of the tuberculum. He thinks that the olfactory tract fibers, if present, exist only rostrally in this layer. It looks otherwise here, but this is not really decisive material.

In front of the stro-tubercular fusion (see Figs. 29-30), which takes place behind the caudal end of the posterior part of the anterior olfactory nucleus (see page 191) essentially in the fashion so clearly described by Livini (1908) in *Hypsiprymnus*, a rather wide *deep* plexiform layer, continuous with the superficial encircling plexiform of the section, intervenes between the tuberculum and the rest of the cellular formation of the section. This layer is crowded with a wealth of fibers of diverse origin and destination, whose adequate analysis is impossible in this series. They include fibers from the lateral olfactory tract, an-

terior olfactory nucleus, intermediate olfactory tract (probably both crossed and uncrossed), from the tuberculum, which are destined for the septal nuclei, hippocampus, frontal neopallial pole. Probably all of these systems are to some extent doubly oriented. And some of them also apparently contribute to the median forebrain bundle, fasciculus medialis telencephali (*f.med.t.*, Figs. 29-35), which begins collecting in the base of the septum quite far forward; these fibers are projection fibers to stem centers and probably from them also. It is the multitudinous *ascending* precommissural fibers which are mainly responsible for the differentiation of the rostral portion of the hippocampus in lower mammals.

The histological development of the tuberculum is in *Caenolestes* spectacular in the highest degree. The external cell layer of medium darkstaining pyramidal or polymorphic cells is thrown into battlement-like folds, interrupted irregularly by islands of Calleja (*i. C.*, Figs. 29-32), composed of extremely small, pale, round cells densely crowded, glomerulus-like roundish or vermiculate areas, and including sometimes a few pale giant cells. These masses vary greatly in size and shape, and they are so sharply delimited and so different from their surroundings as to suggest pathological growths. They probably correspond to Beccari's (1910) Type 2 islands, while deeper ones of the same general character belong to his Type 3 islands. The Type 1 islands consist of thickenings of the crenulations of the external cell layer; these are sometimes fringed with pale granules like those of the other islands. While these types are sharply differentiated, there are, as Beccari found, intermediate types. Small isolated cell masses in the external plexiform layer of the more caudal sections especially are all traceable into the main mass of the tuberculum. None of Beccari's figures show so great a histological complexity as *Caenolestes*. The conditions in the Virginia opossum are much less complex (Gray, 1924).

What is the function of these highly elaborated and integrated *organs within an organ?* They suggest some sort of elaborate rehandling and sorting of incoming stimuli—a physiological analysis by means of differential thresholds, effecting a secondary specificity from mass stimuli dissociated, reenforced and more or less independently projected? A searching study of the tuberculum at its most bizarre stage of development in the lower mammals ought surely to discover valuable clues to modes of nervous organization.

The deep layers of the tubercular “cortex” are best described in connection with the immense fiber and giant cell stream which, like a great diagonally slung hammock, extends from the ventral pyriform cortex

and lateral anterior commissure region across the base of the hemisphere to the ventro-medial "regio innominata", the vestibule to the thalamus and lower stem centers. This great and complex system, composed of an immense number and variety of fibers, both projection and associational, is certainly one of the striking features of the middle subventricular region of the hemisphere. It is generally called the basal olfactory bundle (of Wallenberg) in these lower mammalian brains. It forms a part of the practically unanalyzable mass of fibers (in this series) traversing the basal region of the hemisphere, and including such systems as the olfactory projection of Cajal, striatal systems (*ansa lenticularis*), etc., the whole mass, save the association fibers, drifting ventro-medially to join the medial forebrain bundle and continue spinalward with it. Therefore, following some writers, I have called it the *lateral limb of the medial forebrain bundle* (*fasciculus medialis telencephali, pars lateralis, f.med.t.l.*, Figs. 29-33). It is largely, in all probability, a doubly oriented system. Its more rostral portion is characterised by the presence of a great multitude of pale giant cells strewn among the fibers (nucleus of the basal olfactory bundle, Figs. 29-33). A similar condition occurs in the more median fiber tangle, whose giant cells correspond probably to the "border nucleus" of Völsch (1906). The *ansa lenticularis* component contains few cells. But for many of its fibers the cells of origin are the giant cells characteristic of the *globus pallidus* (*gl.p.*, Figs. 12, 15; *glob. p.*, Fig. 34), and these are just like those strewn so thickly among the fibers of the more rostral stream of the medial forebrain bundle, especially in its lateral limb and in the more medial portion, where they seem to correspond to the "border nucleus" of Völsch (1906). The *globus pallidus* cells are certainly motor projection cells, and very likely the other giant cells mentioned also send long axons to stem centers. The fact that the red nucleus is also mainly composed of pale giant cells of the same type further tends to support this supposition.

With the reduction of the lateral and basal olfactory centers in higher mammalian brains, the more posterior *ansa lenticularis* complex becomes so preponderant as to throw the more anterior olfactory complex into the shade, and so the name "*ansa lenticularis*" comes to be applied to the whole stream. But in lower mammalian brains it is the more anterior component, mediating correlated olfactory stimuli, which seems more conspicuous. Many longitudinal fibers and fiber bundles (association tracts between rostral and caudal regions of the base of the hemisphere) further complicate the situation.

*Septal region.*—The precommissural area of the median surface of the hemisphere is the external surface of the thick paraterminal body of Elliot Smith or septum of ordinary terminology. This region contains the ascending olfactory systems already enumerated (olfacto-septal, olfacto-cortical) and the descending precommissural fornix, septo-amygadaloid (Johnston's stria terminalis bundle 4), septo-habenular (of stria medullaris system) and median forebrain bundles. The bundle labelled olfacto-frontal (*tr.ol.fr.*, Fig. 27), extending from the frontal pole of the neopallium into the septum, where it mingles with the septal fibers which sweep laterally beneath the ventricle or below the lateral mass of the anterior commissure, cannot itself be disentangled and followed with precision in these sections. Arising in the frontal pole of the neopallium just in front of the laterally directed corona radiata fibers destined for the internal and external capsules, these fibers inevitably suggest the possibility of part of the coronal fibers being diverted, or rather persisting, medially into the septum as projection fibers to stem centers by way of the median forebrain bundle, as a vestige of what Edinger has called the septomesencephalic tract of submammalia. In this connection Pedro Cajal's findings (1917, 1919) in *Varanus* and *Lacerta*, of a septal passage for descending fibers from the entire cortex, including the depressed portion between the medio-dorsal hippocampal cortex and the lateral pyriform cortex, which he considers the "general cortex", seem highly significant. One is led to recall also that the only cortical projection tract in birds is a septal one, and that it does not proceed from what seems to be olfactory cortex. It is not inconceivable that in the neopallial frontal pole of the lowly mammalian type of brain, at a level where the hippocampal formation is still rather insignificant, the more medial neopallial fibers might have preserved the shorter septal path.

Two well developed nuclei lie in the septum—the *lateral* and *medial parolfactory nuclei* (Herrick). The lateral parolfactory nucleus (*nuc.pol.l.*, Figs. 28-30) occupies the septal wall lateral to the precommissural fornix fibers. It corresponds to Johnston's (1913) primordium hippocampi and not to his lateral parolfactory nucleus, which is here the nucleus accumbens (*nuc.ac.*), the medial portion of the head of the caudate nucleus. The medial parolfactory nucleus (*nuc.pol.m.*, Figs. 30-31), located medially and ventrally, corresponds to Johnston's nucleus of the same name, and, as he finds in the Virginia opossum and in other forms (Johnston, 1923), it passes back insensibly into the *nucleus of the diagonal band of Broca* (*nuc.d.b.*, Figs.

32-33). Apparently it grades also into the *preoptic nucleus* of the telencephalon medium (*nuc. prop.*, Fig. 34).

The *dorsal (d.)* and *anterior (c.a.) commissures* have already been briefly described in connection with the median section of the brain. The dorsal commissure will be considered also below in connection with the hippocampus. The *composition* of the anterior commissure offers in *Caenolestes* nothing of unusual interest. But in view of the disagreement among zoologists with regard to the assignment of *Caenolestes* to one or the other of the two marsupial subgroups—Diprotodontia and Polyprotodontia—with its bearing on marsupial distributional problems, the *arrangement* of the fibers of the anterior commissure was, since it seemed to be the only remaining anatomical evidence to be expected on the question, a matter of great interest (Obenchain, 1923a, 1923b). After an examination of the brains of every marsupial genus except *Caenolestes* (which was not available) Elliot Smith (1902a and b) found that all diprotodont brains exhibit one feature never found in any polyprotodont brain, or indeed in any other vertebrate brain. This exclusive diprotodont character he named the aberrant bundle (*fasciculus aberrans*) of the anterior commissure, considering it a true diagnostic character of diprotodont brains. It is merely the dorsal portion of the anterior commissure which in diprotodonts splits off from the rest of the commissure to pass upward by way of the internal instead of the external capsule, the common route in all other brains. The aberrant bundle is absent in *Caenolestes*, a fact which, if this feature be decisive, would ally it with the polyprotodonts. The brains of the fossil caenolestids, however, can never be known, but the presumption of the absence of the aberrant bundle in them also would perhaps be justifiable. The effect of this would occasion no further disturbance of Dr. Osgood's marsupial "family tree" than the lengthening of the polyprotodont bracket to include *Caenolestes*, leaving it still in place between the generalised polyprotodont *Perameles* and the diprotodonts of Australia; or at most, in view of the intermediate position of the exposed gyrus dentatus of *Caenolestes*, the latter might be shifted to a position between *Perameles* and *Notoryctes*.

*Pyriform Lobe*\*.—The pyriform lobe consists of two distinct parts: (1) the pyriform cortex, mostly confined to lateral wall of the hemi-

\*The limits here assigned to the pyriform lobe do not exactly coincide with those assigned either by Cajal or Johnston, although the actual descriptions of the areas involved vary little or not at all. Cajal (1911) restricts the pyriform lobe to include, besides the amygdala, only the median pyriform cortex

sphere, between the rhinal fissure above and the rhinal arcuate and amygdaloid fissures below; and (2) the amygdaloid complex, mostly in the ventral wall between the amygdaloid and choroid fissures.

The *amygdaloid complex*, thanks to Johnston's illuminating comparative analysis (1923), which builds upon and completes Völsch's intensive study (1906), is no longer the mysterious territory it has been. Since it is, strictly speaking, a subcortical center, it will be described first here, leaving the pyriform cortex to precede the hippocampus. Owing to its enormous extent, the amygdaloid complex is perhaps the most spectacular part of the brain—unless it share this distinction with the tuberculum olfactorium. The superficial extent of the amygdaloid complex has already been described. Internally it exceeds this both in length and width, overlapping the posterior portion of the tuberculum anteriorly and the pyriform cortex laterally, and, as Johnston (1923) points out in the Virginia opossum, stretching rostrally far towards the anterior commissure. Behind the caudate nucleus and the putamen (*put.*) it floors the ventricle, while the cellular bed of its great fiber system, the stria terminalis (*st.t.*, Figs. 32 ff.) forms the median strip of the floor behind the anterior commissure. I am not, however, able to follow the stria bed in these sections into the anterior olfactory nucleus, as Johnston does in the opossum. It is clear anteriorly here only as it lies upon the anterior commissure and more caudally upon the internal capsule or cerebral peduncle.

The nuclei of the amygdaloid complex in *Caenolestes* comprise the six described by Johnston (1923), and include also the extra seventh one he found in the Virginia opossum: the nucleus of the lateral olfactory tract, the central, medial, lateral, basal, accessory basal, and cortical amygdaloid nuclei.

(his *anterior* pyriform cortex), receiving terminals of the lateral olfactory tract, and the *posterior* pyriform cortex, receiving no direct olfactory fibers (his superior temporal cortex). This makes it coincide approximately with the gyrus hippocampi of primates. Johnston (1915) defines the pyriform lobe as the gray matter underlying the lateral olfactory tract, which would include the entire anterior olfactory nucleus, but not the posterior pyriform cortex. By this definition the pyriform lobe and hippocampus are *directly* continuous anteriorly, but not in contact posteriorly, since the posterior pyriform cortex would be included in the neopallium. Since this area is the field of origin of the temporo-ammonic tract (Cajal), the main afferent tract to the hippocampus in mammals, it seems more logical to include it within the pyriform lobe. Its exclusion by Johnston would explain the complete caudal separation of the pyriform lobe and hippocampus in the turtle, *Cistudo carolina* (1915). The anterior pyriform cortex here coincides with Cajal's "frontal lobe", which he excludes from the pyriform lobe, on the basis that it, like the peduncular gray (anterior olfactory nucleus) receives mainly *collaterals* of the lateral olfactory tract.

The well delimited *nucleus of the lateral olfactory tract* (*nuc.tr.ol.l.*, Figs. 12, 15, 36-38) is a duplex structure, consisting of a large-celled dorsal part and a small-celled ventral part, separated by a narrow plexiform layer. It is tilted up rostrally, and shifted forward for about half its length above the caudal portion of the tuberculum, and therefore only its posterior half lies beneath the medio-ventral tubercle which in *Caenolestes* is apparently not so pronounced as in *Oreolestes*, of which no sections are now available for comparison. The nucleus of the diagonal band (*nuc.d.b.*, Figs. 32, 33) curves around from the median wall here, and the diagonal band fibers pass laterally in the diffuse region above the posterior end of the nucleus of the lateral tract towards the pyriform cortex, probably also effecting connections with the intermediate region. The ventral small-celled portion of the nucleus is so sharply delimited as to appear almost encapsulated, an appearance heightened at its caudal pole, which extends beyond the dorsal part as a sort of island of cells in the plexiform layer of the hemisphere. The corresponding nucleus of the Virginia opossum exhibits neither the forward shifting above the tuberculum nor the histological differentiation seen in *Caenolestes* (Gray, 1924). The nucleus of the lateral olfactory tract receives secondary olfactory fibers from the pars ventralis of the lateral olfactory tract (unlabelled, Figs. 36-38), and dorsally a great fan of fibers from the stria terminalis (*st.t.1*, Figs. 33-36), its most anterior contingent. Johnston (1923) identifies this with the commissural bundle of the stria, but these sections do not actually permit this.

The *central nucleus of the amygdala* (*c.*, Figs. 12, 15; *nuc.amg.c.*, Figs. 35-37) lies above the nucleus of the lateral olfactory tract. It is confluent with the strongly developed "intercalary plate" (*int.plate*, Fig. 36) of Johnston (1923), which is the most hypertrophied part of the stria bed. The central nucleus advances farther forward than any other amygdaloid nucleus, but apparently not so far as Johnston found in the Virginia opossum, up to the region of the anterior commissure. Its limits are not well defined nor its cellular structure striking.

The *medial amygdaloid nucleus* (*m.*, Figs. 12, 15; *nuc.amg.m.*, Figs. 36, 37) occupies the ventro-medial angle of the hemisphere, and also lacks well defined limits or strikingly marked cell structure. It is impossible to fix its caudal limit here. It also is continuous with the intercalary plate and with the central nucleus, as Johnston found.

The *lateral amygdaloid nucleus* (*l.*, Figs. 12, 15; *nuc.amg.l.*, Figs. 35-39) is the "poststriatum" of earlier writers. It is a large and ex-

tremely well defined antero-posteriorly elongated nucleus, oval in section and characterized by good-sized pyramidal or polymorphic cells. It lies in the concavity of the external capsule (*cap.e.*), between it and the ventral part of the putamen (*put.*), and behind the latter it rises to form the more lateral part of the ventricular floor. It clearly receives external capsule fibers, more probably originating in the pyriform cortex, and it seems also to receive a large number of stria terminalis fibers, coursing horizontally just above the basal amygdaloid nucleus (*st.t. 3*, Fig. 38). This last is contrary to Johnston's observations.

The large-celled well defined *basal* nucleus of the amygdala (*b.*, Figs. 12, 15; *nuc.amg.b.*, Figs. 37-42) arises medial to the more caudal portion of the lateral nucleus, near its ventral border, and increases to large proportions as the lateral nucleus diminishes. Behind the flattened tail of the caudate nucleus it occupies a large part of the floor of the ventricle, extending far medialward and lying caudally directly beneath the ependyma. Both it and the lateral nucleus are in cellular continuity with the deep cells of the ventral border of the pyriform cortex at the level of the amygdaloid fissure. Johnston (1923) considers them to have been derived from the pyriform cortex by a process of infolding along this line, and the situation in *Caenolestes* seems to support this view.

The *accessory basal* nucleus of the amygdala (*b.ac.*, Fig. 15; *nuc.amg.b.ac.*, Figs. 37-38) is a less clearly defined nucleus of medium dark cells lying among the ventral fibers of the external capsule as they fan out in the postero-ventral amygdaloid region, below the caudal ends of the lateral and basal nuclei and obscurely confluent with them. It is not only present in *Caenolestes*, but it would be only too easy to subdivide the heterogeneous caudal amygdaloid region into further nuclei.

The *cortical* amygdaloid nucleus (*amg.*, Fig. 12; *nuc.amg.cort.*, Figs. 38-43) forms almost the entire superficial portion of the amygdaloid complex. Laterally it approaches or adjoins the ventral edge of the pyriform cortex and medially the ventral edge of the hippocampus behind the choroid fissure (*fs.ch.*) along an internally well marked and an externally partially obvious medial continuation of the amygdaloid fissure (*fs.amg.m.*). Its histological structure assumes in places a structure similar to that of the pyriform cortex. Its deeper portion is very heterogeneous. Some confusion, however, results from the tangential nature of the posterior sections of the hemisphere. The cortical amygdaloid nucleus receives secondary fibers by way of the pars ventralis of the lateral olfactory tract. The hippocampal-amygda-

loid junction (*subic. (amg.)*, Figs. 40-42) along the median extension of the amygdaloid fissure is also evidence of fiber connections, and Johnston (1923) has demonstrated them in the Virginia opossum.

The *stria terminalis* (*st.t.*, Figs. 32-38), the great fiber system related to the amygdaloid complex, has also been carefully analyzed by Johnston (1923). Practically its entire course is quite clear in these sections, and rostrally and caudally its five component bundles as identified by Johnston, can easily be recognized, but in the compact medial portion of the tract, where it lies in the stria bed between the cerebral peduncle and the ependyma of the lateral ventricle they cannot be individually identified. Johnston's numbers have been affixed to these bundles as traced by him in the Virginia opossum. Rostrally they are certainly correctly applied, but caudally they are applied without direct evidence from the brain of *Caenolestes* of continuity with the respective rostral bundles.

The lateral part of the anterior olfactory nucleus passes without break directly over into the least differentiated anterior pyriform cortex behind it. The *cortex of the pyriform lobe* covers most of the lateral surface of the pyriform lobe. Antero-laterally it may be divided into three regions: the anterior pyriform cortex (*cx.pir.a.*, Figs. 13, 15, 26-31; area piriformis anterior, Gray, 1924; frontal lobe of Cajal, 1911), which passes more caudally by very gradual transition into still more differentiated medial pyriform cortex (*cx.pir.m.*, Figs. 13, 15, 32-34; area piriformis medialis, Gray; anterior pyriform cortex of Cajal; this in turn merges more abruptly into the most specialized posterior pyriform cortex (*cx.pir.p.*, Figs. 12, 13, 15, 42-44; area piriformis posterior, Gray; superior temporal or angular nucleus or center of Cajal. Since the lateral part of the anterior olfactory nucleus merges insensibly with the anterior pyriform cortex, and the latter merges insensibly into the medial pyriform cortex, no definite boundaries can be made out between them. The second cortical layer (not counting the external fibrillar layer) becomes progressively more and more condensed, and any lines of demarcation are, in these sections, merely arbitrary. But the posterior pyriform cortex (*cx.pir.p.*, Figs. 42-44), which is on a different plane functionally from the remainder of the pyriform cortex because (by Cajal's definition) it receives no secondary olfactory fibers, also differs histologically. Its histological development is connected not only with the absence of secondary olfactory fibers, but perhaps even more with the increase of non-olfactory fibers, and its consequent elevation into an associational area second

in rank only to the neopallium. It displays a very striking anatomical character. This is mainly due to the development within it of a wide and very dense plexus in the third layer of the cortex. In *Caenolestes* this plexus, which according to Cajal is in the mouse of extraordinary density, almost fills the pyriform wall dorso-caudally. Its broad, rounded head rises slightly above the level of the rhinal fissure. It contains many pale giant cells, found nowhere else in the pyriform cortex of *Caenolestes*. The posterior pyriform region is the field of origin of the great temporo-ammonic or angular bundle of Cajal (1911, spheno-ammonic, 1906), which delivers a huge stream of highly correlated olfacto-somatic impulses to both the ammon's horn and the gyrus dentatus, for almost their entire length—certainly reaching as far forward in *Caenolestes* as the anterior level of the commissural region, where its structural influence is suddenly and strikingly felt. Since it mingles with other pyriform and with neopalial association fibers to form the cingulum limitans (*ci.lim.*, Figs. 30-42) at the inner dorsal angle of the lateral ventricle, and the cingulum ammonis (*ci.am.*, Figs. 30-42) in the outer plexiform layers of the ammon's horn and gyrus dentatus, it is not separately named in the sections given here. In the posterior region of the hemisphere this avalanche of fibers may be seen pouring above and behind the ventricle into the presubicular and subicular regions and through them, either directly or indirectly, as perforating fibers to the ammon's horn and gyrus dentatus.

Anteriorly the lateral olfactory nucleus certainly sends tertiary olfactory fibers above the olfactory ventricle into the anterior hippocampal formation (Figs. 26-27). The sections suggest that the dorsal path between the pyriform and hippocampal cortices might perhaps be patent for practically the entire length of the neopallium, in the deep layer of the corona radiata. Owing to the height of the rhinal fissure the distance is nowhere very great, and this would certainly be the shortest path for the more dorsal pyriform cortex. The anterior pyriform cortex must also contribute very largely to the subventricular systems, both to the olfacto-septal, olfacto-hippocampal and olfacto-frontal systems anteriorly, and to the more posterior and extensive complex included under the head of the lateral limb of the medial forebrain bundle, as explained above (see page 198). The great efferent pyriform path to stem centers is of course the olfactory projection path of Cajal, probably, like so many of these fiber systems, a doubly oriented one. The stria terminalis component of this system (Johnston's bundle 2, 1923) arises from the amygdaloid complex (so far as it is a descending bundle). The fiber connections between the

pyriform cortex and the amygdaloid complex have already been mentioned (page 203).

In addition to the antero-posterior divisions of the pyriform cortex, Gray (1924) has described several narrow longitudinal bands along the boundary fissures in the Virginia opossum. Three such areas accompany the rhinal fissure: the area perirhinalis, the area piriformis dorsalis, and the area piriformis fissuralis, in order from above downwards. The extreme shallowness of the rhinal fissure in *Caenolestes* is not conducive to great development of these areas. The area perirhinalis, the transition area between neopallial and pyriform cortex, is probably individualized, but the other two are feebly developed and not distinct from one another. Ventrally also the area piriformis ventralis and the area subpiriformis of Gray tend to fuse into one band quite well marked, the ventral pyriform cortex (*cx.pir.v.*, Figs. 27-34), especially anteriorly where it describes a deep reentering angle subjacent to the massive lateral olfactory tract. This band is here regarded as following caudally upon the latero-ventral part of the anterior olfactory nucleus (*nuc.ol.ant.l.v.*, Fig. 26). Behind the tuberculum, and even more rostrally, where the diffuse anterior perforated space (*l.perf.a.*, Figs. 35-38) of Johnston (1923) intervenes between it and the nucleus of the lateral olfactory tract, the pyriform cortex exhibits a very sharp ventral margin back to the point where it gives evidence of infolding at the level of the lateral and basal amygdaloid nuclei. Still further back it becomes more or less continuous with the outer layer of the cortical amygdaloid nucleus, and histological differentiation tends to fade out. The tangential nature of the sections in this caudal region is somewhat confusing, and control by sections in other planes is unfortunately lacking.

#### HIPPOCAMPAL FORMATION

The hippocampal formation of *Caenolestes* (Figs. 6, 12, 17, 26-43) begins with a small patch of cells condensed upon the outer aspect of the rostral border of the anterior olfactory nucleus, at its dorso-medial angle, that is to say, immediately caudal to the bulbar formation (*hip.a.*, Figs. 12, 17; *cx.hip.a.*, Figs. 26-29). It thus takes part in the formation of the rhinencephalic ring surrounding the olfactory ventricle, by means of which the two olfactory cortices are indirectly continuous with one another through the anterior olfactory nucleus. It is to be noted that while the hippocampal formation begins at the *very* rostral margin of this ring, in its intrabulbar portion, just caudal to the olfactory formation itself, a similar lateral (pyriform) condensation falls

short of this, being separated from the bulbar formation by uncircumcated anterior olfactory nucleus. The explanation of this precocity of hippocampal differentiation might conceivably be tied up with the prevailing latero-ventral drift of the secondary olfactory fibers toward the lower olfactory correlation centers of the lateral wall and base of the hemisphere—pyriform lobe and tuberculum olfactorium. This trend is clearly brought out in the bulb, where there is never any considerable accumulation of secondary fibers in the dorso-medial region, those arising there apparently for the most part making as rapidly as possible for the laterally and ventrally situated lateral, intermediate and medial olfactory tracts. The only exception to this is the presence of the small more median portion of the pars dorsalis of the lateral olfactory tract (*tr.old.m.*, Fig. 26), which may, and probably does (as silver preparations indicate in the Virginia opossum, Herrick, 1924a), give off some collaterals to the hippocampal formation, which is, however, already strongly under the influence of tertiary olfactory fibers. It seems but natural that such a region, receiving only a minimum of direct olfactory fibers and beginning almost, if not quite, at once to receive tertiary olfactory fibers from the more lateral portions of the anterior olfactory nucleus (these can be seen crossing above the olfactory ventricle) and presently still more highly correlated olfactory stimuli from the tuberculum by way of the septum, should undergo accelerated differentiation in comparison with a region preponderantly invaded by secondary olfactory fibers (see page 219).

Dorsally the continuity between the hippocampal formation and the pars dorsalis of the anterior olfactory nucleus becomes transformed at the junction between the neopallium and the rhinencephalon into a continuity between the hippocampus and the neopallium on the one hand, and between the pyriform cortex and the neopallium on the other (Figs. 26-27). Ventrally the hippocampal formation, at first continuous with the pars posterior of the anterior olfactory nucleus (*nuc.ol.ant.p.*, Figs. 27-28), breaks away from the latter and becomes separated from it by an increasing interval of diffusely scattered small cells through which some fine pale fibers pass from the deeper septal region to the plexiform layer (Fig. 29). This area is replaced more caudally by the medial parolfactory nucleus (*nuc.pol.m.*, Figs. 30-31).

The ventral end of the precommissural hippocampus (Fig. 29) thins to a slender needle point which, as it recedes upward in the septal wall, approaches the pial surface. This slender column of cells widens

above very quickly as it merges with the neopallial gray. It soon begins to show a slight concavity toward the pial surface (*fs.hip.*, Fig. 29), which more caudally comes to expression as the external hippocampal fissure (*fs.hip.*, Fig. 30). The cells diminish in size and increase in density from above downward, to the sharply pointed ventral end of the hippocampal formation, which curves upwards and backwards in line with the ventral (medial) edge of the definitive gyrus dentatus at the fimbrio-dentate fissure near its rostral end at the antero-dorsal angle of the hippocampal commissure (*fs.fim.d.*, *c.d.*, *cx.dent.*, Figs. 30-31). As the hemisphere increases in height the hippocampal formation lengthens, the upper thicker and larger-celled portion more rapidly than the lower, so that it comes to exceed the lower smaller-celled portion in length. It becomes at the same time thinner and denser. It is interesting to note that rostrally the hippocampal formation differentiates more rapidly at its peripheral (dentate) border, and that differentiation travels upward, the orderly condensed files of definitive ammon's pyramids appearing tardily. Caudally also we find the cortex dentatus apparently leading the way in the formation of the recurved temporal pole of the hippocampus (see page 215).

When I was making the first Edinger drawings I noted a curious breaking up or disorganization in the precommissural hippocampal cell plate, due to the loosening up and paler staining of some of the cells of the upper region (\*, Figs. 12, 17a). This rift or line of fracture I interpreted as the locus of the *interpositio medialis*, the break between the definitive gyrus dentatus and the ammon's horn. But to my great surprise the *interpositio medialis* formed rather suddenly at a distinctly lower (more ventral) level at the anterior border of the dorsal commissure (*ip.m.*, Fig. 31). A provisional explanation of this puzzling rift in the cell plate suggested itself later, however, in connection with Cajal's statement (1911, II., p. 754) that the gyrus dentatus and the more ventral half of the ammon's horn (his extra-ventricular ammon's horn or region of grand pyramids) seem to form an indissoluble anatomical and functional unit, owing to the exclusive distribution of efferent gyrus dentatus axons (the "mossy fibers") to the extra-ventricular ammon's horn. The line of fracture in question might presumably be interpreted, then, as the upper limit of the distribution of the "mossy fibers", the boundary between intra- and extra-ventricular ammon's horn. (For a provisional explanation of its absence in the supra- and postcommissural ammon's horn, see page 209 below). The material available here does not furnish proof of this hypothesis, which is offered merely as a suggestion.

At the level of the anterior face of the dorsal commissure the precommissural hippocampus, which, as Elliot Smith (1896c) long ago pointed out, exhibits in marsupials all stages of development to be seen in the reptilian hippocampus, suddenly assumes the definitive mammalian appearance of double interlocked arcs by the abrupt formation of the interpositio medialis separating the ammon's horn and the gyrus dentatus, and the synchronous humping up of the latter into a horse-shoelike form into whose ventral concavity the terminal lamina (Levi, 1904; nucleus fasciae dentatae, Elliot Smith, 1896c) of the ammon's horn is displaced. The explanation of these sudden changes is probably three-fold: external pressure, internal pressure and neurobiotactic influence. External pressure is exerted on three sides: from above by the downward pressure of the neopallium (as pointed out by Elliot Smith, Levi and many other neurologists), medially by the opposite hemisphere, and ventrally by the rigid barrier of the dorsal commissure and subpallial structures, beneath the choroid fissure (the atrophic choroid barrier so strongly emphasized by Levi, 1904). The internal pressure arises from the intrinsic growth of the hippocampus, chiefly the ammon's horn, which must crumple or roll to adjust itself to the space allotted. The neurobiotactic influence is in the first place due to the "perforating fibers" of the great temporo-ammonic tract and fibers associated with it in the cingulum limitans and cingulum ammonis (see pages 201 and 205). These fibers distribute equally to the gyrus dentatus and the ammon's horn. Those fibers which discharge into the granule cells of the gyrus dentatus break across the hippocampal fissure as it deepens and cause a more or less partial obliteration of the fissure by a secondary fusion of its two lips. They pull the sheet of granules upward through its entire length along a longitudinal axis (nearly median in *Caenolestes*), so that in cross section the gyrus dentatus describes a horseshoe curve. The efferent fibers of the gyrus dentatus (axons of the granules, "mossy fibers"), converging upon the terminal lamina of the ammon's horn, cause a break at the position of the interpositio medialis (*ip.m.*, Fig. 31), and the displacement of the lamina terminalis into the ventral concavity of the gyrus dentatus. Figure 11a, b, c illustrates diagrammatically the mode of formation of the definitive mammalian "hippocampal figure" in *Caenolestes* under the three influences named. The arrows indicate the directions in which the force is applied and its relative strength.

It might be possible to invoke also Kappers' ever useful concept of neurobiotaxis to explain the obliteration of the precommissural rift or fracture in the hippocampal formation (\*, Figs. 12, 17a) noted above

page 208) as the possible boundary line between the intra- and extraventricular ammon's horn; the extraventricular ammon's horn alone receives "mossy fibers" from the gyrus dentatus, a circumstance that might be held to account for the rift or fracture line in question; but the grand pyramids of this region, according to Cajal, send recurrent collaterals into the external plexiform layer of the ammon's horn (*stratum lacunosum*) which rake the whole extent of the ammon's pyramids, both intra- and extraventricular, and so tend to close any gap in them. Furthermore the afferent commissural fibers in the alveus might contribute to the same result, as well as to the formation of the *interpositio lateralis*, by a general neurobiotactic compacting of the whole line of pyramids. More than this, the temporo-ammonic fibers which distribute to the ammon's pyramids either by way of the superficial plexiform layer external to the *stratum lacunosum*, or by way of the alveus (Cajal's temporo-alvear tract), engage, according to Cajal, not only the intraventricular but also some of the nearer extraventricular pyramids, perhaps most of them. At any rate it would seem as though the initial agent in the production of such dislocations as those considered is always the functional activity of the intrinsic structures concerned, and not the mechanical action of the fibers which may later not only occupy the break, but enlarge it, even to the extent, conceivably, of interfering with the function which originally produced it.

The *dorsal or hippocampal commissure* (c.d., Fig. 31) exhibits a narrower and denser dorsal portion, the *psalterium dorsale* (ps.d.), which Cajal (1911) considers the commissural path of the crossed portion of the temporo-ammonic system, and the wider and much more diffuse *psalterium ventrale* (ps.v.) the commissure of the ammon's axons. Many cells are mingled with these latter fibers (the nucleus of the commissure), so that on the whole the dorsal commissure in comparison with the much denser anterior commissure seems larger than it really is. The precommissural fornix fibers (f.prcom., Fig. 30) may be seen passing vertically downward in front of the commissures, and above the *psalterium dorsale* the dense short mass of the fornix longus, bending downward and partly interweaving with the *psalterium dorsale*, forms the "knieförmiges Bündel" (Koelliker; Livini, 1908); they belong to the median striae Lancisii (Johnston, 1913). The *descending columns* of the *fornix* (c.for., Fig. 31) collect in the usual way close to the midline as deeply stained oval bundles above the anterior commissure and pass down behind it into the hypothalamic region. Two similar oval bundles of pale fibers located between the

fornix bundles and the anterior commissure on either side of the inferior recess (*r.i.*) may be the supracommissural bundle of the stria terminals (Johnston's bundle 4, 1923). They seem to be receiving more lateral fibers disposed in the same diagonal direction as some of the darker fibers entering the fornix bundles. I cannot tell whether they are of septal or hippocampal origin, or both. These bundles cannot in my sections be definitely followed laterally into the stria bed above the anterior commissure. There is also the possibility that they belong to the stria medullaris system, but I cannot follow them to the habenula.

As Johnston (1913) was the first to point out, marsupials possess well developed *medial striae Lancisii* above the dorsal commissure, a level at which full-bodied hippocampus also exists, proving that the lateral and not the medial stria of the indusium are the vestigial remnants of degenerate hippocampus in "callosal" brains. These median striae are perfectly clear in *Caenolestes*, but they are omitted from the reduced sections figured here. They are seen as cross cut fibers upon the dorsal surface of the hippocampal commissure and as vertical fibers cutting across the anterior dorsal commissure fibers and partly interwoven with them (see knieförmiges Bündel, page 210).

In connection with the structures under discussion it may be well to describe the form taken by an interesting ventral diverticulum of the superior recess (of Elliot Smith), which has been described and figured in sagittal section of Johnston (1913) for the Virginia opossum (Fig. 16b). In *Caenolestes* this subcommissural pouch (Fig. 16a) runs its course between section 510 (Fig. 30 shows the beginning of the glial mass in which it is embedded) and section 528. The dorsal recess or sac bends down around the rostral surface of the dorsal commissure, carrying with it membranous roof tissue which hypertrophies in the septum between the commissures and in the pial side of the precommissural area to form a rather thick mass of glial tissue between the medial fornix fibers. This mass, composed of densely crowded fine pale granules, is sharply separated from the nervous tissue adjacent to it. Rostrally it is bifurcated and caudally it comes to a median point in the septum beneath the dorsal commissure. It contains a lumen of similar shape, lined with ependyma, which ends caudally as a median recess in front of and above the inferior recess and bifurcates rostrally to end in two smaller diverticula in the precommissural septal walls. In *Caenolestes* the communicating canal to the dorsal recess or pouch is collapsed and obscured in dark-stained membranes and blood vessels. Figure 16a shows a reconstruction of

the ventral diverticulum of the dorsal recess in *Caenolestes* in the horizontal plane below the entrance of the communicating canal; figure 16b the sagittal section of this diverticulum in the Virginia opossum from Johnston (1913, part of figure 35, redrawn).

The middle portion of the hippocampus (Figs. 32-37) is naturally less interesting than the two extremities, which offer more developmental and adaptational clues, and it therefore calls for but few remarks here. With respect to the amount of gyrus dentatus exposed upon the median surface of the hemisphere, *Caenolestes* is intermediate between *Perameles* and *Notoryctes*, a fact which indicates that the neopallial pressure, apparently the chief varying factor here, exceeds that in the latter and falls below that in the former. According to Elliot Smith (1895b, Fig. 6) *Notoryctes* has the least extensive neopallium found among mammals, and "in no other animal does one find the simplicity of arrangement which the hippocampus of *Notoryctes* presents, an appearance which recalls the foetal hippocampus of *Perameles* or *Macropus*." (This statement refers only to what I have called the "hippocampal figure" as seen in cross section and not to the development of the temporal pole of the hippocampus, which will be discussed below.) The intermediate condition of the exposed gyrus dentatus in *Caenolestes* is especially interesting in view of the similarly intermediate condition of the cerebellum in *Caenolestes*.

It should be held in mind that the more caudal sections of the hippocampus become progressively more tangential to the structure itself and present an increasing distortion of the "hippocampal figure" of double interlocked arcs, as well as an exaggeration of its size. We should have a true picture of the hippocampus only if we could make all sections vertical to the hippocampal axis, which, since that is curved, would make them radial. The sections show that the hippocampus as a whole has in *Caenolestes* not yet "turned the corner"; that is to say, the typical "hippocampal figure" does not appear twice, like an object and its inverted image, in any one cross section, as it does, for example, in the rabbit's brain (Fig. 20a, b, c, Winkler-Potter, redrawn); or once, the "mirror image" only, as, for example, in the lion (Fig. 21, Elliot Smith, redrawn) and in man. In *Caenolestes* the gyrus dentatus alone has recurved and therefore it occurs in two places, one dorsal and one ventral, in some sections (Fig. 39). Neither the fimbria nor the ammon's horn has, however, recurred, and hence the ventral hippocampal figure of double interlocked arcs is incomplete and the temporal hippocampus is practically unrecognizable at first glance. The Virginia opossum has advanced one step farther in

the recurring process by the formation of a small forwardly directed pouch on the rostral face of the ammon's horn at its ventral border below the caudal end of the fimbria (Fig. 18a-g, cross sections, from unpublished drawings, Streeter, redrawn; Fig. 18h, reconstruction made from same). This pouch is evidently formed in response to the neurobiotactic attraction of the gyrus dentatus, which has here grown forward beyond the field of the unrecurred ammon's horn. This change still does not result in a complete "hippocampal figure". But in higher marsupials, like *Hypsiprymnus* (Fig. 19a, b, c, Livini, 1908, redrawn), the temporal development has advanced to a point which allows the typical hippocampal figure to appear twice in the same section.

In *Notoryctes* (Fig. 22, Dart, 1920, Fig. 13, redrawn), to my great surprise, the temporal pole of the hippocampus is apparently quite as well developed as in *Hypsiprymnus*, and considerably better developed than in *Caenolestes* and the Virginia opossum. *Notoryctes* is a sightless form without external ears, and the elongation of the hippocampus and great amount of recurring of its temporal pole is perhaps to be regarded as compensatory, in view of the absence or extreme reduction of the visual and auditory systems. The median surface of the hemisphere (Elliot Smith, 1895b, Fig. 1) has a peculiar peaked appearance, which may perhaps be due to the elongation of the hippocampus and its consequent caudal bowing. The pressure of the slightly developed neopallium is not sufficient to cause a great degree of inrolling, not so much as in *Caenolestes*. *Ornithorhynchus* also has an elongated slender but well formed temporal pole of the hippocampus (Elliot Smith, 1896b, Figs. 4, 5, 5", pp. 472-3—the section given through the "tail" of the hippocampus is not very near its temporal end, however). In this case the elongation of the hippocampus and its temporal recurring, which is pronounced, is probably to be correlated with the very great size of the neopallium and consequent compression of the hippocampus. I do not know the condition in *Echidna*, but should expect a similar situation from similar conditions. The temporal pole of *Perameles* is also unknown to me.

In the rabbit's brain, a "callosal" one, in which the hippocampal commissure is caudally displaced by the corpus callosum, there are also two typical hippocampal figures, posed in opposite directions, joined by the tangentially cut fimbria (Fig. 20a, b, c, Winkler-Potter, 1911, pls. XII, XIII, XIV, redrawn). Here we have two exactly identical and completely detached images in front of the middle of the fimbria (Fig. 20a and b). I do not know whether this is

the case also in *Hypsiprymnus* (Fig. 19b). Livini does not give a section showing the fimbria in two parts. The more rostral section (Fig. 19a) shows, however, a little ventral "island" which may be the projecting tip of the uncus, and between this and the next caudal section given the fimbria may appear in two parts; but even so it would probably be less recurved than in the case of the rabbit.

In the case of the higher and more microsmatic mammals, as in the lion (Fig. 21), and in man, the dorsal "figure" disappears as the corpus callosum elongates and the supracallosal hippocampus (lateral striae Lancisii and the accompanying gray) stretches, and only the ventral figure persists completely. We can thus easily assemble a short series which will adequately illustrate the remarkable complete reversal of the hippocampus in the course of phylogeny by the agency of the combined action of callosal growth, tremendous neopallial hypertrophy, and the anchoring of the hippocampus in a rostral position by the pyriform cortex, which is itself strongly anchored to the bulbar formation. The tuberculum and the amygdala, as they diminish, retain their old places one behind the other between the bulb and the temporal end of the hippocampus, and medial to the lateral peduncular gray (lateral olfactory gyrus) and pyriform cortex. The neopallium expands enormously in the caudal direction, further accentuating the hippocampal reversion. The pyriform cortex loses its distinctive histological character and assumes a progressively more neopallial appearance, until the primate condition is attained, where, as "gyrus hippocampi" it becomes histologically practically identical with the neopallium (save in the presence of the external fibrillar layer in its anterior portion). The posterior pyriform region, that devoid of secondary olfactory fibers and richly supplied with non-olfactory fibers, begins, even in the Virginia opossum, (Gray, 1924) to resemble neopallial cortex rather closely along the border for the caudal prolongation of the rhinal fissure. In the mouse, as Cajal's (1911) intensive studies show, this area has developed an exceedingly characteristic histological structure of its own, and assimilation to the neopallial cortical pattern has not apparently made so much progress. The same is true in *Caenolestes*, in which the boundary between the neopallium and the posterior pyriform area is pretty definite (Figs. 41-42), so far as can be construed from frontal sections. The conditions existing at the temporal extremity of the hippocampus in *Caenolestes*, the Virginia opossum, *Hypsiprymnus* and the rabbit certainly stress the dynamic character of the temporal displacement of the hippocampus—"the brain is not a rigid mosaic of morphological units which were laid down in the primordial vertebrate

and thereafter preserved inviolate" (Herrick, 1922, p. 199). The little, rostrally directed ammon's horn pouch in the Virginia opossum is clear evidence of the regulative nature of the changes going on. In *Caenolestes* the forward advance of the temporal gyrus dentatus has not removed it from the unrecurved ammon's field, but in the Virginia opossum this would have happened if the ammon's horn had not responded by the formation of the pouch.

It is to me rather surprising to find the gyrus dentatus leading in the reversal of the hippocampus when rostrally it appears *in definitive form* tardily. But this tardiness is perhaps more apparent than real, since the lower portion of the precommissural hippocampus is in mammals, as Elliot Smith has stated for the same region of the posterior part of the reptilian hippocampus, clearly "on the way" towards differentiation into definitive gyrus dentatus. In the mammalian precommissural hippocampus it is the ventral portion, that directly continuous with the definitive gyrus dentatus, which takes the lead in differentiation. Differentiation apparently travels from below upwards, and the definitive ammon's horn or rather, perhaps, its "intraventricular" portion, is perhaps the last to develop its distinctive structure and extent. It is at least the last to begin differentiating. Pedro Cajal's illuminating studies on the reptilian brain (*Varanus* and *Lacerta*, 1917, 1919) by the silver methods show that in the ventral or medial small-celled portion of the hippocampal formation (*quasi* gyrus dentatus) there is a clear transition in cell type from the deeper to the outer cell ranks. The cells of the outermost cell ranks (nearer the pia) are practically true granules, the innermost true pyramids of the ammon's type. This is very significant, and it would not, I think, be surprising to find in full-bodied precommissural hippocampus of lower mammals an analogous state of affairs. The situation in this *Caenolestes* series strongly suggests, far in advance of the interpositio medialis and the inrolling of the gyrus dentatus, that the ventral cells of the more ventral region of the hippocampus are rapidly verging towards the true granule type, so that the transition to definitive gyrus dentatus involves apparently no sudden cytological changes. The hippocampus is apparently affected by two distinct waves of differentiation, both starting at the ventral border and traveling upward. The first develops cells of pyramidal type: the second, following in its wake, transforms pyramids into granules (phylogenetically speaking). The first wave affects the entire width of the hippocampal formation, reaching its dorsal border (locus of the interpositio lateralis), the second stops at the level of the interpositio medialis, affecting the "dentate" region but

never the ammon's region above it. The two main types of cells are perhaps to be interpreted as an expression of the enhancement of function in the hippocampus by its organization into a highly integrated duplex structure, the ammon's horn from which spring the long projection axons (which alone form the efferent path of the hippocampus), and the gyrus dentatus, whose shorter axons of a specialized type ("mossy fibers") deliver stimuli to part of the ammon's pyramids directly and to many others indirectly (recurrent collaterals of grand pyramids). We can never perhaps get the complete phylogenetic story in any one form, certainly not in the lowest and highest, where either later or earlier steps fail to appear.

Although the general form of the ammon's horn and the gyrus dentatus cell sheets in *Caenolestes* is really simple, it is difficult to show them both in the same diagram. Therefore dissected reconstructions (Figs. 17a and 17b) attempt to show them separately, one or the other being cut away at the commissural level of the hippocampus. The two parts are shown in place together in figure 12. It is seen that the gyrus dentatus takes the form of a sort of helmet or hood with the top of the crown or apex pointing caudally; the front or visor of the helmet corresponds to the elongated dorsal portion of the gyrus dentatus extending above the commissure where it ends in a little pouched thickening (Fig. 30); the back or neck portion corresponds to the ventral or temporal recurved part of the gyrus dentatus. The ammon's horn sheet takes the form of a loose scroll, greatly widened posteriorly in the sections (Figs. 38-40), so that it is really more like a cornucopia, with the wide end caudo-ventral. The upturned median flap of this scroll, covered with a thin coating of alveus fibers, is exposed upon the median surface of the hemisphere, save where its caudally directed corner is inserted into the hooded portion of the gyrus dentatus. This upturned ammon's horn forms Elliot Smith's extraventricular or inverted hippocampus ("dorsales Blatt" of Koelliker). It is seen in the sections to diminish in length as its lower edge recedes upward between the approaching dorsal and ventral portions of the gyrus dentatus (Figs. 34-40), which still more caudally unite to form an oval ring (the "crown" of the hood) containing the caudal tip of the inverted hippocampus (a few scattered cells, Fig. 41). At the caudal end of the choroid fissure the continuity of the two parts of the ammon's horn (in sections) is dissolved (Figs. 40-42), and the lower end of the extraventricular ammon's horn begins to recede upward, while that of the intraventricular ammon's horn seems to turn laterally under the median angle of the ventricle (Völsch's

subventricular hippocampus, 1906), where it comes in contact with the amygdaloid complex (stria bed and cortical amygdaloid nucleus). This contact extends backward along the line of the medial continuation of the amygdaloid fissure (*fs.amg.m.*, Figs. 40-43), always very strongly marked internally and sometimes externally apparent. As the sections show, the more temporal extremity of the gyrus dentatus (Fig. 39) is contiguous with the ammon's horn and perhaps with the amygdala where the two structures adjoin. The fiber connection between the hippocampus and the accessory basal nucleus of the amygdala (Johnston, 1923, Fig. 55) is not apparent in this series. This by no means proves its absence.

The emphasis here placed upon the amount of recurving of the hippocampus is intended to apply specially to mammals, where it is to be considered in connection with the inrolling of the hippocampus under the double necessity of enhancement of function and economy of space. Even mammals, as we have seen above (*Notoryctes*), do not present a quite orderly series in this respect. The degree of recurving alone is not a criterion of advancement in hippocampal development. In some reptiles (*e.g.*, *Cistudo carolina* (Johnston, 1915, Figs. 6, 12, 13, 45) the recurving of the temporal pole is more pronounced than in *Caenolestes*—in single cross sections two separate "hippocampal figures", complete for this brain, appear. The factors provoking the recurving in such cases are easily recognisable and need not be detailed here. The factors operating in mammals to bring about inrolling have apparently provoked a method of increase for the hippocampus, which, in concert with other existing conditions, may result in less recurving of the temporal pole than in lower forms. In higher forms the caudal displacement of the hippocampus due to callosal elongation, reverses or recures the *inrolled* hippocampus exactly as in the case of simpler brains alluded to. What we seem to have always before us is the structural record of the solution of various problems of regulative behavior, from which we may attempt to reconstruct a phylogeny of function. We should remember that there are always a great number of factors working in concert or as more or less independent variables, and that the outstanding potency of any particular factor does not mean its exclusive activity.

Above the medial amygdaloid fissure (*fs.amg.m.*, Figs. 6, 12, 17, 40-43) the dorsal or subicular border of the ammon's horn adjoins, as it curves upward, the posterior pyriform cortex along a line reaching upward to the medial extension of the rhinal fissure (*fs.rh.m.*) thus completing the great horizontal rhinencaphalic cortical ring, as de-

scribed in the earlier part of this paper dealing with the external form of the brain (page 185). In *Caenolestes* this line is longer than in the Virginia opossum, because the position of the rhinal fissure is considerably higher. The exact point at which the rhinal fissure hits the subiculum edge of the hippocampus is not determinable, owing to the fading out of histological differentiation, and therefore the extended portion of the fissure is shown as a broken line (*fs.rh.m.*, Figs. 6, 12, 17, 42).

Elliot Smith (1895b, p. 183), in discussing the hippocampus of *Notoryctes*, makes the following remarks: "The hippocampus is equally convoluted in all mammals, because it reaches its maximum development quite early in the phylogenetic history of the individual. Thus in *Platypus* it possesses a histological differentiation quite as complex and fine as is found in the highest mammals. Like the pyriform, it is developed early both in phylogeny and ontogeny in accordance with the development of the olfactory apparatus. Because part of the smell center should reach a high state of development, when the pallium is not proportionately intricate, is no argument that the cortex of the smell center does not behave like the rest of the cortex in similar circumstances. It should be noted, however, that, intimate as is the connection between the hippocampus and the olfactory lobe, the relative sizes of the two parts are by no means constant. Thus, in spite of the marked difference in the sizes of the olfactory bulb in *Ornithorhynchus* and *Perameles*, there is no appreciable difference in the sizes of their hippocampi. In *Notoryctes* the size of the hippocampus is relatively small, considering its huge olfactory. *What determines the size of the hippocampus is hard to say.*" (Italics mine.)

These statements are very suggestive, and in my study of the cerebral hemisphere of *Caenolestes* they have often recurred to me. Are we, however, warranted in saying that the hippocampus reaches its "maximum development" in the lower mammals, and that in *Ornithorhynchus* the histological differentiation is "quite as complex and fine as is found in the highest mammals"? It is true, as explained above, that the definitive mammalian "hippocampal figure" appears suddenly and at a constant level in the lowest mammals. But the amount of inrolling and the development of the temporal pole of the hippocampus both vary considerably, as we have seen, in the marsupials alone. Now in the marsupials we find also a great variation in the amount of neopallium present, without, however, a greatly elongated eutherian type of corpus callosum to account for the temporal pole by mere displacement of the entire supra- and postcommissural hippocampus. Fur-

thermore, in considering the histological differentiation of the hippocampus, we now know that if we take into account not merely the simple ranks of ammon's pyramids and the granules of the gyrus dentatus as they are stained by ordinary cell methods, such as Nissl, but also the many types of cells in the other layers of the hippocampal cortex, as they were demonstrated by Cajal (1911) in the mouse by the silver methods, we get a tremendously suggestive picture of the possibilities for progressive complication within the hippocampus. I attempted to count the different types of intrahippocampal reenforcing and stepping-up devices as described and figured by Cajal in the mouse, and found some twenty-five or thirty of them. Only a comparative study by the silver methods (such as that being carried on by del Rio-Hortega, 1919) of the whole range of mammalian brains could reveal the stage at which the maximum development (maximum histological differentiation) of the hippocampus was attained. I should rather expect to find it nearer the upper than the lower end of the mammalian phylum, among those brains in which the discrepancy between the olfactory bulbs and the neopallium is marked, but in which smell is still an active function. As Elliot Smith remarks, the hippocampus does not, like the pyriform lobe and the tuberculum olfactorium, decrease *pari passu* with the olfactory bulbs. On the contrary, it holds its own (disregarding the ammosmatic brains, and even they manage to retain some recognizable hippocampus), perhaps because it can so efficiently combine enhancement of function with economy of space (see page 217) as the neopallium increases, and this, apparently because of the increasing activity back and forth between the two. In this connection it is to be noted (see Herrick, 1922, page 196) that the primordium hippocampi has as early as the preganoidean stage no direct somatic connections, and in the ganoidean stage begins to lose direct olfactory connections, and very soon begins to develop a characteristic structure in the presence of indirect correlation and associational connections from various sources, "resulting in a topographical rearrangement which prepared the way for the differentiation within this area of true hippocampal cortex in higher forms" (Herrick, 1922, page 196). The ability of the hippocampus to preserve a sort of structural constancy or individuality with almost total loss of direct olfactory connections, and in the face of great reduction of primary and secondary olfactory centers, has apparently undergone no abatement in the presence of the developing mammalian neopallium. Its peculiar structural pattern has merely unfolded in its own way; it has not approximated the neopallial structural pattern.

Functionally the increasing neopallial-hippocampal bond is of tremendous import. On reflex and lower psychic levels olfaction is mainly if not exclusively linked with food and sex; on higher psychic levels it becomes increasingly significant esthetically and intellectually, in correspondence with the increase of the neural connections between the hippocampus and the somatic pallium which apparently accompanies the *decrease* of neural connections between the hippocampus and the diminishing olfactory bulbs and their immediately dependent secondary olfactory centers. This does not mean that the hippocampus increases phylogenetically in the same ratio with the somatic pallium, or in any constant ratio with it. Apparently neither is true. But it seems hard to believe that a direct relation does not exist between the neopallium and the hippocampus, a relation which is responsible not only for the remarkable preservation of pattern (not its *initiation*) and maintenance of size of the latter structure in higher and relatively microsmatic brains, but finally for the sublimation of smell into a "nobler" sense, practically as truly subservient to higher psychic life as are vision and audition. Language is a form of behavior, and the rich poetic and spiritual imagery clustering around such words as "fragrance" and "incense" amply testifies at once to the importance of the existing sense of smell in man and to its sublimation. So too does the tremendous evocatory power of smell, when it recreates vanished experiences which arouse high and beautiful thoughts or emotions.

#### CORPUS STRIATUM

The corpus striatum consists of a caudate nucleus (*nuc.caud.*, Figs. 12, 15, 28-38) projecting into the ventricle and extending farther rostrally and caudally than any other part of the striatum, and a lentiform nucleus lateral and ventral to it, in two parts, the putamen (*put.*, Figs. 29-35) and globus pallidus (*gl.p.*, Figs. 12, 15; *glob.p.*, Fig. 34). The medial or septal part of the head of the caudate nucleus, the nucleus accumbens (*nuc.ac.*, Figs. 12, 20-30; the lateral parolfactory nucleus of Johnston, 1913—see page 199), has already been mentioned in connection with the fusion of the head of the caudate with the tuberculum (page 196). Rostral to this fusion the large head of the caudate is laced with small diagonal fiber bundles, like darning stitches, and heavily fringed on its ventral border with diagonal fibers, all the way from the septum to the lateral arm of the anterior commissure (Fig. 29). It is split dorsally by a small caudally directed ventral diverticulum of the lateral ventricle, roofed by the lower surface of the anterior commissure which here breaks across the ventricle to reach

the median wall (Figs. 30-31). The large and compact internal capsule (*cap.i.*, Figs. 29-34) separates the caudate nucleus from the large putamen, whose lateral boundary is the curve of the external capsule (*cap.e.*, Figs. 28-35). The caudate nucleus, including the nucleus accumbens, and the putamen are in this series characterized by a peculiar dark, gun-metal gray background, seen also in the lateral and basal amygdaloid nuclei, setting all these structures sharply off from neighboring ones. I do not know what it may be worth as a criterion, but it is interesting to note that the nucleus accumbens, which Johnston (1913) considers to be the lateral parolfactory nucleus, is uniform with the rest of the caudate in this respect, being sharply delimited from the septum by this ground color.\*

The globus pallidus (*gl.p.*, Figs. 12, 15; *glob.p.*, Fig. 34) is a prominent mass of pale giant cells in a rich tangle of fibers, situated near the center of the sections in which it appears, just below the internal capsule as it passes into cerebral peduncle, and not very far behind the anterior commissure level. Small giant cells trailing irregularly towards the basal forebrain bundle in the innominate region (prethalamus, border nucleus of Völsch) may belong to the basal nucleus of the palaeostriatum (De Vries, 1910; Kappers, 1921b).

#### NEOPALLIUM

No attempt has been made to analyze the neopallium of *Caenolestes* into anatomical regions, although even this inadequate series gives some evidence of its possibility. It is hoped that the two series to be made from the brains of *Oroestes* may, with the aid of the intensive cortical analysis of the Virginia opossum in this laboratory (Gray, 1924), render a fairly adequate analysis of the somatic cortex possible in *Caenolestes* and *Oroestes*.

The *claustrum*, which Brodmann and others consider to be a neopallial derivative, is certainly present in the more dorsal part of the

\*I was much interested to read (Kappers, 1923, page 365) of the "Spatz reaction" of sulphur ammonium, based on the presence of iron, which gives a much stronger blue color in the palaeostriatum than in the neostriatum. While not inclined to attribute very great test force to his reaction, Kappers thought it interesting that results on the chick and man corresponded. In this iron-haematoxylin series of *Caenolestes* the dark coloration has a very different distribution. The globus pallidus is conspicuously without it. The caudate nucleus (nearly all but the tail) and parts of the tuberculum fusing with it, the putamen, and the two newest amygdaloid nuclei (according to Johnston, 1923), the lateral and the basal, are the regions strikingly affected by the dark coloration. Very pronounced in the rostral portion of all the structures named, it tends to fade out caudally in each of them. I do not know enough about either the Spatz reaction or the dark coloration here to form an opinion as to any relation between them.

anterior pyriform region, but is not clearly delimited. It apparently forms an irregular cell plate between the external capsule and a cell-poor strip in which some fibers appear which may be an incipient *capsula extrema* (*clau.*, *cap.ex.*, Figs. 27-34). Elliot Smith (1919a, b) considers the claustrum a derivative of the upturned lower edge of the pyriform cortex. This material affords no real evidence either way, although the claustrum here seems to be continuous with the deeper layers of the neopallial cortex.

The cells of this brain, which are remarkably well stained, considering the method used, may be divided first of all into two groups, which Völsch (1906) has called round and pyramid cells, referring to the hemisphere only. The pyramidal cells (using the term very loosely for any angular cell) are black and show dendritic stumps, sometimes very long. The round cells are pale-stained with the nucleus clearly visible. The variation in size is very much greater for the round cells than for the pyramidal cells. All the giant cells of the hemisphere belong to the former type, those of the basal olfactory region, in the anterior portion of the lateral limb of the median forebrain bundle (see page 198), those of the *regio innominata*, prethalamus etc. The smallest cells also belong to this type, the olfactory granules, those of the gyrus dentatus, the exceedingly fine granules of some of the islands of Calleja in the tuberculum, and the scattered masses of very tiny granules tucked between adjacent structures like packing. Völsch considers these last to be non-nervous, I do not know on what evidence other than their size and resemblance to stained glia nuclei. The largest cells of the pyramidal or dark angular type are probably those found in the basal nucleus of the amygdala, for the hemisphere at least.

#### GENERAL CONSIDERATIONS

In the beginning of this study of a type of brain totally unknown to me I saw that no rational progress was possible save upon a broad and strictly comparative basis. In the course of parallel studies of the literature and of the sections of this particular brain, some more general considerations arose, first as persistent questions, usually entirely unanswerable by me at least, but sometimes coming halfway to rest in my mind. Two of these are briefly outlined below.

One of the most puzzling aspects of such neurological studies as this comes out in connection with the very great diversity of anatomical pattern of structures whose afferent and efferent connections seem almost or practically identical. How shall we explain the enormously

discrepant anatomical structure? The real functional adequacy of every existing structure must of course be taken for granted as the basis of its existence. But more than this must apparently be called in to explain its particular anatomical type of structure. Phyletic tradition clarifies some things—inherited type of anatomical pattern (or the potency to develop it) retained, embellished, even accentuated, so long as it is functionally utilisable or perhaps not actually disadvantageous. The hippocampus is perhaps the classic example under this head. Even when no longer adequate, as evidenced by reduction and degeneration, it seems very hard to be got rid of entirely. Fortunately for the comparative neurologist, it hangs on, sometimes only a pale and shrunken relic, long after it has been more or less supplanted by other structures, with similar or unlike functions, which have become more important in the action-system of the animal either because of fundamentally more serviceable type of anatomical structural pattern, or because of more useful afferent or efferent connections, or for both reasons. Thus a sort of natural selection (Roux's "struggle of parts"?) is constantly operating among structural patterns. A structural pattern is safe so long as the demands upon it are not too heavy, or so long as a competing pattern with greater possibilities does not outrun it. The superiority and final supremacy of the competing pattern may depend not only upon its intrinsic possibilities, but also upon its topographical position and the character and activity of neighboring structures. Thus the early "physiological isolation" (to use Child's now familiar term, 1915, 1921) of the primordium hippocampi from direct sensory stimuli (see page 219) led to "topographical and physiological relationships [which have] prepared the way for the differentiation within this area of true hippocampal cortex in higher forms" (Herrick, 1922, page 196). The trail of the Law of Neurobiotaxis is to be seen everywhere, and this is apparently the most potent single factor which can be invoked immediately to "explain" structural pattern (i.e., to translate it into functional pattern) within the central nervous system. Acting in concert with phyletic tradition, it might well result in exaggerations of structural pattern which do not seem to parallel the development of functional pattern. We must, of course, in comparing similar lists of afferent and efferent connections of very dissimilar structures, take into account the quantitative and positional differences of all the factors, as well as the selective operation of synapses. On the surface, perhaps the discrepancies seem much more striking on the structural than on the functional side, although sometimes the reverse seems to be true. We must of course believe that no two

structures that are visibly different do have absolutely identical functions, not even right and left members of paired structures in the same brain. On the whole, however, the physiologist's frequently voiced objection to the anatomist's too great emphasis upon structural pattern may not perhaps be an unjustifiable one. The modern anatomist, of course, regards structure as merely a useful and convenient clue to function.

Another question which naturally arises in such a study as this concerns what, if any, light is thrown upon the method of progressive evolution in the central nervous system. Davidson Black (1913, page 366) quotes Roux's definition of the two phases of the development of an active tissue: "self-differentiation", which goes on without regard to functional differentiation, and "dependent differentiation", which cannot proceed normally in the absence of functional connections—in the nervous system, functional continuity of neuron systems, as Bechterew pointed out. The transition point between these two phases of growth Black calls the "critical point". Apparently the essential character or activity of progressive evolution in the central nervous system is the pushing forward of this "critical point", relegating more and more of the period of "dependent differentiation" back into the period of "self-differentiation", where it undergoes compression, abridgement, and, so to speak, distortion, thus building the foundation for newer and higher development in the period of dependent differentiation—like using the capstones of a newer structure to strengthen and enlarge the old foundation and so to fit it for still newer and more ambitious structures. What this "antedating" of structure implies in physiological terms, what metabolic changes or reorganization by which, or accompanying which, dissociations take place, some phases dropping out, others being temporally dislocated with reference to the stimuli formerly necessary to elicit them, or whether the dissociations are more apparent than real, I am not competent to discuss.

In attempting to reconstruct the phyletic history of any form, it is to be remembered that not all the foundation blocks, original or "second-hand", have been retained in the enlarged foundation—some have been rejected entirely, all have been recut, and many have altered their relations with reference to others. The higher the form the greater the compression, abridgment and rearrangement, and therefore the greater the necessity of prudence and hesitation in the reconstruction of the *detail* of phyletic pattern, no matter how simple and obvious, perhaps deceptively so, the ontogenetic pattern may appear.

## SUMMARY

1. The brain of *Caenolestes* (and of *Orolestes*) is of the extreme macrosmatic type, characterized by the great size of the olfactory bulbs and the great development of the higher rhinencephalic centers (Herrick, 1921).
2. The neopallium, in contrast, forms only the shallow cap of the cerebral hemisphere above the high rhinal and hippocampal fissures, and may perhaps be relatively the least extensive or the second least extensive among mammals (Herrick, 1921).
3. The olfactory cortices—pyriform and hippocampal—form, with the aid of the anterior olfactory nucleus, two periventricular rhinencephalic rings partially united anteriorly: a smaller *quasi*-vertical one rostrally, in which the pyriform and hippocampal cortices are doubly (supra- and infraventricularly) but indirectly united through the anterior olfactory nucleus; and a much larger horizontal ring formed by the additional direct union of the posterior pyriform cortex and the subiculum margin of the ammon's horn on the median surface of the hemisphere between the medial prolongations of the rhinal and amygdaloid fissures. The two olfactory cortices are split apart dorsally by the wedgelike neopallium and ventrally by a similar wedgelike formation composed of the tuberculum olfactorium rostrally and the amygdaloid complex caudally.
4. The marked antero-posterior foreshortening of this brain is one of its characteristic features, frequently in evidence. It is probably to be explained, in part at least, by the exaggeration of the subcortical centers.
5. The hippocampus begins immediately behind the olfactory (bulbar) formation, passes through practically all reptilian stages precommissurally, and at the dorsal commissure rather suddenly assumes definitive mammalian form, under the three-fold influence of external pressure, internal pressure and neurobiotactic attraction. Its temporal end has just begun to recurve, the gyrus dentatus alone being involved. In the Virginia opossum the ammon's horn has begun to follow suit. More advanced critical stages can be added to these to form a complete and illuminating series of the phyletic development of the mammalian hippocampus, omitting the monotremes and the lowly marsupial *Notoryctes*, aberrantly advanced in this respect.
6. In the amount of gyrus dentatus exposed upon the median surface of the hemisphere (an index of the degree of inrolling of the hippocampus) *Caenolestes* is intermediate between *Notoryctes* and *Perameles*.

7. The enormous size of the amygdaloid complex is a striking characteristic of this brain, as is also its prolonged contact with the temporal hippocampus, both ammon's horn and gyrus dentatus.

8. The absence of the aberrant bundle of the anterior commissure would on the basis of Elliot Smith's definition of it as a diagnostic character of diprotodont brains, seem to put *Caenolestes* among the polyprotodonts, and even to raise the question of the exclusion of the diprotodonts from America.

9. The cerebellum of *Caenolestes* and *Oroolestes* is almost exactly intermediate between those of *Notoryctes* and *Perameles*, the two simplest mammalian cerebella hitherto described.

10. In consideration of the marked specialization and aberrancy of the two monotreme brains, the brain of *Caenolestes* (and of *Orolestes* so far as can be judged from the external anatomy) ranks as one of the three simplest and most generalised mammalian brains known at the present time. In view of the exaggerated development of the temporal pole of the hippocampus in *Notoryctes*, it really takes first rank. But on the whole, it is fairly intermediate between *Notoryctes* and *Perameles*, the two simplest and most generalized mammalian brains hitherto described (Elliot Smith), which it most closely resembles. It should offer—and actually does offer—especially promising clues for the reconstruction of the presumptive phyletic stages involved in the transition from the reptilian to the mammalian type. And since it is at once a mammalian brain and so simple and generalized—almost, indeed, a mammalian brain reduced to lowest terms—it also offers hints of unusual legibility for the verification of the structural activities of the nervous system, viewed as regulatory behavior of a more or less plastic material. The cerebral hemisphere of *Caenolestes*, the only part of the brain yet studied in any detail, fairly swarms with exquisitely clear examples of structural evidences of the operation of neurobiotaxis, the principle whose conception and definition by Dr. Kappers of Amsterdam has transferred the study of brain morphology from a static to a dynamic basis.

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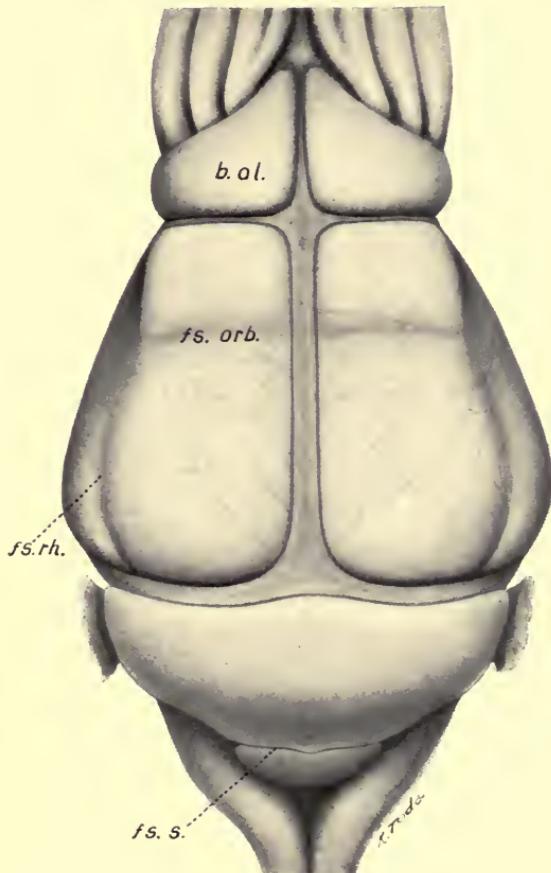
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## ABBREVIATIONS

al.	alveus	cx. pir. m.	cortex piriformis me-
a. ln.	area lunata cerebelli	cx. pir. p.	dialis
amg.	nucleus amygdalae;	d. b.	cortex piriformis pos-
	amygdaloid complex	d. v.	terior
a. prcom.	area precommisuralis	diverticulum ventralis	diagonal band of Bro-
a. pt.	area pteroidea cere-	(of superior re-	ca
belli		cess)	diverticulum ventralis
aq.	aqueduct of Sylvius	fila ol.	(of superior re-
b.	nucleus basalis amyg-	fim.	cess)
dalae		floc.	fila olfactoria
b. ac.	nucleus basalis acces-	f. med. t.	fimbria
sorius amygdalae		f. med. t. l.	flocculus
b. ol.	bulbus olfactorius		fasciculus medialis te-
b. ol. ac.	bulbus olfactorius ac-		lencephali (medial
cessorius			forebrain bundle)
c. (Fig. 8)	brachium conjuncti-		fasciculus medialis te-
vum			lencephali lateralis
c.	n u c l e u s centralis		(lateral limb of m.
	amygdadae		f. b.)
c. a.	commissura anterior	form. bul.	formatio bulbaris (ol-
	sive ventralis; see v.	f. prcom.	factory)
c. am.	cornu ammonis	fs. amg.	fornix praecommis-
cap. e.	capsula externa	fs. amg. m.	suralis
cap. em.	capsula extrema	fs. circ.	fissura amygdaloidea
cap. i.	capsula interna	fs. ch.	fissura amygdaloidea
ch., ch. op.	chiasma opticum	fs. di-tel.	medialis
ci. am.	cingulum ammonis	fs. erh.	fissura circularis
ci. lim.	cingulum limitans	fs. f. d.	fissura choroidea
clau.	claustrum	fs. fim. al.	fissura di-telencepha-
c. c.	corpus callosum		lica
c. d.	commissura dorsalis;	fs. fim. d.	fissura endorhinalis
	see d., ps. d., ps.v.	fs. h., fs. hip.	fissura fimbrio-dentata
c. g. l.	corpus geniculatum	fs. pln.	fissura fimbrio-alvea-
laterale		fs. pnod.	ris
c. g. m.	corpus geniculatum	fs. orb.	fissura fimbrio-dentata
mediale		fs. pr.	fissura hippocampi
col. a.	colliculus anterior	fs. prcul.	fissura postlunata
col. p.	colliculus posterior	fs. rh.	fissura postnodularis
cort.	nucleus corticalis	fs. rh. a.	fissura orbitalis
	amygdalae	fs. rh. arc.	fissura prima cerebelli
cul.	culmen, pars culmina-	fs. rh. m.	fissura preculminata
	ta cerebelli	fs. s.	fissura rhinalis
dec. pyr.	decussatio pyramidali-	fs. spry.	fissura rhinalis ante-
deep nuc.	deep nuclei of cere-	fs. tr. cb.	rior
	bellum (undivided)	g. bas. op.	fissura rhinalis arcua-
em. nat.	eminentia natiformis		ta
ex. am.	cortex ammonis	g. 5	fissura rhinalis me-
cx. am. iven.	cortex ammonis intra-	gl. p., glob. p.	dialis
	ventricularis		fissura secunda cere-
cx. am. xven.	cortex ammonis extra-		belli
	ventricularis		fissura suprapyrami-
cx. dent.	cortex dentatus		dalis
cx. hip. a.	cortex hippocampalis		fissura transversa ce-
	anterior (precom-		rebelli
	missuralis)		ganglion basale op-
cx. pir.	cortex piriformis		ticum
cx. pir. a.	cortex piriformis an-		ganglion semilunaris
	terior	globus pallidus	
		gyrus dentatus	

hab.	habenula	nuc. ol. ant. l. v.	n u c l e u s olfactorius
hip. a.	hippocampus anterior (praecommissuralis)		anterior, pars late- ro-ventralis
i. C.	island of Calleja	nuc. ol. ant. m.	n u c l e u s olfactorius
inf.	infundibulum		anterior, pars me- dialis
interpos. l.	interpositio lateralis	nuc. ol. ant. p.	n u c l e u s olfactorius
interpos. m.	interpositio medialis		anterior, pars pos- terior
int. plate	intercalary plate of Johnston (1923)	nuc. pol. l.	nucleus parolfactorius
ip. m.	interpositio medialis		lateralis
l.	nucleus lateral is amygdalae	nuc. pol. m.	nucleus parolfactorius
lg.	lingula cerebelli		medialis
lob. a. cb.	lobus anterior cere- belli	nuc. tr. ol. l.	nucleus tracti olfacto- rii lateral is; see n. t. o. l.
lob. m. cb.	lobus medialis cere- belli	ped. floc.	pedunculus flocculi
lob. p. cb.	lobus posterior cere- belli	pfloc.	paraflocculus
l. perf. a.	locus perforatus ante- rior	pl. ch. 3 (4)	plexus choroidea ven- triculi tertii (quar- ti)
m.	nucleus medial is amygdalae	p. prcul.	pars preculminata ce- rebelli
med.	medulla oblongata	p. spyr.	pars suprapyramidalis
m. i.	massa intermedia	put.	cerebelli
neop.	neopallium	pyr.	putamen
n. 2	nervus opticus	r.	pyramis cerebelli
n. 5	nervus trigeminus	rec. i.	corpus restiforme
nod.	nodulus cerebelli	rec. s.	recessus inferior
n. t. o. 1.	nucleus tracti olfacto- rii lateral is	rad. thal.	recessus superior
nuc. ac.	nucleus accumbens	st. glom.	radiatio thalamica
nuc. amg. b.	nucleus basalis amyg- dalae	st. gr.	stratum glomeruli
nuc. amg. b. ac.	nucleus basalis acces- sorius amygdalae	st. m. c.	stratum granulare
nuc. amg. c.	nucleus central is amygdalae	st. med..	stratum cellularum mi- tralium
nuc. amg. cort.	nucleus cortical is amygdalae	st. t.	stria medullaris, see st.
nuc. amg. l.	nucleus lateral is amygdalae	st. t. 1	t. 5
nuc. amg. m.	nucleus medial is amygdalae	st. t. 2	stria terminalis
nuc. caud.	nucleus caudatus	st. t. 3	stria terminalis,
nuc. d. b.	nucleus of diagonal band of Broca	st. t. 4	bundle 1 (Johnston, 1923)=com. bundle
nuc. ip.	nucleus interpeduncu- laris	st. t. 5	stria terminalis,
nuc. ol. ant.	n u c l e u s olfactorius anterior (Herrick)		bundle 2 (Johnston, 1923)=ol. proj. tr. (amg.)
nuc. ol. ant. d.	n u c l e u s olfactorius anterior, pars dorsa- lis		stria terminalis,
nuc. ol. ant. ex.	n u c l e u s olfactorius anterior, pars exter- nus		bundle 3 (Johnston, 1923)=subcom.
nuc. ol. ant. l.	n u c l e u s olfactorius anterior, pars late- ralis	st. t. bed.	bundle
		tect.	stria terminalis,
			bundle 4 (Johnston, 1923)=supracom.
			bundle
			stria terminalis,
			bundle 5 (Johnston, 1923)=st. med.
			bundle
			stria terminalis bed
			tectum mesencephali

t. ol.	tuberculum olfacto- rium	tr. t. a.	tractus temporo-am- monis of Cajal (1911; sphenotemp., 1906); see ci. lim. (cingulum limitans) and ci. am. (cingu- lum ammonis)
tr. ol.	tractus olfactorius		
tr. ol. d. m.	tractus olfactorius dorso-medialis		
tr. ol. fr.	tractus olfacto-fronta- lis	t. v. 4 uv.	taenia ventriculi quarti
tr. ol. i.	tractus olfactorius in- termidius (commis- suralis)	v. cb. v. l. v. m. a.	uvula cerebelli ventriculus cerebelli ventriculus lateralis velum medullare ante- rius
tr. ol. l.	tractus olfactorius la- teralis (massive part)	v. ol. v. 3 (4)	ventriculus olfactorius ventriculus tertius (quartus)
tr. ol. l. d.	tractus olfactorius la- teralis, pars dorsa- lis	xven. alv. xven. cx. ani.	extraventricular alveus extraventricular cor- tex ammonis
tr. ol. l. p. d.	tractus olfactorius la- teralis, pedunculus dorsalis	*	line of fracture sup- posed to mark boundary between extra- and intraven- tricular precommis- sural ammon's cor- tex.
tr. ol. l. p. v.	tractus olfactorius la- teralis, pedunculus ventralis	→	arrows to show direc- tion and approxi- mate degree of force operating in the formation of the definitive mamma- lian "hippocampal figure", figure 11
tr. ol. l. v.	tractus olfactorius la- teralis, pars ventra- lis		line of amputation of cortex dentatus, fig- ure 17a
tr. ol. m.	tractus olfactorius me- dialis		line of amputation of cortex ammonis, figure 17b
tr. ol. s. + c.	tractus olfacto-septa- lis et corticalis	I	
tr. op.	tractus opticus	2	
tr. st. thal.	tractus strio-thalamici- cus		

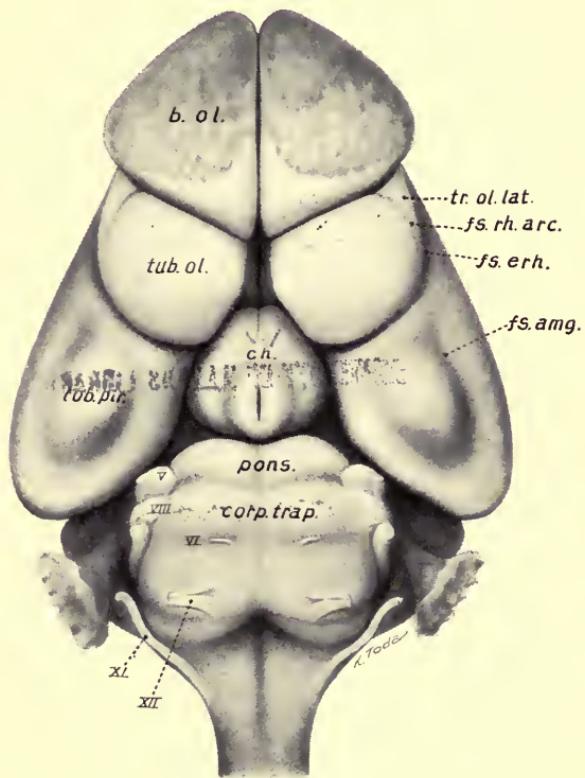


1

OROLESTES INCA.  
DORSAL VIEW OF BRAIN.  
Five times natural size.

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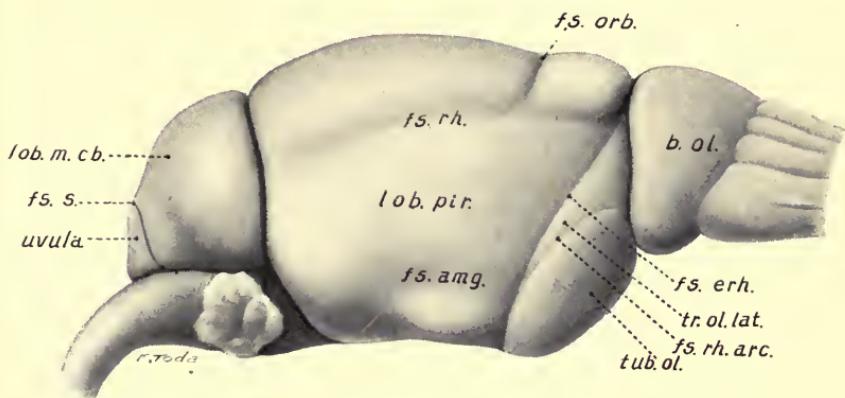


2

OROLESTES INCA.  
VENTRAL VIEW OF BRAIN.  
Five times natural size.

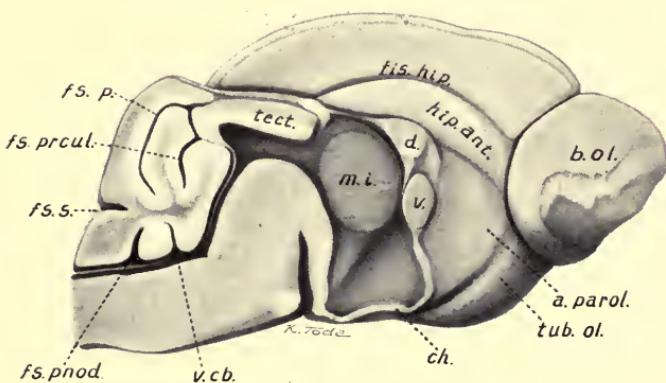
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3

## OROLESTES INCA.



4

## OROLESTES INCA.

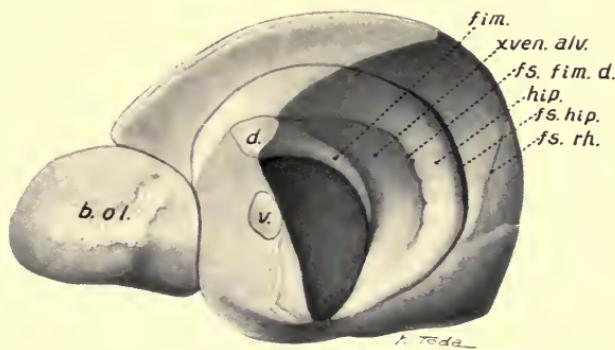
FIG. 3. LATERAL VIEW OF BRAIN.

FIG. 4. MEDIAN SECTION OF BRAIN.

Five times natural size.

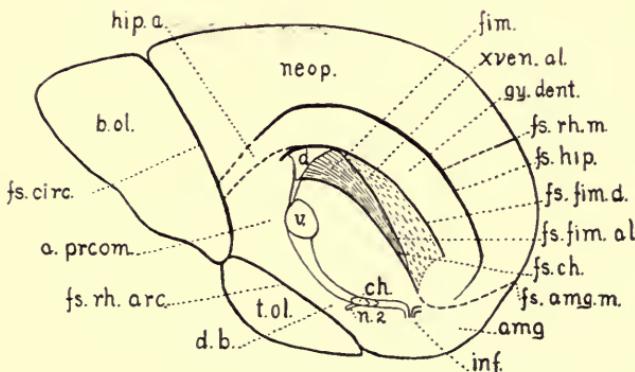
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5

## FIGURE 5. RECONSTRUCTION OF THE MEDIAN SURFACE OF THE HEMISPHERE OF OROLESTES INCA.



6

## MEDIAN SURFACE OF HEMISPHERE.

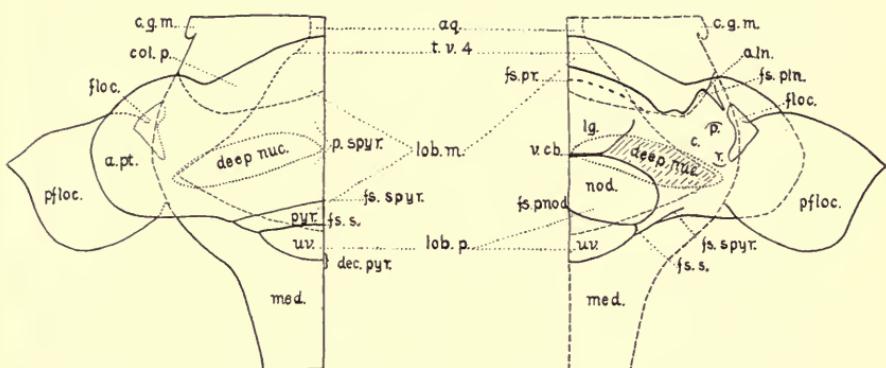
FIG. 5. OROLESTES INCA.

FIG. 6. CAENOLESTES OBSCURUS. RECONSTRUCTION.

Five times natural size.

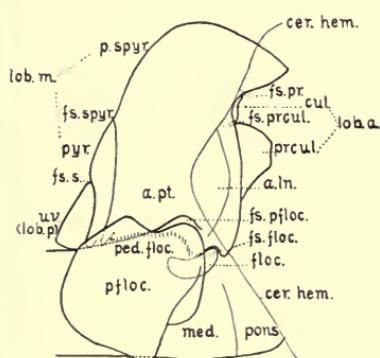
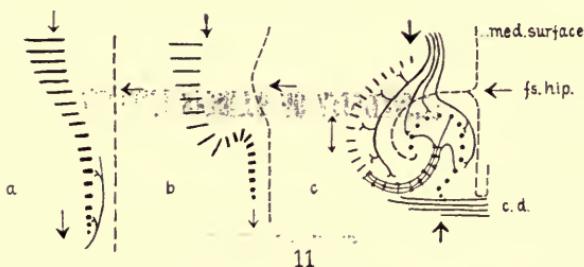
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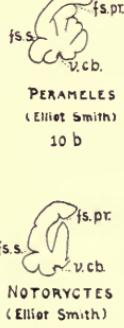
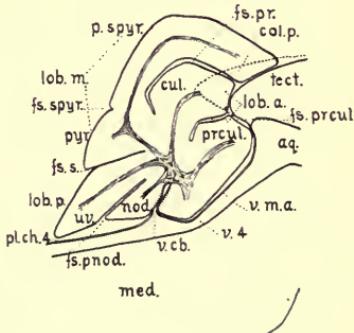


7. DORSAL

8. VENTRAL



9. LATERAL

10 b  
10 a

10. MEDIAL

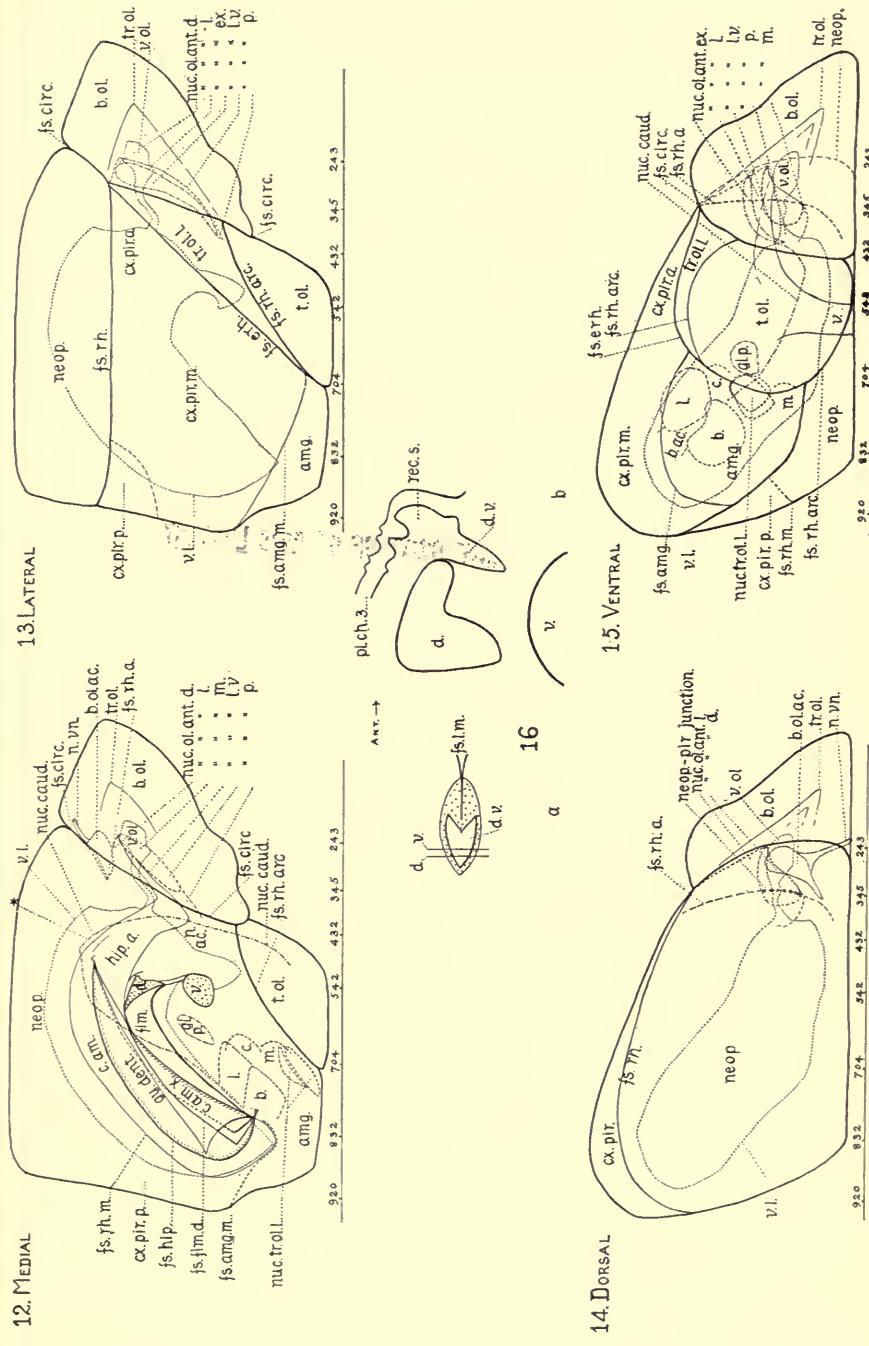
FIGS. 7 TO 10. *CAENOLESTES OBSCURUS*. CEREBELLUM. RECONSTRUCTIONS. X 8.

FIGS. 10a-10b. CEREBELLA OF NOTORYCTES AND PERAMELES.

FIG. 11. DEVELOPMENT OF MAMMALIAN "HIPPOCAMPAL FIGURE."

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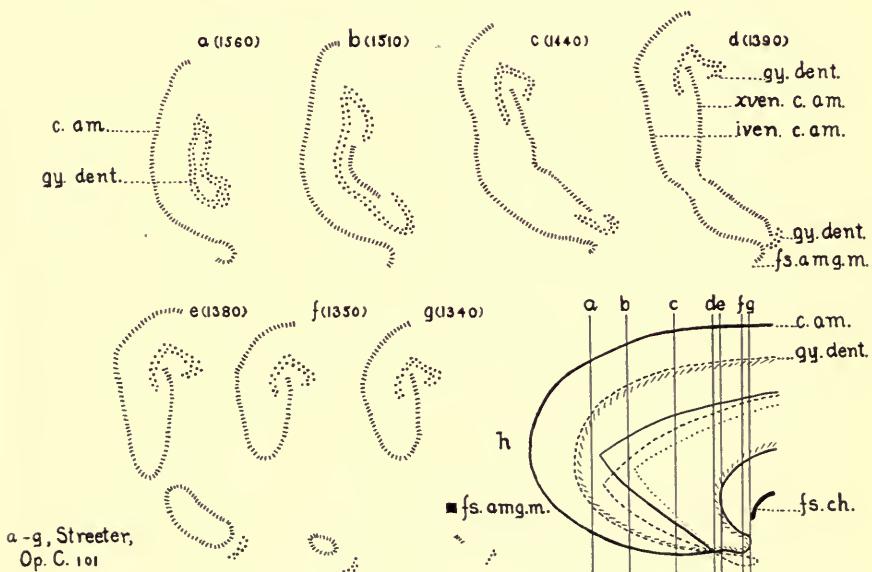
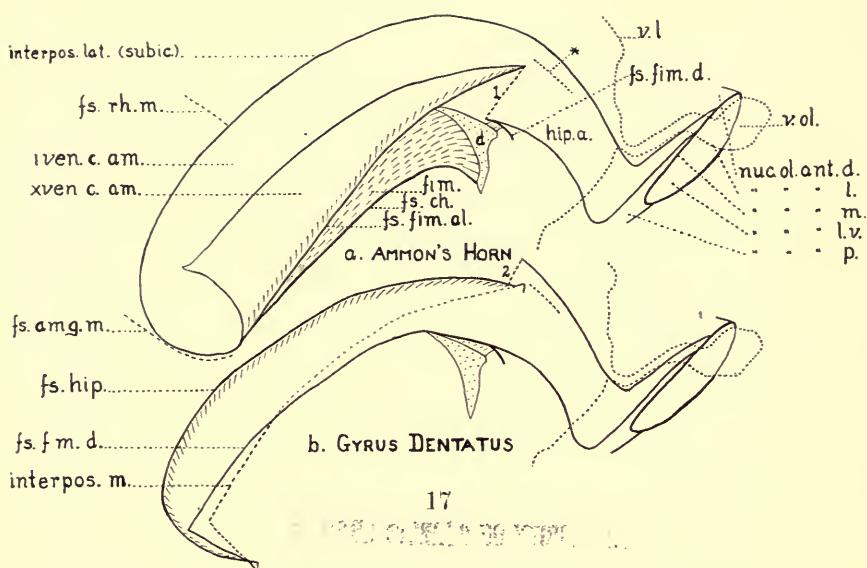


FIGS. 12 TO 15. CAENOLESTES OBSCURUS.

RECONSTRUCTIONS OF HEMISPHERES.

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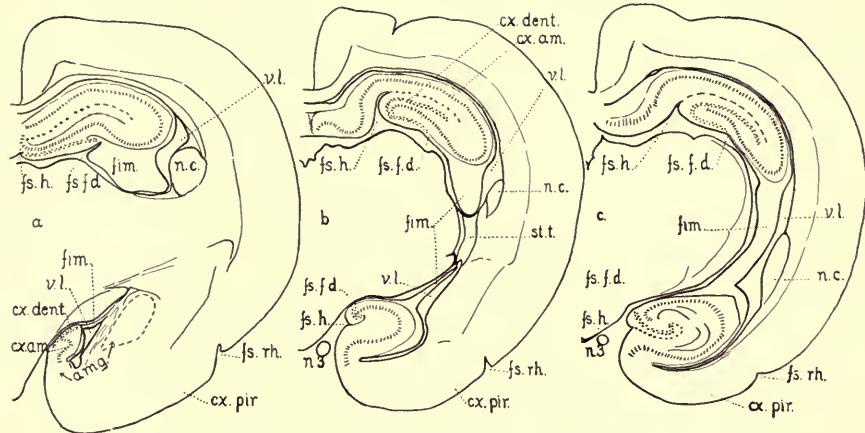




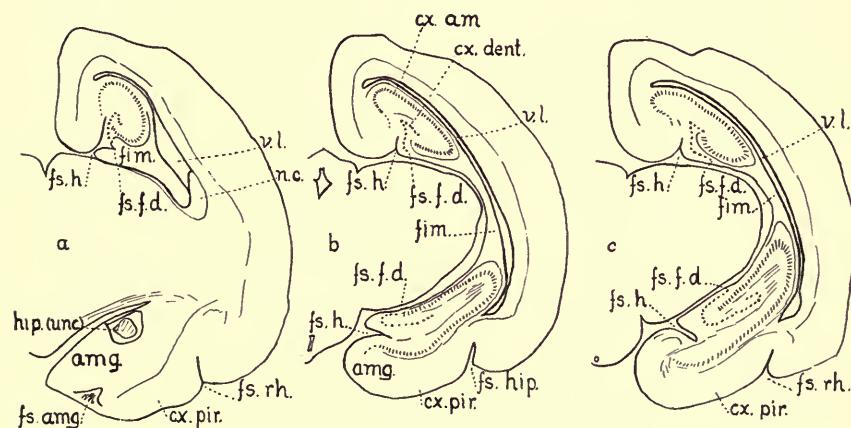
18

FIG. 17. CAENOLESTES OBSCURUS. DISSECTED DIAGRAM OF HIPPOCAMPUS. X 12.  
 FIG. \*8. DIDELPHIS VIRGINIANA. TEMPORAL HIPPOCAMPUS. X 5.

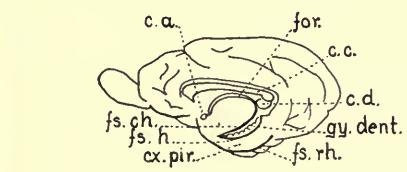




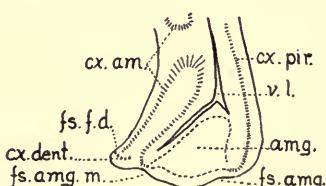
19



20



21



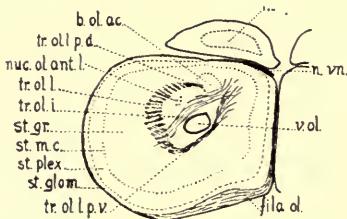
22

## TEMPORAL RECURVING OF HIPPOCAMPUS.

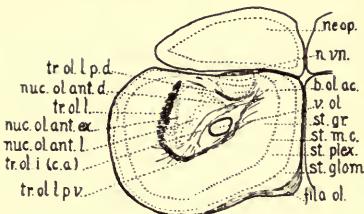
FIG. 19. *HYPSPRYMNUS* (LIVINI) X 3.FIG. 21. *FELIS LEO* (ELLIOТ-SMITH) X ½.FIG. 20. *RABBIT* (WINKLER-POTTER).FIG. 22. *NOTORYCTES* (DART).

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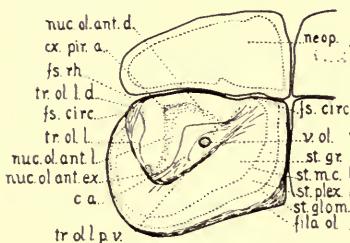




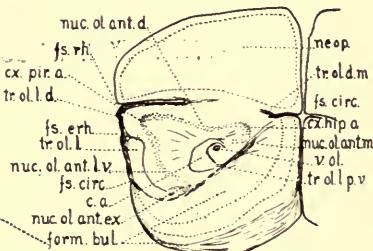
23 (SEC. 243)



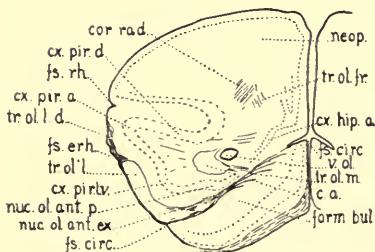
24 (SEC. 271)



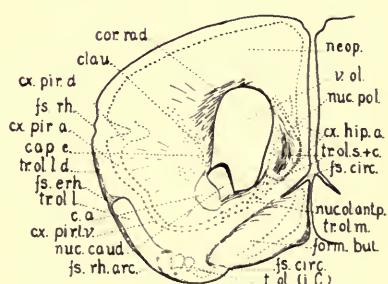
25 (SEC. 307)



26 (SEC. 345)



27 (SEC. 382)



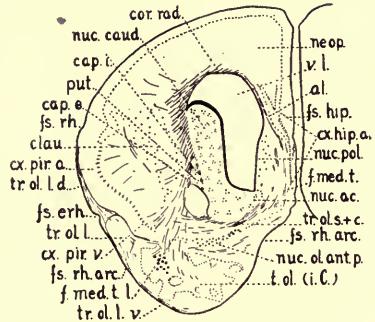
28 (SEC. 410)

## CAENOLESTES OBSCURUS.

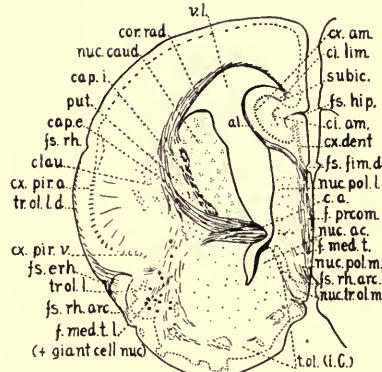
x 8.

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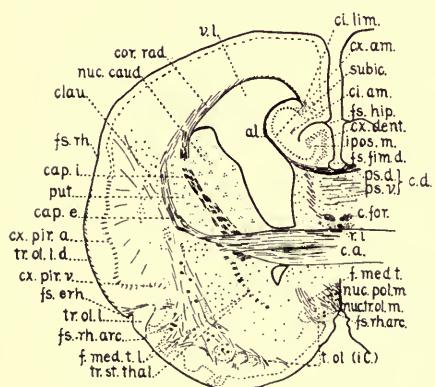




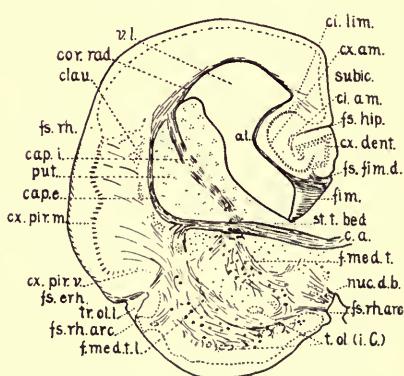
29 (SEC. 432)



30 (SEC. 510)



31 (SEC. 542)



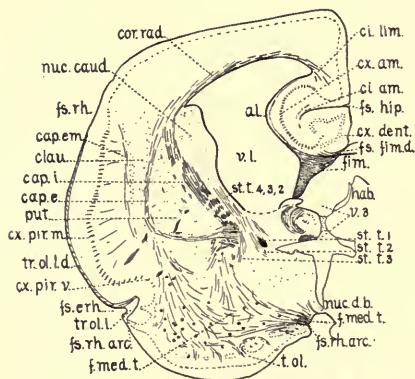
32 (SEC. 581)

## CAENOLESTES OBSCURUS.

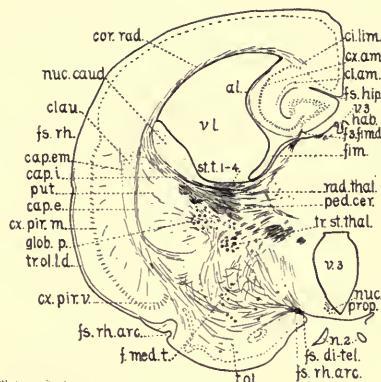
X 8.

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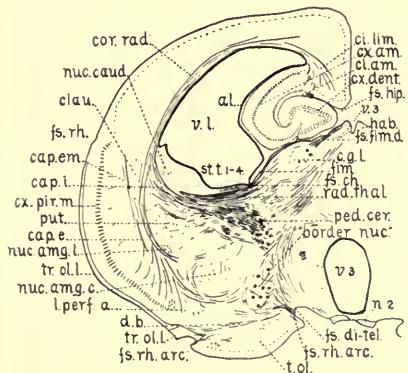




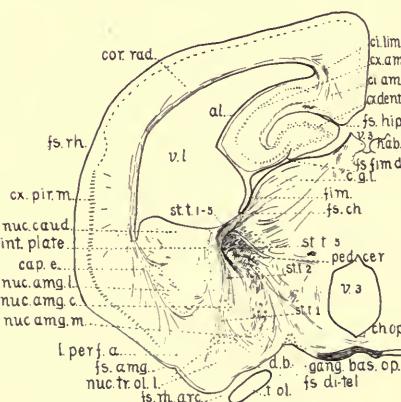
33. (SEC. 593)



34. (SEC. 642)



35. (SEC. 668)



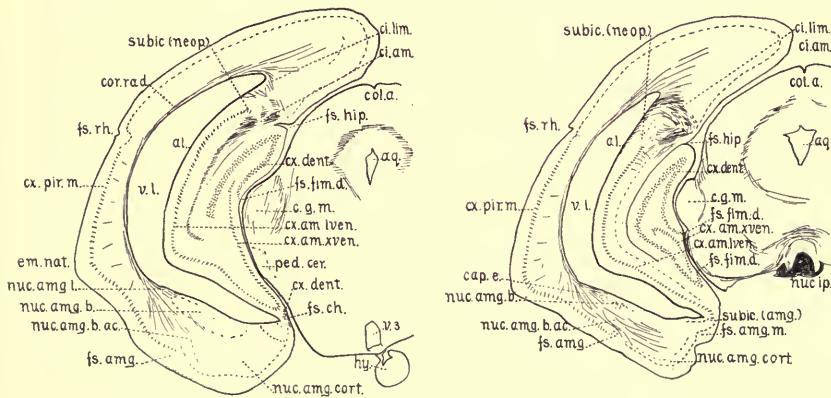
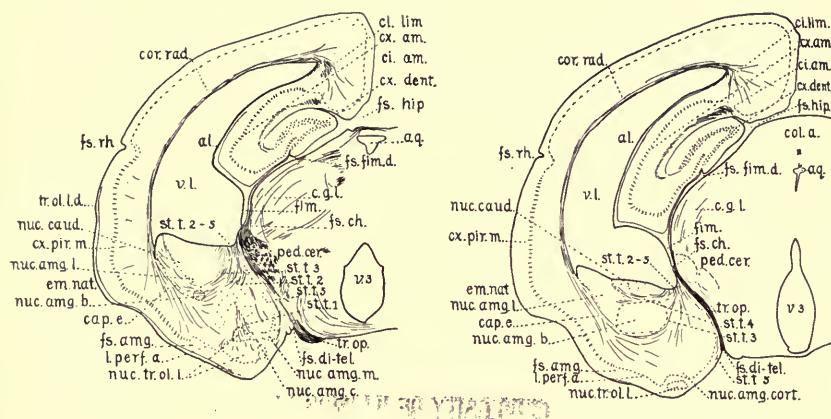
36 (SEC. 704)

## CAENOLESTES OBSCURUS.

X 8.

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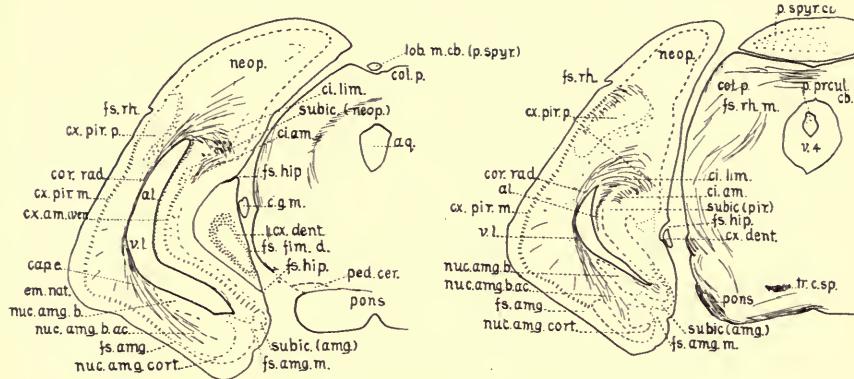


## CAENOLESTES OBSCURUS.

X 8.

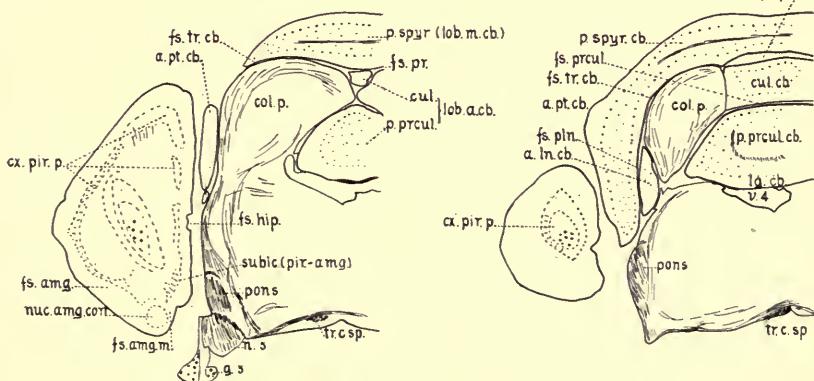
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41 (SEC. 851)

42 (SEC. 879)



43 (SEC. 900)

44 (SEC. 920)

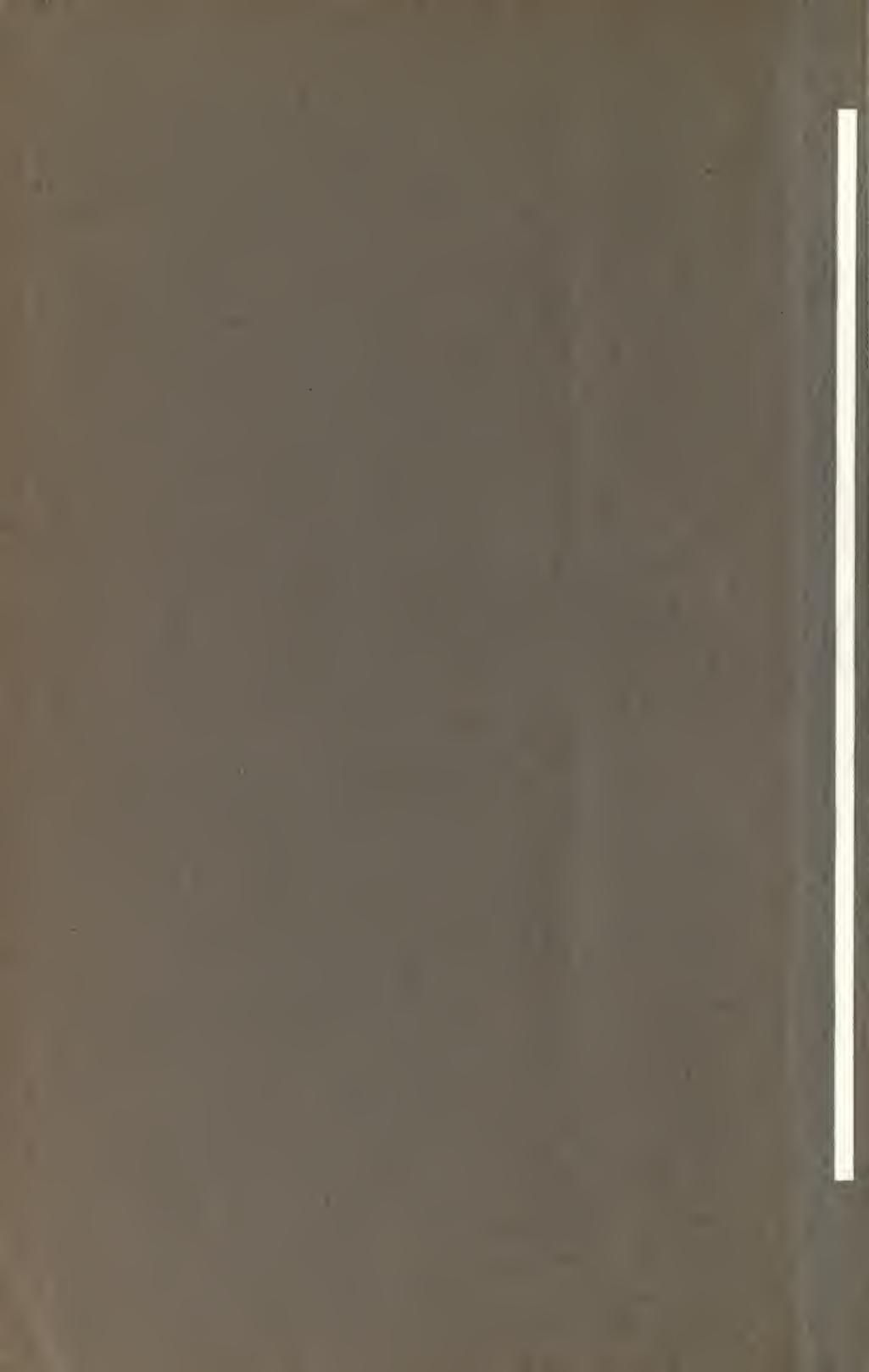
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