ON THE BRAIN OF THE MACROSCELIDIDAE
(*MACROSCELIDES* AND *ELEPHANTULUS*)

By Professor W. E. LE GROS CLARK, F.R.C.S.
Medical College, St Bartholomew's Hospital

THE elephant shrews are of particular interest to morphologists, partly because they form a family usually grouped with the Tupaiidae in the sub-order Menotyphla which is believed by many authorities to bear an important relation to the forerunners of the primate phylum, and partly because these Insectivores display in their anatomical structure a number of remarkably primitive and metatheroid features which have from time to time been noted by zoologists. Of all these features, the brain of *Macroscelides* appears to be unique amongst Mammals. In 1902, Elliot Smith(13) drew attention to this interesting point. He described the astonishing development of the hippocampal formation and the curiously metatheroid psalterium and noted the association of these primitive features with a small ventral commissure and an elongated and Primate-like corpus callosum. The unusual conformation of these parts of the brain, together with the uncertainty regarding the systematic position of the Macroscelididae which still exists, has prompted me to carry out in as complete a manner as possible a detailed study of the brain.

The original genus of *Macroscelides* was divided by Oldfield Thomas(15) in 1906 into three separate genera, mainly on the basis of the characters of the molar teeth and the tympanic bulla, *Macroscelides*, *Elephantulus* and *Nasilio*. This communication deals with the brain of the first two genera.

MATERIAL

I have to express my great indebtedness to the Director of the Transvaal Museum, South Africa, for having sent me three specimens of *Elephantulus myurus jamesoni*, in two of which the brains were excellently preserved. These brains have been studied macroscopically, and from them the text-figs. 1 to 4 have been prepared. To Prof. Elliot Smith I owe gratitude for a complete series of transverse sections through the brain of *Macroscelides* (species unknown) which had been sent to him by Dr Broom. These sections had been stained with a combination of Weigert-Pal and neutral red, with very good results. The fine medullated fibres are sharply delineated and the cyto-architecture can also be readily studied in the same sections as a result of the neutral red staining. I wish to thank Prof. Elliot Smith, also, for reading through this paper before publication. Owing to the kindness of Sir Arthur

Keith, I have also been able to study the brain of a specimen labelled *Macroscelides* which had been preserved for many years in the museum of the Royal College of Surgeons. From this specimen the outlines of text-figs. 5 (*a*) and 9 were drawn. This specimen and the specimen from which the sections were prepared correspond accurately with the figures of the brain of *Macroscelides proboscideus* in Elliot Smith's original paper. It will be seen that there are notable differences in brain structure between *Macroscelides* and *Elephantulus*, the characteristic features of the brain of the Macroscelididae being more emphasised in the former than in the latter genus.

GROSS ANATOMY

In general form, the encephalon of the Macroscelididae is relatively short and broad. The divergence of the cerebral hemispheres caudally with the exposure of the enormous anterior colliculi on the dorsal aspect of the brain is one of the most striking features of the undissected brain.

The following detailed account refers to the brain of *Elephantulus myurus jamesoni*.

The weight of the brain as a whole amounted to 1·14 gm. The ratio of the brain weight to the body weight (35·8 gm.) works out at 1 to 31·4.

The *olfactory bulbs* measure 5·5 mm. in length (on their ventral aspect), and 3 mm. in breadth. They project beyond the extremity of the frontal poles for a distance of 2 mm. The bulbs, which are sessile, terminate in blunt points anteriorly and are closely pressed against each other. The ventral surface is only slightly inclined to the horizontal plane. The *fissura circularis* is shallow on the ventral surface where it separates the bulb from the tuberculum olfactorium, and on the dorsal part of its extent, it is joined by the rostral end of the endorhinal sulcus. If, however, the olfactory bulb is here drawn away from the frontal pole of the hemisphere, it may be seen that in the depths of the interval between them, the fissura circularis and the endorhinal sulcus remain distinct for a short distance to leave a small space for the dorsal olfactory tract. The fissura circularis shows a slight posterior concavity where it crosses the lateral olfactory tract.

The *tuberculum olfactorium*, viewed from the ventral aspect, forms an oblique oval with the long axis extending postero-laterally. It measures 4·5 mm. in length by 4 mm. in breadth. Its surface is not markedly convex and slopes laterally in conformity with the general contour of the piriform region. A broad shallow groove crosses the surface antero-laterally and serves to accommodate the optic nerve. The tubercle is limited laterally by the olfactory tract, while postero-laterally and posteriorly it is separated from this and from the locus perforatus anticus by an evident *fissura rhinalis arcuata*, in which a small blood vessel runs. The part corresponding to the *fissura diagonalis* of Beccari can be seen running antero-medially into the septal region.
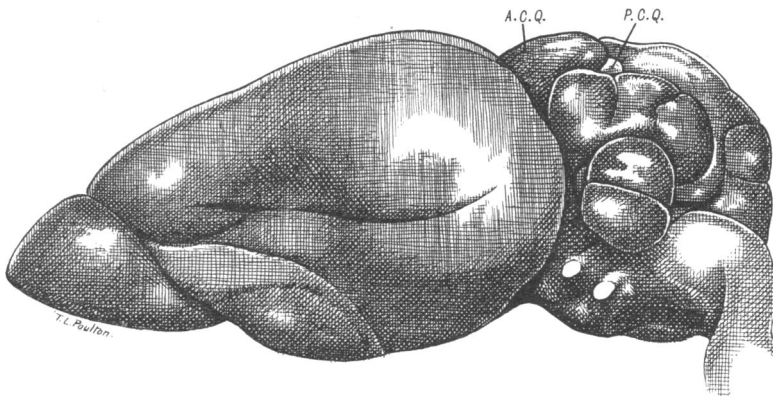
Text-fig. 1. Brain of *Elephantulus*. Lateral view.
A.C.Q. Anterior corpus quadrigeminum, *P.C.Q.* Posterior corpus quadrigeminum.
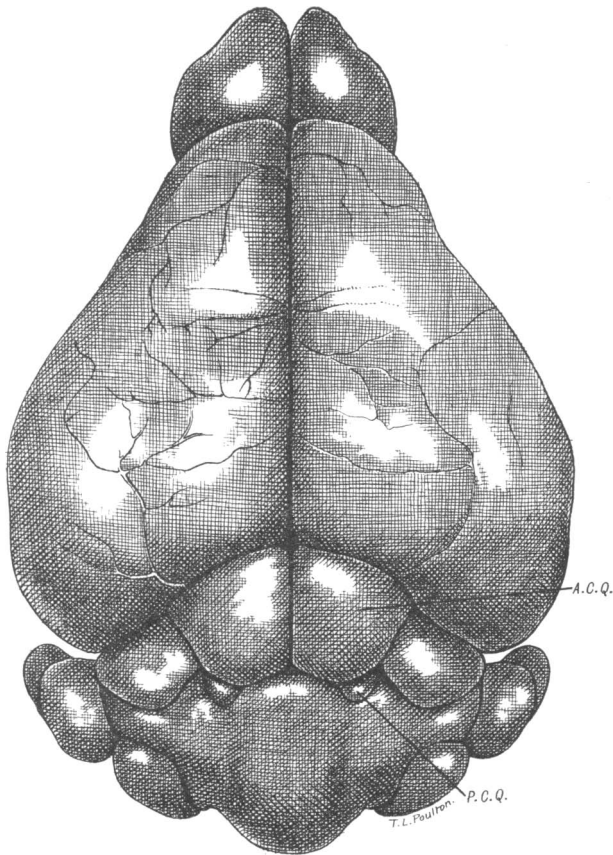
Text-fig. 2. Brain of *Elephantulus*. Dorsal view. Lettering as in previous figure.

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The *lateral olfactory tract* narrows gradually as it is traced caudally. From the olfactory bulb it extends backwards and a little outwards, and then, at the point where it is crossed by a blood vessel, and where the arcuate fissure first becomes apparent, it turns rather abruptly medialwards, ventralwards and backwards, fading out on the surface of the piriform lobe at the posterior extremity of the olfactory tubercle. At its termination, the surface of the piriform lobe is raised into a small and indistinct eminence, the elevation marking the position of the nucleus of the lateral olfactory tract. The fissura endorhinalis is not evident on surface view as a real fissure, its position being merely marked out by the lateral margin of the white olfactory tract.

The *rhinal fissure* runs more or less horizontally backwards. It becomes smoothed out at the site of the orbital depression on the hemisphere, and is thus divided superficially into two parts, anterior and posterior. The anterior portion terminates rostrally by fading away on the lateral surface of the frontal pole. It does not join the fissura circularis. The posterior portion of the rhinal fissure runs caudally with a faint downward convexity. Posteriorly it curves upwards and gradually disappears before it reaches the caudal margin of the cerebrum. It is continued on as a small vascular groove only. No clear indication of a *fissura rhinalis medialis* can be detected on the medial surface of the hemisphere.

The *piriform lobe*, traced from its anterior extremity, broadens out at first gradually, and then with some abruptness where the lateral olfactory tract turns medially. The surface of the lobe is curved in harmony with the orbital excavation of the ventro-lateral surface of the hemisphere. The most medial portion (as seen from the ventral aspect) which abuts on the tuber cinereum is marked off from the rest of the lobe by a short antero-posterior groove, the *fissura amygdalae*.

From the olfactory tubercle, the ventral surface of the piriform lobe slopes evenly upwards and backwards, and no definite natiform eminence is produced. The rounded surface lateral to the amygdaloid fissure corresponds to the position of this eminence.

The *neopallium* is smooth laterally and dorsally. The hemispheres rapidly narrow towards the frontal poles. The dorso-medial border measures about 10 mm. in length. The caudal margin of the hemisphere extends postero-laterally from the median line, with which it makes an angle of some 120°. Laterally the contour of the cerebrum is adapted to form a broad shallow orbital excavation.

The basal view (text-fig. 3) shows the *optic chiasma* to be of moderate size. Superficially no distinction can be made between the optic decussation proper and the commissure of Gudden as can be seen, for instance, in the brain of the mole (Ganser). The first millimetre or so of the optic tract can be seen before it dives under cover of the medial border of the piriform lobe, and it shows a faint groove where it comes into contact with the free border of the tentorium cerebelli.

A broad low convex *tuber cinereum* is seen behind the chiasma, and behind this, also visible in the undissected brain, a narrow pale band representing the mammillary region.

The *oculomotor nerve* is conspicuous as it emerges from under cover of the anterior border of the pontine region about 3 mm. distant from its fellow
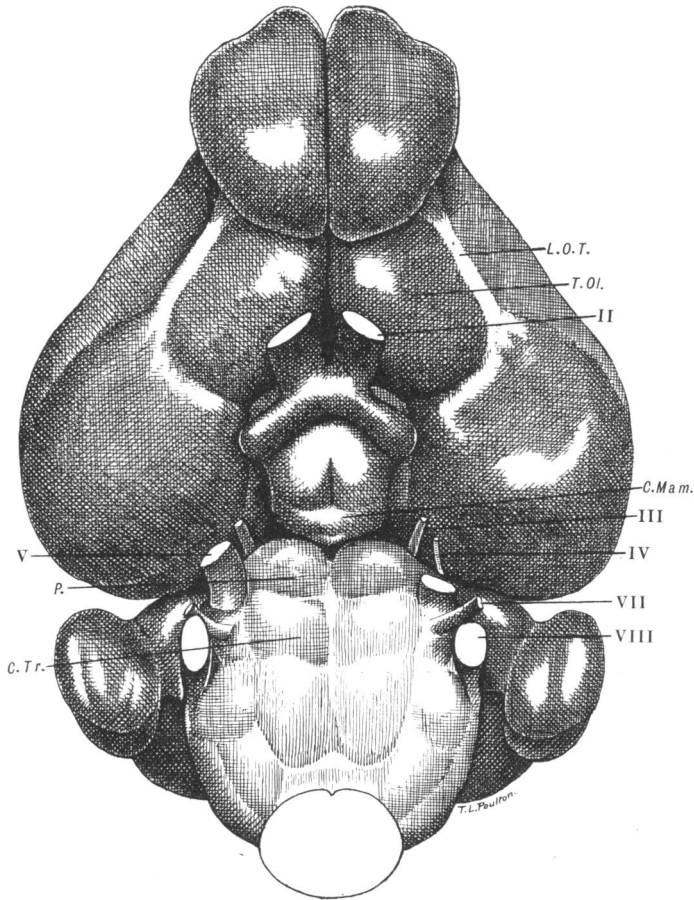
Text-fig. 3. Brain of *Elephantulus*. Ventral view. *L.O.T.* Lateral olfactory tract. *T.Ol.* Tuberculum olfactorium. *C.Mam.* Corpus mammillare. *P.* Pons. *C.Tr.* Corpus trapezoideum. The cranial nerves are numbered.

and overhung by the medial border of the piriform lobe. Lateral to the commencement of this nerve the delicate trochlear nerve may be seen if the root of the large trigeminal nerve is carefully lifted. Immediately caudal to the tuber cinereum and the origin of the third nerves are two transversely oval elevations (text-fig. 3, *P*), one on either side of the mid-line, of a conspicuous reddish brown colour. These appear to bear a very close resemblance

to the ganglion infrapedunculare described by Ganser (5) in the brain of *Talpa*. A study of the transverse sections, however, indicates that this grey matter lies actually in the pons, the transverse fibres of which are spread out in a very thin layer over the surface of it. Behind the pons is the corpus trapezoideum, distinguished from the pons in front and the ventral surface of the medulla behind by its white colour. The pons and the trapezoid body are both deeply grooved in the mid-line by the basilar artery. Laterally, in the interval between the pons and the corpus trapezoideum issues the root of the trigeminal nerve, and postero-lateral to this the origin of the small seventh and the large eighth nerve. A glimpse of the tuberculum acousticum immediately lateral to the root of the acoustic nerve is also visible from this aspect.
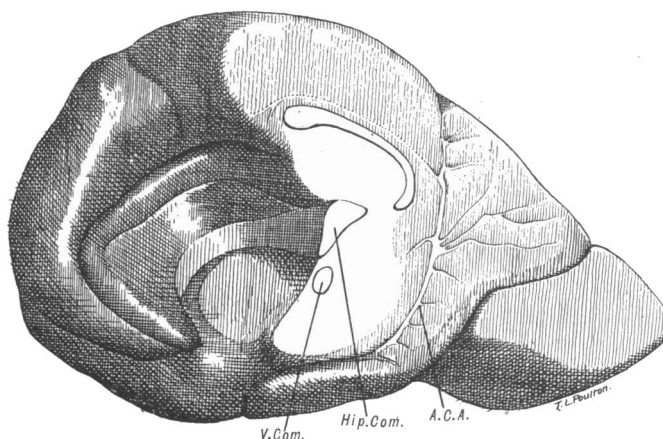

Text-fig. 4. Medial aspect of cerebral hemisphere of *Elephantulus* dissected to show the hippocampal formation. *Hip.Com.* Hippocampal commissure. *V.Com.* Ventral commissure. *A.C.A.* Anterior cerebral artery (groove).

On the dorsal aspect of the brain, the anterior colliculi (text-figs. 1, 2, *A.C.Q.*) are exposed to a considerable degree between the cerebrum and cerebellum. The exposed area of each colliculus measures 3 mm. anteroposteriorly and 3·5 mm. laterally. A small triangular portion of each posterior colliculus is also exposed to view in the undissected brain between the median and lateral cerebellar lobes.

The medial surface of the cerebral hemisphere (text-fig. 4). It is in the appearance of the medial surface of the brain that the main differences between the brains of *Macroscelides* and *Elephantulus* are to be seen. As before, this description applies mainly to the brain of *Elephantulus*.

The details of the commissures are perhaps one of the most interesting features of the brain of these animals, as Elliot Smith has already pointed out. The *corpus callosum* is elongated, slightly convex dorsally, and shows

a well-marked splenium with a splenial bend, a conspicuous genu, and a slightly bulbous rostrum. It measures about 4 mm. in length. Below it, but separated by a broad, flat, cut surface, is the fornix commissure which is of large size and approaches the crescentic shape so characteristic of Marsupials. The cut surface between these two commissures is formed (as can readily be seen by reference to the transverse sections (Plate I, figs. 16, 17)) by the relatively enormous dorsal extremity of the hippocampus, which here in an inverted form is closely pressed up against and actually fused with its fellow of the opposite side. In *Macroscelides* (text-fig. 9 *b*) this exaggeration of the subsplenial flexure is even more impressive, and the corpus callosum has been stretched out and thinned by the pressure of the hippocampus, so that in section it appears as an elongated strip approaching close to the dorso-medial border of the hemisphere. In this genus, also, the fornix commissure is more conspicuously metatheroid in shape.
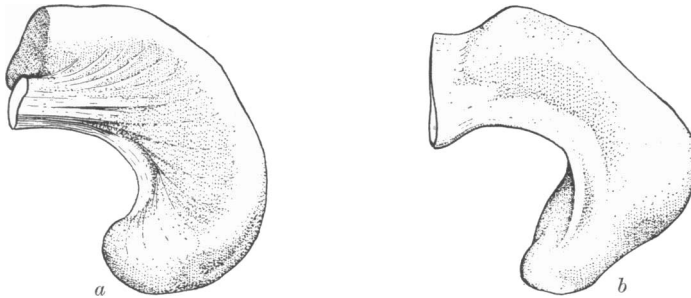

Text-fig. 5. The hippocampus and fornix of (*a*) *Macroscelides rozeti*, and (*b*) *Erinaceus*, dissected out and viewed from the antero-medial aspect to indicate the remarkable development of the subcallosal portion of the hippocampus in *Macroscelides*. (*a*) ×5. (*b*) ×4.

The ventral commissure lies immediately below the fornix commissure. Its small size is in marked contrast with the relatively large commissure found in the lipotyphlous insectivores. Below and in front of the anterior commissure is the paraterminal or septal region, fused across the mid-line as far forward as the level of the genu of the corpus callosum. Ventrally, this area is separated from the medial margin of the tuberculum olfactorium by the *fissura rhinalis arcuata*, from which emerges rostrally a large vascular groove which accommodates the anterior cerebral artery (text-fig. 4, *A.C.A.*). This groove ascends vertically, giving off branches, and just above the level of the corpus callosum divides into two main terminal branches, of which one courses dorsally to reach the dorsal aspect of the hemisphere, while the other runs back immediately above and parallel to the corpus callosum. On superficial inspection, this groove gives the corpus callosum the appearance of being much thicker than it really is.

With the removal by dissection of the mid-brain, the hippocampal formation is brought into view. The fimbria runs back from the hippocampal

commissure and terminates close to the ventral extremity of the extra-
ventricular alveus. The latter forms a relatively broad band exposed on the
medial aspect of the cerebrum. Below it expands somewhat to form a low
flat hippocampal tubercle. Above it disappears immediately caudad of the
hippocampal commissure by the fusion of the fimbrio-dentate with the
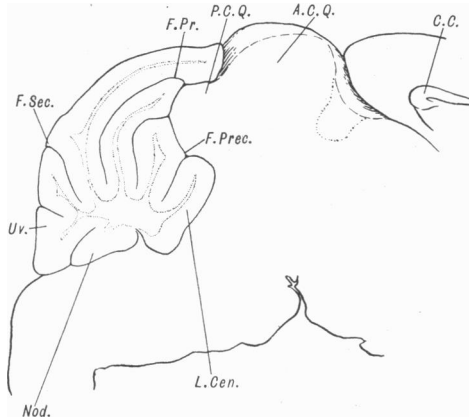
Text-fig. 6. Sagittal section through the mid- and hind-brain region of *Elephantulus*.   × 5.
C.C. Corpus callosum. *A.C.Q.* Anterior corpus quadrigeminum. *P.C.Q.* Posterior corpus
quadrigeminum. *F.Pr.* Fissura prima. *F.Sec.* Fissura secunda. *F.Prec.* Fissura preculminis.
L.Cen. Lobus centralis. *Uv.* Uvula. *Nod.* Nodule.
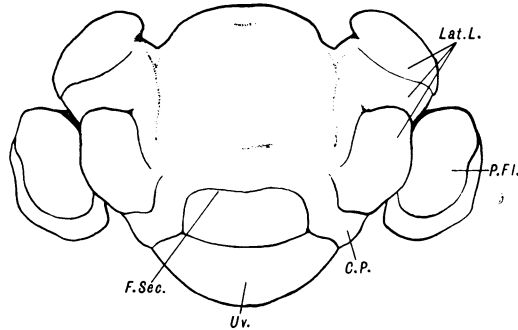
Text-fig. 7. Cerebellum of *Elephantulus*, viewed from the postero-superior aspect.   × 5.
Lat.L. Lateral lobe. *Pfl.* Paraflocculus. *C.P.* Copula pyramidis. *F.Sec.* Fissura secunda.
Uv. Uvula.

fimbrio-alvear (of Obenchain) fissures. The dentate gyrus forms a simple
uncrenated band of grey matter of fairly even width. It is sharply marked
off from the neighbouring pallium by a continuous hippocampal fissure which
at its ventral extremity turns forwards and ventralwards to limit ventrally
the hippocampal tubercle. Immediately below the latter, a faint furrow runs
horizontally backwards, the *fissura amygdaloidea medialis*.

The *cerebellum* (text-figs. 6, 7) is of a very simple type. In a sagittal

section, the main *fissura prima* and *fissura secunda* can readily be recognised. A very faint *fissura suprapyramidalis*, only evident superficially in the mid-line, separates the pyramid from the declive. The pars suprapyramidalis, which with the pyramid forms the lobus medialis of the cerebellum, is thus quite smooth. Faint antero-posterior depressions indicate the separation of the lobus medialis from the lateral lobes. The latter are each divided by well-marked but incomplete fissures into three folia of approximately equal size (superficially), of which the middle is in most direct superficial continuity with the middle lobe.

An inspection of the anterior surface of the cerebellum shows that the middle lobule is really the largest of the three. Its anterior surface, which is moulded round the lateral aspect of the posterior colliculus, is subdivided again into two folia by a vertical sulcus.

The pyramid is connected by a simple unfissured copula pyramidis with the paraflocculus. The latter is divided by a horizontal sulcus into two folia of which the upper is very slightly the larger. In front of and below the base of the paraflocculus is the simple unfissured flocculus, approximately equal in bulk to the upper folium of the paraflocculus.

Behind the fissura secunda is the *uvula*, divided superficially by a complete transverse sulcus reaching to the copulae pyramidis on either side. The *nodule* is not visible in the undissected brain but can be seen in sagittal section.

On the anterior surface of the cerebellum, a *U*-shaped *sulcus preculminis* separates the simple undivided *culmen* from the *lobus centralis*. The latter is again subdivided by a transverse sulcus. The *lingula*, seen in sagittal section, is hardly significant enough to be regarded as a separate lobe of the cerebellum.

MICROSCOPICAL ANATOMY

The transverse sections of the brain of *Macroscelides*, on which the account in this section is based, were cut at a thickness of $15\,\mu$. The total length of the cerebral hemispheres occupied 967 sections.

Primary Olfactory Areas.

A study of the sections indicates that the olfactory bulbs (Plate I, figs. 10, 11) in the brain from which they were prepared were complete. The bulbar formation can be traced back as far as Section 371, the frontal poles of the neopallium appearing at Section 162. Thus the bulb is about 5·5 mm. in antero-posterior extent and projects beyond the level of the frontal pole by 2·4 mm. There is no need to describe in detail the structure of the bulb, for it conforms in general respects to the structure of the bulb of other mammalian brains. In section, the bulb is a vertical oval, narrower ventrally. Anteriorly, it is surrounded on all sides by rootlets of the olfactory nerves which terminate in a conspicuous stratum glomerulosum. As the sections are traced back, the stratum glomerulosum disappears, first on the medial

half of the dorsal aspect of the bulb, the vomero-nasal nerve being left isolated in this position. At Section 145, the accessory bulb appears, that is, slightly rostrad of the frontal pole of the neopallium. The accessory bulb (Plate I, fig. 10, *Ac.B.*) shows the usual structure. It has a broad stratum moleculare filled with medium-sized pale staining cells, which are in continuity with the single layer of mitral cells of the bulb proper. Medullated fibres from the accessory bulb run laterally to contribute to the dorsal peduncle of the lateral olfactory tract. The stratum granulare of the accessory bulb lies deep (ventral) to these fibres, whereas in the rest of the bulb, this stratum is superficial to the fibres which collect to form the lateral olfactory tract. The position of the accessory bulb is marked on the dorsal surface by a very faint furrow.

Secondary Olfactory Areas.

In Section 156, a clump of medium-sized cells, pyramidal and angular in shape, appears dorsal to the central core of the bulb, ventral to the compact stratum granulare of the accessory bulb, and immediately in front of the anterior extremity of the ventricle of the bulb. This marks the commencement of the anterior olfactory nucleus of Herrick (Plate I, fig. 11, *N.O.A.*). Traced back, this mass of grey matter rapidly spreads down the lateral aspect of the olfactory ventricle and further posteriorly sends a medial limb down the medial aspect of the ventricle, forming an inverted *U* in the concavity of which lies the intermediate olfactory tract. The medial and lateral limbs eventually meet on the ventral aspect of the ventricle at Section 334 and thus complete the periventricular ring. From the inner aspect of this ring, fibres pour out into the intermediate olfactory tract. As described thus far, the anterior olfactory nucleus shows no differentiation. The only part of the anterior olfactory nucleus, using the term in Herrick's sense, that can be described as differentiated is the pars externus. This appears at Section 182. At this level, the lateral olfactory tract has the appearance of a query mark in transverse section, with the convexity laterally. Along the dorsal part of the inner concave margin of the tract a small compact group of cells, similar to those which form the main part of the anterior olfactory nucleus, makes an appearance. This is the pars externus (Plate I, figs. 11, 12, 13, *N.O.A.* (*p.e.*)). A few sections more caudally, where the lateral olfactory tract becomes exposed to the surface of the bulb on its dorsal aspect, this external nucleus slides down ventrally until it soon becomes a small localised clump of cells on the medial aspect of the ventral end of the lateral limb of the olfactory tract. Eventually it fades away close to the caudal limit of the bulbar formation. This well-defined cell group has been described in the opossum (Herrick)(7), rat and *Caenolestes* (Obenchain)(11). In the two former Mammals, the nucleus is described as being caudally swallow-tailed in shape. There is no trace of such a splitting of the nucleus in *Macroscelides*. Obenchain has discussed at some length the significance of this nucleus, and suggests

that it is some sort of reinforcing device, discharging its fibres into the subjacent lateral part of the anterior olfactory nucleus. Its diminutive size in relation to the massive lateral olfactory tract is hardly explicable on this hypothesis. In the sections here studied, the nucleus commences laterally in very close association with the accessory bulb, its cells actually intermingling with the cells of the stratum granulare of the accessory bulb. It is forcibly suggested to one that this external nucleus is related to the accessory bulbar formation in the same way that the main bulk of the anterior olfactory nucleus is related to the bulb proper, and that it slides down the lateral olfactory tract in association with the fibres contributed to this tract by the accessory bulb.

If the different parts of the anterior olfactory nucleus are traced caudally in the sections, they are found to behave as follows. The pars dorsalis becomes lodged in between the extreme rostral end of the anterior hippocampal formation and the anterior piriform cortex. Here it forms a conspicuous mass of cells lying ventral to the anterior extremity of the centrum ovale. This mass soon disappears, however, and gives way to a relatively cell-free zone which in turn is replaced by the anterior horn of the lateral ventricle. The pars dorsalis thus appears to maintain its individuality until it disappears altogether, and it would not be correct to say that it merges with the cell mass of the frontal pole of the neopallium. The pars lateralis becomes continuous with the anterior piriform cortex, but when these two formations first come into contact, they are separated by a dipping in of the lamina zonalis at a level which corresponds to the dorsal margin of the main mass of the lateral olfactory tract. In this region, the cortex of the piriform lobe is readily distinguishable from the pars lateralis of the anterior olfactory nucleus, for its cells are more compactly and regularly arranged in a narrow superficial band, they are more pyramidal and more darkly stained. Close to the posterior end of the bulbar formation, the distinction between piriform cortex and pars lateralis disappears. At Section 291, where the pars medialis abuts on the cortex of the medial surface of the frontal pole of the neopallium, a small condensation of moderately large pyramidal cells appears, the rostral extremity of the cortex hippocampi. With this anterior hippocampal formation and the undifferentiated "primordium hippocampi" of Johnston the pars medialis becomes continuous.

The ventral part of the anterior olfactory nucleus is prolonged back as the pars posterior between the tubercular cortex and the head of the caudate nucleus (Plate I, fig. 15, *N.O.A. (p.p.)*). When these latter structures first appear rostrally, the pars posterior expands somewhat to form a conspicuous mass of polygonal cells notably larger than the cells which form other parts of the anterior olfactory nucleus. Among these cells stream the medullated fibres of the olfacto-septal and olfacto-cortical tracts. More caudally, the pars posterior becomes flattened out as though by pressure of the superjacent head of the caudate and its cells become gradually replaced by the small

granules of the tuberculum olfactorium. It should be noted that there appears to be no continuity between the tubercular cortex and the anterior olfactory nucleus, the one becomes replaced by the other in a manner which is quite abrupt in spite of the fact that the cells of the two formations intermingle somewhat at their junction. In *Orycteropus*, Woollard[18] notes that the anterior olfactory nucleus forms a definite cortex with a wavy outline, and that this cortical layer appears to run directly into the tubercular cortex.

The olfactory tracts in these sections need not be described in any detail. In their origin, course, and destination they conform to the usual mammalian condition. The medial olfactory tract is small and ill-defined.

The *tuberculum olfactorium* (Plates I, II, figs. 15–19, *T.Ol.*) first shows itself at Section 379 and the last traces of it are seen posteriorly at Section 592. Anteriorly it commences on the ventral aspect of the pars posterior of the anterior olfactory nucleus, and as it is traced caudally, it extends evenly in a medial and lateral direction. The medial limb at first extends vertically upwards in the septum, close to the surface. This presumably corresponds to the nucleus of the medial olfactory tract of Livini. Further back, it sends up a prominent process which lies on a deeper plane, and, running between the nucleus accumbens and Johnston's medial parolfactory nucleus, expands into a club-shaped extremity which actually reaches the ependymal layer of the lateral ventricle at Section 450. The tubercular cortex shows the usual structure, being composed of small, round, darkly-staining cells which are arranged in a slightly wavy outline and here and there collected into clumps forming the characteristic islands of Calleja. A short distance behind its rostral margin, cells of a similar type appear, forming a narrow layer in close contact with the convex ventral margin of the head of the caudate nucleus, so that in this region the pars posterior of the anterior olfactory nucleus appears sandwiched between a dorsal and ventral lamina of cells characteristic of the tuberculum. A study of the sections suggests that this dorsal lamina represents a rostral extension of the small-celled element of the basal amygdaloid nucleus (*vide infra*). Further caudally, the dorsal lamina disappears and soon after this the last remaining portion of the anterior olfactory nucleus, so that the caudate nucleus becomes covered by the tubercular cortex, only separated by a fine felt-work of medullated fibres which appear partly to contribute to the formation of the medial fore-brain bundle. The latter formation is certainly not at all conspicuous in these sections. The organisation of the olfactory tubercle in *Macroscelides* is not so complex either in the irregularity of the tubercular cortex or in the degree of differentiation of its cellular elements as is indicated by Obenchain for *Caenolestes*, and it also appears simpler when compared with Johnston's figures of this region in the opossum[8].

These sections provide no certain evidence for the still-disputed question as to whether the olfactory tubercle receives secondary olfactory fibres.

The septal region. Immediately rostrad of the anterior extremity of the corpus callosum the anterior hippocampal formation appears. Below the genu of the corpus callosum (Plate I, fig. 14, *A.H.*) it becomes well differentiated, and a conspicuous cortex of ammon pyramids, four or five cells thick, appears. Further back, this becomes replaced by a relatively thick undifferentiated mass, the lateral parolfactory nucleus of Herrick, or Johnston's primordium hippocampi (Plate I, figs. 15–17, *N.P.L.*). In so far as this mass represents the residue of undifferentiated tissue, out of which the anterior hippocampal formation appears to be differentiated dorso-medially, Johnston's term may have some basis of justification. Dart's criticism of the term, however, seems a very pertinent one, and for this reason, Herrick's nomenclature is undoubtedly preferable. Lower down, in the pars inferior of the paraterminal body, is the medial parolfactory nucleus, consisting of scattered medium-sized, pale-staining cells in among which numerous septal fibres run (Plate I, figs. 15, 16, *N.P.M.*). Posteriorly, at Section 502, the cells at the ventral extremity of this ill-defined nucleus congregate at the medial aspect of the olfactory tubercle to form a conspicuous *nucleus of the diagonal band* (Plate I, fig. 17, *N.D.B.*). There is thus no line of demarcation between the latter nucleus and the medial parolfactory nucleus. The pars superior of the paraterminal body fuses with that of the other side at Section 442, relatively far forward, and this fusion proceeds ventrally as the tubercular cortex shrinks down from the medial surface. Thus the nucleus of the diagonal band never lies under the free medial surface of the cerebral hemisphere. Ventro-laterally, the nucleus is demarcated off superficially from the olfactory tubercle by a distinct fissura rhinalis arcuata. The *nucleus accumbens* is prominent as a portion of the caudate nucleus lying medio-ventral to the lateral ventricle (Plate I, figs. 15, 16, *N.A.*). It may be noted that in these sections it shows no characteristics beyond its relative position by which it can be distinguished from the main mass of the caudate nucleus, and there appears here to be no justification for dignifying it with a special name. There is no evidence in these sections of the presence of the olfacto-frontal bundle described in *Caenolestes* by Obenchain (11), and which is believed in that animal to represent Edinger's septo-mesencephalic tract of lower vertebrates.

The amygdaloid complex. Like other workers in this field, I have relied very largely on Johnston's detailed account for an analysis of the amygdaloid complex in my sections of the brain of *Macroscelides*. It will probably be most convenient to study the constitution of this complex from behind forwards. The amygdaloid complex commences at Section 825. Here, at the most dependent part of the temporal horn of the lateral ventricle, the cortex ammonis is to be found turning sharply lateralwards on to the ventral aspect of the cerebrum to become continuous with a somewhat diffuse layer of medium cells resembling in formation the zona presubicularis. This irregular cortical layer becomes slightly infolded towards the ventricle floor, and the site of this infolding is marked a little further forward by a faint surface furrow

(*fissura amygdaloidea medialis*) which serves superficially to separate the cortical amygdaloid nucleus from the lower margin of the hippocampal formation. The cells which appear to have migrated inwards from the surface at the site of this furrow form the medial amygdaloid nucleus which Johnston(8) has described in mammalian brains (Plate II, figs. 21–24, *N.A.M.*). This nucleus is continued laterally into the cortical amygdaloid nucleus whose cells are rather larger, and, caudally, are arranged fairly regularly in a cortical layer. More anteriorly, the cells of the cortical nucleus lie in a more diffuse layer. At the junction of the cortical nucleus and the piriform cortex, there is only the faintest suggestion of an amygdaloid fissure (the caudal prolongation of the fissura endorhinalis), but the turning inwards of the superficial cells at the junction of these two areas to connect up with the large basal nucleus is quite evident. This is in support of Johnston's view that the basal nucleus has been derived from an infolding of the medial margin of the piriform cortex.

The lateral amygdaloid nucleus (Plate II, figs. 19–23, *N.A.L.*) appears at the very caudal extremity of the amygdaloid complex as a well-defined oval group of medium pyramidal and polygonal cells which stain fairly deeply, lying up against the ventro-lateral wall of the ventricular cavity. Traced forwards, the lateral nucleus increases rapidly in size and soon forms a prominent elevation in the floor of the lateral ventricle. It is bounded laterally by the external capsule and in its posterior part by an extension downward of the cavity of the lateral ventricle which here separates it from the piriform cortex. In this region, therefore, the lateral nucleus projects relatively freely in the cavity of the ventricle, covered on its medial and lateral aspects by the ependymal lining of the ventricle. Ventrally, it is separated from the medial and cortical nuclei (at its caudal extremity) by prolongations of the external capsule. Rostrally, the lateral nucleus is continued as a darkly staining band of cells pressed up against the lateral surface of the putamen, and can be traced forwards as far as Section 568, at the level of the anterior commissure and well in front of the level of the posterior margin of the olfactory tubercle. In the anterior half of its extent, the lateral nucleus is traversed dorsally by fibres from the internal capsule. The large bulk of the lateral nucleus in *Macroscelides* is very impressive. Johnston notes that this nucleus is massive at its anterior end in the bat (*Myotis*) and that in the monkey (*Macacus*) it projects forward to an unusual extent.

The large-celled basal nucleus (Plate II, figs. 20–22, *N.A.B.* (*m.*)) appears first at Section 724, lying ventral to the medial extremity of the transversely oval lateral nucleus. Traced forwards, the basal nucleus is found to extend ventrally to the junction of the piriform cortex and the cortical amygdaloid nucleus as already mentioned, and here it appears to come into structural continuity especially with the piriform cortex. Medially to the basal nucleus lie scattered medium and small cells, forming the central nucleus through which run the caudally directed fibres of the stria terminalis,

Ventrally, the central nucleus is continuous with the medial amygdaloid nucleus. Ventro-medial to the anterior part of the basal nucleus is found a clump of small darkly-staining granule cells, and separated from the large-celled basal nucleus by a fibre layer. This would appear to represent the small-celled element of the basal nucleus in the rabbit's brain, described by Johnston (Plate II, fig. 20, *N.A.B.* (*p.*)). Traced caudally, these small cells wander medially to take up a position ventral to the central nucleus, still separated from the large-celled basal nucleus by a fibre layer. Eventually, further back, they come to lie up against the ventro-lateral wall of the ventricular cavity, dorsal to the medial nucleus and medial to the large-celled basal nucleus. Here, its cells tend to group themselves into clumps, and, as Johnston notes for the accessory basal nucleus which he describes in the brain of the opossum, bear some resemblance to the formation of the islands of Calleja. I am in some doubt, however, as to the identity of this small-celled group in the caudal region of the amygdaloid complex of *Macroscelides* with Johnston's accessory basal nucleus. It would be a matter of some interest to arrive at a definite conclusion, for Johnston states that this accessory nucleus is found in Marsupials and not in eutherian mammals, and although not a Marsupial, *Macroscelides* presents a number of curiously metatheroid features in its anatomical structure.

Rostrally, the small-celled basal element extends further than the large-celled element, and comes to lie immediately ventral to the lateral nucleus. It appears to be continued forward as small detached clumps of cells to the region of the olfactory tubercle where similar cells are found lying ventral to the head of the caudate nucleus and dorsal to the pars posterior of the anterior olfactory nucleus.

At Section 648, the well-defined nucleus of the lateral olfactory tract appears (Plate II, fig. 20, *N.L.O.T.*) to fade away again anteriorly at Section 609. It replaces the medial nucleus in position. There is no small-celled element of this nucleus as described by Obenchain for *Caenolestes*, but the middle of the nucleus is divided into two large-celled parts as described by Woollard[18] for *Orycteropus*, the main ventral element, and a small less circumscribed element consisting of cells of the same type as the main portion, intermingling with the caudal ramifications of the commissural bundle of the stria terminalis. The nucleus, though very clearly circumscribed, is not conspicuously large. It is certainly relatively smaller than the lateral olfactory nucleus of the opossum. The basal and central nuclei become indistinct at about Section 635, and fade away into the structure of the globus pallidus and diagonal band nucleus.

Fibre connections of the amygdaloid nucleus. The stria terminalis can be followed throughout its course, but an analysis of its constituent bundles cannot be made from these sections. The most conspicuous and well-defined element to be seen is the fasciculus which runs caudally to the lateral olfactory nucleus, Johnston's commissural bundle. It was not found possible to trace

the bed of the stria in an uninterrupted course from the bed of the anterior commissure back to the amygdaloid nuclei.

The piriform lobe. Rostrally the pars lateralis of the anterior olfactory nucleus is directly continuous with the piriform cortex. The latter, when it first appears anteriorly, is composed of small subpyramidal cells which are somewhat diffusely arranged to form a broad band comprising the second and third layers of the cortex. Traced caudally, the more superficial cells, forming the second layer, become smaller, more darkly stained, and more compactly arranged, while the larger pyramidal cells of the third layer become scattered over a broader zone. Thus the area piriformis anterior of Gray passes quite indefinitely into his area medialis. This latter area is essentially similar to the corresponding area which Gray has described in *Didelphys*(6). Lying above the caudal extremity of the area medialis is a small patch which corresponds in structure with Gray's area posterior (text-fig. 9 (*b*), *J*). It shows a looser arrangement of the cells forming the second layer and the addition of a fourth layer. The latter extends also for a short distance into the dorsal margin of the area medialis. The superficial cells of the area posterior are more darkly stained than those of the area medialis. No pale giant cells were observed in the area posterior, such as have been recorded by Obenchain(11) in the brain of *Caenolestes*. The area posterior first appears anteriorly at about Section 680 (Plate II, fig. 21, *A.P.P.*) and in the region of Section 750 the rhinal fissure disappears. At this level, also, and no doubt resulting in the disappearance at this point of the rhinal fissure, the lateral cortex appears much compressed and thinned out by the huge subjacent hippocampus, so that the dorsal limit of the area posterior is not easy to demarcate. This difficulty is enhanced by the fact that the structure of the area posterior closely approximates to that of the neighbouring neopallial cortex. The area extends over on to the medial surface of the cerebrum to a very small extent where it abuts on the area presubicularis and the hippocampal-amygdaloid junction. This specialised area posterior, according to Cajal, does not receive fibres directly from the lateral olfactory tract and may be regarded as subserving entirely associational functions. In *Macroscelides* it is of very small extent compared with *Didelphys*, but it is developed to relatively the same extent as it is in *Caenolestes*. The other divisions of the piriform area described by Gray can also be observed in this brain, but except for the area subpiriformis, they are hardly definite enough here to deserve separate names.

The hippocampal formation. Rostrally, the anterior hippocampus begins at Section 280 as a short band of small pyramidal cells continuous with layer 2 of the frontal neopallial cortex but more lightly stained than the neopallial cells (Plate I, figs, 13, 14, *A.H.*). This band extends ventrally to meet the anterior olfactory nucleus at the junction of the pars medialis and pars dorsalis. The cortex hippocampi anterior bends round ventral to the genu of the corpus callosum for a short distance. Here it forms a conspicuous band stretching in a vertical direction from the corpus callosum down on to the

surface of the medial parolfactory nucleus. At its dorsal extremity, close to
the callosal fibres, is differentiated a clump of closely-packed small cells
representing the gyrus dentatus formation in this region. These cells are
slightly dislocated from the line of hippocampal cells ventrally by a suggestion
of the interpositio medialis. Above the corpus callosum, the hippocampal
formation disappears entirely except for a few pale-staining pyramidal cells
pressed against the mid-dorsal line of the corpus callosum. These cells, which
never amount to more than ten or so in each section, are 'not always visible,
and indeed disappear altogether over the caudal part of the corpus callosum.
There is thus no well-defined indusium and the striae longitudinales are not
visible. The atrophy of the supracallosal hippocampus has been carried to
an extreme. The hippocampal commissure is relatively large. These sections
show no sharp distinction between the psalterium dorsale and ventrale, though
the ventral fibres are less dense than the dorsal fibres of the commissure.
Among the fibres, especially those of the ventral part, are numerous small
cells forming the nucleus proprius fornicis (Plate I, fig. 17, *N.P.F.*).
Precommissural fibres are evident, passing down in front of the ventral
commissure into the septal region (Plate I, fig. 16, *F.Pr.*). Immediately
ventral to the fornix commissure are the descending columns of the fornix
(Plates I, II, figs. 17–23, *D.C.F.*). Traced posteriorly, these are found to
run directly backwards until they lie under the ependymal lining of the third
ventricle. Just behind the level of the ventral commissure many of their
fibres pass into the habenular region, forming the fasciculus rhinencephalo-
habenularis, and the descending columns then pass down through the sub-
stantia grisea centralis of the third ventricle towards the corpora mammillaria.
Projecting for a short distance between the descending columns of the fornix
above the ventral commissure and ventral to the fornix commissure is the
recessus inferior.

The outstanding feature of the hippocampus of *Macroscelides* is the
inordinate development of its subcallosal portion, and especially the intra-
ventricular alveus. The extent of this development is illustrated by the
sections and the illustration of the hippocampus which has been dissected
from the lateral ventricle (text-fig. 5). The lateral ventricle is distended by
the ammon's horn to an astonishing degree, and this has led to a stretching
and thinning out of the overlying neopallial cortex, so that the latter in parts
appears atrophic. The intraventricular part of the hippocampus reaches
rostrally as far as the anterior end of the corpus callosum, fitting closely into
the concavity of the genu. This huge subspenial flexure has led to a complete
separation of the corpus callosum from the fornix commissure. Elliot Smith [13],
owing to the condition of the brain on which he based his account, was unable
to state what connection really exists between the two commissures, but he
surmised the possibility that the bridge might not contain any nerve fibres,
thus realising the condition found in the *Hapalidae*. These sections indicate,
indeed, that no transverse fibres run through this bridge. Dorsal to the

massive hippocampus in the mid-line and ventral to the corpus callosum, is a band of well-medullated fibres running antero-posteriorly and forming the *fornix longus* (Plates I, II, figs. 17–19, *F.L.*). Anteriorly, just caudal to the genu of the corpus callosum, these fibres pass ventrally between the two hippocampal formations to join the other fornix fibres in the region of the psalterium. Caudally, the fibres of the fornix longus become sandwiched in between the two layers forming the splenium of the corpus callosum, and eventually they disappear at about Section 640. The corpus callosum has been stretched out into an attenuated lamina by the pressure of the large hippocampus to a degree which is much more marked in *Macroscelides* than in *Elephantulus*, and this displacement dorsally of the callosal fibres has led to further displacements in the neopallial cortex as will be seen later. The hippocampal formations of either side, between the corpus callosum and the fimbria, are closely pressed together and fused in the mid-line. Such a fusion is to be seen in the subsplenial flexure in other mammals, e.g. the rabbit, but in no mammal has this condition reached the development seen in *Macroscelides*. The extraventricular alveus forms a relatively broad band which runs down within the concavity of the gyrus dentatus on the medial surface of the hemisphere, and terminates below in a low rounded hippocampal tubercle (text-fig. 4). Here the hippocampus becomes exposed on the surface and runs into the cortical amygdaloid nucleus but separated superficially by a very shallow furrow, representing the *fissura amygdaloidea medialis*. Posteriorly there is a slight recurving of the hippocampal formation to form a temporal pole, so that in a few sections the hippocampal figure is shown twice in the same section. The dentate gyrus is thus duplicated for 68 sections (815 to 748), and the hippocampus for 24 sections only (760 to 737). This slight degree of curvature is a little more pronounced than in *Caenolestes*, in which the gyrus dentatus is alone involved in this hippocampal reversal.

The almost complete disappearance of the supracallosal hippocampus and atrophy of the indusium must be attributed to the pressure exerted by the phenomenal development of the subcallosal portion of the hippocampus. As Elliot Smith has pointed out in various publications, the atrophy of the supracallosal hippocampus in Eutherians is generally to be ascribed to the pressure exercised by the growing corpus callosum. In the present instance, however, the corpus callosum is exposed to the same influence which also leads to the atrophy of the indusium. In discussing the factors concerned in the formation of the typical hippocampal figure of Mammals, Obenchain enumerates the following: external pressure, internal pressure, and neuro-biotactic influences. Of the former, downward pressure of the neopallium can be excluded in the present case, for here it is the neopallium which has clearly been displaced by the growth of the hippocampus. Internal pressure and neuro-biotactic influences must be assumed to be the main operating factors if a mechanical explanation of the hippocampal figure in *Macroscelides* is sought.

The Optic Thalamus.

No attempt has been made here to identify and homologise the numerous collections of cells which go to make up the thalamus. Malone(10) has pointed out how widely variable the structure of the thalamus is in different mammals (with the exception of the hypothalamic region) and how impossible it is to homologise the component nuclei without the study of a closely-graded comparative series of brains. He also emphasises the arbitrary nature of attempting to subdivide the thalamus into "nuclei" by reference to the medullary laminae which lie in the substance of the thalamus rather than by a study of the characters of the nerve cells which form definite homogeneous groups. The general proportions of the thalamus of *Macroscelides* can be readily seen from the transverse sections through the brain figured in Plates I and II. One of the outstanding features is the bulk of the optic tract. It will be seen that a large proportion of the fibres of this tract terminates in the anterior corpus quadrigeminum. The lateral geniculate body is distinct though not conspicuously large in relation to the size of the optic tract. A close study of this nucleus shows that it consists of two distinct parts, separated by a medullary lamina, a small dorsal portion (*C.G.L.* (*d.*)) which is absent altogether at the rostral extremity of the nucleus and becomes larger at the caudal extremity, and a ventral portion (*C.G.L.* (*v.*)) which comprises by far the greater part of the nucleus but is absent in the sections through the caudal extremity. The ventral nucleus is formed of small cells fairly closely packed together. On its lateral aspect it is bounded by the optic tract from which it receives numerous fibres. From its medial border medullated fibres emerge and collect together to form a large part of the ventral medullary lamina (*L.M.V.*). The dorsal nucleus is formed of cells which are larger than those of the ventral nucleus, especially posteriorly, and which are much less closely packed. Moreover no fibres emerge from it to pass into the ventral region of the thalamus. There seems to be little doubt that these two nuclei correspond to the dorsal (pars magnocellularis) and ventral (pars parvicellularis) nuclei found generally in the lateral geniculate body of mammals (Kappers, Winkler, Minkowski, Woollard) of which it is believed that the dorsal nucleus is related to the optic radiations and the area striata of the neopallium, while the ventral nucleus is associated with the mid-brain and is concerned rather with mid-brain visual reflexes. It is to be expected therefore that the ventral nucleus should be so large in *Macroscelides*, in which the anterior corpus quadrigeminum is remarkably developed, while the small size and the feeble differentiation of the dorsal nucleus is correlated with the poorly differentiated area striata of the cortex.

The medial geniculate body (*C.G.M.*) forms a conspicuous elevation immediately caudo-ventral to the lateral geniculate body. It is, however, much smaller than the latter, and shows no differentiation in its structure.

The Neopallium.

The combined method of staining with Weigert-Pal and neutral red was sufficiently successful in the present instance to allow a complete study of the lamination of the cortex to be made, as a result of which it has been possible to indicate several distinct cortical areas which can be separated by reference to their particular and characteristic structure. Some of these areas are sharply limited at their margins, while others pass so gradually into the neighbouring areas that their boundaries can only be fixed very approximately. As is naturally to be expected in a primitive brain of this kind, cortical differentiation is by no means so perfect as it is in many mammalian brains, and this lack of differentiation is very obvious by comparison with the brain of *Tupaia*(3) and, to a much lesser degree, with that of *Ptilocercus*(4). If sections of the neopallial cortex of the other Menotyphla are compared with those of *Macroscelides*, it will be seen that the latter is generally poorly developed. The cortex is thin, not very densely packed with cells, and the supragranular layers are relatively shallow. In the temporal area, the enlarged hippocampus has stretched out the cortex into a thin atrophic-looking layer, and the anomalous development of this structure has also led to a considerable dislocation of the cortical areas from the positions in which they are usually found in mammalian brains. It will be convenient to describe separately the different cortical areas which can be distinguished in this brain.

Area retrosplenialis granularis (text-figs. 8 (*d*) and 9, *H* and *K*). This area may be described first because of its highly distinctive appearance. It can be subdivided into two parts, area *H*, which appears to correspond to areas 29 *a*, 29 *b*, 29 *c*, and 29 *d*, of Brodmann(1), and area *K*, which evidently corresponds either to his area 29 *e* or 27, area presubicularis These areas are characterised by the astonishing development of the lamina granularis interna. The small round and deeply-staining cells which form this layer are closely packed together, sometimes disposed in vertical or horizontal rows, to form a very conspicuous band. It is rendered still more conspicuous by the presence in this layer of fine interlacing myelinated fibres, which represent a highly developed outer line of Baillarger. The lamina zonalis is of moderate width, broader over the mesial part of the area than over the lateral. The lamina pyramidalis is very narrow and contains very small pyramidal cells. The lamina ganglionaris is wide and contains large pyramidal and polygonal cells scattered rather sparsely. The sixth layer is narrow, and the cells in it are rather crowded and flattened in a horizontal direction. This area corresponds almost precisely in its structure with the retrosplenial area of the rabbit as figured and described by Brodmann and Winkler and Potter(17). It is also figured by Brodmann(1) in *Pteropus*, *Lemur* and the kangaroo, by Watson(16) in *Erinaceus*, *Talpa* and *Sorex* (this author's specialised postero-mesial cortex), by Gray(6) in *Didelphys*, etc., and I have studied it in *Tupaia* and *Ptilocercus*, but in none of these animals is the granular layer so con-

spicuously developed as it is in Rodents (*Lepus, Mus, Cavia*(1), (12)) and *Macroscelides*. Area *K* shows a marked increase in the development of the internal granular layer, a broad lamina zonalis, the practical disappearance of layers 2 and 3, and a great reduction of the infragranular layers which no longer contain large deeply-stained cells. These two areas may be regarded as together forming the *area retrosplenialis*. The extent of this area in *Macroscelides* is no less striking than its structural differentiation. It reaches forward above the corpus callosum as far as the anterior quarter of this commissure. Up to this level, also, it extends over the dorso-medial border of the hemisphere
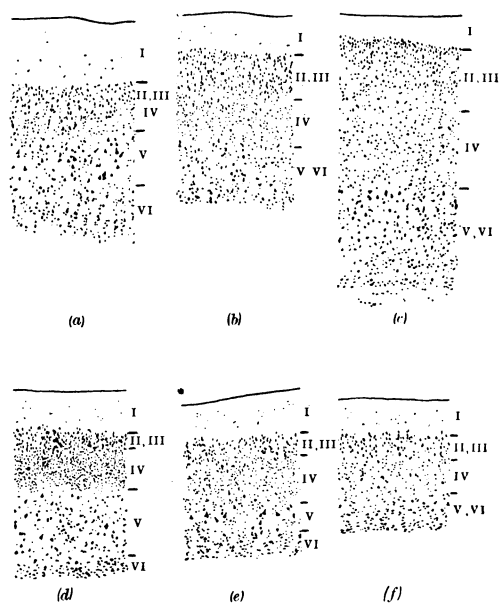
Text-fig. 8. Cortical areas of *Macroscelides*. Traced with a projectoscope. (*a*) Sensorimotor area. (*b*) Parietal area. (*c*) Insular area. (*d*) Retrosplenial area. (*e*) Striate area. (*f*) Temporal area. (The figures refer to Brodmann's system of lamination.)

on to the dorso-lateral surface of the brain. Here the lateral border, which is very sharply defined, is bounded by a shallow furrow on the surface which is reflected in a local thickening of the lamina zonalis and a corresponding indentation of the pyramidal layer of cells (Plate II, fig. 19, *I.S.*). This subzonal sulcus is also represented in the rabbit's brain in Winkler and Potter's figures where these authors label it the *fissura sagittalis lateralis*. From its relation to the retrosplenial area, however, it is clear that this sulcus represents the splenial element of the intercalary complex pushed over on to the lateral surface of the hemisphere by the extension of the retrosplenial area, and also in *Macroscelides* by the displacement of the corpus callosum. This was recognised by Elliot Smith(14) in the brain of *Tragulus*, in which

a similar condition is to be found (see also Brodmann (1), p. 215). In almost all mammals, the retrosplenial cortex is limited to a small area immediately behind and below the splenium of the corpus callosum. Its great extent in *Macroscelides* is, however, not entirely unique, for it is to a considerable degree approached by the condition found in Rodents and *Tragulus*.

Area retrosplenialis agranularis (text-fig. 9, *I*). This name is applied to a small but well-differentiated area lying on the posterior border of the cerebrum between the posterior piriform area and the presubicular area. It seems to correspond to the area of this name (area 30) of Brodmann. The lamina zonalis is broad, the pyramidal layer is well developed and consists of relatively large polygonal cells which hardly vary in size at different levels and stain very lightly as compared with the pyramids in other cortical areas, small granules seem to be quite absent, and the lamination is very indistinct. The margins of this small localised area are peculiarly abrupt, especially where it borders on the presubicular area.
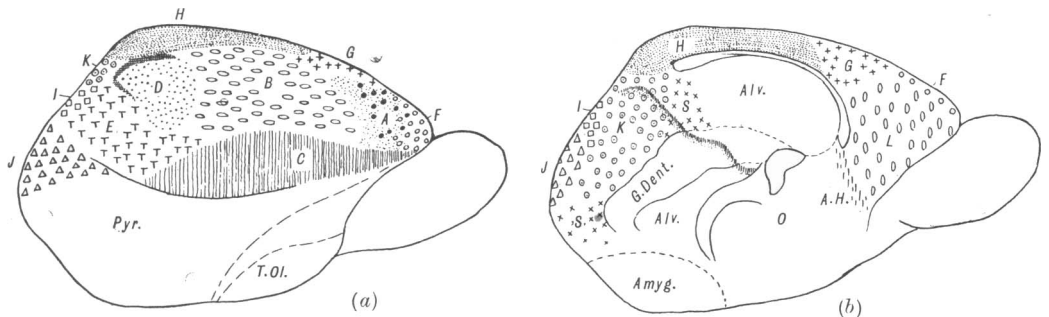
Text-fig. 9. Brain of *Macroscelides* from (*a*) the lateral aspect, and (*b*) the medial aspect, mapped out to show the extent of the various cortical areas described. *A*. Sensorimotor area. *B*. Parietal area. *C*. Insular area. *D*. Striate area. *E*. Temporal area. *F*. Frontal area. *G*. Posterior cingular area. *H*. Retrosplenial area. *I*. Area retrosplenialis agranularis. *J*. Posterior piriform area. *K*. Presubicular area. *L*. Anterior cingular area. *A.H.* Anterior hippocampus. *Alv.* Alveus. *G.Dent.* Gyrus dentatus. *Amyg.* Amygdala. *S.* Subicular cortex. *Pyr.* Piriform lobe. *T.Ol.* Tuberculum olfactorium. × 5.

The *subicular area* (text-fig. 9, *S*) has the usual characteristic structure, a broad zonal layer and a single broad layer of medium pyramids rather widely scattered. Most of the subiculum is buried from the surface in the *fissura hippocampi*, but portions appear on the medial aspect of the brain in the two regions indicated on the map.

The sensorimotor area (text-figs. 9, *A*, and 8 (*a*)). This name is applied to a small area at the anterior end of the dorso-lateral surface of the cerebrum. It is characterised by the presence in the lamina ganglionaris of a layer of large broad pyramidal cells which stain very deeply, and a well-marked band of fine myelinated fibres in the same lamina further adds to the distinctive nature of this cortical area. The lamina zonalis is broad, the pyramidal layer is relatively thin, and the lamina multiformis is moderately developed. The

internal granular layer is variably developed. It is poorly represented at the anterior extremity and along the mesial border of the area, while posteriorly and laterally it becomes more conspicuous and even well developed. This area seems to combine the features of the motor and sensory (precentral and postcentral) areas found in most mammalian brains, and it seems probable that the former is represented by the mesial and anterior (relatively agranular) and the latter by the lateral and caudal (relatively granular) part of this common sensorimotor area. It must be emphasised that the term "sensorimotor" is here applied in a tentative manner only, for Gray found that, in the opossum, the electrically excitable area of the brain did not accurately correspond to the agranular area of the cortex which might be regarded as the area precentralis on the basis of histological evidence.

The *frontal area* (text-fig. 9, *F*) is confined to the rostral extremity of the cerebral hemisphere, and is characterised by a deep pyramidal layer, a complete absence of small granules, the absence of large pyramidal cells in the infragranular layers and imperfect lamination.

The *parietal area* (text-figs. 8 (*b*) and 9, *B*) shows a pyramidal layer rather broader and more regular than in other areas. The inner granular layer is well developed, and there is a lack of large pyramids in the lamina ganglionaris. The boundary line between this area and the two areas next to be described is very indistinct.

The *visual area* (text-figs. 8 (*e*) and 9, *D*) was identified by the broad layer of granules forming lamina IV, the presence of darkly-staining pyramidal cells with broad bases in the lamina ganglionaris (evidently representing the cells of Meynert), the narrow lamina multiformis and the narrow pyramidal layer. It is regarded as the visuosensory area solely by comparing its structure and relative position on the surface of the brain with these features of the visual area found in many other mammalian brains. No trace of the stria of Gennari was found in these specimens although they were stained by the Weigert-Pal method, and it may be assumed to be absent. The anterior and ventral boundaries of this area are very ill-defined. Above, it is separated from the retrosplenial area by a narrow band of cortex in which the inner granular layer is thinner. This band of cortex may be regarded as the peristriate area and it closely resembles this area which is figured by Gray for the opossum (6).

The *temporal area* can only be recognised by its negative characters. The pyramid layer is not well developed, the inner granular layer is of moderate thickness, and there are no conspicuous pyramids in the infragranular layers. As has been already indicated, this area grades insensibly into the parietal and visual areas, so that the junction of these three areas cannot be fixed with any precision. It is clear, therefore, that the boundaries of these three areas as represented on the accompanying map are only approximate. The temporal cortex is relatively thin throughout its extent, consequent on the pressure which appears to be exerted on it by the subjacent hippocampus.

The insular area (text-figs. 8 (*c*) and 9, *C*). This cortical area is characterised by its great depth and rather imperfect lamination. The moderately developed pyramidal layer, which is apt to be rather irregular, is followed by a broad internal granular layer. The infragranular layers are also broad and imperfectly divided into lamina ganglionaris and lamina multiformis. The former contains many medium-sized pale pyramidal cells. The claustrum appears to be represented by a clump of darkly-staining cells lying deep to the rhinal fissure, so that it comes into relation superficially with the ventral margin of the insular cortex above and the dorsal margin of the piriform cortex below. There is at least no other separate cell mass which could be regarded as the claustrum.

The cingular area (text-fig. 9, *G* and *L*). This area is situated on the mesial surface of the hemisphere in front of the area retrosplenialis. The posterior part consists of rather poorly stratified cortex with an inner granular layer. This part, of small extent, reaches over to the dorso-lateral surface of the brain, and would appear to correspond to Brodmann's area 23. The anterior part of the cingular area is agranular, extends down over the mesial surface of the brain in front of the corpus callosum and probably corresponds to Brodmann's area 24.

General. The displacement of the cortical areas from the usual positions in which they are found in the mammalian cerebrum by the enlarged subsplenial flexure of the hippocampus has already been noted. The charts indicate sufficiently clearly the lateral displacement of the retrosplenial area and the posterior part of the cingular area on to the dorsal aspect of the brain. With this is associated a lateral displacement of the visual area which does not occupy the dorso-caudal pole of the hemisphere in *Macroscelides* as it does in mammals generally. A similar position of the corresponding area is to be noted in Rodents and *Tragulus*.

The relatively great extent and the advanced degree of differentiation of the retrosplenial, subicular and presubicular areas stand in marked contrast to the ill-defined nature of the visual, temporal, sensorimotor and parietal areas. This contrast is undoubtedly associated with the conspicuous development of the hippocampal cortex, for the retrosplenial and associated areas are to be regarded as annectant between the old and new pallium. The resemblance between the retrosplenial region of the cortex in *Macroscelides* and Rodents is certainly striking, though its significance is obscure. It may be noted that the area retrosplenialis agranularis, which though of limited extent is so clearly differentiated in *Macroscelides*, is said by Brodmann to be absent in Rodents.

DISCUSSION

The brain of the Macroscelididae is clearly a macrosmatic brain, but not remarkably so. Thus, comparing the brain with those of *Erinaceus* and *Talpa*, two lowly insectivores, the olfactory bulbs, the tuberculum olfactorium, and the piriform lobe are not so proportionately large. The general resemblance

in the contour of the cerebrum to that of the mole has been noted by Elliot Smith. In the elephant shrew the antero-posterior shortening and the transverse width of the hemispheres which are so characteristic in the mole are not shown to the same degree. In the mole, also, the optic nerves are reduced to fine threads, while in the elephant shrew they are nerves of conspicuous size. This is correlated with a marked development of some of the visual centres of the brain and especially the anterior corpora quadrigemina which reach such dimensions that they are exposed on the dorsal aspect of the undissected brain. Compared with the brain of the mole the impression is gained that the exposure of the corpora quadrigemina in this manner is due rather to their own unusual development than to a relatively feeble development of the cerebral hemispheres. As already mentioned, the primary and secondary olfactory areas are well developed but not in any way to an unusual degree. In contrast to this, the relatively large size and differentiation of the amygdaloid complex and the enormous mass of the hippocampal formation stand out as two of the most striking features of this brain. The great expansion of the subcallosal portion of the ammon's horn has led to a distortion of the corpus callosum and the neopallium, and has displaced the septal formation altogether from the interval between the hippocampal and callosal commissures. It has likewise led to an extreme atrophy of the supracallosal portion of the hippocampus. This immense and seemingly bizarre development of the hippocampus is out of all proportion to the development of the primary and secondary olfactory areas, and this fact serves further to confirm what has been suggested by Elliot Smith's remark that the hippocampus does not diminish in size *pari passu* with the diminishing of the olfactory bulb like the tuberculum olfactorium and the piriform lobe, and by the observations of other authors, namely, that the hippocampus may well be concerned with the elaboration of other than purely olfactory stimuli. It does not follow from this, of course, that the hippocampus is not an organ which is predominantly associated with olfactory stimuli, but it indicates that it is at least not so closely related to the primary olfactory regions as are the olfactory tubercle and the piriform lobe. In connection with the piriform lobe, it may be noted that the specialised area piriformis posterior, which is regarded as being entirely concerned with functions of an associational nature, is not developed to any marked extent. Correlated with the size of the hippocampus is the size of the hippocampal commissure which in cross-section is triangular or crescent-shaped, and thus closely resembles the typical appearance of the metatheroid psalterium. It may be doubted, however, whether this appearance can be regarded as indicative of marsupial affinities. The shape of the cut commissure would seem to be the direct result of the large size of the commissure coupled with the pressure of the superjacent hypertrophied subsplenial hippocampus which evidently exerts a pressure downwards and forwards between the corpus callosum and the psalterium leading to a bending downward and forward of

the dorsal part of the latter commissure. A comparison between the brains of *Macroscelides* and *Elephantulus* adds some force to this suggestion, for in the former, in which the hypertrophy of the subsplenial portion of the hippocampus is more exaggerated, the psalterium is distinctly more crescentic and metatheroid in appearance.

In regard to the amygdaloid complex, the most notable features are the clear differentiation of the various nuclei and the predominating size and organisation of the lateral nucleus. The significance of the latter is not known. Johnston(8) notes that it appears to be least intimately related to the other parts of the amygdala, and that it does not seem to share in the distribution of stria terminalis bundles. Johnston's comparative studies of the amygdala do not indicate that there is any relation between the development of the hippocampus and the relative size of the lateral amygdaloid nucleus, and in his description of the brain of *Orycteropus*, in which the hippocampus is described as being a massive structure, Woollard does not note that the lateral amygdaloid nucleus is unusually large. The basal amygdaloid nucleus is conspicuously marked out by the large size of its component cells, but this nucleus is not so large relatively as it is, for instance, in the brains of *Tupaia* and *Ptilocercus*, two other menotyphlous insectivores.

The shape of the corpus callosum differs notably in *Macroscelides* and *Elephantulus* and this difference, again, allows us to conjecture how far the appearance of this commissure is correlated with mechanical influences exerted by the hypertrophied hippocampus. In the former species the larger sub-callosal hippocampus has pushed the corpus callosum further dorsally, so that the mesial surface of the cerebral cortex is reduced to a narrow strip, and at the same time the commissure has evidently been more elongated and thinned as the result of the mechanical pressure. In *Elephantulus* these effects have been produced to a much less marked degree, and the corpus callosum is shorter and thicker. It would appear, therefore, that the length of the commissure is at least in part resultant from the development of the hippocampus. The pronounced curved genu is likewise produced by a moulding of the commissure around the rostral extremity of the enlarged hippocampus. It seems possible also that the presence of the splenial kinking of the corpus callosum may be partly associated with the subsplenial flexure of the hippocampus. It is more conspicuous in *Macroscelides* than in *Elephantulus*, and I have noted in the study of the brains of *Tupaia* and *Ptilocercus* (in which the brains are very similar in external contour) that in the latter where the corpus callosum shows a well-marked splenium there is also a conspicuous subsplenial flexure of the hippocampal formation, whereas in the former there is no such hippocampal flexure and the corpus callosum has no proper splenium. But even if these features of the corpus callosum are effected by such mechanical influences, they are only produced by virtue of the relatively large size of the commissure. Even were the distorting influences of the hippocampus to be removed, the corpus callosum would remain an astonish-

ingly large commissure for a primitive brain. It is difficult to advance an adequate reason in explanation of this feature. The neopallium is poorly developed, and is not only limited in its surface area but is also considerably thinned out by pressure of the hippocampal formation. On the other hand, the ventral commissure is correspondingly small, and appears from the sections to be formed to a greater extent by the intermediate olfactory tract and by fibres of the stria terminalis than by fibres from the external capsule. The idea suggests itself that the growing hippocampus has exerted such pressure laterally against the pallium and the corona radiata (and the existence of such pressure is indicated by the thinning out of the pallium in this region) that the commissural fibres from the greater part of the neopallium are prevented from taking the phylogenetically older path through the ventral commissure and, instead, cross over through the corpus callosum. One is tempted to go further and to suggest that the pressure of a rapidly enlarging hippocampal formation originating in this way may have decided the initial appearance of a callosal commissure in the evolutionary development of eutherian mammals from metatherian forerunners. However this may be, such a large corpus callosum as is found in the Macroscelididae, coupled with a diminutive ventral commissure, is to be regarded as a progressive trait, and its association here with such a poorly developed neopallium renders the difficult problem of the significance of the callosal commissure still more obscure.

The large size of the optic nerves is reflected in the great development of the anterior corpus quadrigeminum (already referred to) and in the differentiation of the lateral geniculate body. The fact that this body is formed mainly by the ventral element and that the dorsal element is so relatively insignificant is correlated with the large size of the anterior corpus quadrigeminum and the undifferentiated condition and small extent of the area striata of the cortex. Ganser[5] has noted the very small size of the lateral geniculate body in the mole's brain, and he found much difficulty in differentiating it from the mass of the optic thalamus. A similar lack of differentiation is to be found in the hedgehog's brain. The other extreme among insectivores is to be found in the brain of *Tupaia*, in which the optic nerves are large and the striate cortex elaborately differentiated. In this brain, the ventral nucleus is large, in association with the great size of the anterior corpora quadrigemina (Woollard[19]), but what appears to be more significant is the large size of the dorsal element, the large size of the individual cells of which it is composed, and its conspicuous lamination. In *Ptilocercus*, in association with the moderate size of the optic nerves, the lateral geniculate body is smaller. The ventral nucleus is absolutely and relatively smaller than in *Tupaia*, and this is evidently correlated with the much smaller size of the anterior corpus quadrigeminum. The dorsal nucleus, on the other hand, although larger relatively to the ventral nucleus than is the case in *Tupaia* for the reason just mentioned, is not so large relatively to the brain as a whole, and not nearly so conspicuously organised. This series of insectivore brains affords

an excellent illustration of the correlation between the development of the optic nerves, the anterior corpus quadrigeminum, the lateral geniculate body, and the area striata of the cortex.

The neopallium is characterised by its general thinness, the relative poverty of its cell content, the poor development of the pyramidal layer and, except in certain regions, its lack of differentiation. On the other hand, the retro-splenial areas show a degree of differentiation and a surface extent which are quite remarkable. The significance of this feature, however, is by no means apparent. It may be surmised that there is some association between the development of this cortical area and the development of the subsplenial portion of the hippocampus. But the retrosplenial area is almost as well developed in many rodents, and in *Tragulus*, in which the subsplenial part of the hippocampus, even if conspicuous, is not to be compared with the condition found in *Macroscelides*.

It is disappointing to find that the anatomical details of the brain seem to be of little use in the determination of the taxonomic position of the Macroscelididae. Indeed, a comparison with the brains of the other family of the Menotyphla, the Tupaiidae, is even a little disturbing, for it would be difficult to find brains of small insectivorous mammals of similar size which show more divergent characteristics. *Tupaia* is a diurnal, arboreal mammal, with well-developed eyes and rudimentary ears, and shows evidence of a reduction of the olfactory regions of the brain. The anterior corpus quadri-geminum is very large, and the posterior very small. The lateral geniculate body shows an advanced degree of development of the dorsal nucleus. The visual cortex is highly differentiated and extends on the medial surface of the hemisphere right down to the dorsal surface of the corpus callosum. Reduction of the hippocampal formation is indicated by the complete absence of any subsplenial flexure. The piriform lobe is relatively diminished, and is largely pushed down from the lateral aspect of the cerebrum by the extension downward of the temporal lobe of the neopallium. The neopallial cortex shows a conspicuous differentiation.

Ptilocercus is a nocturnal arboreal mammal with well-developed external ears. Its brain is distinctly more primitive than that of *Tupaia*. The olfactory bulbs are larger, the piriform lobe relatively bigger, and there is a well-marked subsplenial hippocampal flexure. The anterior corpus quadrigeminum is small, while the posterior is more prominent. The moderate development of the lateral geniculate body contrasts with the size of the medial geniculate body. The visual cortex is not well differentiated and appears to be of small extent. The temporal area of the cortex, however, shows a more pronounced lamination. In both these tree shrews, the fornix commissure is of moderate size, and bears no resemblance to that of the elephant shrew. In the size of the corpus callosum there is certainly a point of similarity between the Macroscelididae and the Tupaiidae, and in this feature there is perhaps an argument for separating them as the Menotyphla from the other members of the Insectivora.

But it seems doubtful whether this argument is really valid, especially as Elliot Smith (14) has recorded that *Chrysochloris* has an "extraordinary elongation" of the corpus callosum. It must be admitted, indeed, that the cerebral anatomy supplies no justification for associating the Macroscelididae with the Tupaiidae. On the contrary, it suggests that the two families represent widely divergent forms. Carlsson (2), in 1909, reviewed the question of the relationship of the Macroscelididae to the other Insectivora, and concludes that, in the absence of fossil remains to indicate otherwise, the general anatomical evidence suggests that they branched off from the ancient Erinaceidae, inheriting from the latter a multitude of primitive characters. The evidence of cerebral anatomy is quite compatible with this hypothesis.

SUMMARY

1. The brain in the Macroscelididae is a primitive, macrosmatic brain in which an unusual development of the subsplenial portion of the hippocampus has led to certain distortions and displacements of other cerebral structures.

2. It is thought possible that this hippocampal hypertrophy may (at least in part) account for the unusual features of the cerebral commissures.

3. The amygdaloid complex of nuclei is conspicuously differentiated and the lateral amygdaloid nucleus is notable for its relatively large size.

4. The optic nerves and tracts are large, and this is correlated with a great development of the anterior corpus quadrigeminum (which as a result of its own size becomes exposed on the dorsal aspect of the undissected brain). The lateral geniculate body is likewise clearly differentiated from the rest of the optic thalamus, but by far the greater part of it is formed from the ventral nucleus, and, in conformity with the very small size of the dorsal nucleus, the *area striata* of the cortex is poorly differentiated and of relatively small extent.

5. The neopallium is, on the whole, poorly developed, appears to be largely thinned out by the pressure of the intraventricular portion of the hippocampus, and many of the cortical areas into which it can be subdivided can only be approximately delimited.

6. The retrosplenial areas of the cortex, on the contrary, are remarkably differentiated and their surface extent on the cerebral hemisphere is unusually great. Herein the Macroscelididae show a striking resemblance to the condition recorded in many rodents and in the primitive ungulate *Tragulus*.

7. In spite of the poor neopallial development, the corpus callosum is obtrusively large. No explanation can be offered for this association of a conspicuous callosal commissure with such a primitive brain.

8. As a result of this study and of a comparison with the brains of the Tupaiidae, there seems no adequate reason for associating the Macroscelididae with the Tupaiidae in a common group, the Menotyphla, at least on the basis of cerebral anatomy. On the contrary there seem to be good reasons for widely

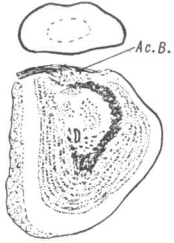separating the tree shrews from the elephant shrews in a natural system of classification.

9. The brain of the Macroscelididae may readily have been derived from the brain of a primitive Erinaceid in which a progressive and unique enlargement of the subsplenial hippocampus has produced certain very aberrant features.

10. This enlargement of the subsplenial hippocampus and its disturbing effects on other parts of the brain have progressed to a much greater degree in *Macroscelides* than in *Elephantulus*.
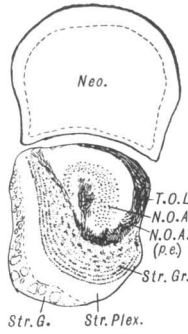
11. The marked difference between the brains of *Macroscelides* and *Elephantulus* justifies the separation of these forms into two distinct genera as originally proposed by Oldfield Thomas.

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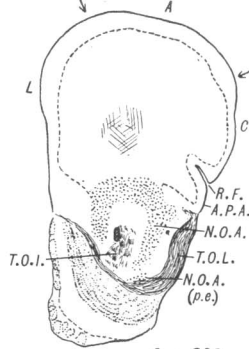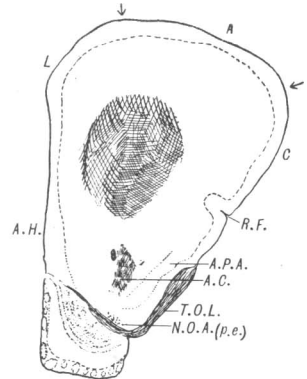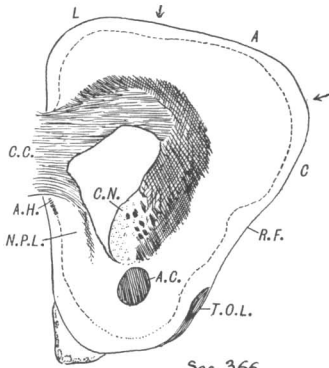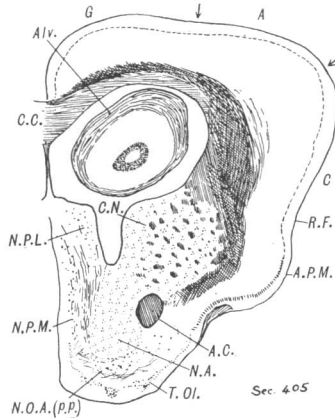
Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.

Fig. 15.

Fig. 16.

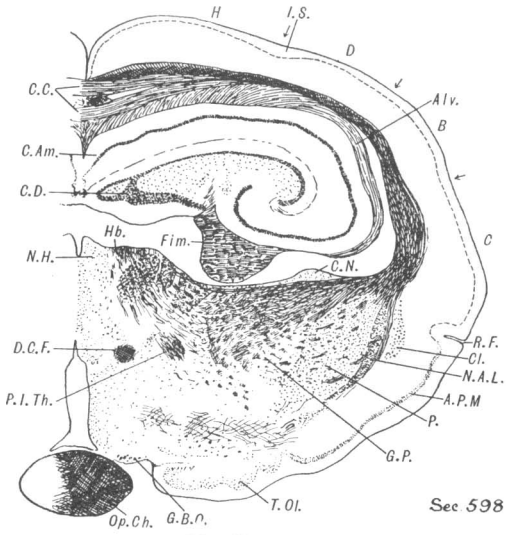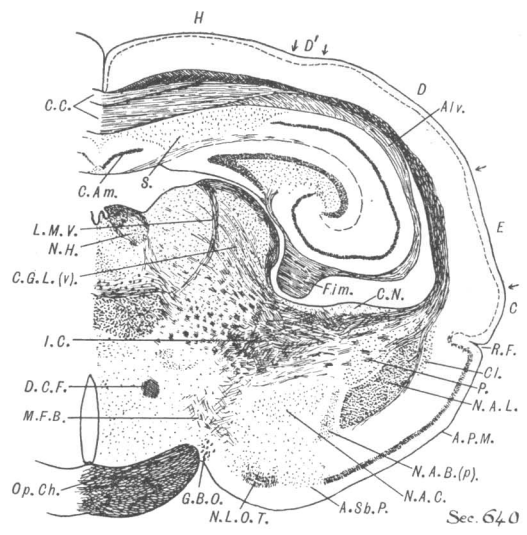Fig. 17.

Fig. 18.

LE GROS CLARK—ON THE BRAIN OF THE MACROSCELIDIDAE
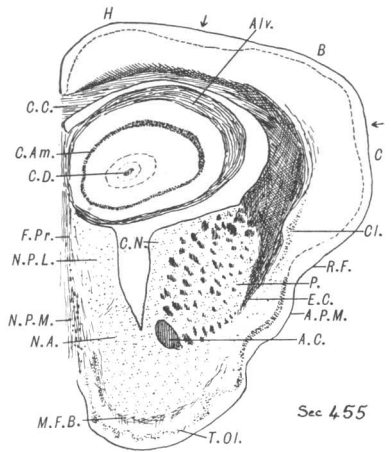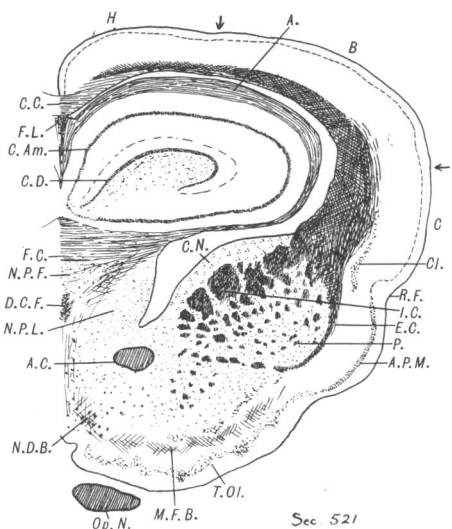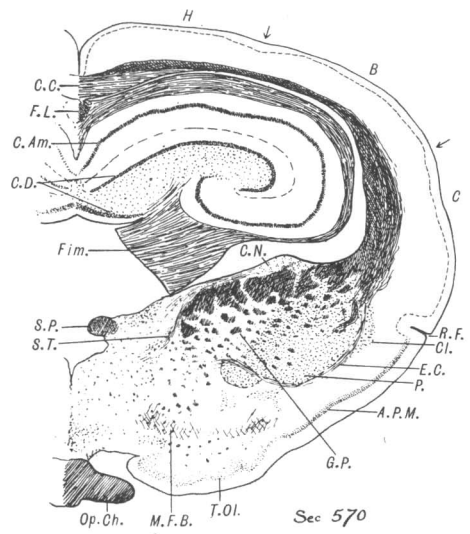
Fig. 19.

Fig. 20.
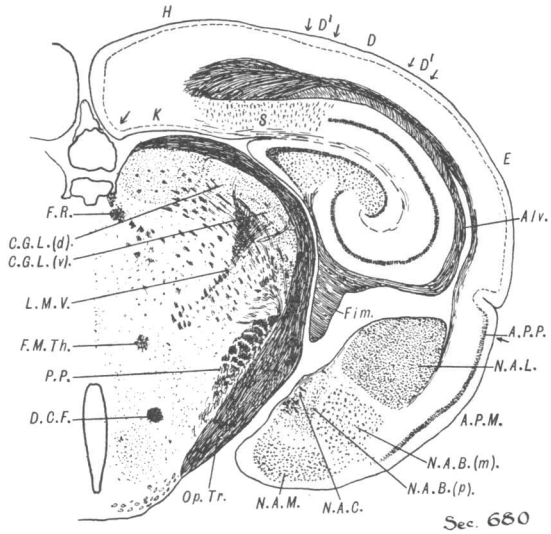
Fig. 21.

Fig. 22.
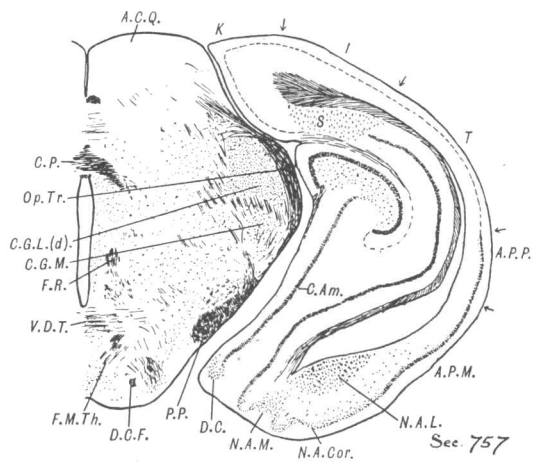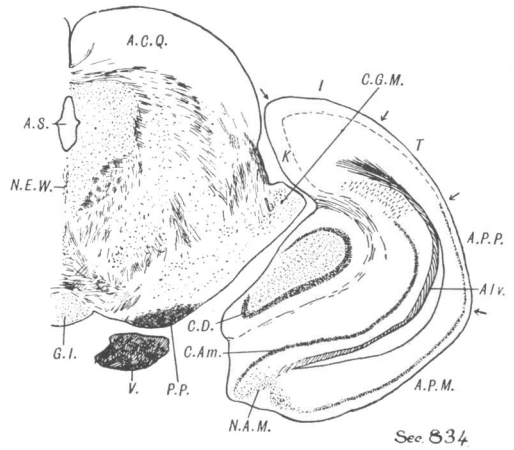

Fig. 23.

Fig. 24.

LE GROS CLARK—On the Brain of the Macroscelididae
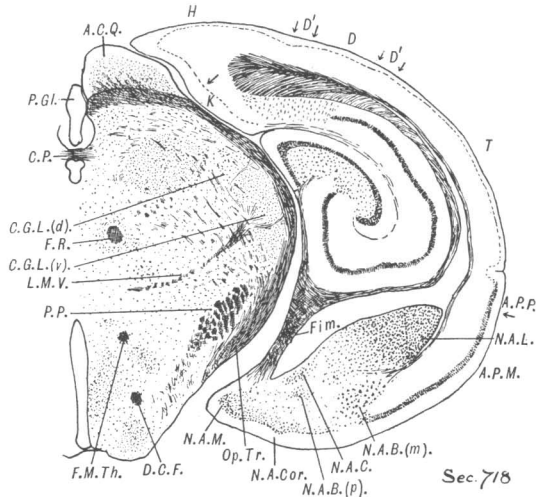
KEY TO ILLUSTRATIONS

A.	Sensorimotor area of cortex
Ac.B.	Accessory bulb
A.C.	Anterior commissure
A.C.Q.	Anterior corpus quadrigeminum
A.H.	Anterior hippocampus
Alv.	Alveus
A.P.A.	Area piriformis anterior
A.P.M.	Area piriformis medius
A.P.P.	Area piriformis posterior
A.S.	Aqueduct of Sylvius
A.Sb.P.	Area subpiriformis
B.	Parietal area of cortex
C.	Insular area of cortex
C.C.	Corpus callosum
C.D.	Cortex dentatus
C.G.L. (d.).	Lateral geniculate body (dorsal nucleus)
C.G.L. (v.).	Lateral geniculate body (ventral nucleus)
C.G.M.	Medial geniculate body
Cl.	Claustrum
C.N.	Caudate nucleus
C.P.	Posterior commissure
D.	Area striata of the cortex
D.C.F.	Descending column of fornix
E.	Temporal area of the cortex
E.C.	External capsule
F.	Frontal area of the cortex
F.C.	Fornix commissure
Fim.	Fimbria
F.L.	Fornix longus
F.M.Th.	Fasc. mammillo-thalamicus
F.Pr.	Precommissural fornix
F.R.	Fasc. retroflexus
G.	Posterior cingular area of the cortex
G.B.O.	Ganglion basale opticum
G.I.	Ganglion interpedunculare
G.P.	Globus pallidus
H.	Area retrosplenialis granularis
Hb.	Habenula
1.	Area retrosplenialis agranularis
I.C.	Internal capsule
I.S.	Intercalary sulcus
K.	Retrosplenial area (29 *e*) or Area pre-subicularis
L.	Anterior cingular area of the cortex
L.M.V.	Lamina medullaris ventralis
M.F.B.	Medial fore-brain bundle
N.A.	Nucleus accumbens.
N.A.B. (m.)	Nucleus amygd. basalis (pars magnocell.)
N.A.B. (p.)	Nucleus amygd. basalis (pars parvicell.)
N.A.C.	Nucleus amygd. centralis
N.A.Cor.	Nucleus amygd. corticalis
N.A.L.	Nucleus amygd. lateralis
N.A.M.	Nucleus amygd. medialis
N.D.B.	Nucleus of the diagonal band
Neo.	Neopallium
N.E.W.	Nucleus of Edinger Westphal
N.H.	Nucleus habenulae
N.L.O.T.	Nucleus of lateral olfactory tract
N.O.A.	Anterior olfactory nucleus
N.O.A. (p.e.)	Anterior olfactory nucleus (pars externus)
N.O.A. (p.p.)	Anterior olfactory nucleus (pars posterior)
N.P.F.	Nucleus proprius fornicis
N.P.L.	Nucleus parolfactorius lateralis
N.P.M.	Nucleus parolfactorius medialis
Op.Ch.	Optic chiasma
Op.N.	Optic nerve
Op.Tr.	Optic tract
P.	Putamen
P.Gl.	Pineal gland
P.I.Th.	Pedunc. inferior thalami
P.P.	Pes pedunculi
R.F.	Rhinal fissure
S.	Subiculum
S.P.	Stria pinealis
S.T.	Stria terminalis
Str.G.	Stratum glomerulosum
Str.Gr.	Stratum granulare
Str.Plex.	Stratum plexiforme
T.Ol.	Tuberculum olfactorium
T.O.I.	Intermediate olfactory tract
T.O.L.	Lateral olfactory tract
V.	Trigeminal nerve
V.D.T.	Ventral decussation of the tegmentum

EXPLANATION OF PLATES

Plates I and II, figs. 10 to 24. Transverse sections through the brain of *Macroscelides*, traced with a projectoscope. × 8⅓.