THE CELL STRUCTURE OF THE MAMILLARY BODY IN THE MAMMALS AND IN MAN

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INTRODUCTION

It may be reasonably assumed that the mamillary body represents an important structure within the hypothalamus, since a number of large nerve tracts originate or terminate in it. Although there is no lack of descriptions of the architecture of the mamillary body in the principal mammals, most of the authors who have dealt with this subject tend to disregard the comparative anatomical point of view, so that the phylogenesis of this structure and the significance of the individual nuclei remain obscure.

Former degeneration experiments, as made by Gudden (1889), Edinger & Wallenberg (1902), and other authors, have already pointed to the fact that degeneration of the fibre tracts of the mamillary body often produces only a partial degeneration of the nuclei. This leads to the assumption that the nuclei are not single functional units. In this paper the phylogenetic development of the cell structure of the mamillary body has been studied.

Gudden, who made an intensive study of the mamillary body in rodents (mouse), carnivores (cat and dog), monkey and man, distinguished a medial and a lateral nucleus in this structure, the lateral nucleus showing the larger nerve cells. Later he separated off a dorso-anterior and a ventro-posterior section in the medial nucleus of mammals, and stated that in the former the nerve cells are larger and less closely packed than in the latter. In man, Kölliker (1896) described a medial and a lateral nucleus, but in his opinion the medial, unlike that in lower mammals, is not subdivided. In addition, he mentions a nucleus accessorius whose nerve cells are smaller than those in the other two nuclei. In rodents, Cajal (1904) speaks of a medial and a lateral nucleus. The area antero-dorsal to the medial nucleus he terms "foco limitante". Malone (1910) describes in man a medial nucleus with medium-sized nerve cells, which is not subdivided, and a lateral nucleus with large nerve cells which he considers to extend deeply into the region of the infundibulum. The lateral nucleus with its continuation into the infundibulum, Malone calls the n. mamillo-infundibularis. Besides these two nuclei he distinguishes also a small large-celled nucleus situated between the medial and lateral nuclei, which he calls the n. intercalatus.

The findings of Friedemann (1912) in *Cercopithecus* are essentially the same as those of Malone in man. The description of the mamillary body in man as given by Malone has been modified by Foix & Nicolesco (1925), Gagel (1928),

and Greving (1925). Within the medial nucleus Foix & Nicolesco describe two parts, a small-celled inner and a small-celled outer part. By them, Malone's n. intercalatus is termed n. magnocellularis. Greving distinguishes between the ventro-medially situated n. magnocellularis and the dorso-lateral n. parvocellularis. Lateral to these two nuclei stretches the small-celled n. cinereus. The n. intercalatus, identical with that of Malone, is found lateral to this group of nuclei. In man and the dog, Roussy & Mosinger (1935) distinguish a lateral nucleus and two segments within the medial nucleus of other authors.

In the rabbit, whose mamillary body has been subjected to the most detailed investigation, Winkler & Potter (1911) described two nuclei. Nissl divided the ventral posterior portion of the medial nucleus, as described by Gudden, into two parts, a medial with large cells and a lateral with small cells. M. Rose (1935), whose nomenclature has been adopted in this paper, distinguishes in the mamillary body of the rabbit the n. mamillaris medialis seu dispar, n. mamillaris basalis, n. mamillaris intermedius seu papilioformis, n. mamillaris lateralis and n. supramamillaris.

METHODS

The investigation was carried out on paraffin-embedded material and entailed the examination of complete series of frontal sections. The sections, 20 μ in thickness, were stained with cresyl violet.

The volume of the different nuclei was determined as follows: By means of a microprojector the outlines of the nuclei were drawn under a known magnification on cardboard, the thickness of which corresponded to the degree of magnification used. The cardboard was then cut to the shape of the outlined nuclei and the individual pieces pasted together. Each cardboard reconstruction was covered with hominite to prevent swelling in water. The volume of the cardboard reconstruction was then determined by displacement of water from an appropriate container, the displaced water being weighed. The volume of the reconstruction divided by the magnification 3 gives the actual volume of the object. When, for instance, a reconstruction using a magnification of 40 times was made, every second section was reconstructed on cardboard 2 mm. in thickness. Such a cardboard figure thus represented the section magnified 40 times in every direction. Each section was calculated as 25 μ, as it is known from M. Rose's (1928) investigations that the number of sections obtained will be about 20 % less than might be expected from the length of the object.

1. CHIROPTERA

Bat (Synotus barbastellus)

Fig. 1 shows the mamillary body near its rostral extremity. Around the ventricle is a dense collection of nerve cells which, analogous to the nucleus described by M. Rose in the rabbit is called the n. medialis postremus hyp. (*psi*). Lateral to this cell group is a well-defined nucleus with rather loosely packed medium-sized nerve cells, dorso-lateral to which extends an ill-defined region of scattered cells which is adjacent to the pes pedunculi (*pp*) and c. subthalamicum (*cs*). Again, as with similar nuclei in the rabbit, these two nuclei can be called the n. hyp. posterior lateralis (*pl*) and n. hyp.

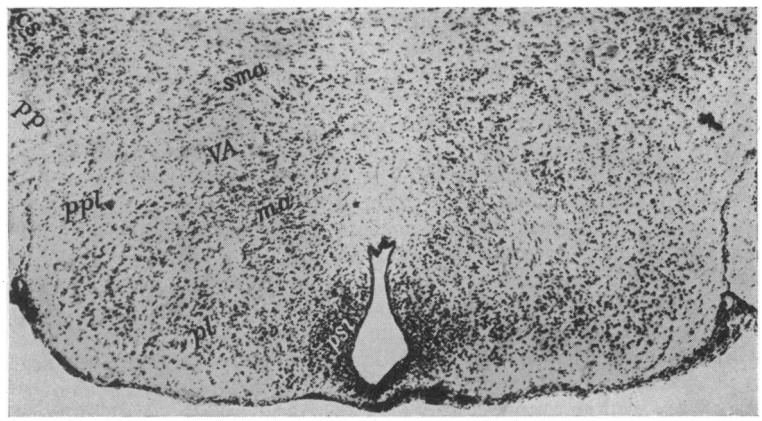

Fig. 1. Bat (*Synotus barbastellus*). N. 4. 207. ×50.

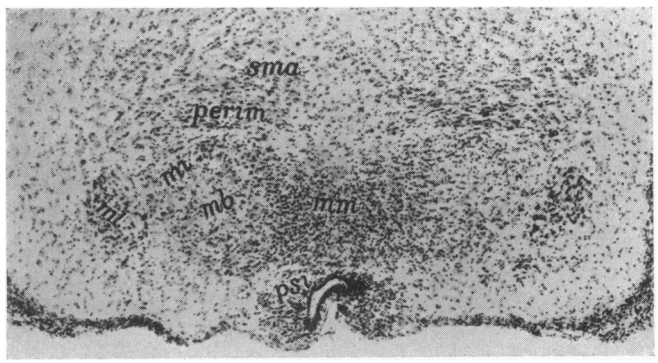

Fig. 2. Bat (*Synotus barbastellus*). N. 4. 215. ×50.

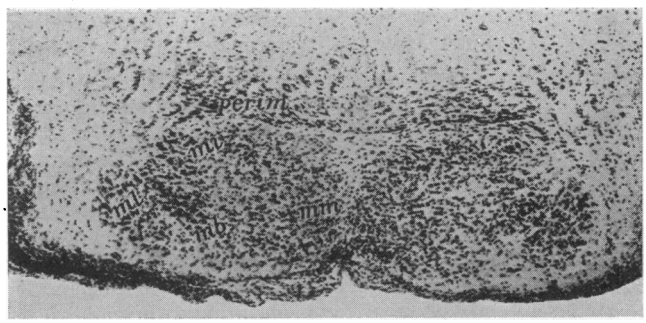

Fig. 3. Bat (*Synotus barbastellus*). N. 4. 219. ×50.

posterior postlateralis (*ppl*). Dorso-lateral to *psi* is a paired nucleus consisting of small, round and medium-sized oval nerve cells, which may be called the anterior mamillary nucleus (*ma*). More caudally the anterior mamillary nucleus passes on directly into the medial mamillary nucleus.

The splitting up of the bundle of Vicq d'Azyr within the anterior mamillary nucleus can be followed in succeeding sections.[1] In Nissl preparations of the bat, however, it is rather difficult to trace this bundle and the fornix.

Above the anterior mamillary nucleus, covering it like a roof, extends the supramamillary nucleus (*sma*) consisting of loosely packed nerve cells which are larger and more deeply staining than those of the anterior mamillary nucleus. There is a partial fusion of the supramamillary nucleus from each side in the mid-line. The supramamillary nucleus does not stand out sharply from the other nuclei.

Fig. 2 shows the mamillary body fully developed. Parts only of the n. medialis postremus hyp. (*psi*) are left, the n. hyp. posterior lateralis (*pl*) and n. hyp. posterior postlateralis (*ppl*) having disappeared. The mamillary body has moved ventrally to the base. In place of the anterior mamillary nucleus (*ma*) an unpaired nucleus has arisen which is the medial mamillary nucleus (*mm*). The nerve cells of the latter nucleus (*mm*) are seen as round, closely packed, granular cells. Ventro-lateral to the medial mamillary nucleus lies the basal mamillary nucleus (*mb*), whose nerve cells, whilst being more loosely arranged, resemble those of the medial mamillary nucleus. On the lateral margin of the basal mamillary nucleus (*mb*) the nerve cells condense into a band which stretches from its base to the lateral aspect of the medial mamillary nucleus, forming a semicircle around the basal mamillary nucleus. In rodents, as will be shown, it is very well developed. It may be termed the intermediate mamillary nucleus (*mi*). Lateral to the medial group of nuclei a new nucleus has appeared, the lateral mamillary nucleus (*ml*). It is an oval, sharply circumscribed nucleus containing relatively large and deeply staining nerve cells. The supramamillary nucleus (*sma*) extends dorsally, and ventral to it is a sharply defined band composed of deeply staining, elongated nerve cells, which enlarge caudally. This part of the supramamillary nucleus will be called the perimamillary nucleus (*perim*).

Fig. 3. The ventricle has disappeared; the medial mamillary nucleus has diminished, but the basal mamillary nucleus (*mb*) is seen distinctly. The lateral mamillary nucleus (*ml*), still large, is about to disappear, its nerve cells intermingling with those of the intermediate mamillary nucleus (*mi*). The perimamillary nucleus is prominently developed, and its large deeply staining nerve cells are arranged in rows, a characteristic of this nucleus. Compared with the supramamillary nucleus the perimamillary nucleus is also far better defined. In the following five sections the mamillary body disappears altogether.

2. INSECTIVORES

(*a*) *Mole* (Talpa europaea)

Fig. 4 shows the mamillary body fully developed. The n. medialis postremus hyp. (*psi*) is about to disappear. Lateral to *psi* are the remains of a nucleus which is termed the premamillary nucleus (*pre*), and which, as a rule, is found in most mammals immediately in front of the rostral extremity of the mamillary body. It is composed of numerous small nerve cells together with a few large deeply staining cells. As will be shown later, this nucleus is not homologous with the premamillary nucleus described by M. Rose in the rabbit.

Dorso-lateral to the premamillary nucleus (*pre*) is the anterior mamillary nucleus (*ma*). In the mole, it forms a very large round dense nucleus. The nerve cells are of medium size with an abundance of cytoplasm, and the cell processes are quite

[1] In all the figures the thalamo-mamillary tract and the fibre tracts joining it are given the common name of the bundle of Vicq d'Azyr.

distinct. In Fig. 4 both anterior mamillary nuclei are already connected to the medial mamillary nucleus (*mm*). In the rostral part of the mamillary body, however, only the two anterior mamillary nuclei (*ma*) are present, being sharply distinguished medially from the premamillary nucleus which has taken the place of the medial mamillary nucleus (*mm*). The medial mamillary nucleus is less dense than the anterior (*ma*), its nerve cells being somewhat smaller, rounded and staining less intensely. Dorsally the nerve cells condense, clearly giving rise to a band of more deeply staining large cells. Above the medial mamillary nucleus the supramamillary nucleus is distinctly visible. It forms a large, loose, well-defined nucleus. Its

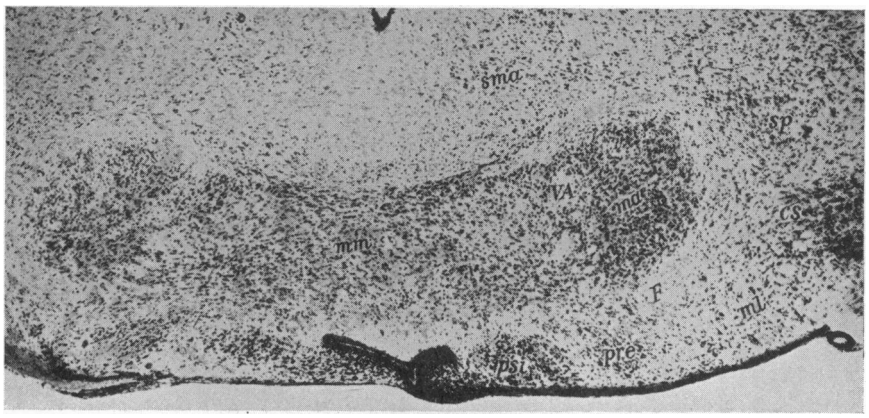

Fig. 4. Mole (*Talpa europaea*). Kt. 384. ×50.

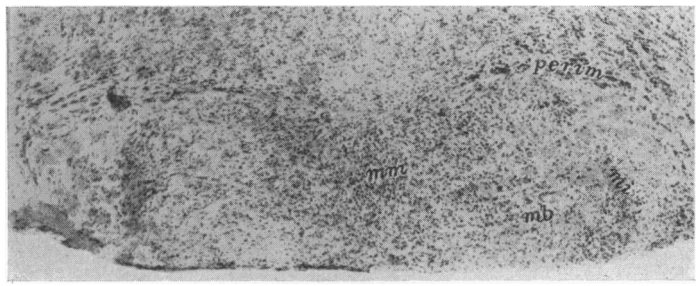

Fig. 5. Mole (*Talpa europaea*). Kt. 394. ×50.

nerve cells are of small or medium size, and the cell processes are abundant. Ventrolateral to the fornix an accumulation of large deeply staining nerve cells is seen, but is not sharply defined. This corresponds most probably to the lateral mamillary nucleus (*ml*), as may be inferred from its typical position as well as from the form and staining of the nerve cells.

Fig. 5. The mamillary body here forms the base of the hypothalamus. The anterior mamillary nucleus on each side has already disappeared. The medial mamillary nucleus shows a distinct condensation of nerve cells in its centre. Ventrolateral to the medial mamillary nucleus is a loosely packed nucleus with smaller nerve cells which corresponds to the basal nucleus (*mb*). The intermediate mamillary nucleus (*mi*) arises lateral to the basal nucleus (*mb*), as a narrow band which is

denser than the basal nucleus (*mb*), though its nerve cells are similar to those of that basal nucleus. Dorsally, on both sides, the intermediate mamillary nucleus (*mi*) fuses with the medial mamillary nucleus (*mm*).

Generally, the differences between the medial mamillary nucleus (*mm*), the basal nucleus (*mb*) and the intermediate mamillary nucleus (*mi*) are not very distinct, particularly caudally, where the nerve cells become scattered so that it becomes difficult to distinguish between the medial mamillary nucleus and the basal mamillary nucleus.

Dorsal to the medial nuclear group, the perimamillary nucleus (*perim*) has taken the place of the supramamillary nucleus (*sma*). In the mole it is enormously developed. The perimamillary nucleus is composed of several rows of large, elongated, oval or polymorphous deeply staining nerve cells with numerous cell processes. It is more sharply demarcated from the other nuclei than the supramamillary nucleus. Within a short distance the perimamillary nuclei fuse.

Within the next twenty sections the mamillary body disappears completely.

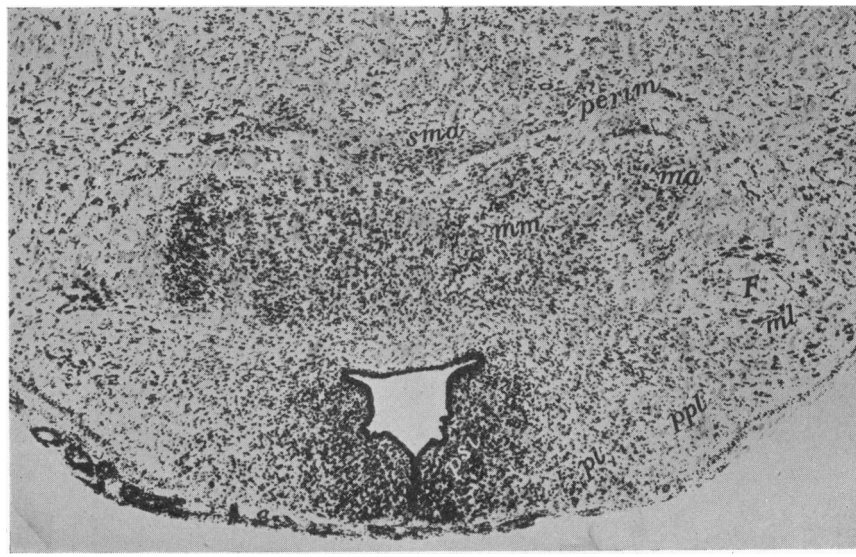

Fig. 6. Hedgehog (*Erinaceus europaeus*). J. 625. ×40.

(*b*) *Hedgehog* (Erinaceus europaeus)

Fig. 6 represents a section from the centre of the mamillary body. The n. medialis postremus hyp. (*psi*), still large, is situated around the ventricle, whilst lateral to it are remains of the nuclei *pl* and *ppl*. The unpaired medial nucleus, which seems to originate from the fusion of the nuclei of both sides, consists of medium-sized nerve cells, round or oval in shape, with a narrow border of cytoplasm and poorly visible cell processes. Lateral to the medial mamillary nucleus (*mm*) the anterior mamillary nucleus (*ma*) is attached to it, being distinguished by smaller and more closely packed nerve cells. The anterior mamillary nucleus is already about to disappear on the right side.

In the hedgehog, although it can readily be seen, the anterior mamillary nucleus (*ma*) is much less developed than in the mole. Its medium-sized, polygonal, closely packed nerve cells show abundant but poorly staining cytoplasm. Above the anterior

mamillary nucleus (*ma*), the supramamillary nucleus develops to the same large size as in the mole. The supramamillary nucleus (*sma*) consists of closely packed nerve cells, both of medium and large size, which are predominantly elongated and oval in shape, with an abundance of clearly visible cytoplasm. The cell processes are broad but can only be followed for a short distance. The supramamillary nuclei show a number of very large nerve cells, and fuse in the mid-line. Lateral to the supramamillary nucleus, the perimamillary nucleus (*perim*) has already appeared, and lateral to the fornix the lateral mamillary nucleus (*ml*) has developed. The latter is much more distinct than in the mole; that it is homologous with the lateral mamillary nucleus of rodents seems beyond doubt. The nerve cells of the lateral mamillary nucleus are large, mainly polymorphous, the cytoplasm being abundant and the cell processes distinctly visible. Both the cytoplasm and the cell nuclei stain intensely.

Fig. 7 shows the mamillary body farther caudally. The medial mamillary nucleus has disappeared almost completely. Its place has been taken by the loosely packed basal mamillary nucleus (*mb*), whose cells are much smaller and less deeply

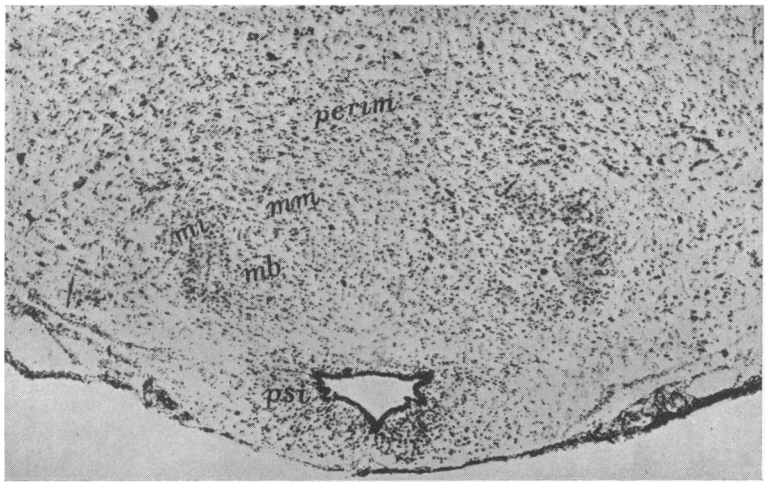

Fig. 7. Hedgehog (*Erinaceus europaeus*). J. 636. ×40.

staining than those of the medial mamillary nucleus, whilst they are rounded and show a narrow border of cytoplasm. Lateral to the basal mamillary nucleus (*mb*) a conspicuous accumulation of nerve cells of the same type is found. This is probably the intermediate mamillary nucleus (*mi*). Dorso-laterally the intermediate mamillary nucleus encircles the basal mamillary nucleus (*mb*) and disappears into the remains of the medial mamillary nucleus. Caudally the intermediate mamillary nucleus (*mi*) becomes still larger. In the rostral parts, however, separation of the intermediate and anterior mamillary nuclei is difficult, as the nerve cells of each show no marked differences.

Dorsally, the perimamillary nucleus has displaced the supramamillary nucleus. It is enormous, its nerve cells being large, elongated and deeply staining with an abundance of cytoplasm. The perimamillary nucleus covers the mamillary body dorsally, and partially on its lateral aspect. The lateral margin of the perimamillary nucleus shows larger cells than the medial. Fusion of both perimamillary nuclei takes place in the mid-line.

3. RODENTIA

(*a*) *Squirrel* (Sciurus vulgaris)

Fig. 8 shows the rostral extremity of the mamillary body. The n. medialis postremus hyp. (*psi*) is visible around the broad ventricle, and to the right a portion of the premamillary nucleus is still present. In the centre of the figure the unpaired anterior mamillary nucleus is seen. Its medium-sized cells are fairly dense. The cytoplasm is readily visible and the cell processes are abundant. The fibres of the bundle of Vicq d'Azyr are distinctly seen penetrating the anterior mamillary nucleus (*ma*). Dorso-lateral to the fornix, the sharply defined oval basal mamillary nucleus can be seen, the cells of which are large, deeply staining, and show numerous cell processes. Above the anterior mamillary nucleus the extremity of the supramamillary nucleus is visible.

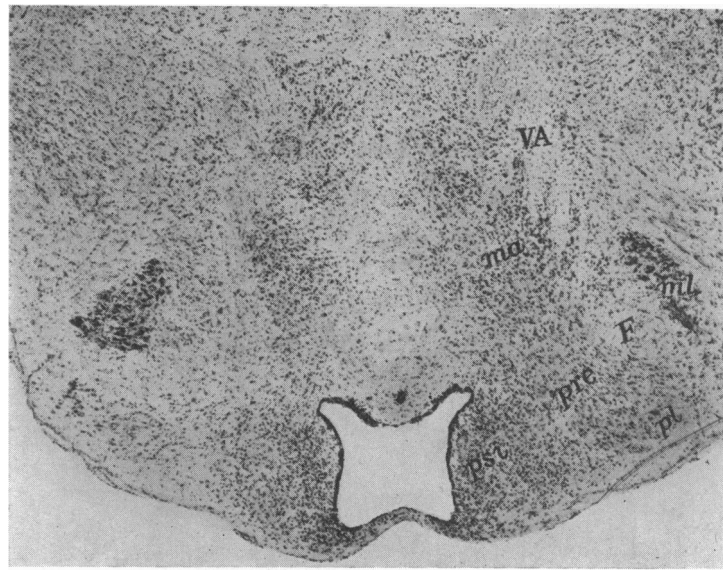

Fig. 8. Squirrel (*Sciurus vulgaris*). W. 1. 513. ×30.

Fig. 9. The mamillary body has moved to the base. In place of the anterior mamillary nucleus, the unpaired large medial nucleus (*mm*) appears. Its cells are closely packed, resembling those of the anterior mamillary nucleus. It is obvious that the medial mamillary nucleus has originated from the fusion of the nuclei of both sides. At the lateral aspect of the medial mamillary nucleus the cells are more scattered. Ventral to the medial nucleus, a collection of considerably smaller nerve cells can be seen forming the beginning of the basal nucleus (*mb*). Dorsally in the figure, the well-developed, large, supramamillary nucleus is seen, forming a roof over the mamillary body. Its cells stain well, and consist of small and also rather large types. The small cells are rounded, whilst the large are angular or polymorphous with an abundance of cytoplasm. Both supramamillary nuclei fuse in the mid-line. This fused portion consists almost exclusively of small nerve cells.

Fig. 10. The medial mamillary nucleus shows a considerable decrease in size, while the basal nucleus (*mb*) has increased. The latter consists of loosely packed, small, feebly staining cells. There is a partial fusion of both basal nuclei (*mb*). From the base of the basal nucleus, the intermediate mamillary nucleus (*mi*) develops,

being composed of cells similar to those of the basal nucleus though more closely packed. The intermediate mamillary nucleus (*mi*) encloses the medial mamillary nucleus (*mm*). Fusion of both intermediate nuclei takes place in the mid-line dorsally. This fused portion, which consists of larger and somewhat more deeply staining nerve cells than those of the individual nuclei, is called the central mamillary nucleus (*mc*), in the rabbit by M. Rose.

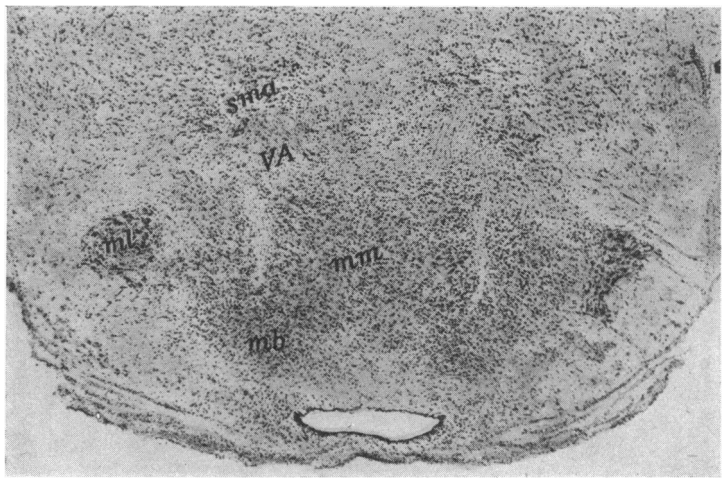

Fig. 9. Squirrel (*Sciurus vulgaris*). W. 1. 527. ×30.

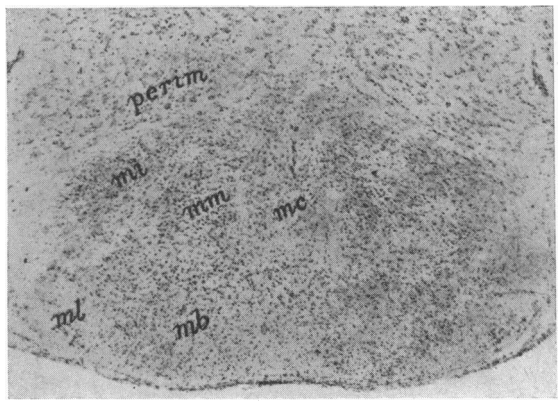

Fig. 10. Squirrel (*Sciurus vulgaris*). W. 1. 547. ×30.

Of the lateral nuclei, only isolated nerve cells are visible. Dorsal to the medial group of nuclei the perimamillary nucleus has arisen in place of the supramamillary nucleus. In the squirrel it is poorly developed. The characteristically arranged rows of elongated and loosely packed nerve cells, however, can easily be recognized.

Caudally the basal nuclei are the only elements representing the medial nuclear group.

(*b*) *Rabbit* (Lepus cuniculus)

The structure of the mamillary body in the rabbit requires no detailed description. It is essentially identical with that of the squirrel, and detailed descriptions and illustrations of its structure have already been given by M. Rose. It may be noted that the nucleus, which in the rabbit, insectivores and the bat I have called the anterior mamillary nucleus, is not considered by M. Rose to belong to the mamillary body, and in the rabbit he has described it as the premamillary nucleus. This may depend on the fact that in the rabbit the close connexion of the mamillary body with the bundle of Vicq d'Azyr is not so obvious and conspicuous as in the squirrel (see Fig. 8).

Regarding quantitative differences in the development of the different nuclei in the rabbit compared with the squirrel, the following may be mentioned: The perimamillary nucleus is even less developed. Only by comparative anatomical investigation can the perimamillary nucleus in the rabbit be regarded as a distinct entity. The lateral nuclei are relatively larger. The intermediate nuclei are particularly well developed and can easily be distinguished from the other nuclei.

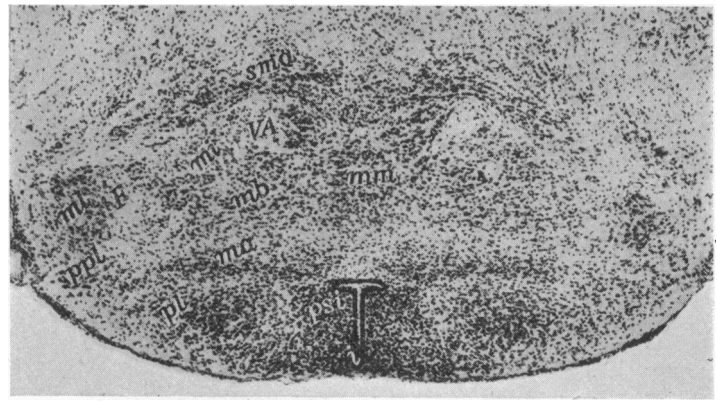

Fig. 11. Mouse (*Mus musculus*). My. 1. 318. ×50.

(*c*) *Mouse* (Mus musculus)

Fig. 11. The n. medialis postremus hyp. (*psi*) is situated round the ventricle, whilst the n. infundibularis (*i*) is ventral to this. Lateral to *psi* extend the well-known nuclei *pl* and *ppl* (nn. hyp. posterior lateralis and postlateralis), dorsal to which is the anterior mamillary nucleus (*ma*). In the mouse the anterior mamillary nucleus is represented by a large oval nucleus which, in rostral sections, runs, as in other rodents, dorso-medially to ventro-laterally. It does not disappear, however, as in other rodents, immediately after the medial mamillary nucleus has arisen, but is displaced downwards. Therefore, after the chief nuclei of the mamillary body have appeared it extends ventral to them as a narrow band, being separated from them by a narrow acellular zone. The anterior mamillary nucleus is fairly dense, its cells being of medium size, oval or angular, and staining well. Both fuse partially in the mid-line.

In the centre of the figure the medial mamillary nucleus (*mm*) can be seen. It is relatively small but dense, and its cells are round or angular and relatively large. Ventro-laterally the basal nucleus (*mb*) is well defined, its nerve cells are more scattered than those of the medial nucleus (*mm*), besides being smaller and mostly round. The

cell processes are scarcely visible. Dorso-lateral to the basal nucleus (*mb*), the intermediate nucleus (*mi*) appears, being well developed in the mouse. Its nerve cells are more closely packed and somewhat smaller than in the basal nucleus (*mb*). The medial margins of the intermediate nuclei, as in other rodents, show larger and more deeply staining cells. In the mouse it is not always easy to distinguish the nerve cells of the medial margin of the intermediate nucleus from those of the supramamillary nucleus. Dorsal to the medial nucleus (*mm*), the supramamillary nucleus is found large and well developed. Its structure shows much resemblance to that of the supramamillary nucleus in the squirrel. The cells are large and deeply staining. In the mid-line the nuclei fuse, the cells in this area being smaller and less deeply staining.

Lateral to the fornix the lateral mamillary nucleus (*ml*) has developed and is almost round. Its cells are round or angular, deeply staining, and show an abundance of cytoplasm.

More caudally than in Fig. 11, both medial and basal nuclei (*mm* and *mb*) become smaller, whereas the intermediate nucleus (*mi*) increases considerably in size and extends as a broad band dorso-medially. In the mouse (as well as in the rabbit and squirrel) the large-celled part of the intermediate nucleus (*mi*) is very well seen. These parts of the intermediate nucleus on each side fuse and, forming a central nucleus, pass on to the medial nucleus.

Dorsally, the perimamillary nucleus (*perim*) has arisen in place of the supramamillary nucleus (*sma*). In the mouse, as in all the investigated rodents, the perimamillary nucleus is poorly developed, but, nevertheless, can be seen clearly. It is narrow, sharply defined and closely attached to the mamillary body, and consists of a few rows of flattened, large, deeply staining nerve cells.

4. CARNIVORA

(*a*) *Polecat* (Mustela putorius)

The mamillary body of the polecat differs considerably from that of the other mammals already described. Its most significant feature is the disappearance of the unpaired nucleus which is present in rodents and insectivores, as well as in the bat.

Fig. 12 shows the medial section of the mamillary body. The ventricle and the nuclei surrounding it have just disappeared. Laterally (to the left) can be seen a narrow band of large deeply staining nerve cells. This nucleus probably corresponds to Grünthal's (1929) nucleus 3 in the dog. The anterior mamillary nucleus (*ma*) is very well seen, and within a short distance a roof-shaped portion (ma_1) can be demarcated. The cells of the anterior nucleus (*ma*) are fairly large, show a dark round or oval nucleus and an abundance of poorly visible cytoplasm, whilst area ma_1 is composed of smaller and more closely packed nerve cells. There is a partial crossing of both anterior nuclei in the mid-line but no distinct fusion. Below, but not sharply defined from the anterior mamillary nucleus (*ma*), is the medial mamillary nucleus (*mm*), into which the bundle of Vicq d'Azyr passes. The medial mamillary nucleus is paired and does not fuse with the medial nucleus of the opposite side, but is always separated from it by a raphe. The cells of the medial nucleus (*mm*) are somewhat smaller than those of the anterior, and the arrangement of the cells is looser. At the dorso-lateral margin the cells are generally more closely packed and slightly larger than in the centre.

With cresyl violet the background stains a deep reddish purple, darker than in the anterior nucleus, so that in the preparation it is considerably easier to distinguish these nuclei than it is in the figure. Ventral to the medial nucleus is the basal nucleus (*mb*), its cells being much smaller and less deeply staining than those of the medial nucleus. The basal nucleus contains many glia-like cells. Lateral to the medial nuclear group the lateral nucleus (*ml*) is seen. It is oval in shape and enormously

developed, and its cells, as in the other animals, are large, deeply staining and provided with numerous cell processes.

Above the anterior nucleus (*ma*) the very well-developed supramamillary nucleus (*sma*) is visible. It covers the mamillary body as a broad band in its typical roof-like manner. Its nerve cells are rather large, deeply staining and loosely arranged.

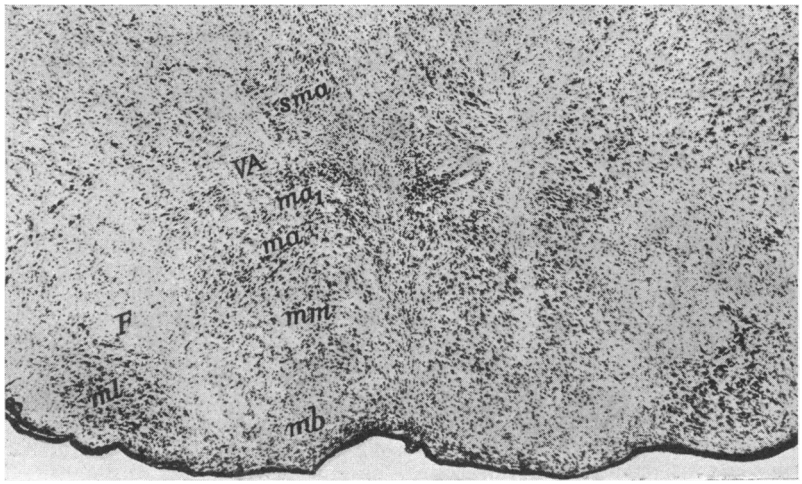

Fig. 12. Polecat (*Mustela putorius*). Tch. 3. 764. ×35.

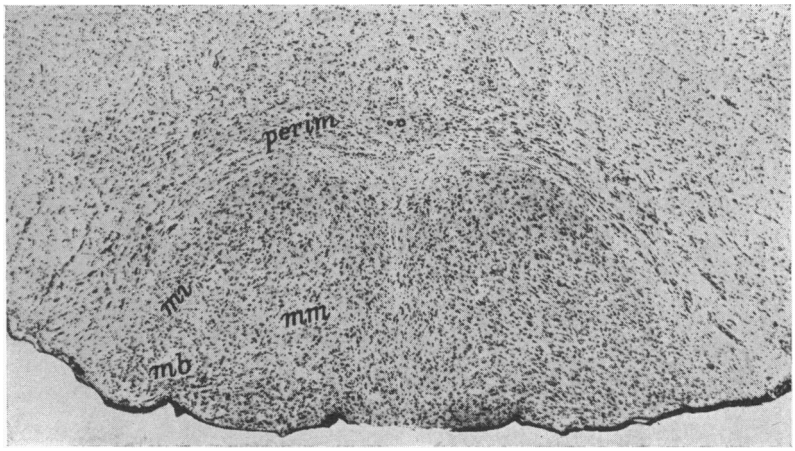

Fig. 13. Polecat (*Mustela putorius*). Tch. 3. 795. ×35.

The thalamo-mamillary tract often divides the supramamillary nucleus into two parts. There is a mingling of the cells of both supramamillary nuclei in the mid-line, whilst they are not sharply demarcated from the other nuclei.

Fig. 13 shows the mamillary body more caudally. The anterior and lateral nuclei have completely disappeared. The medial nuclear group is enormously developed and is surrounded on all sides by a medullary capsule. The deep staining of

the background of the medial nucleus is well seen. Ventro-latero-basal to the medial nucleus (*mm*), the basal nucleus (*mb*) can be recognized by its small, round, feebly staining cells. From the basal nucleus a narrow band of cells, resembling those of this nucleus, becomes separated. It is evidently homologous with the intermediate nucleus (*mi*) of lower animals, but a distinction from the basal nuclei can be made with ease only in some places.

Dorsally, the perimamillary nucleus (*perim*) has appeared in place of the supramamillary nucleus. The perimamillary nucleus surrounds the mamillary body above and on the sides, like a band. It is composed of several rows of elongated, large, deeply staining cells. It shows a distinctly greater development than in rodents.

In the further sections of the medial nuclear group, apart from the perimamillary nucleus, only the medial nucleus is left. Farther caudally, however, the cells of the medial nucleus are more loosely packed. Within about 40 sections caudal to Fig. 13, the mamillary body disappears completely.

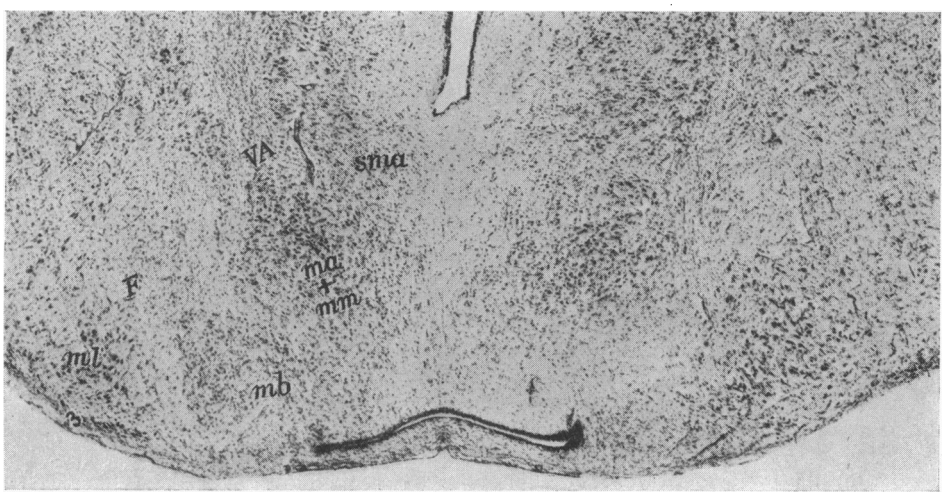

Fig. 14. Dog (*Canis familiaris*). P. 4. 185. ×25.

(*b*) *Dog* (Canis familiaris)

Fig. 14 shows the rostral end of the mamillary body. Ventro-laterally in the figure, Grünthal's nucleus 3 can be seen. Above the ventricle, on both sides, the anterior nucleus (*ma*) is encountered, whilst to the left and ventral to *ma* the basal nucleus (*mb*) is seen and will be described later.

The anterior nucleus is paired and composed of large, deeply staining cells mostly oval in shape. The cytoplasm is abundant and stains well, whilst the cell processes can be traced for long distances. Generally, the cells of the anterior nucleus are somewhat larger and more closely packed than those of the medial nucleus (*mm*) which appears farther caudally. The differences in the dog, however, being slight, the anterior and the medial mamillary nuclei are given the same name.

The well-developed lateral nucleus (*ml*) on each side is situated between the ventricle and nucleus 3, ventro-lateral to the fornix. The cells of the lateral nucleus are large with abundant deeply staining cytoplasm. This nucleus, however, is somewhat less well defined than in the polecat.

Above the medial group of nuclei the supramamillary nucleus has just appeared and will be described in the next figure.

Fig. 15. The lateral nucleus (*ml*) has already gone completely. The anterior and medial nuclei have enlarged considerably, and they are paired. A triangular-shaped collection of small elongated cells unites both the anterior nuclei dorsally. Ventrolateral to the anterior and medial nuclei the basal nucleus (*mb*) becomes obvious. Its cells are more scattered than those of *ma* and *mm*, and are small and less deeply staining. The border of cytoplasm too, is much narrower, whilst the large nucleus of the cells is remarkably light and has an inflated appearance. The cell processes are thin and on the whole readily visible. Lateral to the basal nucleus (*mb*) the intermediate nucleus (*mi*) appears but is poorly developed.

Above the medial nuclear group the supramamillary nucleus is well developed. It covers the mamillary body in its typical roof-like manner. Its elongated oval cells are large and loosely packed, with abundant deeply staining cytoplasm and light oval nuclei. The cell processes are thick and very distinct. The supramamillary nucleus is interrupted by the fibre bundles coursing into the mamillary body.

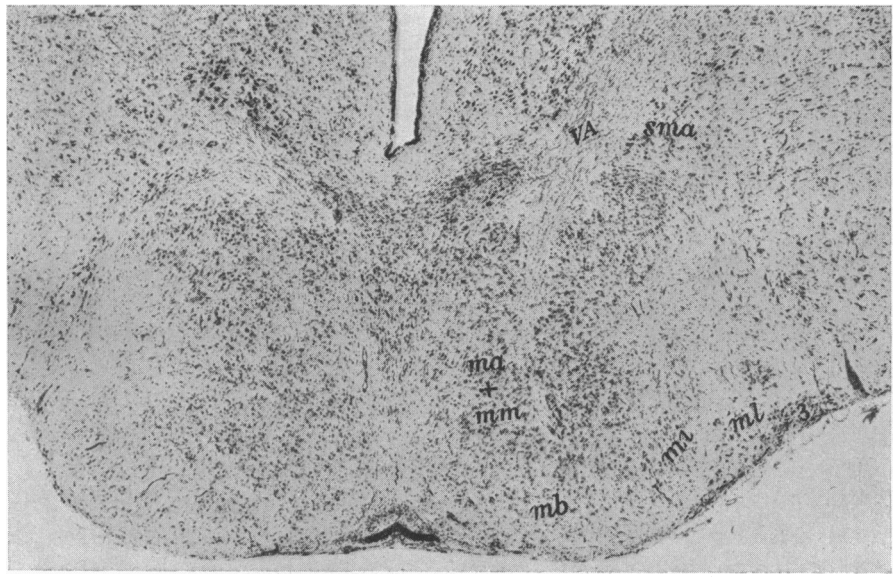

Fig. 15. Dog (*Canis familiaris*). P. 4. 208. ×25.

More caudally the combined anterior and medial nucleus becomes more loosely packed so that it is less sharply defined from the basal nucleus (*mb*). Still farther caudally, the whole of the medial group of nuclei becomes more and more deficient in cells. Caudally, too, the supramamillary nucleus is displaced by the perimamillary nucleus. In the dog the perimamillary nucleus is only incompletely developed. The arrangement of the nerve cells in rows, together with a looser type of formation than in the supramamillary nucleus, however, can be recognized, and the cells are seen to be somewhat elongated, medium-sized and deeply staining.

5. PRIMATES

(*a*) *Rhesus monkey* (Macaca mulatta)

Fig. 16 represents the rostral extremity of the mamillary body. The medial mamillary nucleus (*mm*) occupies the greater part of the figure. In the monkey, the anterior mamillary nucleus (*ma*) cannot be distinguished from the medial mamil-

lary nucleus, and at no point does fusion of the latter nucleus take place with its fellow of the opposite side. Its cells are of medium size and not sharply defined. The background has a dark reddish tinge. The cytoplasm of the cells is abundant but poorly visible, whilst the round or oval nucleus is large. Ventro-laterally, the basal nucleus (*mb*) is seen. Here the ground substance is considerably lighter, the cells are round and small (much smaller than in the medial nucleus), are loosely packed, and show a narrow rim of cytoplasm. There is also an abundance of glia cells. On the lateral margin of the basal nucleus (*mb*) the small nerve cells condense into a narrow band so that they may be spoken of as an intermediate mamillary nucleus (*mi*), but as in the dog it is only feebly developed.

Lateral to the medial nuclear group the lateral nucleus (*ml*) is seen. It is almost round, is sharply demarcated, and its position and composition are typical. The cells are large with an abundance of cytoplasm and deeply staining cell processes.

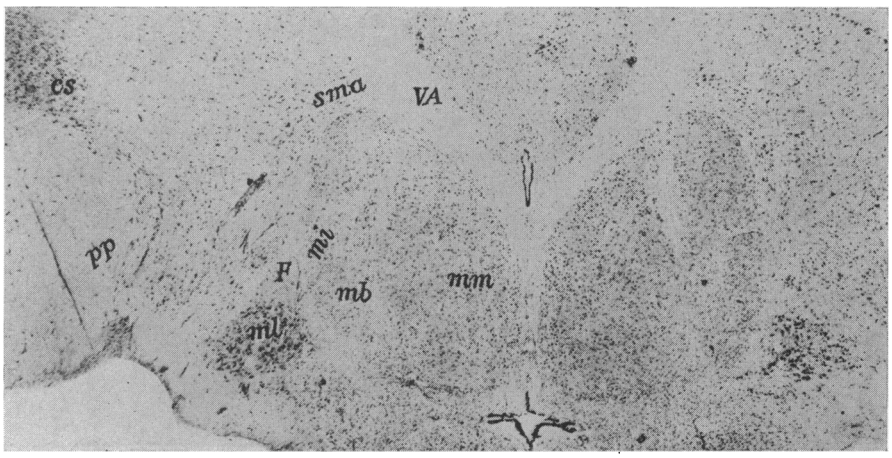

Fig. 16. Macaque monkey (*Macaca mulatta*). M. 2. × 20.

Above the medial nucleus (*mm*) the supramamillary nucleus is seen to begin, and farther caudally becomes fully developed. The supramamillary nucleus covers the mamillary body in its usual roof-like manner and is composed of medium-sized, loosely packed, deeply staining nerve cells. Caudally, a rather large perimamillary nucleus is seen, closely attached to the mamillary body. It stretches as a band, with its maximum width laterally, to surround the mamillary body almost as far as the ventral surface. Its cells, elongated and well-staining, are about the same size as those in the supramamillary nucleus.

Caudally, the medial nuclear group, too, becomes altered because on the medial margin and the upper half of the lateral margin of the nucleus (*mm*) a very narrow zone is seen consisting of more closely packed cells resembling those of the medial nucleus. It is missing only at the junction of the medial and basal nuclei (*mm* and *mb*). Still farther caudally the intermediate and basal nuclei (*mi* and *mb*) disappear completely, and of the medial group of nuclei only the medial nucleus is left.

About 35 sections caudally to Fig. 16 the mamillary body disappears completely.

(*b*) *Man*

Owing to the size of the microphotograph the mamillary body is discussed in relation to a series of sections prepared from the brain of a 3-months-old child. These did not differ from a similar series in the adult.

The structure of the mamillary body in man is very similar to that of the rhesus monkey. There is no fusion of the medial nuclei. The nuclear group on each side forms the well-known eminence which can be seen macroscopically.

Fig. 17 shows the rostral extremity of the mamillary body, and at this level both the medial and basal mamillary nuclei are encountered. The medial nucleus (*mm*) consists of medium-sized, well-staining, round or polygonal cells with abundant cytoplasm, whilst the ground substance shows a reddish tinge. Ventro-laterally, the basal nucleus (*mb*) is readily seen. As in the monkey, it consists of cells which are

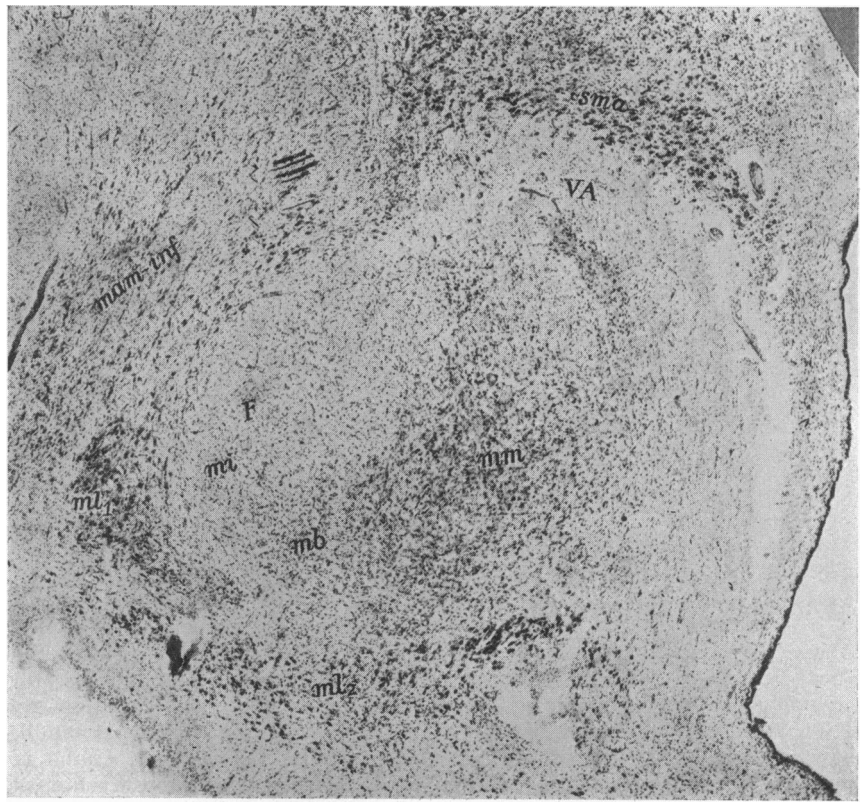

Fig. 17. Man. H. 45. 659. ×30.

much smaller, rounder and more scattered than those of the medial nucleus (*mm*), whilst glia-like cells are also present.

Lateral to the basal nucleus (*mb*), a narrow band of nerve cells appears which may be considered homologous with the intermediate nucleus (*mi*) of lower mammals.

Ventral and lateral to the medial nuclear group, the lateral nucleus (*ml*) is distinctly visible, as in most mammals, although it is divided into two parts. The position and structure of the lateral nucleus is absolutely typical. Its cells are large, polymorphous and deeply staining.

Above the bundle of Vicq d'Azyr the supramamillary nucleus, clearly developed, extends in its typically roof-like manner. It consists of large, deeply staining, polygonal nerve cells.

Farther caudally the medial nucleus attains its full development. Only traces of the lateral nucleus (*ml*) are left, whilst both the basal and intermediate nuclei (*mb* and *mi*) are much reduced.

The supramamillary nucleus quickly decreases in size and is interrupted by fibre tracts. Thus the medial nucleus (*mm*) forms the chief part of the mamillary body. Proceeding farther caudally the mamillary body is represented by the medial nucleus only, and is enclosed on all sides by a medullary capsule. Some rows of loosely packed, elongated nerve cells are closely attached to the capsule and obviously represent the perimamillary nucleus in man.

It may be noted that the lateral mamillary nucleus corresponds not only to Malone's n. intercalatus, but also forms part of his n. infundibulo-mamillaris. Probably Malone's n. intercalatus corresponds only to the nucleus which in Fig. 17 is indicated as ml_1.

According to Malone's description, ml_2 would correspond only to an expansion of the n. infundibulo-mamillaris.[1] From the comparative anatomical aspect, however, one is entitled to regard these parts as homologous with the lateral mamillary nucleus of lower mammals. Malone's nucleus infundibulo-mamillaris is composed of several nuclei which, from a comparative anatomical point of view, are different. The following nuclei, at least, enter into its formation: the n.n. perifornicatus, supra-fornicatus and premamillaris, rostral to the mamillary body; and the supramamillary nucleus, part of the lateral mamillary nucleus and the nucleus, which in Fig. 17 is indicated as the infundibulo-mamillary nucleus (n. mamillo-infundibularis), in the mamillary body itself.

Greving's n. magnocellularis corresponds to the medial mamillary nucleus as described in man and mammals, his n. parvocellularis to the basal mamillary nucleus (*mb*), and the nucleus intercalatus to the lateral mamillary nucleus. Possibly Greving's n. cinereus corresponds to the intermediate mamillary nucleus.

DISCUSSION ON THE STRUCTURE OF THE MAMILLARY BODY FROM THE COMPARATIVE ASPECT

In the mammals which have been investigated for the purpose of this paper, the nuclei may be divided into three groups which are common to all: medial, lateral and dorsal.

(*a*) *The medial group of nuclei*

The main part of the mamillary body is nearly always formed by this group, and, in regard to the structure of its individual nuclei in the different orders, it shows the greatest variations. The thalamo-mamillary tract terminates in it.

In the bat and in rodents this nuclear group shows a similar structure, consisting of an anterior paired nucleus (*ma*), a medial unpaired nucleus (*mm*), and very clearly developed basal and intermediate nuclei (*mb* and *mi*). In all mammals the basal nucleus lies ventral or ventro-lateral to the medial nucleus, and is composed of smaller and less closely packed cells than the medial. The intermediate nucleus in all mammals shows the same cellular type as the basal nucleus, though its cells are more closely packed. It always arises as a narrow

[1] There is good reason for most authors (Greving, Grünthal and others) identifying Malone's n. intercalatus with the lateral mamillary nucleus as described here. This supposition, however, does not accord with Malone's description and drawings.

band, and, when it is well developed, surrounds the medial nucleus on its lateral side. In the insectivores the anterior nucleus has reached a high development. In the mole it is especially well marked, but not to the degree seen in the hedgehog. It may be inferred, though probably it is not absolutely certain, that the anterior mamillary nucleus in insectivores is homologous with the element of the same name in the bat and rodents.

In the hedgehog and mole the paired medial nucleus is very well developed. Though the basal and intermediate nuclei are undoubtedly present, they are very much less differentiated than in rodents and bats.

In carnivores a modification in the structure of the medial nuclear group can be observed. In the polecat the anterior mamillary nucleus may still be defined quite easily, but in the dog it cannot be clearly separated from the medial nucleus.

In addition, the unpaired nucleus disappears in carnivores as well as in the higher mammals. In its place a large paired nucleus develops, which in the polecat is most probably homologous with the unpaired nucleus of rodents, insectivores and bats. In the polecat the nucleus is large, whilst in the dog, where as already stated it cannot be separated with certainty from the anterior nucleus, it already forms the chief part of the mamillary body.

In carnivores the basal and intermediate nuclei (especially the latter) show a regression in development, so that the characteristic appearance of the mamillary body, in rodents, bats and (partly) in insectivores, is altered appreciably.

In the dog, appearances resembling those seen in the monkey and man are found. The cell structure of the mamillary body in the polecat forms a link between the lower and higher mammals.

In the monkey, an anterior mamillary nucleus cannot be defined. Perhaps the condensation of nerve cells on the dorso-medial and partially on the lateral margins of the medial mamillary nucleus may be taken as representing remnants of the independent anterior mamillary nucleus. The similar position of the anterior mamillary nucleus to the medial nuclei of the polecat would favour this assumption.

A further regression has occurred in the basal and intermediate nuclei, the largest nucleus in the monkey being represented by the medial mamillary nucleus.

In man, conditions similar to those in the monkey are found. The medial nucleus is large, the basal nucleus is much reduced, and only traces of the intermediate can be seen, whilst nothing can be found to indicate the anterior nucleus. Thus, from what has been stated, it is probable that in man and monkey the medial nucleus corresponds to the combined anterior and medial nuclei of rodents, insectivores and bats. In the dog this fusion can be seen taking place, but in the polecat they are still readily distinguishable from one another.

In all mammals the basal and intermediate nuclei can be distinguished

throughout, but they show a definite regression from the carnivores upwards.

Attention may be drawn to the staining reaction of the medial nuclear group. In insectivores, carnivores, monkeys and man the ground substance, as a rule, takes on a reddish tinge with cresyl violet, but in the rodent and the bat this is not so constant or so marked. The ground substance of the medial nucleus always stains the deepest, and that of the anterior, basal and intermediate nuclei less deeply. This fact can be observed from the photograph where the ground substance of the medial nuclear group appears a uniform grey.

Investigations regarding the function and connexions of the whole medial group of nuclei in rodents (for instance in the rabbit which is commonly used for laboratory purposes) do not allow reliable conclusions to be inferred regarding the fibre connexions of this nuclear group in man, because, in the rabbit, this group consists mostly of those nuclei which are only feebly developed in man. On the other hand, it may be assumed that the medial nuclear group of the dog, and particularly that of the monkey, subserves the same functions, and therefore has similar fibre connexions, as in man.

(*b*) *The lateral group of nuclei*

This consists of a single nucleus, the lateral mamillary nucleus. Throughout the mammalian scale this shows a typical shape and position. It is always situated lateral to the medial group, and ventro-lateral to the fornix. Its shape is generally oval or round, and its cells are always the largest and most deeply staining of the whole mamillary body. In the series of animals investigated it shows neither a complete regression nor a differentiation.

In bats and rodents it is very clearly formed, and in the rabbit it produces a macroscopically visible swelling in the hypothalamus.

In insectivores it is remarkably indistinct; in the hedgehog it is present no doubt, though feebly developed, whilst in the mole it cannot be defined as a distinct nucleus. As I have already mentioned, when describing the mamillary body of the mole, I consider that the scattered nerve cells found ventro-lateral to the fornix show distinct characteristics which allow them to be considered as the homologue of the lateral nucleus.

In the carnivores the lateral nucleus is very well developed, though in the dog it can only be followed for a short distance. In the monkey its shape and position are typical. In man it is clearly developed but is divided into two bands. From its typical position near the fornix it can be inferred that it is closely associated with that structure, confirmation being found in the fact that it generally appears when the fornix can no longer be traced as a distinct bundle (at least in Nissl preparations). Its small size, however, makes it most improbable that it receives all or even the majority of the fibres of the fornix. In fact, degeneration experiments have proved the lateral nucleus to be independent at least of the majority of the fibres of the fornix.

Within the whole mammalian scale the elements included under the term lateral mamillary nucleus are no doubt homologous, and the function of the nucleus can be assumed to be the same in all mammals. The shape, size, density and cell processes of the nerve cells of this nucleus are prone to great variations in the animals investigated.

For experimental operations on the lateral mamillary nucleus, the rodents, and especially the rabbit, seem to be the most suitable. The lateral nucleus of the rabbit is particularly large, sharply demarcated, and relatively distant from the other nuclei.

(*c*) *The dorsal group of nuclei*

The supramamillary and perimamillary nuclei comprise this group and show a close topographical relationship to the mamillary body. It cannot be stated with certainty how far they are functionally related to it. In all mammals (including man) the dorsal nuclear group can easily be defined, but the development of the component nuclei varies.

In the bat, the supramamillary nucleus and the perimamillary nucleus are both very well developed, and this dorsal nuclear group is particularly well differentiated in the insectivores. Both these nuclei in the hedgehog and the mole are large and broad. In rodents, the supramamillary nucleus is well developed, but the perimamillary is only poorly so, being best developed in the mouse, poorly in the squirrel and poorest in the rabbit.

In the carnivores also, the dorsal nuclear group is well developed, more so in the polecat than in the dog. The monkey shows a moderately developed supramamillary nucleus and an easily discernible perimamillary nucleus. In man the supramamillary nucleus can readily be seen, but only extends for a short distance, whilst the perimamillary nucleus is very feebly developed. In dog, monkey and man this group is interrupted by the thalamo-mamillary tract.

The fact that I found the supramamillary nucleus present in man contradicts the statement of Grünthal (1933) that the absence of the supramamillary nucleus should be considered a human feature.

(*d*) *The volume of the nuclei of the mamillary body*

Examination of the mamillary body from a phylogenetic point of view has shown that some nuclei of the lower mammals are only feebly developed in the higher mammals. Thus the question arises whether the mamillary body, as a whole, has undergone a reduction in the course of evolution, or whether single nuclei increase or, at least, do not diminish in size whilst others are reduced. A superficial examination of this series seems already to favour the second assumption. In the higher mammals the medial nucleus is so large that it is probably more correct to speak of a progressive rather than a regressive development.

This question, however, can be answered accurately only by determining

the volume of the single nuclei, and it is of special interest in so far as Grünthal maintains that the hypothalamus is subjected to a regressive development in the ascending animal scale. This view Le Gros Clark (1936) does not share, pointing to the well-developed medial nuclei in man.

The volume of the three nuclear groups, medial, lateral and dorsal, whose equivalence in the different mammals seemed to me beyond doubt, has been measured separately, and compared with the volume of the thalamus and hypothalamus.

The thalamus is taken to consist of (*a*) the epithalamus (ganglia habenulae, taenia thalami),[1] (*b*) the metathalamus (corpus geniculatum mediale and laterale), and (*c*) the thalamus proper or dorsal thalamus (prethalamic,[2] anterior, lateral, medial, ventral, reticular, central, posterior and prebigeminal nuclear complex (M. Rose)). According to M. Rose the following purely topographical nuclear complexes are implied when speaking of the hypothalamus: dorsal, medial, lateral, ventral, suprapeduncular and mamillary. The substantia nigra has not been included.

The boundary between the thalamus and hypothalamus is not always sharply defined, but the doubtful zone is relatively narrow and occurs infrequently.

Regarding the demarcation of the three nuclear groups of the mamillary body, the sharp outline of the dorsal nuclear group is often artificial whilst the lateral group in insectivores, particularly in the mole, can only be determined approximately.

The volume of the nuclei on each side has been ascertained, and in all animals the volume of the ventricle has also been determined.[3]

Table I

	Volume of the hypothalamus in c.mm.	Volume of the thalamus in c.mm.	Ratio: $\frac{\text{hypothalamus}}{\text{thalamus}}$
Bat	5·0	6·3	1:1·3
Hedgehog	51·2	61·4	1:1·2
Mole	12·4	23·5	1:1·9
Mouse	10·2	14·1	1:1·4
Rabbit	71·3	176·1	1:2·5
Squirrel	84·3	192·2	1:2·3
Polecat	66·0	192·3	1:2·9
Dog	188·7	703·7*	1:3·7
Monkey	273·5	880·0	1:3·2
Man (3 months old)	913·5	4590·0	1:5·0

* The thalamic volume of the dog is a little greater than here indicated because, owing to the technical difficulties, the most posterior parts of the thalamic nuclei could not be reconstructed.

From Table I it can readily be seen that in the ascending animal scale the volume of the thalamus shows a regular increase compared with that of the

[1] The epiphysis has not been included.

[2] Except in the thalamic volume of dog and man.

[3] Embryological studies on the rabbit have since convinced me that the prethalamic nuclear complex does not belong to the thalamus but to the hypothalamus. This nuclear group, however, being rather small, this statement is of no particular importance for the total volume of the parts of the brain measured here.

hypothalamus. Whereas in the bat the ratio of the thalamic volume to that of the hypothalamus is only 1·3, it amounts to 2·5 in rodents, 3·7 in carnivores and as much as 5·0 in man.

Table II

	Volume of the total grey matter of the mamillary body in c.mm.	Ratio: $\frac{\text{mamillary body}}{\text{hypothalamus}}$
Bat	0·23	0·046:1
Hedgehog	1·62	0·032:1
Mole	1·92	0·155:1
Mouse	0·52	0·051:1
Rabbit	5·01	0·070:1
Squirrel	3·22	0·038:1
Polecat	4·99	0·076:1
Dog	15·67	0·083:1
Monkey	7·97	0·029:1
Man (3 months old)	38·02	0·042:1

From Table II it can be seen that the ratio of the volume of the mamillary body to that of the hypothalamus shows rather marked variations. Thus in the mole the relative volume of the mamillary body is particularly great. Similarly, the rabbit and carnivores show a relatively large mamillary body. It may also be pointed out that in both monkey and man the ratio is relatively small, and in view of the fact that the mamillary body in both is well developed one is led to suppose that there has been no relative decrease in the grey matter of the hypothalamus. Man shows about the same ratio as the bat and squirrel, the smallest ratio of the investigated animals being in the monkey.

Table III. *Volume of the nuclear groups as percentage of volume of whole mamillary body*

	Dorsal	Medial	Lateral
Bat	47·8	47·8	4·4
Hedgehog	51·9	42·5	5·6
Mole	40·6	54·8	4·6
Mouse	26·9	67·3	5·8
Rabbit	23·1	65·3	11·6
Squirrel	26·4	70·2	3·4
Polecat	30·7	64·7	4·6
Dog	24·0	70·8	5·2
Monkey	39·1	54·3	6·6
Man (3 months old)	13·3	80·6	6·1

From Table III it can be seen that in almost all mammals the lateral nuclear group has an approximate constant value, the variations in volume relative to the whole mamillary body being rather small in all except the rabbit. This suggests that functionally the lateral nucleus is intimately related to the rest of the grey matter of the mamillary body, otherwise this constant ratio is difficult to understand. Topographically, too, this connexion can be recognized in rodents and in the bat. In monkey and man, where the medial nuclear group is separated by a medullary capsule from the lateral nucleus, the connexion is less conspicuous.

In addition, from Table III it can be seen that as one ascends the animal

scale the volume of the medial nuclear group increases at the expense of the dorsal group. In the bat and insectivores the volume of these two groups is equal, whereas in the hedgehog the dorsal group has an even greater volume than the medial. In rodents and in the polecat the volume of the medial nuclear group amounts to more than twice that of the dorsal, whilst in the dog it is almost three and in man six times the size. In the monkey, however, it amounts to only one and a half. Thus the medial nuclear group not only shows a marked increase as a whole, but this increase is exclusively due to the increase of the medial nucleus. The basal and intermediate nuclei, which in the bat, insectivores and rodents are large and can be estimated to amount to about one-half of the total volume of the medial group, form only a fraction of the volume in the dog, monkey and man.

The comparison of the volume of the different nuclear groups of the mamillary body with that of the thalamus or hypothalamus is given in Tables IV and V.

Table IV. *Volume of the lateral group of nuclei (percentage of the hypothalamic volume)*

Bat	0·20	Squirrel	0·13
Hedgehog	0·17	Polecat	0·34
Mole	0·72	Dog	0·43
Mouse	0·28	Monkey	0·19
Rabbit	0·81	Man (3 months old)	0·25

From Table IV it may be seen that the lateral nuclear group does not show any great variations except in the mole and the rabbit. It has already been shown (Table II) that the mole has a large mamillary body, whilst its lateral nucleus is of average relative volume (Table III). The rabbit, on the other hand, combines an average-sized mamillary body with a relatively large lateral nucleus. As a rule, the lateral nuclear group seems to have a fairly constant volume not only relative to the mamillary body but also to the entire hypothalamus. This would tend to favour the assumption that the lateral nuclear group has no connexions with the thalamus (or, at least, not with those parts that show a progressive development in higher mammals).

With the medial nuclear group the relationship is different, owing to its connexions with the thalamus, and one assumes that there is a definite ratio between the volumes of the grey matter of these two structures.

Table V. *Volume of the dorsal and medial nuclear groups (percentage of the thalamic volume)*

	Medial	Dorsal
Bat	1·70	1·70
Hedgehog	1·11	1·40
Mole	4·50	3·30
Mouse	2·48	0·98
Rabbit	1·86	0·65
Squirrel	1·17	0·44
Polecat	1·67	0·79
Dog	1·57	0·53
Monkey	0·49	0·35
Man (3 months old)	0·68	0·10

From Table V it is seen that in spite of a relative increase in the ratio of the volume of the thalamus to that of the hypothalamus as shown in Table I, the volume of the medial nuclear group, expressed as a percentage value of the volume of the thalamus, differs only slightly in the mammals, apart from monkey and man, and also the mole. That is, the values show no decline until the primates are reached. But even in man this value is only 2·5 times smaller than in the bat.

In man, however, the thalamus is five times the volume of the hypothalamus, whereas in the bat it is only 1·3. Furthermore, in the hedgehog the percentage value of the medial group is not twice that of man; its thalamus, however, is only 1·2 times the size of its hypothalamus. The dog and polecat, in which the thalamus is about three times the volume of the hypothalamus, show the same (or even higher) percentage values for the medial nuclei in comparison with the bat and hedgehog, whose thalamus:hypothalamus ratio is 1·2. The monkey shows a great relative decrease in the percentage value of the medial nuclear group.

As a rule, however, it may be assumed that the volume of the medial nuclear group increases as the thalamus develops, although this increase, as is to be expected, does not run strictly parallel with the phylogenetic increase in volume of the thalamus as a whole. This statement brings out another fact. One can speak of the medial nuclear group as probably showing a progressive development in man and higher mammals; it is certainly not reduced.

Similarly, it may be inferred that the lateral nuclear group is probably not reduced, as it shows a constant relationship to the mamillary body (see Table III).

Unlike the medial nuclear group, the figures in Table V show clearly that the percentage value of the volume of the dorsal nuclear group, calculated in relation to the thalamic grey matter, shows a decrease rather in excess of what might be expected in view of the relative increase of the thalamus. This suggests that the dorsal nuclear group has no connexions with the thalamus.

In man it seems to have undergone a distinct reduction. It cannot be seen with sufficient certainty from the percentage values whether it is also reduced in the higher mammals generally. In rodents and carnivores, however, the dorsal nuclear group appears to have been reduced.

SUMMARY

In all mammals the mamillary body is well developed. Three groups of nuclei can be distinguished: medial, lateral and dorsal.

The medial group consists of nuclei of which some are better developed in the lower mammals, others in the higher.

In the higher mammals the medial nucleus, probably equivalent to the medial and anterior nuclei of the lower mammals, is better developed, whereas the basal and intermediate nuclei show a poorer development.

In the higher mammals the volume of the medial nuclear group, as a whole, shows a relative increase in association with that of the thalamus, a relationship that becomes obvious by determining their respective volumes.

The lateral group of nuclei in all mammals bears a fairly constant relation to the volume of the mamillary body as a whole, as well as to the whole hypothalamus. The lateral nuclear group seems to have no connexion with the thalamus.

The dorsal nuclear group, very well developed in lower mammals, undergoes a reduction in man and probably in the other higher mammals as well, whilst its volume decreases relative to that of the mamillary body, hypothalamus and thalamus. It is probably not connected with the thalamus.

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ABBREVIATIONS IN THE FIGURES

cs, corpus subthalamicum; *F*, fornix; *i*, n. infundibularis; *ma*, n. mamillaris anterior; *mam-inf.* n. mamillo-infundibularis; *mb*, n. mamillaris basalis; *mc*, n. mamillaris centralis; *mi*, n. mamillaris intermedius; *ml*, n. mamillaris lateralis; *mm*, n. mamillaris medialis; *perim*, n. perimamillaris; *pl*, n. hypothalami posterior lateralis; *pp*, pes pedunculi; *ppl*, n. hypothalami posterior post-lateralis; *pre*, n. praemamillaris; *psi*, n. medialis postremus hypothalami; *sma*, n. supramamillaris; *sp*, suprapeduncular nuclear complex; *VA*, bundle of Vicq d'Azyr.