

## OBSERVATIONS ON THE OLFACTORY APPARATUS AND THE TELEENCEPHALON OF *ANOLIS*, A MICROSMATIC LIZARD\*

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Most reptiles have a well-developed olfactory and vomero-nasal apparatus; in only one order, the Crocodylia, is there a complete absence of the vomero-nasal component. Some of the Lacertilia, however, have been described as 'microsmatic', including the anoles which are a group of essentially arboreal New World lizards.

The diencephalon and midbrain of *Anolis carolinensis* were described in detail by Huber & Crosby (1933) but, so far as we are aware, there is no comprehensive description of the telencephalon. Occasional references to certain features of this part of the brain were made by Kappers, Huber & Crosby (1936), including a statement that the olfactory bulbs 'are small masses, conical in outline and situated at the base of the hemisphere, overlapped by its frontal pole'. Crosby & Humphrey (1939*a, b*) placed *Anolis* with certain other iguanids in a group of 'lizards with no accessory olfactory bulbs'; while in a more recent publication by Pratt (1948) it is held that the epithelium of the vomero-nasal organ in *A. alligator* is 'completely non-sensory', and that of the nasal sac 'almost non-sensory' in nature.

Several accounts of the normal anatomy of the typical lacertilian forebrain are already available, and in spite of differences in the species studied, of the various techniques adopted and of conflicting terminologies and interpretations, there emerges a remarkably constant pattern of forebrain morphology. However, since olfactory connexions have been thought to play an important part in determining this morphology, it was decided to investigate the condition of the telencephalon and olfactory organs in specimens of *Anolis* which recently became available. As will be seen, some of our findings differ fundamentally from those of the earlier writers.

### MATERIAL AND METHODS

Specimens of three species of *Anolis* were available, *A. lineatopus*, *garmani* and *grahami*. *A. garmani* is considerably larger than either of the other two species, but no other difference relevant to the present investigation was found between any of them.

The animals were received alive. For microscopical examination they were killed by decapitation and the brains prepared either by Nonidez's (1939) silver impregnation technique or by a Nissl method (thionine) following fixation in formol-acetic-alcohol. In each case complete series of sections were cut from paraffin blocks.

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The following series were available for study of the normal brain:

Series no.	Species	Stain	Plane of section	Thickness ( $\mu$ )
A 7	<i>A. lineatopus</i>	Thionine	Transverse	12
A 6	<i>A. lineatopus</i>	Thionine	Sagittal	10
A 3*	<i>A. garmani</i>	Thionine	Sagittal	15
A 1	<i>A. lineatopus</i>	Nonidez	Transverse	7.5
A 4	<i>A. lineatopus</i>	Nonidez	Transverse	10
A 5	<i>A. lineatopus</i>	Nonidez	Sagittal	10
A 2	<i>A. garmani</i>	Nonidez	Transverse	10

\* In this specimen the olfactory bulbs and peduncles were sectioned separately in the horizontal plane and stained with thionine.

In an attempt to obtain material showing degeneration effects, olfactory bulbs were removed in three specimens which were prepared as follows:

Series no.	Species	Operation	Survival time (days)	Stain	Plane of section	Thickness ( $\mu$ )
A 8	<i>A. grahami</i>	Unilateral bulbar ablation	2	Nonidez	Transverse	10
A 12	<i>A. lineatopus</i>	Bilateral bulbar ablation	2	Nonidez	Transverse	10
A 9	<i>A. grahami</i>	Bilateral bulbar ablation	14	Nonidez	Transverse	10

For examination of the peripheral olfactory apparatus, including the vomero-nasal organ, transverse serial sections were cut through the whole snout (after decalcification) in specimens A1, A2, A4, A6 and A9. The sections from A2, A4, A6 and A9 were stained with haematoxylin and eosin, and those from A1 by de Castro's method. The latter gave no information about the nasal organs which was not obtainable from the haematoxylin and eosin preparations.

For comparative purposes we had a large number of series of sections through the brains of *Lacerta viridis* and *L. vivipara*, cut in all three primary planes and stained by both Nissl and Nonidez methods. Other lacertilian brains available included transverse Nonidez series of *Anguis fragilis* and *Aristelliger praesignis* and Bielschowsky series of *Gecko verticellatus* cut in all three primary planes. We had also the snouts of several specimens of *Lacerta viridis*, cut serially in the transverse plane and stained with haematoxylin and eosin. They included normal specimens and several killed 10–14 days after unilateral ablation of the main and accessory olfactory bulbs.

#### PERIPHERAL OLFACTORY APPARATUS, OLFACTORY BULBS AND PEDUNCLES

##### *The nasal sac*

This is a fairly simple tubular structure and, as in lizards generally, is divisible into anterior and olfactory chambers (Pratt, 1948; Bellairs, 1949). The anterior chamber is short; it is lined by a thin stratified epithelium which extends into the anterior end of the olfactory chamber. The main part of the olfactory chamber, which contains the olfactory receptors, is usually known as the conchal zone. This term

is inappropriate in *Anolis*, for there is no sign of a concha. A thick, sensory epithelium (Pl. 1, fig. 5) is limited to the anterior half of the zone where it covers much of the roof, the entire medial wall and the medial third of the floor. Although relatively much smaller in area, this epithelium is almost identical histologically with the olfactory epithelium in *Lacerta viridis*; it is a little thinner, and Bowman's glands, though present, are small and few in number. Beneath the epithelium many bundles of olfactory nerve fibres can be seen.

#### *The vomero-nasal organ*

This structure is present but small, as noted by Pratt (1948) in *Anolis alligator*. All the usual components are present but less well-differentiated than in most lizards. Two kinds of lining epithelium can be recognized: a ciliated columnar epithelium covers the so-called mushroom body and a much thicker and entirely different epithelium covers the dorsal and medial walls (Pl. 1, figs. 2, 3). In sections stained with haematoxylin and eosin, three layers can be recognized in the latter: (i) superficially, a faintly striated eosinophilic layer containing only occasional small nuclei, (ii) a narrow layer of large, oval, vesicular nuclei which is succeeded by (iii), a much thicker layer of small and deeply staining nuclei. Bowman's glands are not present. The subepithelial tissue contains several fine nerve bundles, blood vessels and pigmented cells.

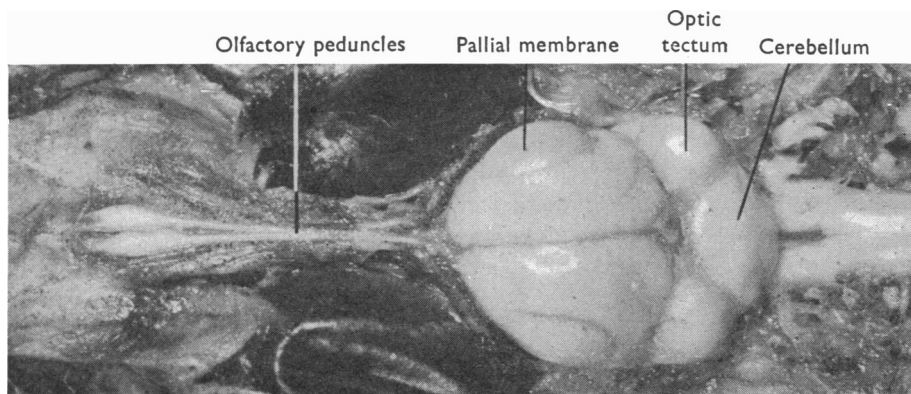
In all these features the epithelium under consideration resembles very closely the sensory epithelium of the vomero-nasal organ in *Lacerta viridis*, and indeed of many other vertebrates (Kolmer, 1927); it differs from that of the nasal cavity only in the greater thickness of the third layer, and in the absence of Bowman's glands. The unequivocal identification of neuro-sensory cells and supporting cells is not possible in sections stained only with haematoxylin and eosin, but from what is known in other forms it appears almost certain that the two superficial layers are formed by the outer parts of the cell bodies and by the nuclei of supporting cells, between which the distal processes of the neuro-sensory cells project, and that the deeper or third layer consists of the nuclei and cell bodies of the neuro-sensory cells. As will be shown, our experimental findings are consistent with this interpretation.

#### *The olfactory bulbs and peduncles*

A dorsal view of the exposed brain (Text-fig. 1) shows at once what appear to be olfactory bulbs attached to the cerebral hemispheres by long peduncles in the manner characteristic of the Lacertilia. The bulbs are small both absolutely and relatively, and under low magnification are seen to be divided by a slight depression on the medial side into larger anterior and smaller posterior portions (Text-fig. 2). It would seem natural to identify these with the main and accessory olfactory bulbs of other lizards. The peduncles are very fine, and are attached to the hemispheres just beneath the frontal poles.

The microscopical evidence is entirely consistent with the above interpretation. The anterior part of the bulb complex surrounds a centrally situated olfactory ventricle which, as in reptiles generally, is patent throughout the length of the peduncle. Superficially it is covered by a network of nerve fibres into which the

nerve bundles from under the olfactory epithelium of the nasal sac could be traced in two specimens in which the bulbs had been left *in situ*. Beneath this are the 'glomeruli', which are succeeded by neurons of medium size with well-stained Nissl substance. These are the mitral cells. Next is a layer of fine fibres and beneath it a periventricular layer of small densely packed granule cells. The fibres and the layer of granule cells extend caudally into the olfactory peduncle.



Text-fig. 1. Brain of *Anolis garmani*, *in situ*, exposed from above. ( $\times 6$ .)



Text-fig. 2. Olfactory bulbs and peduncles of *A. garmani* exposed from above, showing the subdivision into main and accessory bulbs. ( $\times 11$ .)

In the caudal part of the complex the olfactory ventricle is displaced laterally, and olfactory bulbar formation is present only in the medial wall. The deeper layers here are continuous with those more rostrally placed, but there is a distinct break in the glomerular layer at a level corresponding to the depression visible externally. The nerve bundles found in relation to the epithelium of the vomero-nasal organ can be traced caudally until they join to form a single nerve which enters this caudal part of the olfactory bulb complex. There is no doubt therefore that it represents a typical accessory olfactory bulb as the gross appearance suggested.

The peduncles call for little comment except to note their extreme fineness. In *Anolis garmani* they are about 0.1 mm. in diameter. They contain small cells of

uncertain nature forming the periventricular grey matter, external to which are many fine fibres, running rostro-caudally. These are presumably the axons of mitral and other cells in the bulbs: among them are a few scattered cells most of which are probably neuroglial.

#### *Effects of bulbar ablation*

In one specimen (A9) it was possible to examine the effects of bilateral removal of both main and accessory bulbs on the peripheral olfactory apparatus. It was found that 14 days after the operation many of the small cells had disappeared from the deepest layer of the epithelium; this loss was more conspicuous in the thicker epithelium of the vomero-nasal organ (Pl. 1, figs. 3, 4) than in the olfactory epithelium of the nasal sac (Pl. 1, figs. 5, 6), but was quite definite in both. It is interpreted as a retrograde degeneration of neuro-sensory cells in both situations, and is very similar to the secondary degeneration described by Clark & Warwick (1946) in the olfactory epithelium of the rabbit following bulbar ablation; such degeneration does not appear to have been recorded previously in the vomero-nasal organ.

Almost precisely similar changes were seen in the olfactory and vomero-nasal epithelia in the specimens of *Lacerta viridis* examined 10–14 days after unilateral bulbar ablation (Pl. 1, fig. 1). In this species a basal layer of cells, next to the sub-epithelial connective tissue, was unaffected; these may be additional supporting cells, possibly similar to the basal cells mentioned by Clark & Warwick (1946) as persisting in the olfactory epithelium of the rabbit 8 weeks after bulbar ablation.

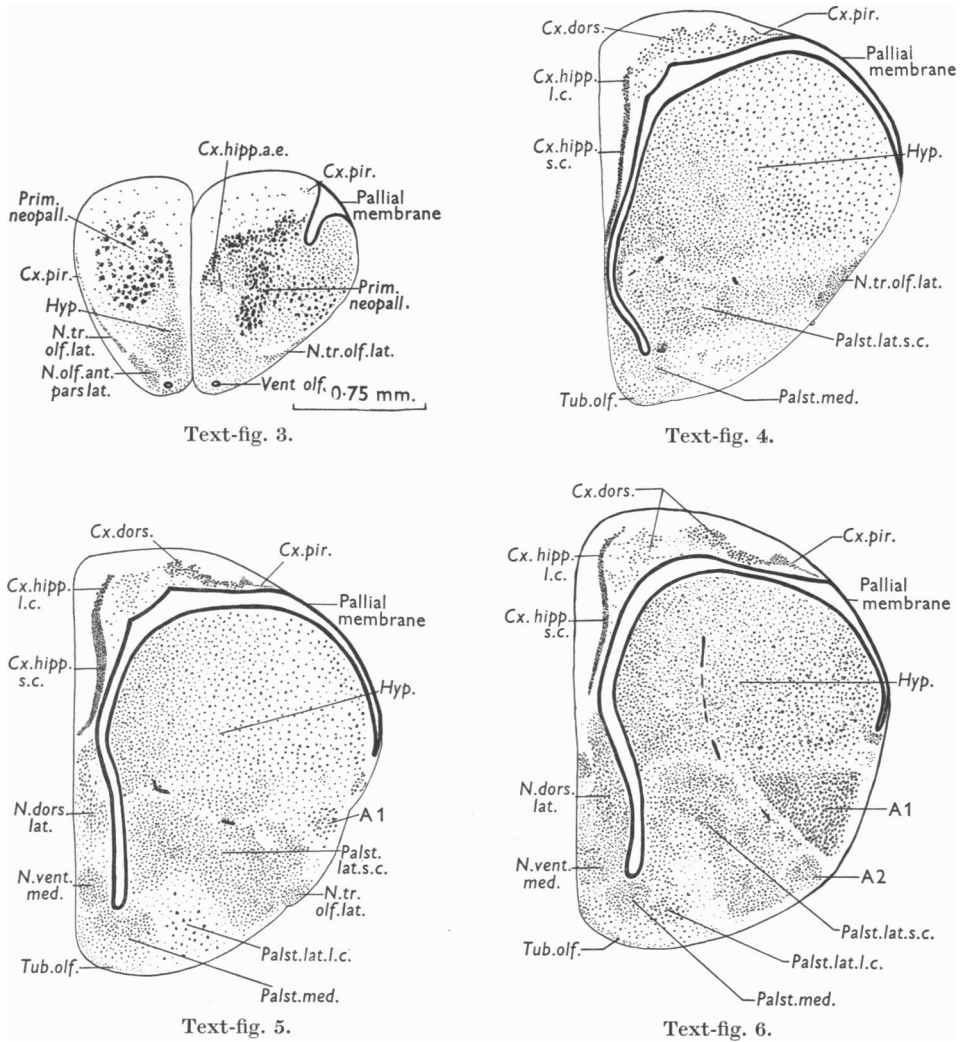
It is reasonable to conclude that in the species of *Anolis* which have been examined the nasal sac and the vomero-nasal organ both contain typical neuro-sensory epithelium and are connected with main and accessory olfactory bulbs respectively. The epithelium and the olfactory bulbs are atypical only in so far as they are reduced in extent, both absolutely and relatively, in comparison with their development in most Lacertilia. There is no reason to doubt that these organs are functional, nor anything to suggest that their functions differ from those of corresponding organs in other reptiles.

#### THE CEREBRAL HEMISPHERES

The general form of the hemispheres is shown in Text-fig. 1. They are foreshortened in comparison with the usual lacertilian condition, and more genuinely hemispherical in shape; in this respect they are somewhat reminiscent of the crocodilian forebrain. The point of junction with the olfactory peduncles is overlapped by the frontal pole and is marked by a small conical projection which represents the anterior olfactory nucleus (this is not visible in Text-fig. 1). The crescentic line seen on the dorso-lateral surface in the photograph marks the dorsal and caudal margins of a region of extreme thinning of the pallium, which is reduced in the area enclosed by the line to a transparent membrane. A thinning in this situation, leading to the formation of a 'pallial membrane', appears to be unique among the reptiles so far described. The strio-amygdaloid complex (including the so-called hypopallium) is relatively very large in *Anolis*, and part of its ventricular surface can be seen through the pallial membrane. The general relationships of pallial and basal

structures and the pallial membrane are best seen in transverse sections, e.g. Text-figs. 3-8.

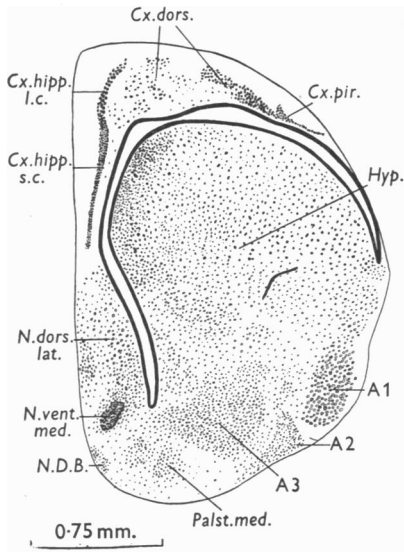
Surface fissures of comparative morphological significance are very poorly developed. On the ventro-lateral surface of the hemisphere there is a constant



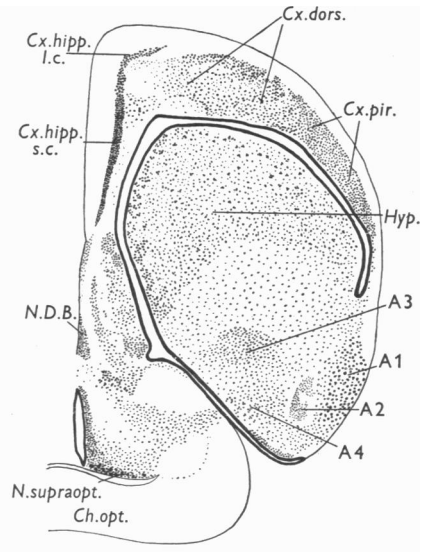
Text-figs. 3-6. Scale drawings of transverse sections through a cerebral hemisphere of *Anolis lineatopus* stained with thionine. For meaning of abbreviations used in all text-figures see p. 307.

small depression which may represent the caudal end of the endorhinal or amygdaloid fissure. Medially, it is only in the region dorsal to the supraforaminal part of the paraterminal body (or septum) that there is any suggestion of a fissura limitans hippocampi, although in other reptiles such a fissure seems to be a constant finding (de Lange, 1911; Johnston, 1915; Goldby, 1934).

Two other points of interest are shown in Text-fig. 1. The very large cerebellum extends rostrally almost to touch the caudal poles of the cerebral hemispheres, and associated with this there is a marked lateral displacement of the optic lobes.

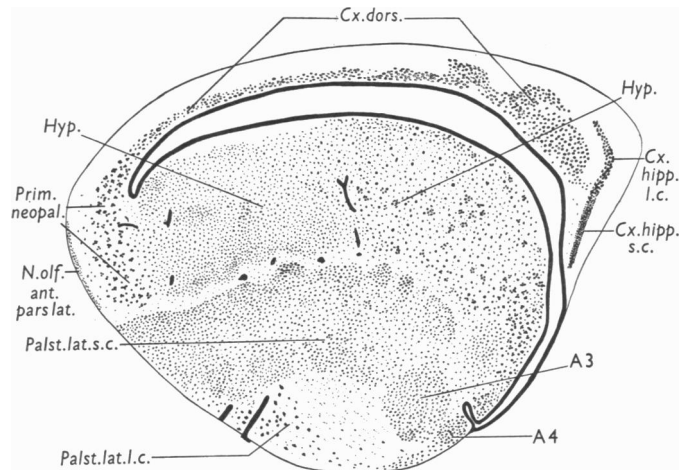


Text-fig. 7.



Text-fig. 8.

**Text-figs. 7 and 8.** Scale drawings of transverse sections through a cerebral hemisphere of *Anolis lineatopus* stained with thionine.



Text-fig. 9.

**Text-fig. 9.** Scale drawing of a parasagittal section through a cerebral hemisphere of *Anolis garmani* stained with thionine.

#### *Anterior olfactory nucleus*

This nucleus is formed by an ill-defined zone of small round cells external to the periventricular grey matter, and appears to correspond with the anterior olfactory nucleus of other lizards such as *Lacerta* (Goldby, 1934) and *Varanus* (Crosby &

Humphrey, 1939b). In *Anolis* it shows cellular condensations dorsally and laterally. The lateral condensation is found to be continuous caudally with two cellular strands on the surface of the hemisphere. The first of these is a row of small, oval cells extending dorso-laterally along the rostral and dorsal margin of the pallial membrane (Text-figs. 3, 4, *Cx.Pir.*), forming the anterior extremity of what appears to be an extremely rudimentary piriform cortex. The second is a collection of cells which can be traced caudally in association with the lateral olfactory tract; in some sections these appear to form a definite interstitial nucleus of the tract, in others they appear as an ill-defined collection of cells difficult to distinguish from those of the underlying palaeostriatum lateralis.

Dorsally the anterior olfactory nucleus has a somewhat tenuous connexion with the anterior extremities of the dorsal and hippocampal cortices, and ventrally it extends as a few small scattered cells overlying the palaeostriatum and forming a very indefinite olfactory tubercle. Medially, the nucleus is represented by only a few scattered cells which are replaced caudally by the anterior end of the paraterminal body. In brief, the anterior olfactory nucleus of *Anolis* is similar to that of other lizards, but is relatively much smaller.

#### *Strio-amygdaloid complex*

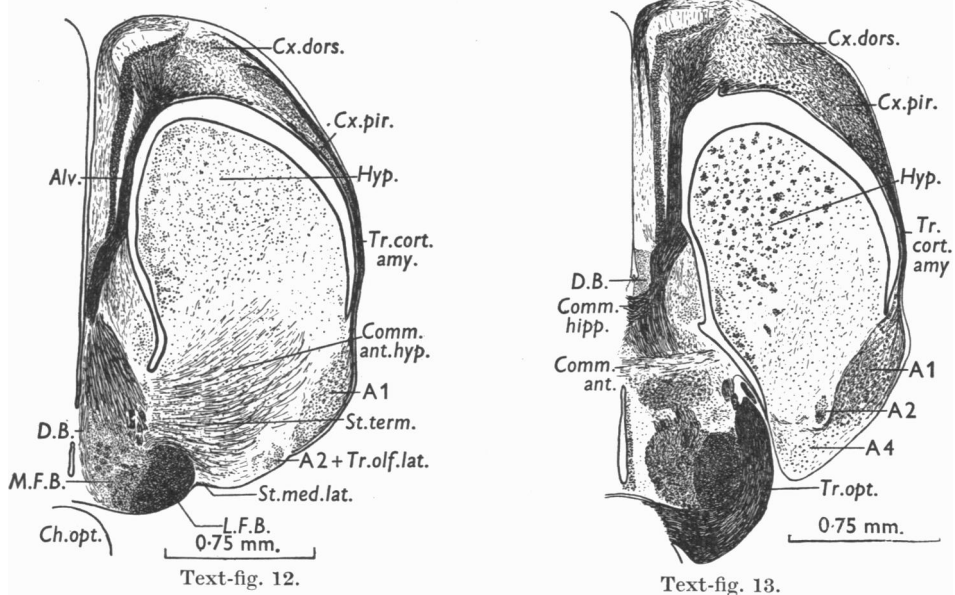
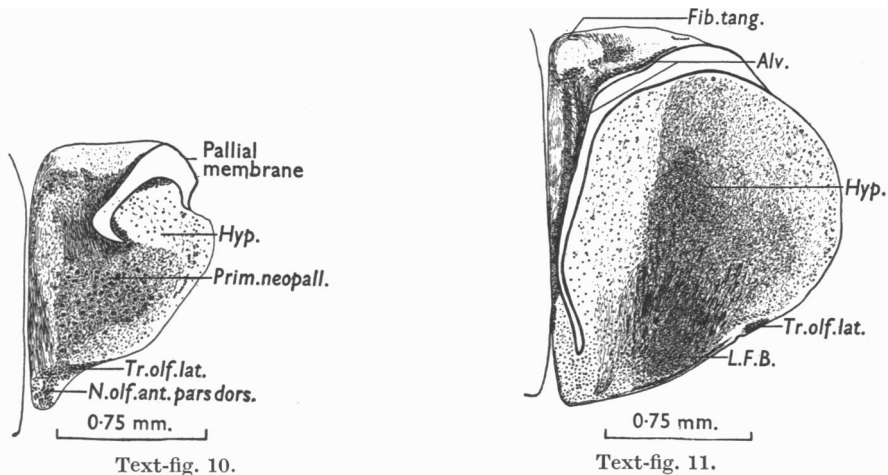
A characteristic feature of the reptilian hemisphere is the large and complex ventro-lateral cell mass which invaginates the lateral ventricle. As the name indicates, this mass develops in the region of the hemisphere wall which is occupied by the corpus striatum and amygdaloid nuclei in mammals. There is considerable uncertainty whether some of the components which can be distinguished in reptiles have any mammalian counterparts, and as a result a cumbersome and inconsistent terminology has grown up in reference to this part of the brain. This terminology was reviewed in detail by Goldby (1934) and by Kappers *et al.* (1936). To clarify the description which follows, it will suffice here to summarize the principal components.

On the basis of more or less well-defined cellular condensations three main components are generally recognized; they are known respectively as the palaeostriatum, the hypopallium and the amygdaloid complex. The palaeostriatum is found rostrally and ventrally and is usually divided into medial and lateral parts, of which the medial extends below the lateral ventricle into the septum as a nucleus accumbens. It lies immediately beneath the surface of the brain in the region of the olfactory tubercle, and its cells are scattered among the fibres of the forebrain bundles. The hypopallium forms the dorsal and rostral part of the region and is usually the largest of its three main components. It commonly appears as a cellular cap immediately beneath the ependyma over the convex dorsal and medial surface. Since it appears to be connected with terminal fibres of the lateral forebrain bundle, it is sometimes grouped with the palaeostriatum as a composite functional unit, the whole being referred to as the 'corpus striatum'.

The amygdaloid complex is situated caudally and has characteristic connexions with the lateral olfactory tract and stria terminalis system of fibres. A 'hypopallium posterior' has been identified in many reptiles and interpreted by a number of authors (e.g. Goldby, 1934) as a part of the amygdaloid complex. When well



developed, as in many lizards and snakes, it resembles in cellular arrangement and certain topographical relationships the hypopallium described above (to which the term 'anterior' has been applied). Its main connexion, however, is with the



Text-figs. 10-13. Scale drawings of transverse sections through a cerebral hemisphere of *Anolis lineatopus*. Nonidez's silver impregnation method.

lateral olfactory tract and it seems better to refer to it as one of the amygdaloid nuclei than to use a term which implies essential similarity to the hypopallium, as described above, of which there is little evidence. Other terms have been applied to this structure, e.g. 'nucleus sphaericus' and more recently 'posterior amygdaloid nucleus' (Curwen, 1939).

In *Anolis* all three main components of the strio-amygdaloid complex can be readily identified. As a whole it is relatively much larger than in most lizards, due principally to the great size of the hypopallium. Other features are as follows: for the most part only those in which *Anolis* differs from at least the majority of lizards are described.

(a) *Palaeostriatum* (Text-figs. 4-6 and 9). In Nissl preparations this is found to be divisible into the usual medial and lateral parts, related to the rostral ends of the medial and lateral forebrain bundles respectively, although in silver impregnated sections the separation of the medial from the lateral bundles in this part of the hemisphere is somewhat arbitrary. The lateral part of the palaeostriatum is further differentiated from the medial by the presence of a dense network of fibres among its cells (Text-fig. 11); it would appear, therefore, to be the main field of distribution for the lateral forebrain bundle, a characteristic which it may share with the overlying rostro-lateral part of the hypopallium.

Most of the cells of the palaeostriatum are small, but there is a conspicuous group of large deeply staining neurons of the motor type ventrally situated in its lateral sub-division (Text-figs. 5, 6 and 9). These cells may give rise to descending fibres in the lateral forebrain bundle, and they suggest comparison with the large cells of the globus pallidus in mammals.

(b) *The hypopallium*. This occupies rather more than the dorsal half of the whole strio-amygdaloid complex. Nissl preparations show that the cell pattern varies to some extent within the hypopallium, although there are no clear-cut subdivisions. Thus, in its caudal part there is a tendency for cells to be arranged in clumps near the ventricular surface (Text-figs. 8, 9 and 13), while rostrally the cells are smaller and more closely packed medially than they are laterally (Text-figs. 4-7). The rostro-lateral part of the hypopallium is also characterized by a dense intercellular network of fibres (Text-fig. 11), which in the material available seems to consist partly of terminal fibres from the lateral forebrain bundle and partly of short fibres connecting with the underlying palaeostriatum. In the rostro-medial and caudal parts of the hypopallium very few pericellular fibres are demonstrable, at least by the methods we have used; a few fibres enter the rostro-medial part from the palaeostriatum and perhaps from the lateral forebrain bundle, but caudally the only extrinsic connexion appears to be through small fibre bundles which converge towards the anterior commissure.

(c) *The amygdaloid complex*. This complex is fairly large in *Anolis* and shows more definite subdivisions than in many lizards, e.g. *Lacerta*, *Anguis* and the geckos. Four nuclei can be distinguished which will be called A1, A2, A3 and A4 in order to avoid suggestions of homology which might be implied if more descriptive terms were used.

Nucleus A1 is conspicuous and well defined. In the rostral part of the complex, it has the shape of a wedge between the hypopallium above and the caudal part of the palaeostriatum lateralis below (Text-fig. 6); at more caudal levels it assumes a distinctly oval outline in transverse sections (Text-figs. 7, 8, 12 and 13). Its cells are of medium size and multipolar; they stain deeply, and are surrounded by a dense network of fibres. The nucleus is bounded on its ventral and lateral sides by a thin capsule of fibres which converge with some of the intercellular fibres to form

a prominent tract which can be followed dorsally along the posterior margin of the pallial membrane, apparently to connect with the caudal parts of the piriform and dorsal cortices. We have named this the cortico-amygdaloid tract (Text-figs. 12, 13). No fibres of the lateral olfactory tract or of the stria terminalis system can be traced to this nucleus, which is included in the amygdala only by reason of its topographical position.

Nucleus A2 (Text-figs. 6–8, 12 and 13) is a collection of small round cells, forming a caudal continuation of the nucleus of the lateral olfactory tract, which passes ventral and medial to nucleus A1. At its caudal extremity it forms a tiny cap of cells around the termination of the lateral olfactory tract, and this part of the nucleus is related to a small ingrowth of ependyma which invaginates the caudal surface of the strio-amygdaloid complex. Nucleus A2 is the only part of the amygdaloid complex which receives olfactory tract fibres directly; although small, and not very clearly defined, its relation to the ependyma and its connexion with the lateral olfactory tract suggest a correspondence with the larger and more clearly differentiated ‘hypopallium posterior’ of *Lacerta* and most other *Squamata*.

Nucleus A3 is a large mass of small cells immediately caudal to the palaeostriatum in the central and medial parts of the amygdaloid complex (Text-figs. 7–9). Medially it extends dorsal to the lateral forebrain bundle. It shows a dense intercellular neuropil, and the main extrinsic connexions clearly pass to the stria terminalis system and the anterior commissure (Text-fig. 12).

Nucleus A4 lies in the ventro-caudal part of the complex (Text-figs. 8, 9). Its cells are small and resemble those of A3. The connexions of this nucleus appear to be of two kinds; many fibres pass dorso-medially into nucleus A3 and thence into the stria terminalis, while others run dorso-laterally into nucleus A1 and possibly through that nucleus into the cortico-amygdaloid tract (Text-fig. 13).

#### *Paraterminal body*

The paraterminal body or septum forms the medial wall of the hemisphere between the hippocampal cortex above and the olfactory tubercle and palaeostriatum medialis below (Text-figs. 5–7). Caudally it forms a bed for the hippocampal and anterior commissures, and extends dorsal to the interventricular foramen as far as the posterior hippocampal commissure.

Rostrally the paraterminal body is very thin (Text-figs. 4, 11). Caudally it is much thicker, forming a characteristic projection into the lateral ventricle (Text-figs. 6, 7); here, as in most reptiles, it shows a subdivision into dorso-lateral and ventro-medial nuclei, the former consisting of larger cells than the latter; neither is very clearly defined. A condensation of small cells, superficially placed immediately anterior to the commissures, represents the nucleus of the diagonal band; ventrally these cells come into close relationship with the large cells of the supraoptic nucleus. Other cellular condensations form bed nuclei for the commissures.

The fibre systems related to this region are very similar to those in *Lacerta viridis*. Dorsally it receives fibres from both the superficial and deep aspects of the hippocampal cortex (tangential and alveus fibres respectively), and ventrally, particularly in its more caudal part, it is very closely related to the medial forebrain bundle.

Whether these fibre systems are afferent or efferent connexions of the para-

terminal body is not known, nor how far they may be fibres of passage, passing, for example, from the hippocampus to the medial forebrain bundle or vice versa.

The nucleus of the diagonal band is accompanied by a well-developed bundle of fibres which can be traced from a position superficial to the hippocampal cortex, above the commissures, ventrally to the region of the supraoptic nucleus. These fibres are practically identical with the medial part of the diagonal band system described by Gamble (1952) in *L. viridis*. Rostrally in the paraterminal body there are many fibres, also quite superficial beneath the pia, which run obliquely or longitudinally, and a few of these can be traced ventrally and laterally across the base of the hemisphere to the stria medullaris lateralis. They may correspond in part to the anterior olfacto-habenular tract and the ventral part of the medial olfactory tract of *L. viridis* (Gamble, 1952). In *Anolis* they do not form definite bundles, and cannot be distinguished with confidence from adjacent fibre systems.

#### *Pallium*

The most striking feature of the pallium in *Anolis* is the presence of the 'pallial membrane' (Text-figs. 3-7, 10 and 11). This consists of an outer layer of pia mater and an inner layer of flattened ependymal cells, and contains no nerve cells, neuroglia or nerve fibres. It occupies much of that region where the piriform cortical area is found in other reptiles. It is quite separate from another membranous area on the ventro-medial aspect of the hemisphere wall, caudal to the commissures, from part of which the choroid plexus of the lateral ventricle is formed. This ventro-medial membranous area is present in *Anolis* and in most, perhaps all other reptiles; it seems to represent the region of the choroidal fissure in mammals but is less completely invaginated into the ventricle.

Hippocampal and dorsal cortical areas can easily be recognized in *Anolis*. Although differing in some details from these areas in other lizards, they conform to the same general pattern, particularly to that found in *Lacerta viridis*, and show no obvious difference in extent and degree of differentiation. The piriform area is less easily recognizable; it appears to be present in *Anolis* but to be extremely rudimentary, at least in the anterior half of the hemisphere. Some additional features of these cortical areas are as follows.

(a) *The hippocampus.* The hippocampal area is situated mainly on the medial aspect of the hemisphere and shows the usual differentiation into large and small-celled parts (Text-figs. 4-9). The small-celled part extends back to form a covering to the whole posterior pole of the hemisphere; otherwise it is entirely confined to the medial surface. The large-celled part is also situated on the medial surface (Text-figs. 4-7) except for a short distance in the caudal part of the hemisphere where it extends on to the dorsal surface (Text-fig. 8). The relatively small extent of the large-celled part on the dorsum of the hemisphere is the only obvious difference in the hippocampus of *Anolis* from that of *Lacerta viridis*.

A well-developed system of tangential fibres lies superficial to the cells of the hippocampal cortex, closely applied to its small-celled part but separated from the large-celled part by a zone of neuropil. This zone which is characteristic of *Squamata* generally contains radially orientated fibres, which seem to connect the tangential fibres with the alveus system of fibres next to the ventricular ependyma. As in

other reptiles, the alveus system extends well beyond the hippocampal area and beneath the dorsal cortex.

(b) *The dorsal cortex.* This forms an almost continuous sheet with the hippocampus in the anterior part of the hemisphere, but is overlapped by the large-celled hippocampus caudally (Text-figs. 6–9). It consists of pyramidal or polygonal cells like those of the large-celled hippocampus, but slightly smaller and more irregularly scattered. At about the middle of the hemisphere (Text-figs. 5–7) it is divided into medial and lateral parts by a comparatively cell-free zone. Rostrally its cells extend ventrally in front of the lateral ventricle, forming an oval cell mass in close relation to the rostral extremity of the hypopallium (Text-fig. 9). This extension, in which most of the cells are arranged in small groups, resembles closely the so-called ‘primordium neopallii’ which has been identified in a wide variety of reptiles since the original descriptions of Crosby (1917) and Smith (1919). It is difficult, however, to find definite criteria whether it should be classified as basal or pallial. In *Anolis* the identity of cell-type with that of the dorsal cortex suggests a pallial derivation, but the cells lie in a dense network of fibres which is continued into the lateral part of the hypopallium. It may be reached directly by some fibres from the lateral forebrain bundle.

In addition to the usual relationship to the tangential and alveus fibre systems, the caudal one-third of the dorsal cortex has a strong connexion with the cortico-amygdaloid tract already described (p. 298); the precise extent of this connexion is difficult to determine since the boundary between dorsal and piriform cortices is indefinite in this region. There is no connexion with the anterior commissure, and the lateral forebrain bundle does not reach the dorsal cortex, except possibly in the region of the ‘primordium neopallii’.

(c) *The piriform cortex.* This appears to be represented in the rostral part of the hemisphere by a narrow strand of small cells along the rostral and dorsal margins of the pallial membrane, overlapping the lateral part of the dorsal cortex (Text-figs. 4, 5). It can be followed rostrally into continuity with the lateral part of the anterior olfactory nucleus, and some fibres from the lateral olfactory tract can be traced to its superficial surface. Caudally it broadens and becomes considerably thicker (Text-fig. 8), and is no longer clearly separated from the dorsal cortex. At the caudal pole of the hemisphere it becomes continuous with the small-celled hippocampus. The caudal part of the piriform cortex, like the dorsal cortex, is very closely related to the cortico-amygdaloid tract (Text-figs. 12, 13).

#### *Olfactory tracts*

In general the secondary and tertiary olfactory connexions are similar to those which have been seen in *Lacerta viridis* (Goldby, 1934), but are more difficult to demonstrate since the fibres are very fine and comparatively few in number.

From the peduncle, fibres can be traced to the anterior olfactory nucleus in which the majority collect laterally. Here they are probably reinforced by additional fibres arising in the anterior olfactory nucleus itself. These lateral fibres can be followed into a small but definite lateral olfactory tract, some fibres from which enter the neuropil overlying the strand of cells identified as piriform cortex. The

main part of the tract passes back to the amygdaloid region (Text-figs. 11, 12); it runs ventral to nucleus A1 and, leaving the surface of the brain, enters nucleus A2. Its termination in that nucleus has already been described (p. 298).

Intermediate and medial olfactory tracts can also be identified, although the fibres concerned are so diffusely spread that the term 'tract' is hardly justified. The intermediate tract is represented by fibres which pass through the ventral part of the anterior olfactory nucleus to be distributed over the surface of the olfactory tubercle. Fibres resembling both dorsal and ventral parts of the medial olfactory tract described in *L. viridis* by Gamble (1952) are present; those corresponding to the pars ventralis can be traced caudally and then laterally across the base of the hemisphere to join a very small stria medullaris lateralis. Yet other fibres in this situation may represent the so-called anterior olfacto-habenular tract, which in *L. viridis* was shown by Gamble (1952) to be a well-developed crossed secondary olfactory pathway; in *Anolis* they do not form a separate and compact bundle.

Some additional information was obtained from examining the effects of bulbar ablation. Fourteen days after removal of both bulbs fibres had completely disappeared from the olfactory peduncles, and there was some loss of fibres from among the cells of the anterior olfactory nucleus. Behind this nucleus there was marked loss of fibres from the surface of the olfactory tubercle, and possibly a slight loss from the lateral olfactory tract. It was obvious that the majority of fibres in this tract arise from cells posterior to the bulb, probably in the anterior olfactory nucleus.

Chief interest lies in the possibility of establishing the presence in *Anolis* of a crossed secondary olfactory pathway such as that which exists in *Lacerta viridis*. Unfortunately, the evidence obtained is equivocal. There seemed to be a definite loss of fibres passing across the base of the hemisphere between the stria medullaris lateralis and the surface of the paraterminal body but no loss was demonstrable in the stria medullaris itself nor in the unusually small habenular commissure.

In the two specimens allowed to survive 2 days after bulbar ablation, fragmentation of fibres could be seen superficial to the anterior olfactory nucleus and over the anterior part of the piriform cortex, thus providing support for the identification of that cortex. No further evidence relevant to this investigation could be obtained from these specimens.

#### DISCUSSION

In the three species of *Anolis* at our disposal the peripheral olfactory apparatus (including the vomero-nasal organ) does not differ fundamentally from that found in other lizards, but the term 'microsmatic' is nevertheless justified. The nasal sac is less complex than usual and the area of its lining epithelium is smaller, while a corresponding reduction in size is found in the vomero-nasal organ. At the same time, the existence of functional sensory epithelium in both chambers is established and this is clearly inconsistent with Pratt's (1948) description of the nasal sac in *A. alligator* as 'almost non-sensory' and of the vomero-nasal organ as 'completely non-sensory'. It is just possible that a species variation is responsible for the discrepancy. It seems more likely, however, that Pratt was influenced in his interpretation by an earlier assertion that no accessory olfactory bulb and only

a very rudimentary main bulb could be demonstrated in *Anolis* (Crosby & Humphrey, 1939*a, b*); certainly he related these earlier findings to his own.

In view of the relatively reduced condition of the peripheral olfactory organs it is not surprising that the olfactory bulb complex in *Anolis* should be small. Our findings, however, differ fundamentally from those of Kappers *et al.* (1936) and Crosby & Humphrey (1939*a, b*). They described the olfactory bulb in *A. carolinensis* as a minute body beneath the frontal pole of the cerebral hemisphere which 'would be missed entirely if it were not so closely associated with the main mass of the forebrain' (Crosby & Humphrey, 1939*a*). Similar findings were reported in *Phrynosoma cornutum* and *Holbrookia maculata*, and no accessory olfactory bulb was recognized in any of these lizards. By way of contrast, the three species of *Anolis* which we have studied possess both main and accessory bulbs. They lie well in front of the hemispheres, and apart from being relatively small do not differ in any essential features from the olfactory bulbs of other lizards.

It seemed that these conflicting accounts might be explained by the fact that different species of *Anolis* were involved; but this possibility was rejected after reference to a paper by Willard (1915) on the cranial nerves in *A. carolinensis*. Although not referred to in the text, the olfactory bulbs are clearly shown in Willard's pl. 2, fig. 4, and pl. 3, fig. 6, and are similar to those described in the present paper. We think, therefore, that the descriptions given by Kappers *et al.* and by Crosby & Humphrey were based upon a misinterpretation. The structure identified by them as an olfactory bulb did not have the histological characteristics of typical bulbar formation, and corresponds topographically with the root of the olfactory peduncle. Their material, presumably, was removed from the head in such a way as to leave behind the olfactory bulb complex and the greater part of the olfactory peduncles. No specimens of *Phrynosoma* or *Holbrookia* were available for the present investigation, but re-examination of the olfactory system in these iguanids is desirable in view of the present findings in *Anolis*.

The central connexions of the olfactory and accessory olfactory bulbs call for little further comment. The general pattern is similar to that in other lizards, although the number of fibres involved in any of the so-called olfactory tracts is clearly much smaller than is usually present. The 'olfactory component' of the anterior commissure could not be recognized at all.

Collections of cells related to the secondary and tertiary olfactory pathways are also relatively inconspicuous in *Anolis*. This is particularly noteworthy in the case of cell groups related to the terminal fibres of the lateral olfactory tract; the anterior part of the piriform cortex is reduced to an almost insignificant remnant, and the main nucleus of termination of the lateral olfactory tract in the amygdaloid region, the 'hypopallium posterior' of many authors, is not recognizable as such. It is represented in *Anolis* by the small nucleus A2. In this context it is worth pointing out that the hippocampal cortical areas, the septal nuclei and the palaeostriatum medialis (sometimes referred to as an 'olfacto-striatum') are all well developed, and show no general reduction or deficiency in their differentiation as compared with other reptiles. Evidently they have not been affected by the reduction of olfactory connexions.

The cause of the reduction of structures concerned with olfaction is of course not

indicated by studies of the kind reported here. Bellairs & Boyd (1951) have suggested that a reduction of the peripheral olfactory apparatus may have been related to the adoption of an aboreal mode of life by ancestral iguanid lizards, although other factors may also be of importance since Crosby & Humphrey (1939*a, b*) and Stebbins (1948) have observed a similar reduction in the desert-living *Phrynosoma* and in other non-arboreal species. Relatively poor development of the olfactory system seems to be characteristic of many iguanids and perhaps of the whole family; it is not a feature acquired only by the recent arboreal forms.

The fact that reduction of the peripheral receptors and the parts of the forebrain which receive connexions from them go together is, of course, not unexpected. Ontogenetically, it has been shown by Burr (1916) that removal of an olfactory placode in an amphibian embryo results in subnormal development of the olfactory regions in the corresponding hemisphere. It appears that Lopaschov (1937) has also shown that the forebrain, acting as a second-grade organizer, induces the formation of the olfactory placodes. The relationship between peripheral receptor and the forebrain is therefore reciprocal; changes in any part of the complex will affect the whole, and this will apply as much to phylogenetic as to ontogenetic development, since a phylogenetic series must consist of a succession of ontogenies. It is often assumed, however, that olfactory connexions are very widespread in the forebrain, and have been of fundamental importance in the determination of fore-brain morphology as a whole. While this may be true in early phylogenetic stages, it is clear that at the reptilian level a reduction of the olfactory apparatus can occur without obviously related changes in any part of the brain except those limited regions to which secondary olfactory fibres have been traced in experimental material (Goldby, 1937; Gamble, 1952). The present observations in *Anolis* therefore support the idea, implicit in a former paper (Gamble, 1952), that olfactory connexions are much less important than is commonly supposed in relation to reptilian forebrain morphology.

The telencephalon as a whole has been treated rather briefly in the descriptive section of this paper. From the results obtained it is clear that it shows in general a typical reptilian pattern. The large size of the ventro-lateral basal centres and the reduction of part of the pallium to a membrane without nervous constituents, suggest developments parallel to those which have occurred in the bird's brain. Similar avian trends were noted in the large size of the cerebellum and the lateral displacement of the optic lobes. These features, however, do no more than emphasize the fact that the reptilian brain in general is related to the avian brain far more closely than to the mammalian.

Differences from other reptiles were, of course, observed. In the pallial and paraterminal regions, with the exception of the reduction of the anterior piriform cortex, these are of a minor character. In the ventro-lateral basal structures they are more marked. The amygdaloid complex shows more intrinsic differentiation than in many other lizards, including *Lacerta* and the geckos. Although lacking a large and highly differentiated 'hypopallium posterior', it resembles that of *Tupinambis*. In this lizard amygdaloid nuclei were classified by Curwen (1939) in two groups: (i) lateral, closely related to the piriform and dorsal cortices by fibres forming a 'primordial external capsule' and (ii) medial, with connexions from the



lateral olfactory tract, anterior commissure and stria terminalis. A similar grouping is applicable in *Anolis*. Nucleus A1 and the lateral part of A4 seems to correspond with Curwen's lateral group, and the cortico-amygdaloid tract in *Anolis* is very like her 'primordial external capsule'; similarly, the medial group is represented by nuclei A2, A3, the medial part of A4 and the nucleus of the lateral olfactory tract. The medial group of amygdaloid nuclei is apparently present in all lizards, but the lateral group with cortical connexions has not been generally recognized. It cannot be identified with certainty in any of the other lacertilian material at our disposal though it may be represented in the lateral part of the diffuse 'central amygdaloid mass' described in *Lacerta viridis* by Goldby (1934).

The remainder of the strio-amygdaloid complex has been divided as usual into a ventral palaeostriatum and a dorsal hypopallium. While this subdivision is supported by the appearance of Nissl preparations it is relevant to point out that a division of this whole region into medial and lateral parts would be more in keeping with the appearance of sections in which fibres have been stained. No conclusion can be drawn from these observations, except that, with the evidence at present available, any subdivision in this region must be regarded as somewhat arbitrary. Much the same applies to the identification of a 'primordium neopallii' in *Anolis*, or for that matter in any other reptile. This structure has none of the characteristics by which the neopallium of mammals can be recognized; the claim that it is a primordium of the neopallium rests only on the fact that it occupies a position where the neopallium might have begun to differentiate, and that the fibres of the lateral forebrain bundle which appear to reach it may be ascending from the thalamus and so represent a primitive internal capsule system.

It is becoming increasingly evident that the terminology commonly used in the description of the reptilian brain must be accepted with reserve. Such terms as 'striatum', 'hippocampus', 'amygdaloid' and so on, are taken from human anatomy, and when applied to brains other than the human they lose their character as simple descriptive labels for particular structures, and come to imply an essential similarity. It is important to be aware of just how much similarity the use of these terms in comparative investigations does imply. In some regions, such as the paraterminal or septal region, the topographical position, intrinsic differentiation and relationship to fibre tracts is so similar in all tetrapod vertebrates, that the correspondence is obvious and the use of a common term justified. In others, such as the amygdaloid region, the position is very different. Here the term means little more than that the structure in question always occupies a similar topographical position in the telencephalon. Intrinsic differentiation may be very different, and though a relationship to the lateral olfactory tract and stria terminalis is always present, too little is known of the components and connexions of these fibre systems for this to have much significance.

To give every definable structure, for which there is no unequivocal representative in the mammalian brain, a new and non-committal name may be desirable, but would lead to a very cumbersome terminology. This is unnecessary provided it is realized that the use of terms like 'amygdaloid' imply little more than a broad classification based on topographical location in the wall of the hemisphere vesicle. If one is to go further than this it is necessary to use methods which will give more

precise and detailed information about neurons and their connexions than can be given by simple cell and fibre stains in normal material. From their inherent limitations, these methods are incapable of giving more than a preliminary classification in somewhat vaguely defined topographical regions. Their use as a basis for the phylogenetic implications of such terms as 'primordium neopallii' and 'palaeostriatum' is of very doubtful validity. Nevertheless, provided it is realized that the terms are highly speculative, their use can be justified if it stimulates further work on the morphogenesis of the nervous system by methods capable of giving evidence more directly relevant to these problems. In short, the terms used here and in other similar descriptions should in no case be regarded as final and definitive descriptions of the structures to which they are applied, but rather as indicating hypotheses which will be substantiated, modified or perhaps discarded in the light of future work in this field.

#### SUMMARY

The vomero-nasal organ, olfactory epithelium and telencephalon of *Anolis lineatopus*, *A. garmani* and *A. grahami* have been examined histologically in normal specimens, and at varying intervals after the removal of the olfactory and accessory olfactory bulbs.

The normal material shows a typical neuro-sensory epithelium in the vomero-nasal organ and in the olfactory chamber of the nasal sac which, in both situations, is less extensive than in most reptiles. In the telencephalon small olfactory and accessory olfactory bulbs are present attached to the hemispheres by long slender peduncles in the characteristic lacertilian manner.

In the hemispheres themselves the strio-amygdaloid complex is relatively very large and shows the usual reptilian differentiation into hypopallium, palaeostriatum, and a complex of nuclei in the amygdaloid region; among the latter no 'hypopallium posterior' can be recognized, but it appears to be represented by a small collection of cells receiving fibres from the lateral olfactory tract. In the pallial region the area occupied by the piriform cortex in most reptiles is largely occupied by a thin membrane containing neither nerve cells nor fibres, and the anterior part of the piriform cortex is reduced to a vestige. Dorsal and hippocampal cortical areas, and the septal nuclei, differ only in details from the comparable structures in other lizards. The anterior olfactory nucleus is present but small, and reduced representatives of the usual olfactory tracts are found.

Removal of the olfactory and accessory olfactory bulbs results in degeneration of neuro-sensory cells in the epithelium of both the vomero-nasal organ and the nasal sac, and some fragmentation and loss of fibres in the olfactory tracts.

We wish to express our thanks to Mr Garth Underwood of the University College of the West Indies who collected and sent the live specimens of *Anolis* on which this work is based; we are also indebted to the Photographic Department, St Mary's Hospital Medical School, for the photograph reproduced as Text-fig. 1.

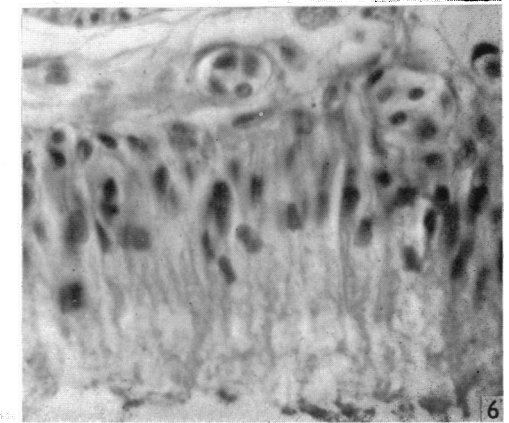
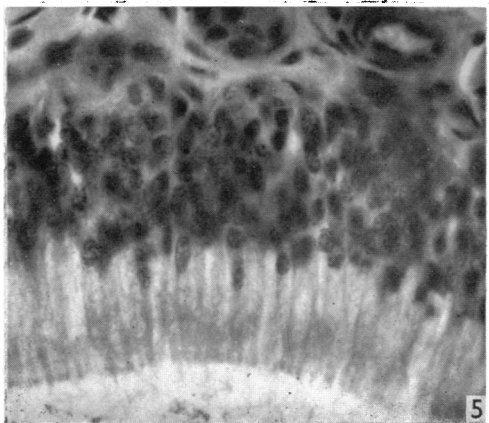
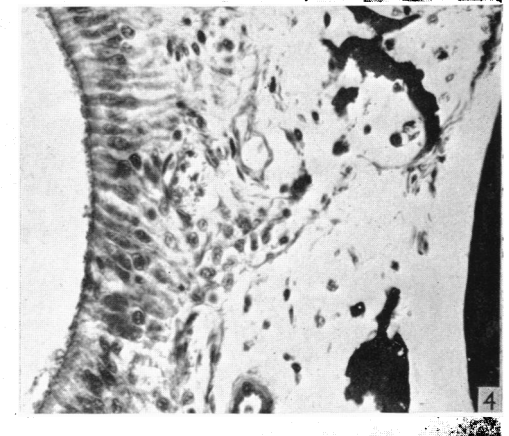
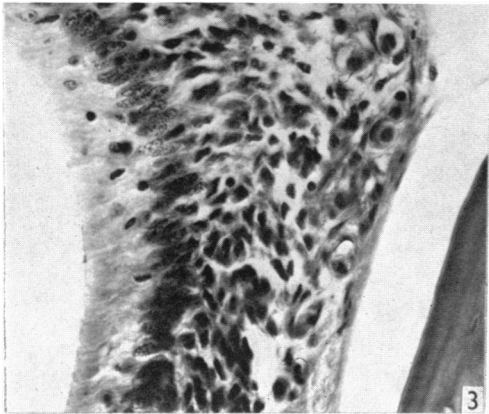
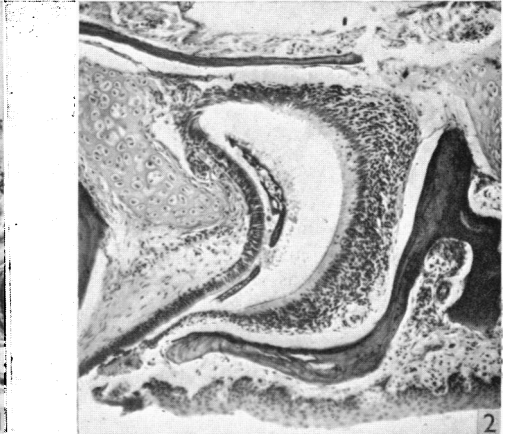
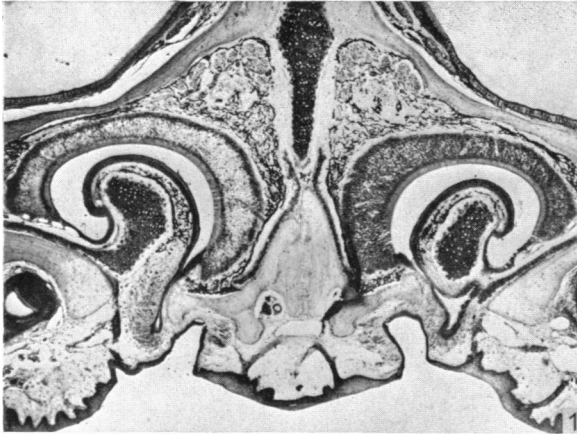
#### ADDENDUM

Since this paper was sent to press we have found a further reference to the brain of *Anolis lineatopus* in a paper by E. Horne Craigie entitled 'Notes on Cytoarchitectural features of the lateral cortex and related parts of the cerebral hemisphere in a series

of reptiles and birds' (*Trans. Roy. Soc. Can. series 3*, **30**, v, pp. 87–113). Craigie gives a description of the pallial membrane, and also notes the vestigial character of the piriform cortical area. He relates this condition to the reduction of the dorsolateral region of the cortex in the bird's brain, but makes no reference to the microsmatic character of *Anolis*. He also gives a brief account of the cell masses which can be differentiated in the ventro-lateral region of the hemisphere, but does not describe them in detail.

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ARMSTRONG, GAMBLE AND GOLDBY—OLFACTORY APPARATUS AND THE TELEENCEPHALON OF *ANOLIS*

EXPLANATION OF PLATE

- Fig. 1. Transverse section through the palatal region of *Lacerta viridis* 10 days after unilateral ablation of main and accessory olfactory bulbs. The section shows loss of nuclei from the third layer of the sensory epithelium of the vomero-nasal organ (left side) with persisting basal and supporting cells. Haematoxylin and eosin. ( $\times 32$ .)
- Fig. 2. Normal vomero-nasal organ of *Anolis lineatopus*. Transverse section. Haematoxylin and eosin. ( $\times 90$ .)
- Fig. 3. Normal sensory epithelium of the vomero-nasal organ in *A. lineatopus*. Haematoxylin and eosin. ( $\times 410$ .)
- Fig. 4. Sensory epithelium of the vomero-nasal organ in *A. grahami* 14 days after bilateral ablation of main and accessory olfactory bulbs. The epithelium is much thinner than normal (compare fig. 3), due mainly to a loss of cells from the third layer. Haematoxylin and eosin. ( $\times 410$ .)
- Fig. 5. Normal sensory epithelium of the nasal sac in *A. lineatopus*. Haematoxylin and eosin. ( $\times 630$ .)
- Fig. 6. Sensory epithelium of the nasal sac in *A. grahami* 14 days after bilateral ablation of main and accessory olfactory bulbs, showing similar changes to those seen in the vomero-nasal epithelium in fig. 4 above. Haematoxylin and eosin. ( $\times 630$ .)

LIST OF ABBREVIATIONS USED IN TEXT-FIGURES

A1-A4	Amygdaloid nuclei	<i>N.olf.ant. pars lat.</i>	Anterior olfactory nucleus, pars lateralis
<i>Alv.</i>	Alveus	<i>N.olf.ant. pars dors.</i>	Anterior olfactory nucleus, pars dorsalis
<i>Ch.opt.</i>	Optic chiasma	<i>N.supraopt.</i>	Supraoptic nucleus
<i>Comm.ant.</i>	Anterior commissure	<i>N.tr.olf.lat.</i>	Nucleus of the lateral olfactory tract
<i>Comm.ant.hyp.</i>	Hypopallial component of anterior commissure	<i>N.vent.med.</i>	Ventro-medial nucleus of paraterminal body
<i>Comm.hipp.</i>	Hippocampal commissure	<i>Palst.lat.l.c.</i>	Palaeostriatum lateralis, large-celled part
<i>Cx.dors.</i>	Dorsal cortex	<i>Palst.lat.s.c.</i>	Palaeostriatum lateralis, small-celled part
<i>Cx.hipp.a.e.</i>	Hippocampal cortex, anterior extremity	<i>Palst.med.</i>	Palaeostriatum medialis
<i>Cx.hipp.l.c.</i>	Hippocampal cortex, large-celled part	<i>Prim.neopall.</i>	Primordium neopallii
<i>Cx.hipp.s.c.</i>	Hippocampal cortex, small-celled part	<i>St.med.lat.</i>	Stria medullaris lateralis
<i>Cx.pir.</i>	Piriform cortex	<i>St.term.</i>	Stria terminalis
<i>D.B.</i>	Diagonal band	<i>Tr.cort.amy.</i>	Cortico-amygdaloid tract
<i>Fib.tang.</i>	Fibrae tangenciales	<i>Tr.olf.lat.</i>	Lateral olfactory tract
<i>Hyp.</i>	Hypopallium	<i>Tr.opt.</i>	Optic tract
<i>L.F.B.</i>	Lateral forebrain bundle	<i>Tub.olf.</i>	Olfactory tubercle
<i>M.F.B.</i>	Medial forebrain bundle	<i>Vent.olf.</i>	Olfactory ventricle
<i>N.D.B.</i>	Nucleus of diagonal band		
<i>N.dors.lat.</i>	Dorso-lateral nucleus of paraterminal body		