# AN EXPERIMENTAL STUDY OF THE VISUAL PATHWAYS IN A REPTILE (*LACERTA VIVIPARA*)

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The structural analysis of the reptilian brain has so far been based almost exclusively on the study of normal material prepared by various neuro-histological techniques. By such means accurate and detailed maps of the disposition of cells and fibre tracts have been made. I refer, in particular, to the studies of Huber & Crosby on *Alligator* (1926) and on *Anolis* (1933), of Cairney (1926) and Durward (1930) on *Sphenodon*, and of Shanklin (1930) on *Chameleon*. Though these form a base on which further investigations can be built, they do not by themselves provide adequate or satisfactory material for morphological and functional interpretation. They give little objective evidence of the precise origin or termination of fibres, or of the direction in which they normally conduct. To gain this information it has been found necessary to make use of methods for the differential staining of degenerating fibres; but such methods have been used extensively only on the mammalian brain.

It is probably in the analysis of the mammalian visual system that the use of degeneration techniques has met with most success. It was therefore decided to apply these methods to that system in the reptile, in order to determine the course followed by fibres of retinal origin through the chiasma and optic tracts, and also the localization of their terminals in the brain. In addition, a large part of the investigation was necessarily devoted to a study of the nature and rate of degenerative changes in the reptilian nervous system.

The methods available fall into three classes, depending on the demonstration of degeneration in: (*a*) the cell body of the neuron; (*b*) the axon and its terminals; and (*c*) the myelin sheath. The Marchi technique for the demonstration of myelin degeneration has been used, but is not very satisfactory in the reptilian brain, where many fibres are unmyelinated; chief reliance has therefore been placed on the demonstration of the degeneration of axons and their terminals by means of a silver impregnation technique. No attempt has yet been made to utilize degenerative changes in the cell body, assuming these to occur in reptiles as they do in mammals.

## MATERIAL AND METHODS

The animals used were specimens of *Lacerta vivipara*. Some were prepared as normal material; in others the left eye was removed under ether anaesthesia, and penicillin-sulphathiazole powder introduced into the orbital cavity. The mortality rate was high, one in three of the animals dying as the immediate result of the operation. The post-operative behaviour of the animals was apparently normal, and infection occurred in only one specimen. In some preliminary experiments, in which snakes

* This work was carried out during the tenure of a post-graduate studentship from the University of London.

as well as lizards were used, the animals were kept at room temperature (approximately 16° C.). Under those conditions no degenerative changes could be detected even 17 days after the operation. In all subsequent experiments, therefore, the lizards were kept in cages heated to approximately 30° C. At intervals between 6 days and 11 weeks after the operation the animals were killed by decapitation. The brain was exposed and fixed *in situ* for 24 hr. prior to removal.

### *Histological methods*

(*a*) Five Nissl series were prepared from normal specimens. The brain was fixed either in 95 % alcohol or in 12 % formol saline with 4 % acetic acid. After alcohol fixation three transverse series were stained with thionin, and after formol-acetic fixation one transverse and one horizontal series were stained in the same way. The sections were all cut in paraffin at 12 $\mu$.

(*b*) In preliminary trials the most complete and consistent silver impregnations were obtained by Nonidez' modification (1939) of the Cajal technique. This method was therefore used throughout, except for two brains prepared by the pyridine-silver method which also gave satisfactory results.

The normal silver material consisted of five brains impregnated by Nonidez' method, of which two were cut transversely and three horizontally. The experimental material included eighteen brains treated by Nonidez' method, of which sixteen were cut transversely and two sagittally. Of the transverse series two were prepared 6 days after removal of the eye, and the remainder 7, 8, 10, 12, 13, 14, 17, 20, 25, 26, 34, 36, 69 and 77 days after. Of the sagittal series one was prepared after 13 days, the other after 15 days. In addition, two transverse series were prepared by the pyridine-silver method 15 and 23 days after the operation. All the silver material was cut at 7 $\mu$.

(*c*) One normal transverse series was stained by the Weigert-Pal method. Two experimental series were prepared by the Marchi technique, 25 and 26 days after the operation respectively. Both were cut transversely.

## The normal anatomy of certain thalamic and mid-brain centres

It appears from the literature that between different species of reptiles there exists considerable variation in the degree of development of certain nuclei, and that normal histological appearances have been variously interpreted. It is therefore necessary to describe, in some detail, the structures in *Lacerta* to which particular terms are to be applied. So far as possible, common usage has been followed in the terminology adopted, but its use does not necessarily imply homology with structures similarly named outside the reptilian class.

## The diencephalic region

*Lateral geniculate nucleus.* This is a well-defined formation situated in the lateral part of the thalamus. The whole nucleus is divisible into medial and lateral parts, which I have called the 'medial cell plate' and the 'lateral neuropil' (Text-fig. 1*b*). The latter is an area of dense neuropil related directly to the concave surface of the optic tract. Small, rounded cells are scattered throughout it. Its dorsal extremity

lies lateral to the conspicuous nucleus rotundus, while ventrally it extends to the lateral aspect of the lateral forebrain bundle. The medial part of the nucleus is a vertical plate of fairly large, fusiform cells. It extends not quite as far dorsally as the lateral neuropil, and its ventral border is formed by a segregated cluster of fusiform cells dorsolateral to the lateral forebrain bundle. Each cell lies with its long axis approximately perpendicular to the optic tract, and from the cell body processes extend both laterally and medially. Those directed laterally are coarse; they enter and ramify within the lateral neuropil, many of their branches reaching up to the optic tract. Those directed medially are fine; they turn ventrocaudally and pass to the tegmentum in a large tract, the fasciculus geniculatus descendens (Text-fig. 3). Although the present material does not reveal the precise termination of this tract, it is seen to converge upon the retro-infundibular decussation, within which it may cross.

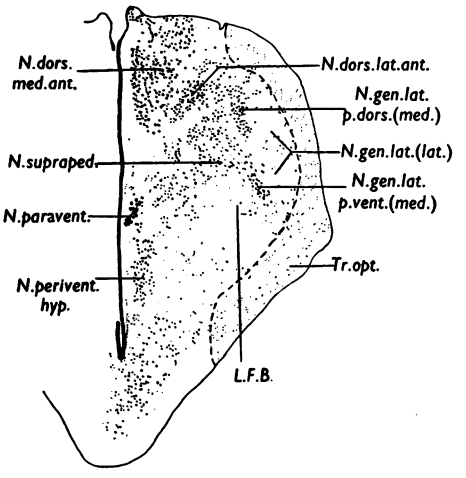



Fig. 1*a*.

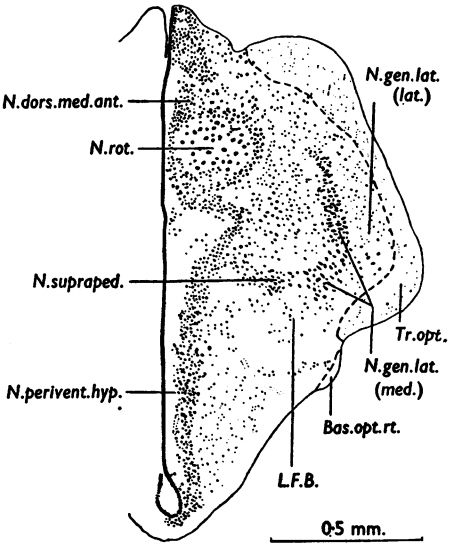



Fig. 1*b*.

Text-fig. 1. Scale drawings of transverse sections stained with thionin: (*a*) through the rostral part of the thalamus; (*b*) through the middle of the thalamus. For key to abbreviations see p. 166.

The extreme rostral end of the geniculate nucleus separates into dorsal and ventral parts (Text-fig. 1*a*). The pars ventralis is closely related to the lateral forebrain bundle, and the fusiform cells forming its medial part are a forward extension of the cell cluster which at more caudal levels forms the ventral border of the medial cell plate. In the pars dorsalis, however, the medial plate cells become small and rounded, and do not appear to give rise to fibres of the fasciculus geniculatus descendens. They are not clearly distinguishable from the cells of the nucleus dorsolateralis anterior of the thalamus. The lateral neuropil of the pars dorsalis is less dense than in other regions of the nucleus.

Comparable descriptions of the lateral geniculate nucleus were given by Edinger (1899) for *Varanus*, and by Beccari (1923) for *Lacerta muralis*, the latter referring to the medial cell plate as the 'cellule a doppio pennacchio'. Elsewhere little stress

has been laid upon a differentiation into medial and lateral parts. In many reptiles the nucleus appears to be less well developed than in *Lacerta*, but it is clear that some authors have regarded the lateral neuropil as the whole nucleus. This is certainly true of Frederikse (1931), who refers to the medial cell plate in *Lacerta* as a separate 'nucleus lateralis'.

Dorsoventral subdivision of the geniculate nucleus has been described in various reptiles, e.g. by Ramón (1896) and by Shanklin (1930) in *Chameleon*, by Cairney (1926) and by Durward (1930) in *Sphenodon*, by Huber & Crosby (1933) in *Anolis*, and by Warner (1947) in *Crotalus*. The subdivisions have varied considerably between the different species with regard to both the number and character of the separate parts so formed. In the present study of *Lacerta* definite separation into a dorsal and a ventral part could be distinguished only in the rostral part of the nucleus where, as described, the pars dorsalis presents certain features in which it differs from the rest of the nucleus. It is true that the segregation of a cluster of cells along the ventral border of the medial cell plate also suggests a division of the nucleus at more caudal levels. But such a division is not justified by any difference in either cellular morphology or connexions, nor by the results of the experimental investigation. Cairney (1926) and Durward (1930) found similar conditions in *Sphenodon*, where separate dorsal and ventral parts of the nucleus could be identified only in the rostral thalamus. It is possible that the pars dorsalis described here in *Lacerta* may correspond to a lateral differentiation of the nucleus dorsolateralis anterior which Huber & Crosby (1926) described in the alligator.

### Pretectal region

Beneath the rostral part of the optic tectum, in a zone of transition from thalamus to midbrain, is the pretectal region. It contains the following nuclei which are of significance for the present investigation.

*Nucleus lentiformis mesencephali.* This is a collection of large and small cells extending obliquely across the base of the rostral border of the tectum (Text-figs. 2*a*, and 3). Its outline is not well defined. The larger cells are fusiform, and lie in the rostral part of the nucleus in relation to optic tract fibres ascending to the anterior aspect of the tectum. The nucleus is pervaded by a transverse band of fibres, the brachium tecti medialis (Shanklin, 1930; Huber & Crosby, 1933). It is succeeded caudally by the nucleus pretectalis.

*Nucleus pretectalis.* This is a clearly circumscribed structure containing closely packed cells of medium size and a fine neuropil. In transverse sections it appears as an ovoid body lying at the level of the posterior commissure, caudal and slightly ventral to the nucleus lentiformis. In sagittal sections its shape is round (Text-fig. 3). Dorsally it is related to the stratum griseum centrale of the optic tectum (vide infra) and it is traversed by bundles of fibres passing to, or from, the deeper layers of the tectum.

*Nucleus geniculatus pretectalis* (Text-fig. 2*a*). This is situated ventral to both of the above-mentioned nuclei. Its rostral end lies dorsomedial to the caudal extremity of the lateral geniculate nucleus to which it is very similar in structure, but from which it is clearly separated. Its medial part consists of quite large fusiform cells,

and the lateral part is a region of dense neuropil related to the inner surface of the optic tract. Its extent is appreciated only after combined study of Nissl and silver preparations. Coarse dendritic processes extend laterally from the fusiform cells into the neuropil. Finer processes are directed medially into a large tract, the fasciculus geniculatus pretectalis descendens. This tract runs ventrocaudally into the tegmentum, in company with the fasciculus geniculatus descendens (Text-fig. 3).

*The nucleus posterodorsalis.* In a transverse series this first appears lateral to the habenula. It contains a few small cells and a diffuse neuropil. Caudally it extends above the posterior commissure as a rounded elevation medial to the optic tectum and close to the midline (Text-fig. 2*a*). It is penetrated by fibres of the tecto-thalamic system, and in normal preparations appears to be reached by fibres from the supra-optic decussations and from the optic tract.

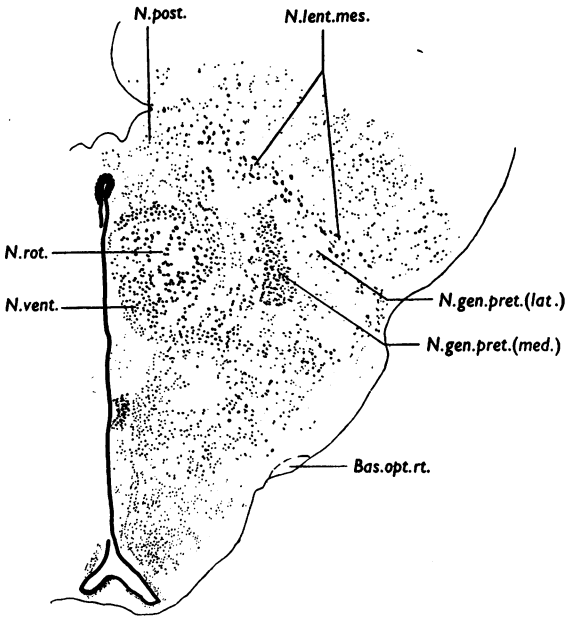



Fig. 2*a*.

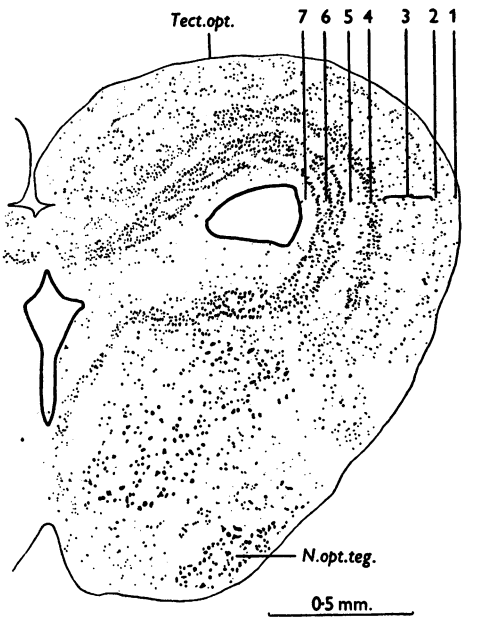



Fig. 2*b*.

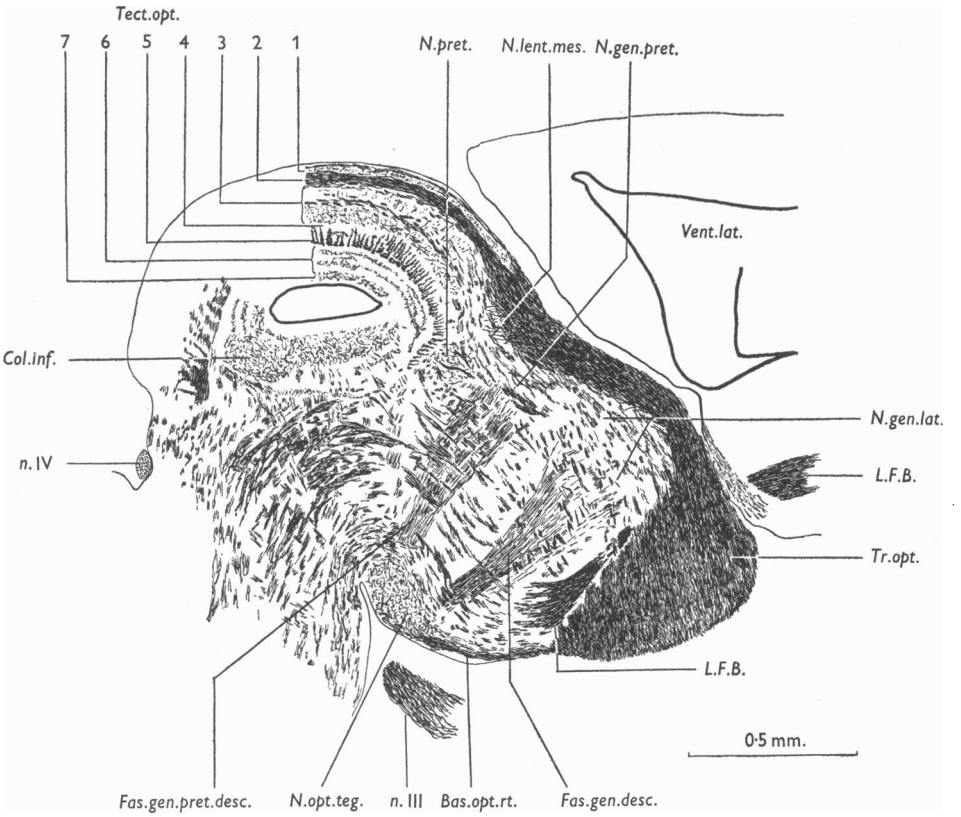
Text-fig. 2. Scale drawings of transverse sections stained with thionin: (*a*) through the pretectal region; (*b*) through the midbrain. For key to abbreviations see p. 166.

The present description cannot easily be reconciled with all previous accounts of the pretectal region in reptiles. It is very similar to that of Beccari (1923) for *L. muralis*, and is comparable with those of Huber & Crosby (1926, 1933) and Cairney (1926). There is no doubt that much confusion has been caused simply by terminological inconsistencies. Thus, the 'nucleus lentiformis' described by Edinger (1899) in *Varanus* is the nucleus pretectalis of many of the more recent workers, while his 'nucleus pretectalis' is probably the nucleus geniculatus pretectalis. Edinger's terminology was adopted by de Lange (1913). The nucleus posterodorsalis of the present work corresponds to the structure of the same name described by Huber & Crosby in *Anolis* (1933) which was later identified by Papez (1935) in turtles as the

'area pretectalis'. Frederikse (1931) failed to distinguish in *Lacerta vivipara* the nucleus geniculatus pretectalis, and much of his interpretation of the pretectal region is not confirmed by the present material.

### Optic tectum (superior colliculus)

The optic tectum of *Lacerta* has a complex laminar structure in which seven principal strata can be recognized (Text-figs. 2*b*, 3). Of these, only the first three




Text-fig. 3. Scale drawing of parasagittal section through the diencephalon and midbrain. (Nonidez' silver method.) For key to abbreviations see p. 166.

are of concern to the present investigation. They are, from the surface inwards, as follows:

*Stratum zonale* (layer 1 in the figures). This is present as a thin layer over the entire surface of the tectum, but is much thicker on the anterior, medial and dorsal aspects. It consists of a neuropil of fine fibres with scattered small cells. Over approximately its rostral half it is characterized by the presence of small fibre bundles just beneath the pia mater; they appear to enter the stratum from the optic tract. Huber & Crosby (1933) indicate that the stratum zonale is poorly developed in many reptiles, but in *Lacerta* and probably in *Sphenodon* (Cairney, 1926) it is a well-defined structure.

*Stratum opticum* (layer 2 in the figures). This is a dense layer of closely packed fibre bundles coming from the optic tract. Small cells are scattered between them.

*Stratum fibrosum et griseum superficiale* (layer 3 in the figures). A broad layer which in silver preparations is readily divisible into four substrata on the basis of differences in the density of the neuropil and the relative number of fibre bundles. Cells are scattered throughout, but apart from a slight concentration in the second substratum the lamination observed in the Nonidez preparations is not evident in the Nissl material. The outer substratum is distinguishable from the overlying stratum opticum only by the presence of areas of coarse neuropil between the bundles of fibres. The second substratum is a broad zone of diffuse, fine neuropil with only a few fibre bundles; the third is narrow, and like the first consists of a coarse neuropil and many fibre bundles; the fourth has a dense, fine neuropil and only a few fibre bundles. The fibre bundles referred to are arranged tangentially, and are derived from a number of sources, including the optic tract, the supraoptic decussations and the so-called thalam-otectal pathways. Traversing the whole stratum fibrosum et griseum superficiale there are, in addition, many radially directed fibres. The origin and termination of these could not be determined on account of the density of the fibre plexus, but they probably include ascending processes from cells lying in the deeper strata of the tectum, including the periventricular layers. de Lange (1913) and Huber & Crosby (1933), using Golgi preparations, showed such fibres to exist in the reptilian tectum.

## EXPERIMENTAL RESULTS

In experimental material prepared by silver impregnation degenerative changes were revealed in the fibres of retinal origin. This provided a positive means of identification, and permitted a more precise analysis of the visual pathways than is possible with normal material. As very little is known about degeneration in the reptilian nervous system it is necessary to describe in some detail the histological characteristics of the degeneration observed in the present experiments.

### *The characteristics of axonal and terminal degeneration*

In specimens prepared 6 days after the operation no change could be detected in axons from the cut optic nerve. In the 7-day specimen they showed a distinctly heavier impregnation, and this increased affinity for silver remained the only indication of degeneration up to 10 days. After 12 days definite changes were evident in axonal structure, and were well established by the 15th day (Pl. 1, fig. 1). Many fibres had lost their smooth contour, becoming sinuous and uneven. Irregular varicosities had developed along the course of the axons, some of which presented very large spherical and ovoid swellings separated by constrictions which appeared to be on the point of rupture. Large irregular vacuities were present in the midst of degenerating fibre bundles, and became an increasingly prominent feature as degeneration proceeded. After 25 days fragmentation of the distorted axons was well advanced. This resulted not only in the formation of many short lengths of tortuous and heavily staining axons (Pl. 1, fig. 2), but also gave rise to a wealth of small, irregular fragments and of large fusiform and spherical bodies along the course of

the visual pathways. By 36 days the original fibre bundles were largely replaced by a dense mass of axon debris and a lightly staining amorphous ground substance. Resorption of the debris appeared to be a slow process, and was far from complete even after 11 weeks.

Degeneration of most fibres followed the sequence described, but certain variations suggest that the rate of degeneration is related to axonal thickness. Unusually coarse axons, such as those of the basal optic root, disintegrated rapidly into blackened granular fragments (Pl. 1, fig. 3*b*), this being already evident after 12 days. On the other hand, structural changes in many of the finest axons and collaterals were not apparent until after 34 days.

In addition to axonal degeneration changes were observed which appear to indicate the terminal distribution of degenerating fibres. These changes were very similar to the mammalian terminal degeneration first described by Hoff (1932), but with one outstanding difference. Mammalian studies have been concerned with the degeneration of terminal boutons (end feet) which are a normal feature of many synaptic junctions. With the technique employed here it was not found possible to demonstrate the existence of boutons in the normal lizard material in any of those parts of the brain related to the fibres of retinal origin; but 6 days after removal of the eye a profusion of minute argentophil rings was demonstrable in some of these regions. Although some of the rings appeared to be isolated structures many were clearly terminal formations, each on the end of a short length of fine fibre (Pl. 2, fig. 4). The point of attachment to the fibre was usually drawn out to form a racquet-shaped outline. The precise disposition of the rings varied, depending upon the particular locality in which they were observed. Sometimes they lay singly or in clusters in relation to cell bodies, but more frequently in relation to dendritic processes. In all of the areas concerned some also appeared in the sections to lie freely in the neuropil, not obviously related to either cells or fibres. The histological appearance of many of these structures was the same as that of the normal terminal boutons as described, for example, in the lateral geniculate body of mammals (Glees & Le Gros Clark, 1941; Glees, 1941, 1942), but their appearance in the lizard must be regarded as a degenerative phenomenon since they were demonstrable only after removal of the eye.

Between 12 and 15 days after the operation the rings were larger and much more numerous, some having become markedly elongated, and the majority showed varying degrees of thickening with consequent reduction of the lumen. In some the lumen appeared to have been entirely obliterated, resulting in the formation of solid bulbs some of which were almost as large as the nucleus in nearby cells (Pl. 2, figs. 6, 8). By this time many fine fibres of the surrounding neuropil showed swelling, vacuolation and fragmentation. This was often seen in fibres bearing a terminal ring or bulb, and a characteristic thickening of the fibres was frequently observed where they divided (Pl. 2, fig. 10*a*). Fibre changes of this kind have been referred to in mammals as 'preterminal degeneration' (Le Gros Clark & Meyer, 1947).

On the 20th day the number of rings appeared to be less, but the proportion of bulbs was increased. Many of the latter were very large, and some showed signs of granular disintegration. At 25 days only a few remained, and there was a noticeable sparcity of neuropil in the regions concerned. Nevertheless, both rings and bulbs

were occasionally found even after 36 days, some being very small and no different in appearance from those first seen at 6 days. None remained 10 weeks after the operation.

*The visual pathways*

In the specimen prepared 11 weeks after the operation no normal fibres could be found in the debris in the central stump of the divided optic nerve, which must therefore contain only afferent fibres. On reaching the chiasma the nerve divides into a number of large bundles which interdigitate with those from the opposite side, presenting in transverse section the dovetail pattern usual in reptiles. The number, size and arrangement of the bundles are very variable. In the present material anything from three to seven bundles were formed in different specimens, and further subdivision within the chiasma was occasionally encountered.

The bundles rejoin after crossing and form the greater part of the contralateral optic tract. Decussation, however, is not quite complete. A small fascicle separates from the most ventral bundle derived from the optic nerve and turns on to the ventral surface of the homolateral optic tract. Degeneration of this fascicle was initially overlooked on account of its small size, and it was first observed in a slightly oblique transverse series in which it was particularly obvious (Pl. 3, fig. 11). Re-examination of the other experimental material confirmed its existence, and in each case a corresponding fascicle of normal fibres was seen to turn on to the ventral aspect of the degenerating optic tract.

While recognizing the existence of a partial decussation, it must also be emphasized that the proportion of uncrossed fibres is in fact very small. Nevertheless, their presence in a reptile was an unexpected finding, and it is therefore appropriate to record here that similar experiments now in progress on the grass snake (*Natrix natrix*) have revealed uncrossed fibres in that species also (Pl. 4, fig. 13).

The degeneration of retinal fibres in the chiasma provided a clear demonstration of the extensive supraoptic system, which was of course totally unaffected by removal of the eye (Pl. 4, fig. 14). It is divisible into the usual dorsal and ventral supraoptic decussations which, as in reptiles generally, lie almost entirely caudal to the chiasma. The division itself is somewhat arbitrary, since there is appreciable interchange of fibres between the two decussations.

The ventral supraoptic decussation consists of a large band of fine fibres situated immediately caudal to the chiasma, from which it is not easily distinguishable in normal preparations. It appears to have extensive connexions with the hypothalamus. When followed laterally its fibres gradually separate into dorsal and ventral groups, which differ in their distribution and correspond to the dorsal and ventral parts of the ventral supraoptic decussation as described in *Sphenodon* by Cairney (1926). In their subsequent course the fibres of the pars ventralis form a compact bundle along the caudal margin of the optic tract. Those of the pars dorsalis swing on to the medial surface of the optic tract; further reference is made to them later.

The dorsal supraoptic decussation is smaller than the ventral. Its fibres cross directly beneath the third ventricle and spread out dorsolaterally, many of them penetrating the basal forebrain bundle. Coarse fibres situated in the caudal part of this decussation represent the 'fibrae ansulatae' of earlier writers.

The optic tract presents the usual gross relationships. It runs dorsolaterally from the chiasma on the ventral surface of the diencephalon. Turning round the lateral forebrain bundle it then passes dorsocaudally on the lateral surface of the thalamus towards the tectum of the midbrain.

Enucleation of the eye resulted in massive degeneration in the contralateral optic tract. Close to the chiasma a few degenerating fibres were seen to separate from its dorsal surface, to pass for a short distance through the supraoptic region of the hypothalamus, and then to rejoin the tract. No evidence was found for the termination of retinal fibres in any part of the hypothalamus.

Just lateral to the chiasma some remarkably coarse fibres become segregated in the caudal part of the optic tract. On nearing the lateral forebrain bundle they separate from the tract and run directly caudally as a compact bundle on the ventral surface of the subthalamus and tegmentum. This is the basal optic root or 'posterior accessory optic tract' (Text-fig. 3). Slightly rostral to the exit of the oculomotor nerve it enters the ventral aspect of the nucleus opticus tegmenti. The latter is a well-defined structure forming a pear-shaped elevation on the ventral surface of the tegmentum. It contains a dense, coarse neuropil and many multipolar cells of medium size (Text-figs. 2*b*, 3). Removal of the left eye resulted in complete degeneration of the contralateral basal optic root (Pl. 1, figs. 3*a*, *b*), and a conspicuous terminal reaction occurred throughout the corresponding nucleus opticus tegmenti. Argentophil rings appeared in relation to the cell bodies and their processes, and after 13 days many of them had developed into massive, heavily staining terminal bulbs (Pl. 2, fig. 8). Several such bulbs were frequently applied to the surface of a single cell body. After 11 weeks the nucleus was markedly shrunken as compared with the normal side, and much of its neuropil had disappeared.

On the lateral surface of the thalamus the optic tract is related medially to the lateral geniculate nucleus, and corresponds to the marginal optic tract of Huber & Crosby (1926, 1933). Degeneration experiments showed that the lateral neuropil of the geniculate nucleus receives a very large number of retinal fibres which turn medially from the tract, some traversing the width of the tract in order to gain the geniculate neuropil. Some are stem fibres, but many are collaterals which arise at right angles from fibres continuing dorsally in the tract.

From the 6th day after removal of the eye a multitude of argentophil rings was present in the contralateral geniculate nucleus (Pl. 2, fig. 4). They were very numerous in the lateral neuropil, being particularly dense close to the optic tract. Many were obviously related to the dendritic processes arising from fusiform cells of the medial cell plate, and others occurred in clusters around some of the small cells which are present in the lateral neuropil (Pl. 2, fig. 5). Rostrally, where dorsal and ventral subdivisions of the geniculate nucleus can be recognized, retinal fibres were traced into both subdivisions but especially into the ventral, where an exceptionally dense terminal reaction was obtained.

In the medial cell plate the terminal reaction was much less striking than in the lateral neuropil, although solitary rings were seen in relation to many of the fusiform cell bodies.

From the 12th to the 20th day after the operation the number of rings in the geniculate nucleus was much increased, and many terminal and isolated bulbs were

now present (Pl. 2, fig. 6). There was also abundant swelling, vacuolation and fragmentation of fibres in the lateral neuropil. After 11 weeks much of the neuropil had disappeared, and together with shrinkage of the optic tract this resulted in pronounced asymmetry of the diencephalon.

The boundary between the optic tract and the lateral geniculate nucleus is not easily defined, for some fibre bundles situated deeply in the tract encroach upon the outer part of the lateral neuropil. In sections through the rostral part of the thalamus a few such bundles of degenerating fibres were followed more deeply into the lateral neuropil of both the dorsal and ventral parts of the geniculate nucleus. Most of them appeared to terminate here, and the remainder rejoined the inner surface of the optic tract. These deeper bundles correspond, in part, to the 'axillary optic tract' of Huber & Crosby (1926, 1933). In the rostral pole of the thalamus a few retinal fibres were followed into a small, ovoid group of closely packed cells, the form and relations of which show that it corresponds to the nucleus ovalis of other reptiles (Huber & Crosby, 1926; Cairney, 1926; Durward, 1930; Addens, 1938). All appeared to be fibres of passage, and no evidence was found for the termination of retinal fibres in the nucleus ovalis.

Beneath the rostral part of the tectum the optic tract is in close relation to the nuclei of the pretectal region. Degenerative changes showed that many retinal fibres, including both stem fibres and collaterals, here turn medially from the tract and pass dorsal to the caudal end of the lateral geniculate nucleus. They enter the nucleus geniculatus pretectalis and the nucleus lentiformis mesencephali.

Six days after enucleation of the eye a profusion of argentophil rings was evident in the lateral neuropil of the contralateral nucleus geniculatus pretectalis. These were accompanied at 12 days by numerous isolated and terminal bulbs, and by the usual preterminal changes in many fibres of the neuropil. In this nucleus, as in the lateral geniculate, the lateral neuropil appears to be essentially an area of axo-dendritic association between incoming retinal fibres and the dendrites of the fusiform cells in the medial part of the nucleus. Only a relatively small number of rings and bulbs appeared actually in relation to the fusiform cell bodies.

The retinal fibres which enter the nucleus lentiformis mesencephali pass dorsal to the nucleus geniculatus pretectalis. They form a part of the so-called brachium tecti medialis, although much of this remained unaltered 11 weeks after removal of the opposite eye. The nucleus also receives retinal fibres which leave the optic tract as it ascends on to the anterior aspect of the tectum. An appreciable terminal reaction occurred throughout the nucleus lentiformis, but was less dense than that in the lateral geniculate nucleus and in the nucleus geniculatus pretectalis. In the rostral part of the nucleus clusters of bulbs and rings lay in relation to some of the larger cells and their processes (Pl. 2, fig. 7), but for the most part they were scattered freely in the neuropil. After 36 days much of the neuropil had vanished, its place being taken by irregular vacuities.

Degenerating fibres could not be followed into the nucleus pretectalis, nor into the nucleus posterodorsalis. In the sagittal series prepared 13 days after the operation several rings and bulbs were found amongst the cells of the contralateral nucleus pretectalis, but as this was not found in other specimens, its significance is questionable.

As the optic tract was followed dorsally in the experimental preparations it was

evident that it contained, particularly in its deeper part, an increasingly large number of fibres which were unaffected by removal of the opposite eye. This was especially clear in material prepared 10 and 11 weeks after the operation, in which crossed retinal fibres had undergone complete degeneration.

The small fascicle of uncrossed retinal fibres accounted for only a very small fraction of the persisting normal fibres. Its course and distribution are considered later, so that here we are concerned with non-retinal components of the optic tract. Most of these come from the ventral supraoptic decussation. Fibres which constitute the pars dorsalis of this decussation swing on to the medial aspect of the optic tract, and pass between it and the lateral forebrain bundle (Pl. 4, fig. 14). Here a few of them enter the tract, and accompany the fibres of retinal origin round the thalamus. The majority, however, form small bundles which sweep dorsocaudally through the lateral part of the thalamus and pretectal region. Many of these bundles incline laterally and join the inner surface of the optic tract, within which they continue dorsally towards the tectum. A relatively small number of fibres separate from the pars ventralis of the ventral supraoptic decussation, and enter the optic tract along its caudal margin.

After complete degeneration of crossed retinal fibres there also remained in the optic tract many normal axons which seemed to have no relation to the supraoptic decussations. They appeared to enter the tract from the lateral geniculate nucleus. Turning dorsally, usually at a right angle, they became mingled with the supraoptic fibres from which they could not then be distinguished. Such fibres were found in relation to all parts of the lateral geniculate nucleus, but the present material does not show whether they arise from or terminate within this nucleus.

When the optic tract arrives at the lower border of the tectum it has already contributed a considerable number of retinal fibres to the visual centres of the tegmentum, thalamus and pretectal region. In spite of this the majority of fibres from the retina eventually reach the tectum of the opposite side. It is likely that many of these have given collateral branches to the various diencephalic and pretectal centres. This was observed to be so in the case of the pretectal region, but from the available preparations it was not possible to be certain that collaterals which enter the lateral geniculate nucleus do indeed arise from fibres which ultimately reach the tectum.

On nearing the tectum the optic tract expands to form a broad sheet of fibres, those from the rostral part of the tract reaching the anterior and medial aspects, while those from the caudal part reach the lateral and posterior aspects. Degenerative changes showed that the great majority of retinal fibres pass from the optic tract into the stratum opticum, but that rostrally a few pass directly into the stratum zonale and also into the stratum fibrosum et griseum superficiale. The stratum opticum suffered almost complete degeneration after removal of the opposite eye. Over the whole extent of the tectum degenerating fibres were seen to leave the stratum opticum and enter the underlying stratum fibrosum et griseum superficiale, within which they ramified in the three outer substrata. The fibre bundles which pass directly into the stratum zonale form a narrow superficial layer of fibres (Text-fig. 3), and this degenerated completely. The few bundles which pass directly into the stratum fibrosum et griseum superficiale are mingled with many other bundles from the deeper part of the optic tract which did not degenerate and are thus not of

retinal origin. The latter include those supraoptic fibres which join the optic tract at thalamic and pretectal levels. No evidence was found to show that retinal fibres cross the midline in the tectum.

The most conspicuous terminal reaction within the tectum was seen in the stratum zonale, especially in its rostral part. Terminal rings and bulbs were distributed throughout the neuropil of this layer, and were associated with considerable varicosity and fragmentation of fibres of the neuropil itself (Pl. 2, figs. 10*a*, *b*). In the stratum opticum a few rings and bulbs were scattered sparsely between the fibre bundles, and in the stratum fibrosum et griseum superficiale they appeared in appreciable numbers in the three outer substrata (Pl. 2, fig. 9). Although such a very large number of retinal fibres enters the tectum it was surprising to observe that terminal changes never approached in density those which occurred in the other visual centres. From the twelfth day after the operation the most obvious feature of degeneration in the contralateral optic tectum was the disappearance of neuropil, especially from the stratum zonale and from the second substratum of the stratum fibrosum et griseum superficiale.

This description has been concerned so far with the distribution of retinal fibres which cross at the chiasma. Analysis of the relatively very small uncrossed pathway presents a problem which these experiments have not entirely solved. Eleven weeks after the operation, i.e. after the disintegration and partial resorption of the crossed retinal fibres, the persisting fascicle of normal uncrossed fibres could be traced along the outer surface of the optic tract from the chiasma to the level of the lateral forebrain bundle (Pl. 3, fig. 12). Here it became dispersed throughout the tract, and some of the fibres were seen to give collateral branches into the pars ventralis of the lateral geniculate nucleus in the rostral thalamus. Beyond this point the uncrossed fibres were indistinguishable from the persisting non-retinal components of the optic tract.

In material prepared between 12 and 26 days after the operation degeneration of the uncrossed fascicle could be followed in the homolateral optic tract, but again only to the level of the lateral forebrain bundle. Beyond this occasional fragments of axon debris were present in the otherwise normal tract, but the fibres could not be traced with precision. A careful search was made for terminal changes in the homolateral visual centres. In three specimens, those killed 10, 17 and 26 days after the operation, a few rings, bulbs and degenerating fibres were identified in the lateral neuropil of the pars ventralis of the lateral geniculate nucleus, but as these were not found in the remaining experimental material they must be regarded as of doubtful significance. No evidence could be found for the terminal distribution of uncrossed fibres in any of the other visual centres.

### *Marchi results*

In the two specimens treated by the Marchi technique a quite considerable reaction was observed in the cerebral stump of the divided optic nerve. Myelin degeneration products were present in the form of droplets of various sizes and more rarely as ellipsoids. They were sufficient to give a general idea of the principal optic pathways.

The decussation of normal and degenerate bundles at the chiasma was clearly

shown, and a distinct Marchi reaction was present throughout the contralateral optic tract. Particularly large and numerous droplets occurred along the contralateral basal optic root, and could be followed as far as the nucleus opticus tegmenti within which there was scattered a profusion of minute osmiophilic particles. Myelin degeneration in the optic tract itself could be followed around the thalamus and into the stratum opticum of the tectum. Rows of droplets throughout the lateral geniculate and pretectal regions indicated the presence of retinal fibres, but this was, of course, insufficient to show whether any of the fibres ended there. A very slight reaction along the outer surface of the homolateral optic tract close to the chiasma was the only indication of the uncrossed fibres.

The results obtained by the Marchi method, although positive, clearly give no more than a general confirmation of the more detailed findings provided by use of the silver technique.

## DISCUSSION

Former attempts to utilize the Marchi technique in reptiles met with varied success. Gross (1903), in a study of the reptilian chiasma, failed consistently to obtain a positive Marchi reaction after removal of an eye. Shanklin (1933) observed droplets of degenerating myelin in the contralateral basal optic root of the chameleon after removal of an eye, but was not concerned with the remaining visual pathways. Goldby (1937) obtained a moderate reaction in *Lacerta viridis* following certain forebrain lesions. The results achieved in the present work by means of the Marchi method compare favourably with those of earlier writers, and are as satisfactory as expected in view of the limitations of the method.

From the present observations on the visual pathways it is apparent that axonal degeneration in the lizard is for the most part very similar to that which occurs in mammals. The succession of changes corresponds to the sequence described by Ramón y Cajal (1928) as secondary or Wallerian degeneration. Such differences as do exist appear to be due to the relatively slow rate of degeneration in the reptile. Even at the high temperature used (30° C.) no changes can be detected less than 7 days after the operation and this is followed by a further interval of about 6 days during which the only change is a progressive increase in the affinity of the axons for silver. The subsequent stages of varicosity, fragmentation and resorption are the same as in mammals, except that they are slower in onset and more prolonged.

Failure to demonstrate terminal boutons in the visual centres of the normal lizard brain may have been due to several factors. It is possible that retinal fibres normally terminate in so-called free endings, or else in boutons so minute as not to be revealed by the technique adopted. Moreover, if boutons are normally present, it may be that they become readily stainable with silver only when degenerating, and this possibility is supported by the fact that the rings observed in the present experiments showed a progressive increase in their affinity for silver from the time of their first appearance. It is of interest to note that difficulty has sometimes been experienced in demonstrating normal boutons in the visual centres of mammals (Glees & Le Gros Clark, 1941; Nauta & van Straaten, 1947).

The question naturally arises whether the rings and bulbs observed in the lizard were in fact terminal structures, or whether they arose on the course of the terminal

arborizations of the retinal fibres. Their appearance in the available material suggests strongly that those seen from the 6th to the 10th day after the operation were predominantly and perhaps entirely terminal structures, but that from the 12th day they probably included many of the swellings and vacuoles which were seen to develop along terminal fibres. There is no doubt that fragmentation of such fibres would lead to the formation of rings and bulbs indistinguishable from those which were genuine nerve endings.

The organization of the reptilian visual system as disclosed by the experimental method is in some respects different from that revealed by the use of normal material.

In a recent paper (Ströer, 1939) it was submitted that in *Lacerta* each optic nerve consistently divides at the chiasma into two bundles, and that each bundle from the left nerve passes dorsal to the corresponding bundle from the right. A similar uniformity was indicated by Gross (1903) in a comparative survey of the reptilian chiasma. In the present investigation it was observed that the number of bundles into which the optic nerve divides is very variable, and also that a constant relationship does not exist between the bundles from the left and right nerves.

More important is the demonstration that some fibres of retinal origin do not cross at the chiasma. Such fibres are generally accepted as a mammalian characteristic, quantitatively related to the extent of the binocular field, and forming part of the anatomical basis of stereoscopic vision. Uncrossed fibres have been suspected in certain birds, but their existence has not been confirmed by experiments utilizing the Marchi technique (Harris, 1904). Partial decussation has never been described in reptiles, but the present experiments show that an uncrossed component is present in the optic tract not only of *Lacerta*, but of *Natrix* also. It remains for future work to demonstrate with precision both the origin and termination of these fibres. In the absence of this data their functional significance must be a matter of pure conjecture. It is tempting to relate them to the binocular field of vision which Kahmann (1935) has shown to exist in *Lacerta viridis* and in *Natrix*, but the problem clearly requires further investigation.

Systematic accounts of the visual system in reptiles all include reference to the basal optic root, which appears to be well developed throughout the class. That it contains crossed fibres of retinal origin was proved experimentally by Shanklin (1933) in the chameleon, and the present results show that in *Lacerta* it is composed entirely of such fibres. Widespread efferent connexions of the nucleus opticus tegmenti were described by Shanklin, including fibres to the oculomotor nucleus and medial longitudinal bundle. This, and the remarkable thickness of the fibres in the basal optic root, suggest that the tract functions, at least in part, as a rapid reflex pathway by means of which the extrinsic eye muscles are influenced by impulses of retinal origin.

There is repeated reference in the literature to a system of optic fibre bundles which are said to separate from the optic tract and pursue a course dorsally through the substance of the thalamus and pretectal region, subsequently rejoining the optic tract. The number of such bundles has been shown to vary considerably between species. Bellonci (1888) showed them as a conspicuous feature in the thalamus of *Natrix*, but they appear to be less obvious in *Varanus* (de Lange, 1913), *Alligator* (Huber & Crosby, 1926) and *Sphenodon* (Cairney, 1926). Later Huber & Crosby

(1933) described them in *Anolis* under the name of 'axillary optic tract', tracing some as far as the tectum before they rejoined the main optic tract. The present experiments indicate the relatively small extent of this system in *Lacerta vivipara*, and this may of course be simply a feature of the species. However, it is also clear that an extremely intimate relationship exists within the thalamus between these retinal bundles and the very numerous bundles from the pars dorsalis of the ventral supraoptic decussation, many of which also join the optic tract; indeed, the two are indistinguishable in normal preparations. This suggests the possibility that in studies based only upon normal material confusion between retinal and non-retinal fibres may have led to some exaggeration of the 'axillary' system.

This difficulty of distinguishing retinal from other fibres in normal material is well exemplified in a recent paper by Warner (1947) on the rattlesnake. In Warner's figure 8 it appears that the fibres labelled 'optic chiasma' actually belong to the ventral supraoptic (post-optic) decussation, while the massive basal optic root illustrated in figure 9 (Warner) is almost certainly composed mainly of the same fibres. This confusion of ventral supraoptic fibres with the basal optic root seems to have led to a misinterpretation of the structure labelled as the nucleus of the basal optic root in Warner's figure 11. The basal optic root itself is still present at a more caudal level (Warner's figure 12), where it is much smaller and obviously comparable to the tract so named not only in *Lacerta*, but also in other reptilian brains.

There has not been complete agreement in the past concerning the status of the reptilian lateral geniculate nucleus as a primary visual centre. Bellonci (1888), in *Natrix*, *Lacerta* and *Emys*, was unable to convince himself that fibres of retinal origin actually terminate in any part of the thalamus. Edinger (1899), using Golgi preparations, described fibres undergoing terminal ramification in the lateral geniculate nucleus of *Varanus*, and considered them to be of retinal origin. Similar observations were made by Beccari (1923) in *Lacerta muralis*. Huber & Crosby (1926), in *Alligator*, and Cairney (1926), in *Sphenodon*, confirmed that many fibres enter the geniculate nucleus from the optic tract, but the latter could follow stem fibres only into the dorsal part of the nucleus in the rostral thalamus. Later, however, Huber & Crosby (1933) expressed the view that the reptilian lateral geniculate nucleus 'serves more particularly as a place of synapse in the course of descending impulses from the tectum to lower centres', passing first along tecto-geniculate fibres and then through the fasciculus geniculatus descendens.

As a result of the present experiments it is established that a considerable number of fibres of retinal origin make synaptic contacts within the contralateral geniculate nucleus, all parts of it receiving both stem fibres and collaterals. Further, it may be that the pars ventralis, and perhaps the whole nucleus, also receives a small number of uncrossed fibres. There can be little doubt that the primary function of the nucleus is that of a relay centre for impulses of retinal and not of tectal origin. The disposition of the fusiform cell bodies and their dendrites, essentially in relation to incoming retinal fibres, necessitates this interpretation.

Retinal connexions with the pretectal region were suggested by Cairney (1926) who, in *Sphenodon*, followed collaterals from the optic tract into the nucleus geniculatus pretectalis. Huber & Crosby (1933), in *Anolis*, indicated connexions with the nucleus lentiformis mesencephali, and traced a fascicle from the optic tract into the

nucleus posterodorsalis. The experiments on *Lacerta* confirm that a large number of retinal fibres enter the pretectal region. Their terminal distribution is seen to be localized within the nucleus lentiformis and the nucleus geniculatus pretectalis, with the added possibility that a very small number reach the nucleus pretectalis. Although no connexion with the nucleus posterodorsalis was found, it may be significant that this nucleus appears to be more highly developed in certain other reptiles. The existence of pretectal visual centres is of particular interest after the demonstration that the pupil-light reflex in mammals is mediated by retinal fibres which terminate in that region (Hare, Magoun & Ranson, 1935; Magoun, Atlas, Hare & Ranson, 1936). Further experiment is necessary, however, before a specific function may be attributed to any part of this region in the reptilian brain.

Little is known about the precise terminal distribution of retinal fibres in the reptilian tectum. Extensive non-retinal connexions render specific analysis of the retinal components extremely difficult in normal material. Huber & Crosby (1926, 1933) described fibres turning from the stratum opticum to undergo terminal arborization in the stratum fibrosum et griseum superficiale. Cairney (1926), in *Sphenodon*, followed optic tract fibres not only into the stratum opticum, but also directly into the stratum fibrosum et griseum superficiale and into a surface layer corresponding to the stratum zonale. The present observations on *Lacerta* show that a large number of retinal fibres pass directly into the stratum zonale, and the extensive terminal reaction which occurred in this layer shows it to be an important area for the terminal distribution of such fibres. Within it they come into synaptic association not only with the small neurones which are found there, but also probably with long ascending dendrites from cells lying in deeper strata, including the periventricular layers. Such processes were described by de Lange (1913) and by Huber & Crosby (1933) in Golgi material, and probably account for many of the radially orientated fibres which were seen in the Nonidez preparations. The presence of retinal terminals superficial to the stratum opticum has also been observed in various mammals (e.g. Barris, Ingram & Ranson 1935; Jefferson, 1940; Nauta & van Straaten, 1947).

The sparsely scattered rings found in the stratum opticum suggest that at least a few retinal fibres end there, but the great majority undoubtedly enter the stratum fibrosum et griseum superficiale, where they terminate predominantly in the three outer substrata. It was therefore surprising to find relatively little positive evidence of terminal degeneration in this region, as compared with the striking changes in the lateral geniculate nucleus and pretectal region. Since the terminal ramifications of retinal fibres in this region are extremely fine, it is possible that they disappear without showing the structural changes which are typical elsewhere. Whatever the explanation, the fact remains that the principal evidence of retinal connexions in these layers of the tectum was negative, namely the widespread disappearance of neuropil.

In the light of the present results some comparison may be made between the organization of the reptilian visual system and those of Amphibia and mammals. Adequate experimental data for Amphibia are lacking at present, but the studies of Herrick (1948) on the normal amphibian brain indicate that the reception and correlation of impulses from the retina are primarily functions of the tectum. Optic terminals of less importance are described in the neuropil of the dorsal thalamus,

including the nucleus of Bellonci, showing a concentration in an ill-defined 'geniculate neuropil'. Other connexions are described with the hypothalamus and the pretectal neuropil, and fibres have been followed from the chiasma to the tegmentum in a somewhat diffuse basal optic tract.

In mammals, on the other hand, it is well known that the thalamo-cortical system has attained a dominant role in visual function at the expense of the midbrain. In the reptile, as typified by *Lacerta*, numerous retinal fibres certainly terminate within a well-developed lateral geniculate nucleus, and there are clearly-defined visual centres in the pretectal region; but the vast majority of the fibres reach the tectum which presents an extremely complex pattern of laminar differentiation. In addition, the basal optic root is well developed and terminates in a prominent tegmental nucleus. In general, the reptilian visual apparatus seems to be no more than an elaboration of the more primitive condition found in Amphibia, and to show no fundamental change in organization such as the 'prosencephalization' characteristic of mammals.

On the basis of comparable relations and assumed connexions it was proposed by Cairney (1926), and again more recently by Addens (1938), that the amphibian nucleus of Bellonci is represented in reptiles by the nucleus ovalis. In the present investigation no evidence was found to suggest that any retinal fibres end in the nucleus ovalis in *Lacerta*. Assuming the homology to be correct, it may therefore be supposed either that this nucleus has been abandoned as a thalamic visual centre in reptiles, or else that its retinal connexions (if they exist at all) arose as an amphibian specialization.

It is obvious that in a general way the diencephalic region of the reptilian brain which receives direct retinal connexions is comparable with the same region of the mammalian brain, where it forms the lateral geniculate body. Difficulties arise if more detailed comparisons are attempted.

Topographically the reptilian lateral geniculate nucleus is most closely comparable with the so-called ventral nucleus of the lateral geniculate body of mammals. This was indicated by Beccari (1923) and Papez (1935), who implied that the dorsal or principal nucleus of mammals is not represented in reptiles. The main efferent connexions of the lateral geniculate nucleus in reptiles appear to be through the fasciculus geniculatus descendens with the tegmentum of the midbrain, while geniculotectal fibres are also said to exist (e.g. by Huber & Crosby, 1933). Similar pathways have been described in relation to the ventral nucleus of the mammalian geniculate body (Rioch, 1929; Barris *et al.* 1935), but a fact which cannot be overlooked is that experimental studies on mammalian visual pathways have so far failed to provide unequivocal evidence for the ending of retinal fibres in that nucleus (Le Gros Clark, 1942).

Another possibility is that the reptilian geniculate nucleus might represent the dorsal nucleus of the mammalian geniculate body. Both are situated in the lateral part of the thalamus, and both receive direct retinal connexions. But it is well known that the dorsal nucleus in mammals functions essentially as a relay centre, projecting impulses of retinal origin through the optic radiations to the visual cortex. Geniculo-tectal fibres have also been described, but their existence is made doubtful by the experiments of Lashley (1934) and of Barris *et al.* (1935). In reptiles

there is no evidence of a forward projection from any part of the geniculate nucleus; on the contrary, its efferent fibres are directed caudally into the midbrain.

In some reptiles the lateral geniculate nucleus shows signs of differentiation into dorsal and ventral parts. This was observed in *Sphenodon* by Cairney (1926), who suggested that the dorsal and ventral parts might represent the dorsal and ventral nuclei of mammals. This view was taken by Le Gros Clark (1932), and by Huber & Crosby (1933). Dorsoventral subdivision of the geniculate nucleus is, however, a very variable feature in reptiles, and is ill-defined in most species. In *Lacerta*, for example, it is distinct only in the extreme rostral part of the nucleus, where the pars dorsalis might be considered as a rudiment of the dorsal nucleus of mammals. In favour of this interpretation is the observation that, unlike the rest of the nucleus, this part does not appear to contribute fibres to the fasciculus geniculatus descendens. Nevertheless, no forward projection has been demonstrated.

It is clear that the absence of evidence for telencephalic connexions from any part of the geniculate nucleus in reptiles makes it difficult to institute precise comparison with the dorsal nucleus of the mammalian geniculate body. Similarly, the absence of retinal connexions with the ventral nucleus of mammals is a difficulty in comparing this structure with the reptilian lateral geniculate nucleus, all parts of which receive abundant retinal fibres. One is forced to the conclusion that the visual system of reptiles is organized in a fundamentally different way from that of mammals, and is in fact more closely comparable with that of Amphibia. The general similarities between mammals and reptiles, such as the presence in both of thalamic, pretectal and tectal retinal connexions, would be perfectly consistent with an independent derivation of both from generalized amphibian ancestors.

## SUMMARY

1. A description has been given of the normal histological appearance of thalamic, pretectal and midbrain centres related to the optic tracts in *Lacerta vivipara*. They are compared with corresponding structures described in other reptiles.

2. Silver impregnation of the brain after removal of an eye has revealed axonal and terminal degenerative changes, essentially similar to those which occur in mammals, except that they develop more slowly.

3. Twenty brains prepared by silver impregnation and two treated by the Marchi method have been utilized for the study of the course and distribution of degenerated fibres of retinal origin. Evidence was obtained for the following main conclusions:

(*a*) That the optic nerve contains only afferent fibres.

(*b*) That decussation of the optic nerves is almost, but not quite, complete.

(*c*) That crossed retinal fibres terminate in the lateral geniculate nucleus, in the nucleus geniculatus pretectalis, in the nucleus lentiformis mesencephali, in the superficial layers of the optic tectum (including the stratum zonale) and in the nucleus opticus tegmenti. A few may also end in the nucleus pretectalis.

(*d*) That the basal optic root is composed entirely of crossed retinal fibres.

(*e*) That uncrossed retinal fibres form a small fascicle on the outer surface of the optic tract, some probably having connexions in the rostral thalamus with the pars ventralis of the lateral geniculate nucleus.

(*f*) That as the optic tract runs on the lateral surface of the thalamus it contains in its deeper part numerous non-retinal fibres. Many of these appear to cross in the ventral supraoptic decussation.

4. The organization of the visual system in *Lacerta* has been compared with those in Amphibia and mammals. The possibility of homology has been discussed, with special reference to the lateral geniculate nucleus.

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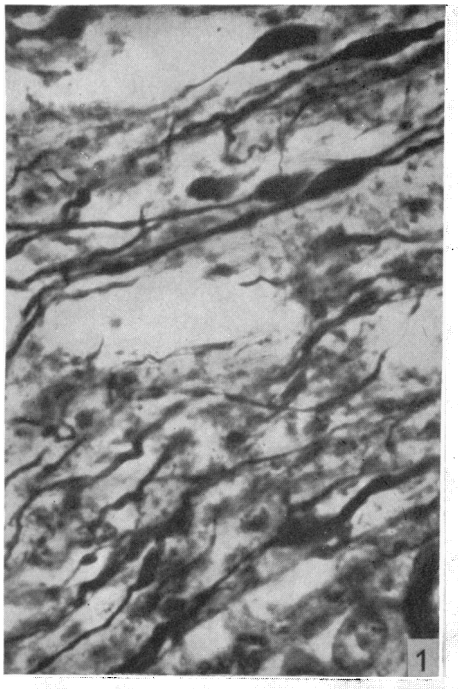
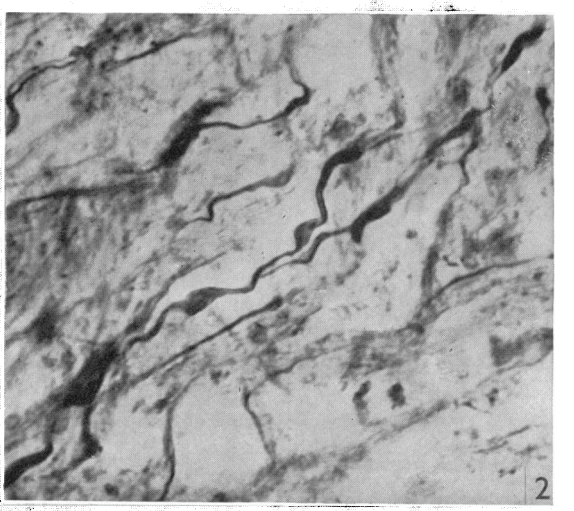
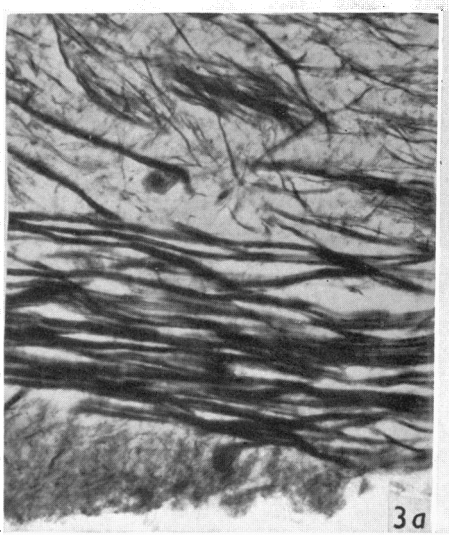
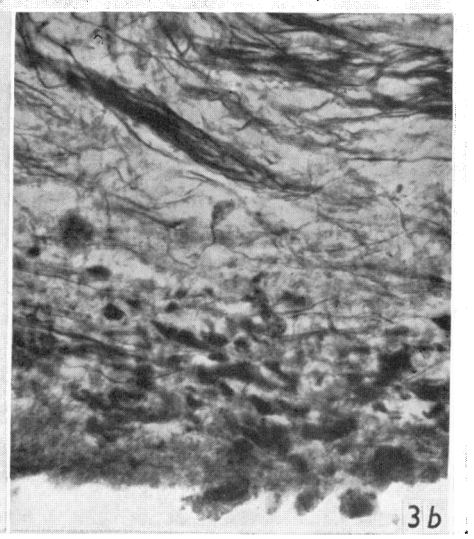
## ABBREVIATIONS

| | |
|---|---|
| *Bas.opt.rt.* | Basal optic root |
| *Col.inf.* | Colliculus inferior |
| *Dec.supraopt.dors.* | Decussatio supraoptica dorsalis |
| *Dec.supraopt.vent.p.dors.* | Decussatio supraoptica ventralis pars dorsalis |
| *Dec.supraopt.vent.p.vent.* | Decussatio supraoptica ventralis pars ventralis |
| *Fas.gen.desc.* | Fasciculus geniculatus descendens |
| *Fas.gen.pret.desc.* | Fasciculus geniculatus pretectalis descendens |
| *L.F.B.* | Lateral forebrain bundle |
| *n.* III | Nervus occulomotorius |
| *n.* IV | Nervus trochlearis |
| *N.dors.lat.ant.* | Nucleus dorsolateralis anterior |
| *N.dors.med.ant.* | Nucleus dorsomedialis anterior |
| *N.gen.lat.* | Nucleus geniculatus lateralis |
| *N.gen.lat.(lat.)* | Nucleus geniculatus lateralis (lateral neuropil) |
| *N.gen.lat.(med.)* | Nucleus geniculatus lateralis (medial cell plate) |
| *N.gen.lat.p.dors.(med.)* | Nucleus geniculatus lateralis pars dorsalis (medial cell plate) |
| *N.gen.lat.p.vent.(med.)* | Nucleus geniculatus lateralis pars ventralis (medial cell plate) |
| *N.gen.pret.* | Nucleus geniculatus pretectalis |
| *N.gen.pret.(lat.)* | Nucleus geniculatus pretectalis (lateral neuropil) |
| *N.gen.pret.(med.)* | Nucleus geniculatus pretectalis (medial cell plate) |
| *N.lent.mes.* | Nucleus lentiformis mesencephali |
| *N.opt.teg.* | Nucleus opticus tegmenti |
| *N.paravent.* | Nucleus paraventricularis |
| *N.perivent.hyp.* | Nucleus periventricularis hypothalami |
| *N.post.* | Nucleus posterodorsalis |
| *N.pret.* | Nucleus pretectalis |
| *N.rot.* | Nucleus rotundus |
| *N.supraped.* | Nucleus suprapeduncularis |
| *N.vent.* | Nucleus ventralis thalami |
| *Tect.opt.* | Tectum opticum |
| *Tr.opt.* | Tractus opticus |
| *Tr.opt.(deg.)* | Tractus opticus (degenerate) |
| *Vent.lat.* | Ventriculus lateralis |

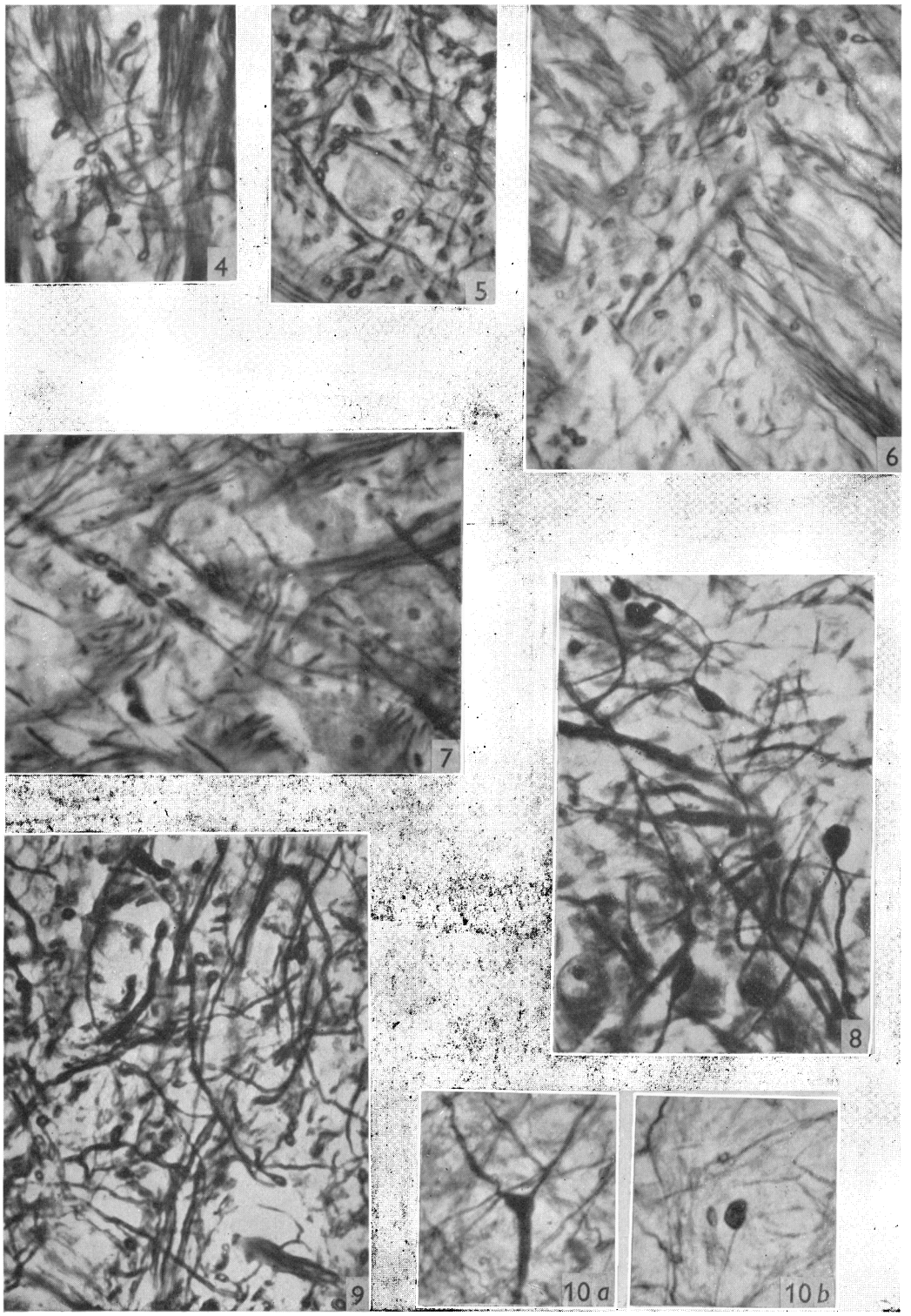



ARMSTRONG—STUDY OF THE VISUAL PATHWAYS IN A REPTILE (*LACERTA VIVIPARA*)

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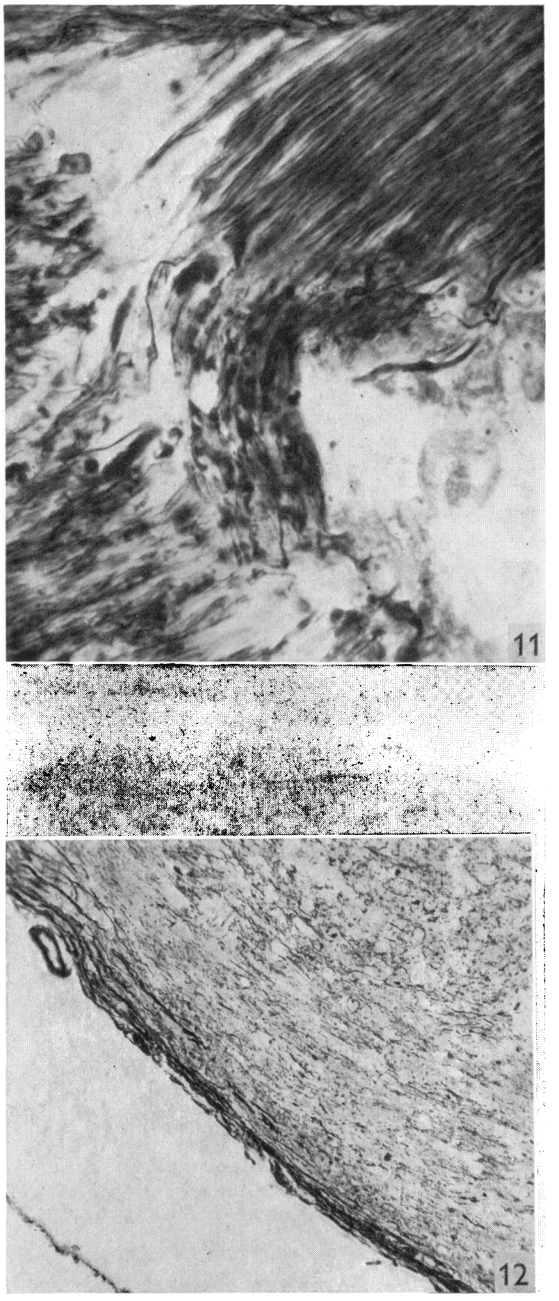


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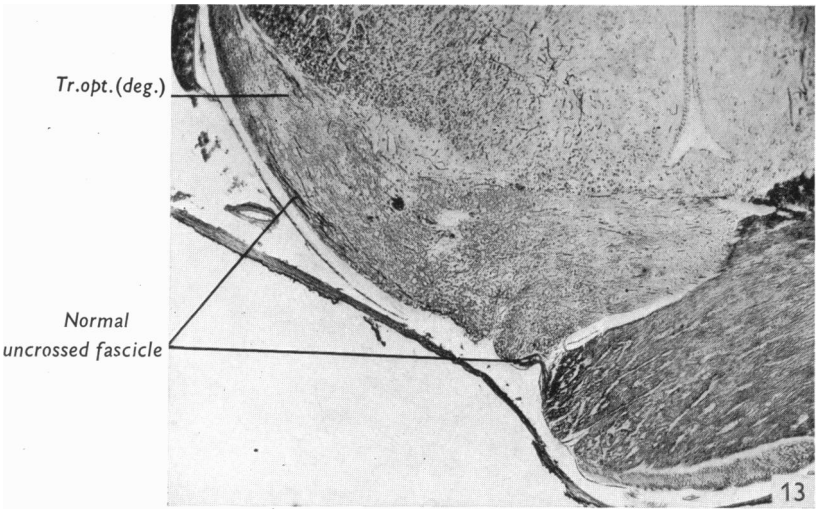
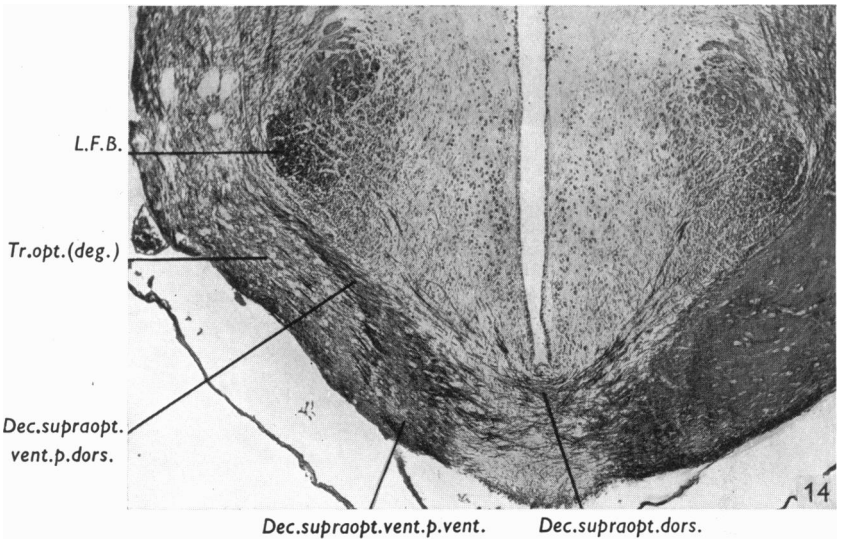

Tr.opt.(deg.)
Normal
uncrossed fascicle
13


L.F.B.
Tr.opt.(deg.)
Dec.supraopt.
vent.p.dors.
14
Dec.supraopt.vent.p.vent.
Dec.supraopt.dors.

## EXPLANATION OF PLATES

### Plate 1

Fig. 1. Axonal degeneration in the right optic tract 15 days after removal of the left eye. The fibres are tortuous, and present irregular and fusiform swellings. Degeneration vacuities are to be seen in the upper part of the field. Nonidez' method. ( × 1340.)

Fig. 2. Axonal degeneration in the right optic tract 25 days after removal of the left eye. Short lengths of distorted axon are seen to be fragmenting. Nonidez' method. ( × 1340.)

Fig. 3. Sagittal sections of (*a*) the left basal optic root, and (*b*) the right basal optic root, 15 days after removal of the left eye. The homolateral tract is normal; the contralateral tract shows advanced degeneration. Nonidez' method. ( × 750.)

### Plate 2

Fig. 4. Terminal rings in the lateral neuropil of the lateral geniculate nucleus 7 days after removal of the opposite eye. One ring shows thickening and a single bulb is seen in the lower part of the field. Nonidez' method. ( × 1340.)

Fig. 5. Rings and bulbs in the lateral neuropil of the lateral geniculate nucleus 12 days after removal of the opposite eye. Some rings are seen in relation to a cell body (cytoplasm unstained). Nonidez' method. ( × 1340.)

Fig. 6. Terminal degeneration in the lateral neuropil of the lateral geniculate nucleus (pars ventralis in the rostral thalamus) 13 days after removal of the opposite eye. Note the profusion of rings and bulbs, and the increased proportion of the latter. Nonidez' method. ( × 1340.)

Fig. 7. Terminal degeneration in the nucleus lentiformis mesencephali 13 days after removal of the opposite eye. Rings and bulbs are applied to a process of a large fusiform cell. Nonidez' method. ( × 1340.)

Fig. 8. Large terminal bulbs in the nucleus opticus tegmenti 13 days after removal of the opposite eye. Nonidez' method. ( × 1340.)

Fig. 9. Terminal rings and bulbs in the stratum fibrosum et griseum superficiale of the optic tectum 13 days after removal of the opposite eye. Nonidez' method. ( × 1340.)

Fig. 10. The stratum zonale of the optic tectum 20 days after removal of the opposite eye. (*a*) Terminal optic fibre swollen at the point of division. (*b*) Large terminal bulb. Nonidez' method. ( × 1340.)

### Plate 3

Fig. 11. Degenerating fascicle of uncrossed retinal fibres turning on to the outer surface of the homolateral (normal) optic tract. Left eye removed 13 days previously. Nonidez' method. ( × 940.)

Fig. 12. Persisting fascicle of normal uncrossed fibres on the outer surface of the degenerate optic tract 11 weeks after removal of the opposite eye. Nonidez' method. ( × 200.)

### Plate 4

Fig. 13. Transverse section of optic chiasma of the grass snake (*Natrix*) 19 weeks after removal of an eye. Uncrossed retinal fibres are seen as a normal fascicle turning on to the outer surface of the degenerate optic tract. Nonidez' method. ( × 85.)

Fig. 14. Transverse section (*Lacerta*) just caudal to the chiasma 11 weeks after removal of the left eye, showing the disposition of the supraoptic decussations. Nonidez' method. ( × 80.)