NOTES ON THE LATERAL EYES OF SPHENODON
WITH SPECIAL REFERENCE TO THE
MACULAR REGION

BY

IDA MANN

LONDON

The unique zoological position of the Tuatera (Sphenodon punctatus) and the fact of its increasing rarity and probable imminent extinction render any opportunity for its investigation of the greatest interest. Its anatomy and the general lines of its development are at present well known (Dendy, Howes and Swinnerton, etc.) as are also the main facts concerning the structure of both its parietal and its lateral eyes. It has, however, been my good fortune recently to examine a living specimen and to be able to correlate the ophthalmoscopic and slit-lamp appearances of its lateral eyes with histological specimens, both embryonic and adult. It therefore seems worth while to record my findings, which are in the main confirmatory of the work of other observers. As far as I can discover, no previous published record of the intra-vitam examination of the eye exists. The most complete account of the histology of the adult retina is that of Bage. The findings of this observer (whose material I have had the opportunity of examining) are given in a detailed paper published in 1912. This paper should be consulted since I am in complete agreement with its conclusions and do not intend to deal minutely here with the ground covered in it. The observations of
Osawa (1898) on the retina of Sphenodon appear to be inaccurate, possibly owing to the poor condition of his material, since he states, among other discrepancies, that no distinct area centralis (or macula lutea) could be found. A year later, however, Kallius corrected this mis-statement by describing and photographing a well-marked fovea, though the state of preservation of his material also left much to be desired. Bage has since (1912) confirmed and extended this work by a detailed description of the fovea in a perfectly fixed specimen.

The present communication is intended to deal mainly with those points which can be observed in the living eye and their histological and embryological confirmation. A short account of the animal itself will first be given, followed by a description of the living eye.

The Animal

The Sphenodon is the only extant representative of the third order of the Reptilia, the Rhynchocephalia. It thus occupies an intermediate position between the tortoises and crocodiles (Testudinata and Loricata) on the one hand and the lizards and snakes (Sauria and Serpentes) on the other. It is at the present time only to be found on a few islets in the Bay of Plenty, New Zealand (N. Island). The animal nests in a large burrow (2 ft. by 1 ft. and 6 ins. high). This it shares as a breeding place with a petrel, the nest of the bird being usually on the right of the chamber, that of the Tuatera on the left. The eggs of the latter (8-10 in number) are laid in the early summer. Development proceeds for about five months and then comes almost to a standstill till the following spring when it recommences and hatching takes place about mid-summer. The earlier embryonic stages resemble those found in tortoises, the more lizard-like characters being acquired relatively late. The embryos are marked with longitudinal and transverse bands of grey and white, while the adults are variable. The animal has been described as the most generalised of living reptiles. Superficially it resembles a lizard but possesses well developed abdominal ribs. There is geological evidence to show that an aquatic form was once widespread throughout North America and Europe. Fig. 1 gives a rough idea of its general appearance. The specimen I examined had a total length of 44 cm. from the snout to the tip of the tail. The head was 8·5 cm. long, the body 17·5 cm. The skin is of a greenish mud colour and is covered with small tubercles and scales. There is a low crest extending from the neck to the tip of the tail. There are no external ears. The eyes are placed laterally, the angle between the optic axes being 160° or more. On the top of the head is a raised spot of a lighter colour marking the site of the parietal eye. This becomes obscured or converted into a depression with
The organ is covered with skin and cannot be seen except on dissection. With regard to the primitive characters and geological antiquity of Sphenodon, Howes and Swinnerton in their monograph on the skeleton state that it "must be regarded as the surviving representative of that group of animals ancestral to all the living Sauropsida and to at least, the Dinosauria, Pterodactyla and Ichthyosaurus of the past."

**The Eyes.**—The eyes are provided with thick moveable lids covered with greenish brown scales. The palpebral aperture is 13 mm. from side to side, and, when the eye is open, 4 mm. from above downwards at its widest part. Since the diameter of the cornea is 5 mm. or slightly more, it follows that the upper and lower corneo-scleral junction is never exposed, and the iris is never seen complete. At the inner and outer canthus a triangular area of ocular conjunctiva is exposed. This is pale green in colour, and is covered with fine capillaries having pale brown walls. The pupil reacts well to direct illumination, changing from a circle to a vertical slit. There does not appear to be any consensual reaction.

**Appearances seen by Focal Illumination.**—The cornea was extremely transparent and completely avascular. Practically no structures could be made out in it. The appearance of the iris is indicated in Fig. 2. The deepest layer of the stroma is a shining silvery buff, but this is only visible in a few very small patches as it is mostly overlaid by splashes of a rich coppery red metallic pigment,
which is in turn obscured in some places by a superficial layer of thin chocolate coloured tissue. The vessels all stand up from this layer in high relief, which becomes more marked towards the pupil, where many of the loops project almost perpendicularly from the surface of the iris. The walls of the vessels are densely coated with chocolate pigment, mixed here and there with the coppery pigment of the stroma. No individual pigment cells are distinguishable, nor is the direction of the circulating blood or its colour anywhere seen.

Fig. 2 shows the arrangement of the vessels. They are all roughly of the same calibre, no distinction being possible between arteries, veins and capillaries. At the margin of the pupil is a narrow flat dark brown zone, which appears to be avascular. Peripheral to this is an anastomotic arcade of large irregular vascular loops, fed by a network of vessels covering the rest of the iris. These vessels, though anastomosing freely, run for the most part a course from above downwards in the upper half of the iris and from side to side in its lower half. The lens appears highly curved and extremely translucent. The shagreen is easily visible but no sutures could be made out. The vitreous could not be seen.

Ophthalmoscopic Examination.—The fundus reflex was a pale silvery green. The details of the fundus (Fig. 3) were very easily seen with an electric ophthalmoscope, the refraction being hypermetropic.

The optic disc was situated below and to the nasal side of the posterior pole. It was slightly kidney-shaped, its long axis vertical, and its concavity towards the temporal side. It was white in colour, with some greyish areas in the centre and round the edges. In the centre were a very few red capillaries, arranged in small loops (see Fig. 3) and not extending to the edge of the disc. There is no pecten.

The nerve fibres can be easily seen radiating from the disc. They
LATERAL EYES OF Sphenodon

have a silky sheen, most marked near the disc and becoming gradually less visible as they pass to the periphery. They are non-medullated and are much more easily seen than are those of mammals, possibly because of the greenish background. Their arrangement is interesting, being almost exactly similar to that found in man. On the nasal side of the fundus they radiate evenly from the disc, while on the temporal side they sweep round in a curve above and below the posterior pole, leaving a very definite area centralis in the situation of the human macula, and meeting in the beginnings of a temporal raphé outside this. The area centralis, although the macula itself was not easily seen, shows modification from the rest of the fundus, being darker in colour and more stippled. The general fundus colour is a speckled greyish green, shading into a browner tint at the posterior pole. The whole retina is covered with minute reflecting dots, almost exactly like Crick's dots, and probably caused by the same structures (Müllerian foot-plates). There are no vessels in the retina, and the choroid is nowhere visible through it.

Comparison of the intra-vitam appearances of the eyes of Sphenodon with those of allied reptiles.—In its ocular structure, as

FIG. 3.
Fundus oculi of Sphenodon.
in its general anatomy, Sphenodon occupies an interesting intermediate position between the Loricata and the Sauria. The main characters to be considered (shape of pupil, vascular pattern and pigmentation of iris, optic disc and type of fundus) illustrate very well its reputation as a "generalised reptile." In the first place, like the crocodiles and most of the geckos, it possesses a vertical pupil. This is bi-convex in form, not showing any of the specialisations (diamond-shaped openings, umbraculae, etc.) found for example in Gekkonidae and Lacertidae. Secondly, the vascular pattern (an easily visible anastomosing radial network) is intermediate between the crocodile type, in which an irregular net is present deeply embedded in opaque stroma, and the true lizard type in which the superficial radial net is seen to be composed of veins only, the arteries of supply running circumferentially and on a deeper plane. In Sphenodon these circumferential iris arteries appear to be absent. In sections of the adult eye the stroma deep to the large vessels of the network was practically avascular. At the root of the iris there were large capillaries in contact with the pigment epithelium and in the ciliary region a thick walled circumferential artery could be made out. It appears likely, therefore, that the iris vessels arise directly from those of the ciliary region and not from inferior and temporal iris arteries such as are found in most lizards. The iris pattern of Sphenodon therefore resembles most closely that of the crocodiles and the skinks, in which latter family also these arteries are in many species, but not all, invisible. (It should be mentioned that in many snakes also a vertical pupil is present with an irregular network of vessels, arteries being indistinguishable from veins.) In Sphenodon the vessel walls are pigmented and neither the colour of the blood nor its direction of flow can be seen. This is also the case in crocodiles, in a few skinks and lizards and in most snakes.

With regard to the presence of metallic pigment in the iris stroma one can only say that this is a general character, occurring throughout the Amphibia and Reptilia, the most notable exceptions being some of the crocodiles, skinks and snakes. As it is found in even greater abundance in amphibians than reptiles it may be accounted primitive.

The fundus oculi of Sphenodon affords a very good example of a primitive unspecialised type. In the first place its greenish silver colour, shewing the presence of a tapetal layer, is a far commoner background among the vertebrates than is the orange red of the human type. Secondly, the absence of a pecten is of interest. This structure is in all probability a specialised development of the proximal end of the hyaloid artery, correlated with an increasing functional efficiency of the eye. It is found in its most simple form in lizards, and becomes extremely elaborated in birds. It is absent
in crocodiles and amphibians. Rudimentary traces of it occur in some of the lowest mammals (Marsupials) only. In Sphenodon the arteria centralis retinae (developed from the proximal end of the hyaloid) is present in a rudimentary and unspecialised form (i.e., a few small branches not extending beyond the disc itself). The same condition occurs in crocodiles and alligators and even in some of the lower mammals. Two diverging lines of specialisation appear to be possible from this primitive vascularisation of the disc, the one culminating in the pecten of the bird, the other in the retinal blood supply of the higher mammals.

The arrangement of the nerve fibres is interesting as it shows that the human arrangement (radial on the inner side, and sweeping round to a temporal raphé on the outer) is also the primitive one and may well be the fundamental vertebrate arrangement although it is not universal. In some of the Marsupialia (e.g., Rat-kangaroo, Perameles) the arrangement is entirely radial, no area centralis being recognisable (Lindsay Johnson7). This should probably be looked on as degenerate rather than primitive. The region of specialised relatively invisible fibres from the posterior pole may well be looked on as the papillo-macular bundle. It is noteworthy that approximately the same extent of the temporal side of the disc is occupied by these fibres in Sphenodon as is taken up by the macular fibres in man. It is thus obvious that specialisation of the posterior pole for form vision begins much lower in the animal scale than was at first thought. It is actually not surprising to find in the ancestor of the Pterodactyls the presence of that macular area which reaches such a high degree of elaboration in its modern avian descendants.

Histological Confirmations. In view of the interesting intra-vitam appearances of the eyes of Sphenodon, especially those of the fundus, it was thought advisable to attempt some histological corroboration. Through the courtesy of Professor Doris Mackinnon, to whom I wish to tender my thanks, I was enabled to examine the valuable material collected by the late Professor Dendy. These specimens had also formed the basis of Miss Bage’s work on the retina mentioned above. The preparations which proved of most value to me were those of the adult eye, and of two advanced embryos (Stages R and S in Dendy’s classification) cut serially, the one transversely, the other longitudinally. A short description of these specimens will now be given.

Histological appearances of the Adult Eye

The Sclerotic, like that of many of the lower animals, is in its greater part cartilaginous. This cartilage (hyaline) forms a thin sheet, which ends anteriorly at the corneo-scleral junction by bifurcating into two thin layers separated by a small amount of
fibrous tissue. Posteriorly it exhibits a large fibrous area in the region of the nerve entrance.

The Cornea.—This is thin. The stratified epithelium on its surface is of three layers only in most places and the cells are large. Bowman's membrane can with difficulty be recognized as a fine refractile line. The substantia propria contains very few cells. Descemet's membrane is extremely thin, and the endothelial cells covering it are large and flattened, and approximate in appearance much more to the typical endothelial cell than do their more specialised homologues in the corneae of mammals.

The Choroid forms a thick, deeply pigmented and richly vascular layer. The innermost layer (chorio-capillaris) is composed of large capillaries closely packed together. This layer is not pigmented, but is embedded in fine fibrous tissue (? tapetal layer). The membrane of Bruch is well marked. The next layer is composed of vessels of varying calibre, many of them extremely large. It is not strictly possible to divide this layer into an intermediate and an outer layer, though doubtless both these typical layers take part in its formation. This portion of the choroid is deeply pigmented. The lamina suprachoroidea is represented by a thin avascular layer of loose pigmented connective tissue in direct contact with the cartilaginous sclerotic.

The Angle of the Anterior Chamber.—Unfortunately most of the preparations were somewhat torn here, so that the exact relationship of parts was not certain. Detailed investigation of this region was not therefore considered. It was possible to make out that the angle was well open and the ligamentum pectinatum well marked and pigmented. A large vascular channel (canal of Schlemm) could be seen in relation with the bottom of the angle. This contained blood cells, which is in keeping with the observation that during life in many reptiles (especially snakes) circulating blood can be seen in this channel with the slit-lamp. This had not, however, been observed in the living Sphenodon.

The Ciliary Muscle.—The longitudinal portion of this could be easily seen. It was composed of striped muscle. The exact relations of its insertion were disturbed in most of the specimens. The circular fibres were not seen.

The Ciliary Processes.—These were very small and scarcely more vascular than the choroid. They were covered by two layers of epithelium, the outer only pigmented.

The Ciliary Nerves were large and medullated. They ran forward external to the ciliary muscle fibres. A very large circumferential nerve trunk could be seen running round the root of the iris on its anterior surface just in front of the bottom of the angle. This trunk (the connective tissue septa of which are pigmented) gave branches of supply to the muscles of the iris and possibly also to the walls of
LATERAL EYES OF SPHENODON

its blood vessels, though this could not be made out with absolute certainty.

The Iris. This is composed of the following layers from the deep surface forwards.

(a) Two layers of pigmented epithelium in apposition. Some proliferation of the anterior of these two layers was visible near the pupil margin.

(b) A layer of longitudinally arranged cells, continuous with the tapetal layer of the choroid. Possibly some unstriped muscle was present in this layer but no differential staining had been used. This layer was not vascular except just at the root of the iris where ciliary capillaries extended into it (Fig. 4). It was not pigmented.

(c) The stroma. This was composed of a very loose tissue, resembling in places unstriped muscle, in places connective tissue. It was continuous with the sphincteric condensation at the pupil margin and also contained pigment cells, these being more numerous in its anterior than its posterior part. It is practically avascular, but contains medullated nerves. The layer is limited anteriorly by a thin pigmented layer which supports the most anterior layer.

(d) The layer of large superficial vessels. These vessels, seen mostly in transverse section in Fig. 4, are large, thick walled and deeply pigmented. They stand up in high relief from the surface of the stroma and many of them are actually free in the aqueous in front of this. There is no limiting endothelial layer separating either the vessels or the stroma from the aqueous. (Raised vessels with pigmented walls are common throughout the Reptilia).

The Retina.—For a detailed account of this structure Bage's paper should be consulted. She states that the macula is situated 3.5 mm. from the optic disc and that the fovea is 136μ deep at its
centre. The retina is thickest in the macular region (306μ) and decreases evenly towards the ora serrata (Pars ciliaris 17μ).

The retina is completely avascular though capillaries are present on the disc. The retinal layers are essentially the same as in all vertebrates. Fig. 5 shows the structure of the macula. It will be seen that it resembles that of man very closely indeed, the main difference being that the layer of bipolar cells shows greater representation.

No rods are present in the retina of Sphenodon (Gamgee\(^8\) has stated that rods are absent throughout the Reptilia) but the cones are of several distinct kinds, both single and double, large and small. They are very long and thin in the fovea.

**Embryological Considerations**

The embryological stages of the Sphenodon macula have not, so far as I am aware, been described, and the examination of Professor Dendy’s stages R and S was undertaken primarily from this standpoint.
**LATERAL EYES OF SPHENODON**

**Embryo of stage R.** This specimen, which was cut transversely, is at the end of the organogenetic period. The eyes are large and occupy a considerable portion of the head, although they are smaller in proportion than would be the eyes of a chick embryo of a corresponding age. The sclera is already cartilaginous in the greater part of its extent although the anterior bifurcated portion is still fibrous. The cornea is very thin and is in close apposition to the anterior surface of the lens. The lens capsule is present. Secondary lens fibres are beginning to form and the annular pad is recognisable. There are no vessels in the vitreous nor is there a hyaloid artery or vascular capsule to the lens. The lid folds are present but are separated by a considerable area.

With regard to the retina one can say that over the greater part of its extent its stage of differentiation corresponds to that seen in a 110 mm. human foetus. That is to say that the three layers of nuclei (ganglion cells, inner and outer nuclear layers) are separate and distinct, but that the inner nuclear layer is still obviously divided into two layers by the transient fibre layer of Chievitz. This is only recognisable as an extremely narrow gap and by the fact that the nuclei internal to it do not take the stain quite so deeply as do those external to it. At the posterior pole the transient fibre layer is more easily recognisable than it is in the equatorial and anterior regions. This points to the beginning of that retardation of differentiation which marks the future macular region in the human embryo from the fifth month onwards. In Sphenodon also the macular region is recognised at this stage, both by the persistence of the transient fibre layer and by the slightly greater thickness of the retina here. This stage was the earliest of the Sphenodon series in which I could find any indication of the position of the future macula. Its earliest appearance therefore, resembles in this animal that already well known in man (190 mm. stage approx.).

**Embryo of Stage S.** This specimen was cut longitudinally, and the macular region could be easily identified. Fig. 6 shows the appearance of a model reconstructed from the sections and then cut transversely through both eyes. It will be seen that the maculae are visible as raised circular areas in each fundus, situated above and to the temporal side of the disc. They appear to become displaced downwards later by subsequent growth of the eye. In this model the optic disc lies considerably nearer the lower pole of the eye than it does in the adult. This is merely an expression of the late development of the lower part of the optic cup which is found through the whole range of vertebrate embryos. Microscopically this embryo shows a slight advance on Stage R. The lid folds are almost in apposition and all the tissues are consolidating. In the retina the transient fibre layer of Chievitz is only recognizable
Model of Sphenodon embryo (Stage S).
1. Lateral view of head.
2. Transverse section of model along line A. M=macular prominence in each eye.

at the posterior pole. The macular elevation is now extremely marked. Fig. 7 shows two strips of retina (at the same magnification) taken (A) in the equatorial region and (B) at the macula. It will be seen that the increase in thickness of the second involves the nuclear layers much more than the fibre layers. The level of the transient fibre layer can be seen more easily in B than in A.

Unfortunately this was the latest developmental stage available for examination so that it is not possible to state the exact time at which the macula assumes its excavated appearance and its final adult characteristics. It seems however fairly certain that its early stages resemble those of the developing human macula in a striking manner. This, together with the arrangement of the fovea and its nerve fibres in the adult justifies us in drawing a very close parallel between the posterior pole of the eye in the two cases. It may appear remarkable that two species so widely separated as the
Primates and the Rhynchocephalia should show such strong resemblance in both embryonic and adult structure in what might have been considered as one of the most highly specialised regions of the body. The fact may possibly be interpreted as showing in the first place how early is the appearance of a retinal area specialised for form vision, or secondly, the human macula may be added to the lengthening list of man’s primitive characters. It is interesting to note how on the one hand we find in birds extreme elaboration of the macula, and extension and even multiplication of the site, while, on the other hand, in most mammals (excluding the Primates) there is
either absence of the fovea altogether, or extreme simplification. It is as if the primitive potentialities for accurate form vision fell into abeyance in the lower mammals only to be re-established again with the acquisition of binocular vision. That the position of the eyes had originally nothing to do with the specialisation of a fovea is obvious from its presence in Sphenodon, which cannot have any binocular vision at all, in birds in which both binocular and unio-

cular vision is found, and in the Primates with true binocular and stereoscopic vision. The abeyance of the fovea in the lower mammals is therefore probably not a correlate of the position of their eyes, but rather of the subsidiary part played by vision which in them is over-shadowed by the rise in importance of the sense of smell. Thus the microsmatic visual human type comes to resemble the primitive ancestor more closely than its own nearer relations.

In all probability further research will reveal that the presence of a well formed fovea centralis is of more common occurrence among reptiles than is now supposed. According to Ovio9 the crocodile shows a specialised area centralis, while Detwiler and Laurens10 have described a definite fovea in an American Agama, Phrynosoma cornutum. Few observations appear to have been made on the subject. I have myself been able to corroborate Ovio's observation on the crocodile, by ophthalmoscopic examination of a young specimen at the London Zoo. The specialisation of the temporal side of the retina was well marked. The reflex from it was greater, the nerve fibres appeared finer and not so easily visible, nor were they arranged in so regularly radial a manner as on the nasal side. No fovea could be seen, nor any true temporal raphé. On the other hand I was able to see ophthalmoscopically a definite macula lutea with fovea centralis in the living eye of a skink, Tiliqua scincoides. This animal has a small conical pecten, with some visible nerve fibres radiating from its base. Well above and slightly to the temporal side of the pecten is a small bright shining spot, the fovea, with a reflex radiating from it suggesting the macular reflex, but seen as a sector, not as a complete circle. No arrangement of nerve fibres in the region could be made out. The appearance was seen in the eyes of two healthy adult specimens, and is probably normal.

BIBLIOGRAPHY


WOUNDS OF THE POSTERIOR CHAMBER OF THE EYE

PART I

FIFTY-THREE cases of wounds of the sclera and other coats of the eye exposing the vitreous, were collected chiefly from Sir John Parsons' clinic at Moorfields; of these eighteen were in the region of the limbus and thirty-five were purely scleral wounds. The period covered was from 1905 to 1931. The above numbers do not include sixteen cases where the injury was so extensive that immediate excision was the only possible treatment.

In the present investigation special attention was paid to the question of immediate infection. It was found that no case of acute infection was observed when the wound was scleral exposing the vitreous. Threatened sympathetic ophthalmitis occurred in five cases, four of which were injuries in the region of the ciliary body, and one was scleral. This is in accordance with the accepted view of the greater liability to sympathetic infection in the case of wounds involving the ciliary region.

Nature of the Injuries. The majority of the injuries were produced by hot fragments of steel. Four were caused by splinters of glass and one of stone. In two cases the injury was due to direct blows from a spanner. Small pieces of steel are usually sterile and rarely convey bacteria into the interior of the eye. At the same time a prolapse or exposure of vitreous to any organisms which may be present in the conjunctival sac is effected. In one case there were