

On the retina of amphibia and reptiles / by J. W. Hulke.

Contributors

Hulke, J. W.
University College, London. Library Services

Publication/Creation

[London] : [Anatomical Society Of Great Britain And Ireland], [1867]

Persistent URL

<https://wellcomecollection.org/works/vwh2xjnf>

Provider

University College London

License and attribution

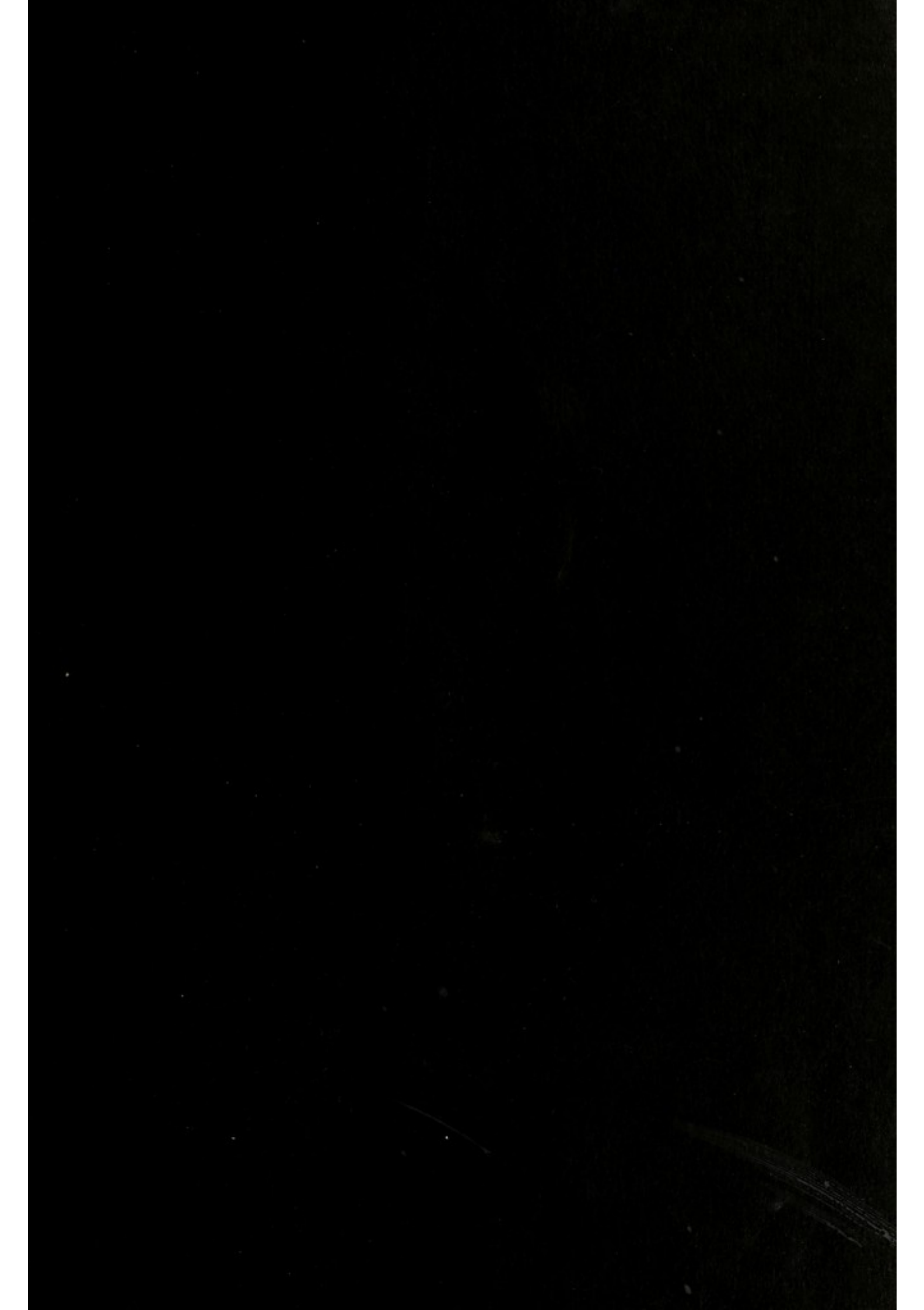
This material has been provided by This material has been provided by UCL Library Services. The original may be consulted at UCL (University College London) where the originals may be consulted.

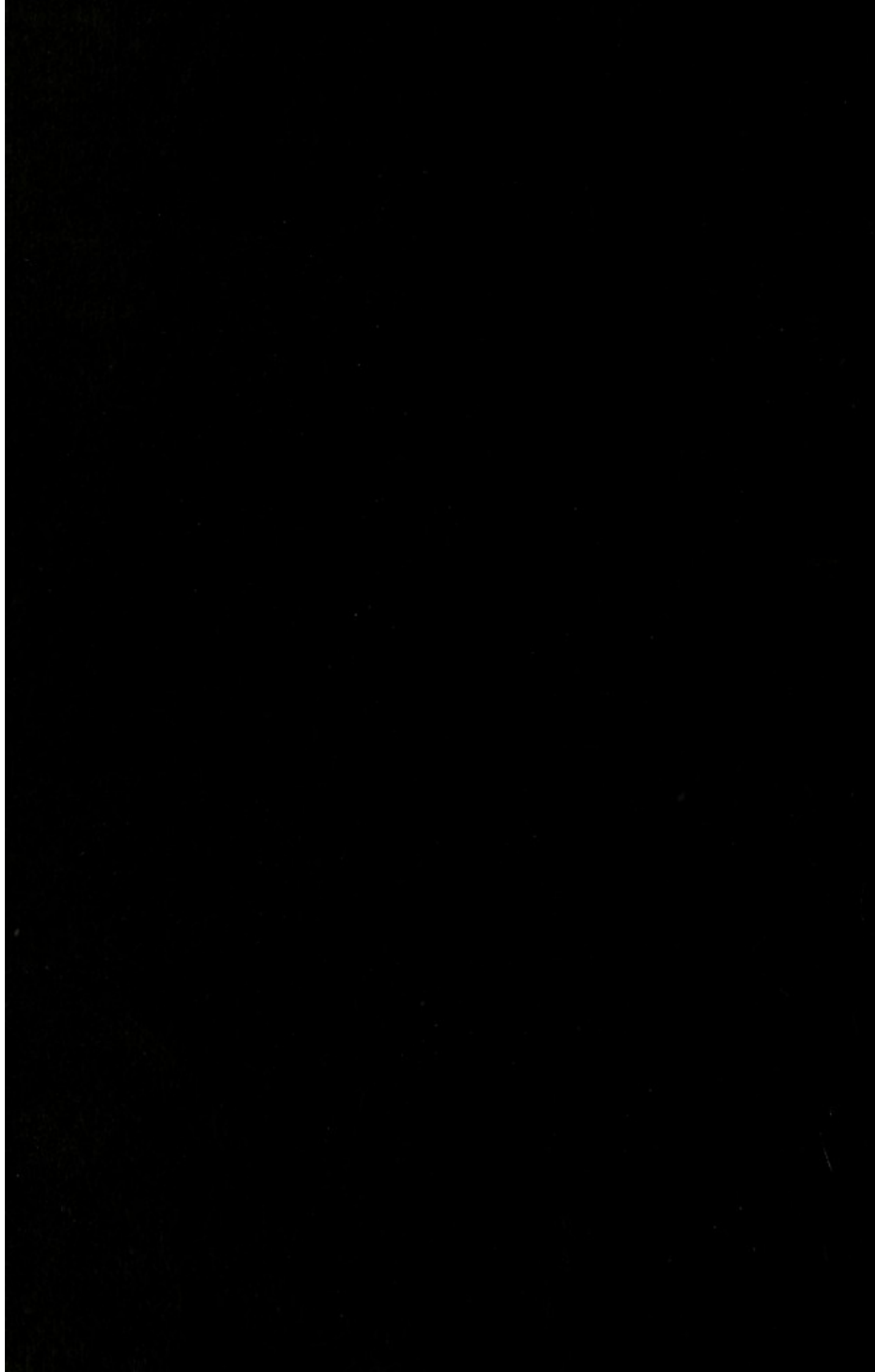
This work has been identified as being free of known restrictions under copyright law, including all related and neighbouring rights and is being made available under the Creative Commons, Public Domain Mark.

You can copy, modify, distribute and perform the work, even for commercial purposes, without asking permission.



Wellcome Collection
183 Euston Road
London NW1 2BE UK
T +44 (0)20 7611 8722
E library@wellcomecollection.org
<https://wellcomecollection.org>





13. fibres of these muscles undergo only a very slight contraction in the passage from extension to flexion of the limb, the much longer fibres of the semitendinosus are in these circumstances contracted to less than half their full length. From this it appears that the semimembranosus and biceps act chiefly in a ligamentous manner; and by the large number of their short fibres combining to maintain the required length of muscle they have great strength in their action, whether they combine with the vasti and crureus to erect the trunk upon the thigh in rising up, or convey the flexing action of the iliopsoas to the knee. The semitendinosus muscle, on the other hand, consisting of fibres few in number and with much more slender tendon than the biceps and semimembranosus, is much less fitted for bearing a great strain; but will move the knee quickly through a large area, and in this will act in company with the sartorius and gracilis.

In the bringing of these remarks to a close, another of the long muscles of the thigh, the rectus femoris, demands special notice on account of the remarkable arrangement of the superior tendon. Perhaps that arrangement, which is by no means peculiar to man, is not to be explained principally by physiological considerations; but it is at least interesting to observe that the advantage of having the fibres rather in medium than in full contraction, gained, as already said, in some long muscles by stretching of the fibres over a joint, is in this instance obtained by the peculiarity of the upper attachments. For if when the thigh is straight the anterior head of the rectus be cut, the muscle will be lengthened at least a quarter of an inch; or if when the thigh is flexed the posterior head be cut, the muscle will in like manner be lengthened. It is obvious therefore that had only one of the heads existed, there would have been a quarter of an inch more contraction of the muscle required, either in passing from the extended to the flexed or from the flexed to the extended position of the hip-joint. To gain that quarter of an inch of shortening without contraction of every fibre to that extent further than is its wont, would require the addition of probably half an inch of muscle; and that addition would require to be made to every fibre in order to be effective. The total addition of muscular action thus required would be considerable; and so also, therefore, is the saving of muscular action caused by the arrangement of the upper heads of origin.

From Tour of Anat & Phys
Vol 1 Nov 1886

L. B. Bland

ON THE RETINA OF AMPHIBIA AND REPTILES, by
J. W. HULKE, *Assistant-Surgeon to the Middlesex and Royal
London Ophthalmic Hospitals, and joint Lecturer on Physiology
in the Middlesex Hospital Medical School.*

IN this paper I have sought to embody the results of a study of the amphibian and reptilian retina begun in 1862, and comprising now *bufo vulgaris*, *rana temporaria*, *triton cristatus*, the black and golden salamander of Europe, *boa constrictor*, *natrix torquata*, *vipera communis*, *anguis fragilis*, chameleon, Spanish gecko, iguana (*tuberculata*?), *lacerta viridis*, a larger blue-spotted lizard, *testudo Graeca*, *emys* or *terrapene*, and *chelonias mydas*. In all of these animals the retina shews the following layers in regular sequence from its outer to its inner surface¹:

1. Bacillary layer = Layer of cones and rods = Jacob's membrane.
2. Outer-granule l. } Collectively these form H. Müller's and
3. Inter-granule l. } Kölliker's Körnerschicht, with its three
4. Inner-granule l. } subdivisions, and Bowman's agglomerated granules.
5. Granular l. = Kölliker's Lage grauer Hirnsubstanz.
= H. Müller's granulöse Schicht, = Bowman's grey vesicular layer.
6. Ganglionic l. = Müller's Nervenzellenschicht, = Bowman's caudate, nucleated vesicles.
7. Optic nerve l.

The plan which I have proposed to myself is to describe these layers seriatim, then to trace the continuity of the nervous and of the connective elements throughout the layers and interpret their physiological offices, and lastly to sketch the important structural modifications which mark the centre and the ora retinæ.

1. *Bacillary layer*.—In most of the animals comprehended in my study this layer contains both cones and rods, but in the chameleon, iguana, gecko, snake and viper, I found only one kind of bacillary element.

Pl. I. figs. 1—12. The cones and rods both consist of an outer and an inner segment, the former termed the shaft, the latter called the appendage or body. These parts are divided by a bright transverse line, at which the slightest force separates them. The constant occurrence

¹ In this paper *outer* always refers to the retinal surface towards the choroid, and *inner* to that towards the vitreous humour.

of the dividing line at the same height, its distinctness in perfectly fresh specimens, the evenness of the separated surfaces, the very facile separation of the segments, and their different refractive powers, speak for the normality of the segmentation and for its existence during life, and against its being merely a post mortem change.

The *shaft* (Pl. I. figs. 1—12 *a*), has sharp, hard outlines. It is a more conspicuous object than the appendage. Its profile figure is a slender rectangle (slightly tapering towards the outer end), but the actual shape is probably a cylinder or long prism. The outer end of isolated shafts is usually uneven from mutilation, but in perfect specimens it is a straight line. The inner end, which joins the appendage, is always limited by a sharp, straight line. A membranous sheath, and a contained homogeneous albuminous substance, granulated by coagulating agents, are the only natural parts recognizable. Ritter's 'axial fibre,' described from chromic acid preparations, is, I believe, the coarcted and drawn-out inner portion of the appendage, the outer portion of which is vesicularly dilated. The fibre always appears to me to pass without interruption into the contour of the vesicle, and never to lie inside this (Pl. I. figs. 3, 4). The true origin of the fibre is easily ascertained by tracing its gradual evolution through the numerous intermediate phases which occur between the stout, bulbous, and the slender-stalked vesicular metamorphoses of the appendage.

The *appendage* (Pl. I. figs. 1—12 *b*) is a pale, club-like, cylindrical or fusiform body. The outer end, that which joins the shaft, is abruptly truncated; while the inner end is either rounded, or it tapers, and it is prolonged into the outer-granule layer as a flattened ribbon or round fibre—the *primitive cone or rod-fibre*, collectively termed primitive bacillary fibres (Pl. I. figs. 8, 9 *e*).

A very constant difference is perceptible in the inner and outer parts of the appendage in perfectly fresh specimens examined instantly after decapitation of the animal, the former being less coarsely granular than the latter, which is either very finely granular or clear. This difference increases soon after death, and in chromic acid preparations the coarser granulation of the contents of the outer half is very obvious. Another difference is observable in the effect of carmine, which tinges the outer part lightly, or not at all, and deeply stains the inner.

The appendage, like the shaft, also consists of a membranous sheath and albuminous contents. In addition to this an outer-granule is always lodged in the inner end of the appendage whenever this latter is large enough to hold it (Pl. I. figs. 8, 12 *d*), and the outer end in the cones of some animals contains a bright globular bead, which always lies close to the line dividing the appendage and shaft (Pl. I.

figs. 2—12 c). Its colour is yellow or pale green in the toad, frog, triton, salamander, blindworm, and lizard; while the land and water tortoises and the turtle have also ruby beaded cones, the green beads lying in the smallest cones, the yellow in the intermediate, and the ruby in the largest. The occurrence of the cone-bead in the blindworm is interesting in connection with its other lacertian affinities. It is wanting in the common snake and viper.

Nothing is yet known of the chemistry of the colouring matter, or of the physiological meaning of these remarkable beads. I have found that rose-aniline imparts to the yellow and pale green beads the intense stain it gives the nucleus of the red blood corpuscle, and that iodine turns the ruby to mauve and the yellow to dark green. In the emys the red beads absorb the violet, indigo, blue, green, and part of the yellow rays of the spectrum to the *d* (soda) line, and transmit the remaining yellow, orange, and red rays. The yellow beads absorb the violet and other rays to about the *b* line of the spectrum, and transmit part of the green, and all the yellow, orange, and red rays. The green beads absorb the violet, indigo, and a small adjacent portion of the blue rays of the spectrum, and transmit all the rest. In short it appears that the beads absorb the rays belonging to the chemical, and transmit those belonging to the heat-domain of the spectrum¹.

Whatever other differences are held respecting the mode of visual perception, all physiologists have long agreed that the cones and rods are the sentient elements. This is concluded (1) from the absence of perception from the optic nerve-entrance, where there are no cones or rods; (2) from the unfitness of the other nervous tissues, by reason of their anatomical arrangement, to receive separate and distinct stimuli; (3) from the obvious fitness of the cones and rods by their serial arrangement in a single stratum, and their insulation, to receive distinct stimuli; (4) by the formation of a superficies by the outer ends of the shafts collectively, upon which correct images may be formed; and (5) by Purkinje's experiment, which demonstrates that the sentient elements lie at the outer surface of the retina.

Universal and decisive characters by which we may distinguish cones from rods are yet wanting, if indeed such will ever be discovered. Size, shape, and the cone-bead will not always serve us, for while the rods much exceed the cones in the toad, frog, triton, and salamander, their sizes differ little in the tortoise and turtle, and in the chameleon's central fovea the cones are as long and as slender as the most typical rods. Again, the bead, which is perfectly

¹ For the use of several spectroscopes and much valuable assistance in these observations, I am indebted to Mr Heisch.

decisive of cones when present, is altogether absent from many reptiles and from all mammalia, so that its absence does not count for anything.

The relations of the cones and rods to the choroid differ from those which obtain in the human retina, where the outer ends of the shafts simply stand on the pigment epithelium. In amphibia and reptiles the outer ends of the shafts similarly rest on the choroidal epithelium, but processes of pigment are prolonged from this inwards between the shafts, sheathing them and separating each one from its neighbour. The pigment is granular, and the grains lie in linear series, perpendicular to the choroidal surface, embedded in a soft interstitial tissue which occupies the spaces between and around the cone shafts.

My observations respecting the relations of the cones and rods to the *membrana limitans externa*, and the nature of this membrane, agree with those of Schultze. It is a fenestrated, glassy membrane, and the cone and rod-appendages perforate it, sitting in its apertures, as Schultze says, like eggs in an egg-board, and prolonging themselves at its inner surface into the next layer in the form of primitive bacillary fibres.

2. *Outer-granule layer*.—Perfectly fresh outer-granules, examined in vitreous humour, are large, circular, or roundly-oval nuclei, occasionally containing a nucleolus (Pl. II. figs. 1—4 *a*). In chromic acid preparations, besides these circular outer-granules, elliptical (myrtle-leaf) ones are not unfrequent, particularly in the salamander and frog (Pl. II. figs. 1, 2 *b*), and these have been distinguished by the name cone-granules from the belief that they are always associated with cones and never with rods. The myrtle-leaf outer-granules belong, however, indifferently to cones and rods, and are not the granules (so called) simply and solely, but they are granules sheathed in a production of the bacillary appendage which shrinks under the influence of the chromic acid (used to harden the retina preparatory to making the sections), and alters the shape of the granule which it encloses.

The number of the outer-granules equals that of the cones and rods, since each of these has one of the granules associated with it in one of two ways: either the bacillary appendage, when its size allows, includes the granule in the manner already described, or when too slender to include it communicates with it by the intervention of the primitive bacillary fibre. The closeness of this relation justifies us in regarding the outer-granules as the nuclei of the bacillary appendages.

The layer is traversed obliquely from its outer towards its inner surface, and in a direction from the centre of the retina

towards the ora by the primitive cone and rod-fibres, the obliquity of these fibres decreasing as their distance from the retinal centre increases; and it is traversed perpendicularly to its surfaces by another set of fibres which course outwards in a direction radial from the centre of the globe towards the inner surface of the *membrana limitans externa*, where they lose themselves. These are the terminations of the connective-tissue fibres, named after their discoverer, H. Müller, and the former set are nervous.

This different arrangement of the two systems of fibres was first discovered by Müller in the chameleon. I have observed it in all the animals included in this paper, but plainest in the lizards (Pl. III. fig. 1). Since it is repeated in the following layers it is of the greatest value, because it enables us to ascertain the anatomical nature of a particular fibre from its direction, and to deduce the nature of the nuclei and cells in the granule and inter-granule layers from their relations to the fibres.

3. *Inter-granule layer*.—This consists of a thin stratum of connective-tissue bounding the outer surface of the inner-granule layer (Pl. IV. fig. 2 *f*), and of a nervous plexus lying between this stratum and the outer-granule layer (Pl. IV. fig. 2 *g*).

The nervous plexus arises out of the union of the primitive bacillary fibres at the inner surface of the outer-granule layer. In the chameleon, iguana, and gecko, it is remarkably conspicuous at the centre of the retina, where it forms a very thick band, which thins out and becomes less apparent towards the ora. In chelonians the arrangement of the plexus is essentially the same, though less evident.

The general direction of the bundles of the plexus coincides with that of the primitive fibres in the outer-granule layer, and the bundles interchange in such a way that the fibres are brought from the outer towards the inner surface of the plexus. Here the bundles are again resolved into delicate fibres, which pass through the connective-tissue stratum into the inner-granule layer.

4. *Inner-granule layer* (Pl. II. fig. 6). Here, as has been mentioned, we find the same two systems of fibres, one obliquely radial from the outer towards the inner surface of the layer, and from the centre towards the ora of the retina; the other having a direction vertical to the surfaces of the layer, and radial from the centre of the globe: the first system is nervous, the second connective-tissue.

The oblique fibres have two sets of cells associated with them.

1. Small, oval, or bipolar nuclei, which lie in the finer fibres. These are more numerous, and occur everywhere throughout the layer.
2. Larger, nucleated, branched cells, receiving on the one side stout fibres, resulting from the union of the finer ones just mentioned, and

on the other side detaching fibres, which obliquely pass through the granular layer, and join the outer branches of the cells of the ganglionic layer. These larger inner-granules are less numerous than the smaller, and occur mostly near the inner surface of the layer.

The vertically radial connective-tissue fibres have long fusiform bodies in close relation with them. The first impression conveyed to the mind is that they are nodal thickenings; but more careful inspection shews that they are independent structures, perhaps homologous with connective-tissue corpuscles, closely clinging to the radial fibres by finely areolated branches.

5. *Granular layer* (Pl. IV. fig. 1 g). This keeps a more uniform thickness throughout the retina, and declines more gradually towards the ora than the other layers. At the thin edges of good sections the tissue, as Schultze pointed out, may be seen with a high magnifying power to be finely areolated. Its derivation, in great part from the radial connective fibres which run vertically through it, shews that it is a connective-tissue. The granular appearance is produced by the fineness of the net, and by the innumerable ends of the extremely delicate fibres divided in the section.

Dark bands, in which a longitudinal fibrillation is sometimes apparent, are very constantly seen in lizards, parallel with the surfaces of the layer.

The oblique nervous fibres mentioned in the inner-granule layer run through this layer also obliquely on their way to the ganglionic layer.

6. *Ganglionic layer*.—The constituents of this layer are (1) large, strongly outlined, circular nuclei, and (2) larger, branched, nucleated cells having a faint contour, and a pale, finely granulated texture (Pl. II. fig. 5). They lie between the vertically radial connective-tissue fibres.

The free nuclei so closely resemble the nuclei of the branched cells, and so frequently have fragments of tissue adhering to them which is not optically distinguishable from the tissue of the cells, that it seems probable they have escaped from cells and that all the perfect cells are nucleated and branched.

The connection of the branched cells with the nervous fibres coming through the granular layer from the inner-granule layer was mentioned in the description of this last layer. On the other side the cells detach branches which join the optic nerve fibres.

7. *Optic-nerve layer*.—The optic nerve pierces the eyeball below the axis, at its temporal side. In lizards the spot at which the nerve appears at the inner surface is marked by a well-developed conical or sword-like pecten. The boa also has a minute globular pecten (Pl. III. fig. 3), and the common viper a still more rudimentary one,

but the common snake, blind-worm, tortoise, and turtle, have none. The base of the pecten is continuous with the choroid. It is formed by a vascular plexus with a little pigmented interstitial connective-tissue; its surface is even and not plaited as in birds, and it is overlaid by a thin stratum of pigment, and by a hyaloid membrane channelled by the blood-vessels, which are distributed between the outer surface of the vitreous humour and the retina.

The bundles of nerve fibres run through the base of the pecten and radiate towards the ora in a plexus with long meshes, in such a manner that those bundles of fibres only which are distributed to the retinal centre pass directly towards this from the pecten, while those bundles proceeding to parts beyond the centre, at its nasal side, arch above and below this latter in increasingly open curves. The bundles are separated from the *membrana limitans interna* by a thin stratum of tissue identical with that of the granular layer.

The fibres resemble axis-cylinders. Fresh ones are perfectly transparent. In *chelon* their diameter is less uniform than in the lizards and snakes, and they are more varicose than in these latter animals and in the frog and salamander. The connection of the nerve-fibres and ganglion-cells has been already mentioned.

We now come to the *membrana limitans interna*, a structureless membrane which bounds, as its name conveys, the inner surface of the retina. The outer surface of the membrane gives origin to Müller's radial fibres, which arise from it by winged, decurrent expansions (Pl. IV. fig. 1 *f*); and the inner surface is so closely applied to the hyaloid capsule which encloses the vitreous humour that it cannot always be artificially separated from it.

I repeat that there are not any blood-vessels in the retina in these animals. Their absence is compensated by the close relation of the bacillary layer to the vascular choroid, and by the net of the blood-vessels in the hyaloid capsule (Pl. III. fig. 4 *e*).

My readers will now be able to follow me as I trace the continuity of the nervous and of the connective-tissues through the different layers, in doing which the different directions of the fibres prove of the utmost service.

Beginning with the nervous tissues, at the outer surface of the retina (that which is furthest from incident light), we find the sentient cones and rods, each one of which, by means of its appendage, or through the intervention of its primitive fibre, is associated with an outer-granule so intimately that we may regard this latter as the nucleus of the appendage, which we may consider a specially modified cell.

The primitive cone and rod-fibres continued from the appendages traverse obliquely the outer-granule layer, and at its inner-surface

form a plexus, which constitutes a large part of the inter-granule layer. The bundles of this plexus keep the same general direction as that of the primitive fibres, and at its inner surface break up again into fine (primitive?) fibres which run through the connective-tissue stratum of the inter-granule layer into the inner-granule layer. Here they take up the lesser inner-granules, and form a second plexus with long obliquely directed meshes. Towards the inner surface of the layer the bundles grow stouter by the union of the smaller fibres, and end in the large branched cells resembling ganglion-cells, which in turn give off other branches that run obliquely through the granular layer to the ganglionic layer, and join here the outer branches of its cells, other branches of which become continuous with the optic nerve-fibres.

Our knowledge is at present too imperfect to allow us to fix with certainty the physiological offices of all the elementary nervous tissues; for while the indications respecting some are so strong as to amount as nearly to demonstration as the case permits, with regard to others they are so weak as to be merely suggestive. The cones and rods fall in the first class; all agree that they are the sentient elements; but if we go beyond this and try to fix the meaning of each of the parts composing them, we stumble at once on great difficulties.

The high refracting power, the straight sides, and the insulation of the shafts by black pigment, suggest a physical, optical office; while the absence of these very qualities, and the presence of a nucleus (outer-granule), hint that the appendage performs a vital role. May it be that at the junction of shaft and appendage light is converted (if I may so express it) into nerve force? The absorption of the chemical rays of the spectrum by the cone-beads which lie here favours this conjecture.

If the outer-granule is rightly regarded as the nucleus of the appendage, we presume its office is the maintenance of the integrity of this latter as a living organ.

The system of oblique fibres, from its structural continuity with known nervous tissues (e.g. the cones and rods, and the ganglion-cells) must be also nervous, and its function internuncial.

It is not certain whether we ought to regard the smaller inner-granules as the nuclei of a particular segment of the oblique-fibre system, or as bipolar ganglion-cells; but the close similarity of the larger inner-granules to ganglion-cells, their relations to the stouter oblique fibres, and their connection with the cells of the ganglionic layer (by fibres running through the granular layer) indicate these inner-granules to be ganglion-cells. Since each primitive bacillary fibre represents a cone or rod, and the stouter fibres going to the

larger inner-granules are composed of several of the finer fibres, it results that each of these granules corresponds with several bacillary elements, and its inner branches serve to convey the nervous currents received from them through the oblique fibres to the cells of the ganglionic layers.

Each ganglion-cell probably communicates with more than one larger inner-granule, and through these with as many groups of cones and rods; and these relations hint that the cones and rods may be disposed in physiological groups, each of which is controlled by a ganglion-cell.

I now proceed to review the connective-tissues in the same manner as the nervous. They consist of (1) the *membrana limitans interna*, and *memb. limit. ext.*; (2) a system of fibres running vertically between these membranes, named after Müller; (3) finely areolated interstitial tissue. The limiting membranes and their relations to the other tissues and the granular layer which properly belongs to this section, have, for convenience' sake, been already described; and the origin of Müller's fibres from the outer surface of the *limitans interna* was noticed, so that it only remains to trace the general course of these fibres. They pass from the *membrana limitans interna* outwards, vertically through all the layers, and branching repeatedly, and becoming ultimately very fine, they end at the inner surface of the *membrana limitans externa*. They evidently form a frame, the office of which is to bind the layers together. In their outward course they first pass through the meshes of the optic nerve plexus, and through the ganglionic layers, where, in vertical sections tangential to the optic nerve entrance, they resemble stout pillars with arcade-like interspaces which transmit the nerve-fibres, and lodge the ganglion-cells. The arches are constructed of branches which the stout trunk-fibres detach before they enter the granular layer. Pursuing their outward course through this layer, the fibres give off within it numerous fine branches which, repeatedly subdividing and interlacing, contribute to the areolated tissue of the layer. I have found this even plainer in the turtle than in the frog, in which Schultze first described it. The designation "grey nervous layer," and others implying a nervous character, are evidently founded on error and should be discontinued. The further distribution of the fibres differs at the centre and at the periphery of the retina. In the former place most of the fibres springing from the inner limiting membrane end, in the turtle and tortoises, at the outer surface of the granular layer, where another set of vertically radial fibres (which

we may distinguish as the *outer* radial fibres) arises, principally out of the areolated tissue of this layer, and to a less extent directly from the fine terminal branches of the inner radial fibres.

These outer vertically radial fibres form a second series of arches, and forking acutely, in the same way as the inner fibres, pass through the outer-granule layer, to end at the outer limiting membrane. In lizards these outer vertically radial fibres arise out of the thin stratum of connective-tissue mentioned in the description of the inter-granule layer. Towards the periphery of the retina the fibres from the *membrana limitans interna* traverse all the layers and reach the *limitans externa*; and here the outer fibres, as a distinct set, are absent.

The interstitial tissue, which is essentially identical in structure with the granular layer, is continuous with and principally derived from the repeated subdivision of the finer branches of the vertically radial fibres. It fills the minute spaces between the elementary nervous tissues, fixing them in their several layers and preserving their stability. It possibly also insulates them, maintains the distinctness of each nervous chain between the cones and rods and ganglion-cells, and prevents the lateral discharge of the nervous current.

The Fovea Centralis, and the Ora Retinae.—Two parts of the retina differ so much in their structure from the rest as to require separate notice: these are the centre and the periphery or ora.

The first notice of the existence of the fovea centralis in reptiles which I can find is by Knox, in the *Memoirs of the Wernerian Society*, 1823, where he describes very accurately the macula and foramen centrale in the chameleon, and says he had also seen it in *lacerta superciliosa*, *l. scutata*, *l. calotes*, and *l. striata*. There was recently in the Anatomical Museum at Frankfort a preparation of the chameleon's eye with an inscription in Soemmering's handwriting describing the foramen, which proves it to have been known to this great anatomist; and there are also in the Museum of the Royal College of Surgeons two old preparations of the chameleon's eye (undated, Hunterian?), which time has spoiled, but which the catalogue says are intended to display the foramen. These preparations and Knox's memoir were overlooked by later investigators, and till very recently it was commonly taught that the macula and central fovea were peculiarities of the human retina and of that of some apes. In 1862 this error was for ever set aside by H. Müller's remarkable memoir on the chameleon's eye¹, in which he described with great exactness the macula and fovea, and the two sets of vertically and obliquely radial fibres here so conspicuously distinct.

¹ *Wurzb. Naturwiss. Ztschr.* 1862.

The large number of chameleons brought to London in 1864 gave me greater advantages than Müller, whose only material consisted of eyes which had been long in chromic acid solutions, and it enabled me, while confirming him in every essential point, to make out some particulars which he had been obliged to leave undetermined¹. Since then I have found the oblique nervous fibres, and a point corresponding to the human fovea centralis, in all the animals included in this paper. In the chameleon's retina, where the fovea is more developed than in snakes and chelonia, it is a minute, deep, circular pit in the inner surface of the retina, at the posterior pole of the eyeball. (Pl. VIII.) The centre (bottom) of the pit is a minute brown dot encircled by a lighter ring corresponding to the sides, and this, in turn, is surrounded by a colourless belt which merges gradually into the surrounding parts. The surface slopes in a rapid and uniform curve from the border to the bottom of the pit, and declines slowly from the border towards the ora retinæ, so that the foveal border is the most elevated, and the foveal centre the most depressed part of the macula.

The pit is produced by the obliquely radial deflection on all sides of the primitive cone-fibres and their prolongations from a point in the inner surface of the bacillary layer, and by the peripheral displacement of the outer and inner granules and the ganglion-cells connected with the central cones from this point.

In vertical sections laid accurately through the centre of the fovea, the optic nerve, granular, and inner-granule layers, the plexus of cone-fibres which forms the principal part of the inter-granule layer, and the inner limit of the outer-granule layer, are seen to bend outwards at the foveal border and, rapidly thinning out, to converge towards the bottom (centre) of the fovea, where they cease; only the cones, with their diverging primitive fibres embedded in a very thin stratum of finely areolated interstitial connective-tissue, occurring at this point. Reviewing the layers at the macula in their order from the outer to the inner surface of the retina, we find first the bacillary which contains cones only. These are very long, and so exceedingly slender that a superficial unit here contains more of them than at any other part, which is evidently connected with the greater visual acuity of the retinal centre, since the sensitiveness of a surface is proportioned to the number of distinct percipient elements it contains. The cones decline slightly in length, and grow slightly stouter from the foveal centre to the periphery of the macula; and hence to the ora, rapidly for a short space, and then gradually for the remaining distance, they become much broader, and shorter.

¹ Cf. a paper in the *Phil. Trans.* of the current year.

The extreme slenderness of the central cones does not allow the appendages to include their outer-granules at this part, and these latter being displaced towards the foveal border, the primitive cone-fibres passing to them from the appendages must necessarily have a correspondingly radial deflection. The result of this displacement of the outer-granules belonging to the central cones is a very rapid growth of the outer-granule layer in a peripheral direction from the foveal centre. It reaches its maximum at the foveal border, where the thickness of the layer is very remarkable, then declines slowly for about $\frac{3}{4}$ mm, and then thins out rather suddenly towards the ora. Succeeding the outer-granule layer, the remarkable plexus of the inter-granule layer formed by the cone-fibres begins in the angle between the outer and inner-granule layers near the foveal centre. Rapidly growing, it reaches its maximum thickness just beyond that of the inter-granule layer. The bundles of the plexus are obliquely deflected, the innermost least so.

The inner-granule layer closely approaches the outer at the bottom of the fovea, in consequence of the extreme thinness here of the plexus just described. At this point it is extremely thin, but, like the preceding layers, it quickly grows broader, and it attains its maximum a little way beyond that of the plexus.

The granular layer, and the granular stratum which elsewhere separates the optic nerve layer from the membrana limitans interna, blend at the foveal centre with the interstitial connective-tissue in which the central primitive cone-fibres are embedded. From this point the granular layer increases in breadth, reaching its maximum at the foveal border, and preserving this nearly to the ora retinæ. The ganglion-cells around the foveal centre lie in a single interrupted series which halfway between the centre and border of the fovea becomes a continuous band of two or three rows, while at the border the cells lie four or five deep. The layer of optic nerve fibres is not absent, as some have thought, but only very attenuated. It is possible to trace fibres nearly to the foveal centre.

The connective-tissue fibres traverse the layers vertically as they do at other places, but, owing to the curve of the inner surface of the retina at the fovea, their direction is not radial from the centre of the eyeball.

The anterior margin, or ora retinæ, is not serrated as in man, but even. All the nervous elements cease here, but the connective-tissues, in a modified form, are prolonged into the ciliary region.

The cones and rods, which for some distance from the ora have declined in length and size, suddenly altogether cease, and the outer and inner-granule layers thin out and terminate. Where the bacillary elements disappear the processes of black pigment prolonged

from the choroid in between them also cease; while the *membrana limitans externa*, approaching the choroidal elastic lamina very closely, yet separated from it by the stratum of pigment epithelium, runs forward upon the ciliary body. The attenuation of the layers towards the ora brings the inner limiting membrane closer to the outer, like which it is also produced beyond the ora. The prolongations of these two membranes in the ciliary region are separated by a very distinct stratum, which in lizards and in the emys is fibrillated vertically to its surfaces, but in the turtle it has a more reticulated structure.

A few horizontal fibres run a little way into this stratum from the granular layer at the ora, but its vertical fibres are continuous with the radial connective-tissue fibres which in the ciliary region lose their retinal characters, and become very short and relatively broad, especially their inner ends. They are often very regularly nucleated. At the tips of the ciliary processes the two membranes coalesce and form a single one, from the inner surface of which the stiff fibres of the *ligamentum suspensorium lentis* arise.

EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Two rods of the frog, $\times 1000$. In all the figures in this plate, *a* marks the shaft, *b* the appendage.

Fig. 2. Cones of the frog, $\times 1000$. In this and in the other figures in this plate, *c* marks the cone-head.

Fig. 3. Transformation of the appendages of the cones and rods forming Ritter's "axial fibres." *d*, stout club-like vesicles; *e*, stalked vesicles; *f*, line of *membrana limitans externa*. From a chromic acid preparation of the frog's retina, $\times 670$.

Fig. 4. Two stalked vesicles displaying stellated vacuoles, $\times 670$. From another part of the same preparation as the preceding figure.

Fig. 5. Rod-shafts of salamander, $\times 670$.

Fig. 6. Cones and rods of *anguis fragilis*, $\times 670$.

Fig. 7. Central cones of the chameleon, $\times 670$.

Fig. 8. Peripheral cones of chameleon, $\times 670$. *d*, the outer-granule in the inner end of the appendage; *e*, the primitive cone-fibre; *f*, *membrana limitans externa*.

Fig. 9. Cones from the macula of the chameleon. The shafts are hidden in the choroid. The letters indicate the same parts as in the last figure, $\times 670$.

Fig. 10. Cones and rods of a large green blue-spotted lizard (spe. incerta), $\times 670$.

Fig. 11. Cones of *emys* or terrapene. *r*, red; *y*, yellow beads, $\times 670$.

Fig. 12. Cones and rods of *chelonina mydas*. (The left three are the rods). *d*, outer-granule lying in the appendages; *r*, red; *y*, yellow cone-beads.

PLATE II.

Fig. 1. Outer-granules of frog; *a*, circular; *b*, myrtle-leaf granules ensheathed in appendages of the cones and rods; *d*, outer limiting membrane; *e*, connective tissue stratum of the inter-granule layer, $\times 1000$.

Fig. 2. Outer-granules of the salamander; *c*, cone or rod-appendix; *f*, primitive cone or rod-fibre, $\times 1000$.

a, *b*, *d*, *e* mark the same parts as in the preceding figure.

Fig. 3. Three cone or rod appendages with primitive fibres and outer-granules. From the turtle, $\times 1000$. The same letters are used as in the last figure.

Fig. 4. Represents a vertical section of the outer and inner-granule, and part of the granular layer of the turtle.

h, outer-granule layer; *i*, inner-granule layer; *k*, granular layer.

a, circular outer-granules; *d*, outer limiting membrane; *g*, inner-granules; *l*, a compound cone or rod-fibre of the plexus, which contributes to the inter-granule layer; *m*, a Müller's vertically radial connecting-tissue fibre.

EXPLANATION OF PLATES.

Fig. 5. A branched ganglion-cell of the turtle, $\times 1300$.

Fig. 6. Represents a vertical section through the outer layers of the retina of the gecko, $\times 670$.

a, outer-granules lying in *c*, the appendages of the cones; *b*, primitive cone-fibres; *d*, outer limiting membrane; *e*, connective tissue portion of inter-granule layer; *f*, finer oblique cone-fibres; *g*, stouter ditto, formed by the union of the finer fibres; *h*, vertically radial connective tissue-fibres (Müller's); *i*, granular layer.

PLATE III.

Fig. 1. A vertical section radial from the fovea centralis, and parallel to the bundles of the cone-fibre-plexus which forms the principal part of the inter-granule layer in this situation. *a*, oblique radial nervous bundles; *b*, vertically radial connective tissue-fibres crossing the nervous bundles, $\times 670$. From the chameleon.

Fig. 2. A vertical section through the outer layers of the retina of the common snake, near the ora, $\times 760$. *a*, cone-shafts; *b*, appendages containing outer-granules; *c*, membrana limitans externa; *d*, obliquely radial cone-fibres in the inter-granule layer; *e*, connective tissue stratum of the same layer; *f*, distant outer-granules (?) with primitive cone-fibres; *g*, inner-granules.

Fig. 3. Vertical section through the centre of the optic nerve of the boa, $\times 20$. *n*, the nerve; *p*, pecten; *v*, a blood-vessel passing out of the pecten and channelling the hyaloid capsular membrane of the vitreous humours; *r*, retina; *ch*, choroid; *sc*, sclerotic.

Fig. 4. A vertical section through the inner layers of the boa's retina, $\times 1000$. *a*, the granular layer; *b*, arcade-like spaces between Müller's fibres which contain the ganglion-cells, and optic nerve fibres; *c*, Müller's fibres; *d*, membrana limitans interna; *e*, divided blood-vessels in the hyaloid capsule of the vitreous humour.

PLATE IV.

Fig. 1. A vertical section through the inner layers of the gecko's retina, $\times 670$.

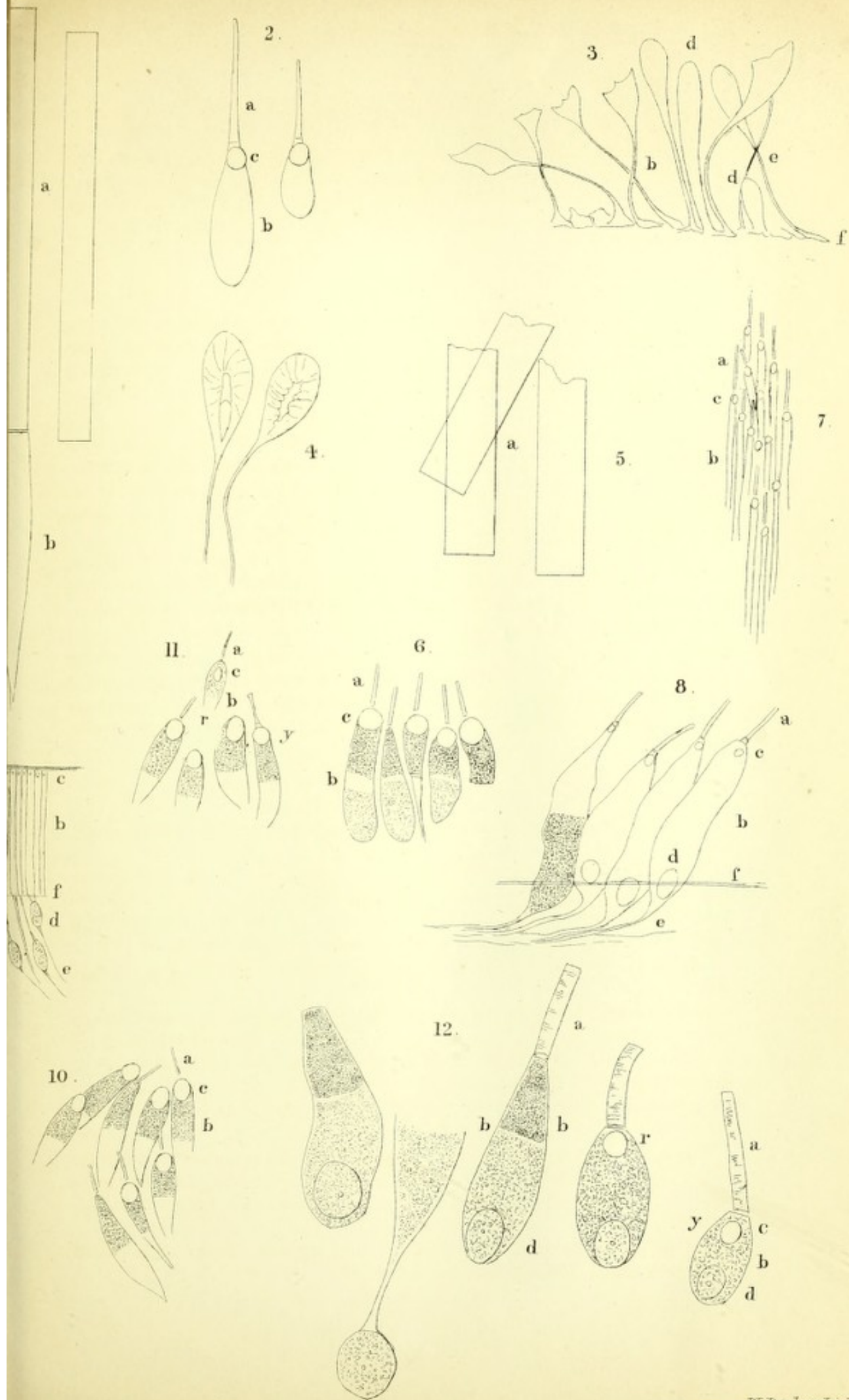
a, finer obliquely-radial nervous fibres in the inner-granule layers; *b*, stouter do.; *c*, fibres passing from the inner-granules through *g*, the granular layer, to the ganglionic layer; *d*, vertically radial connective tissue-fibres arising at *f*, from *i*, the membrana limitans interna; *e*, inner-granules; *h*, optic nerve fibres.

Fig. 2. A vertical section tangential to the fovea centralis of the chameleon, $\times 670$.

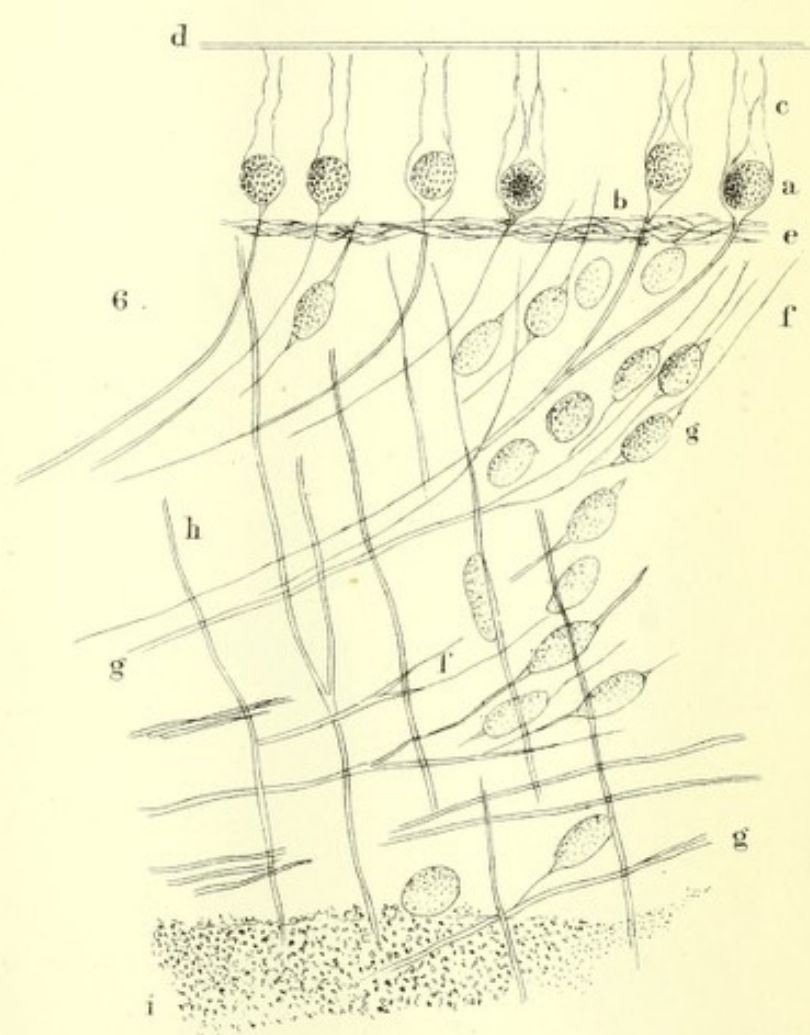
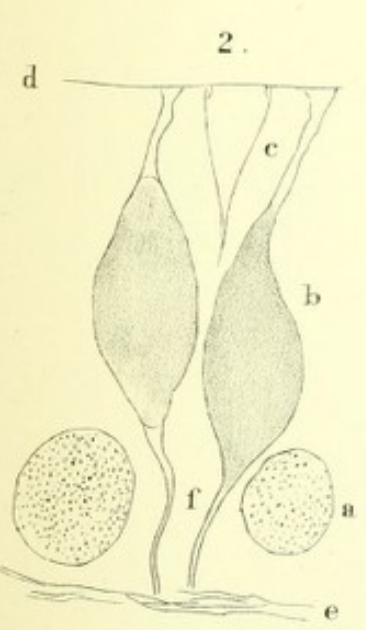
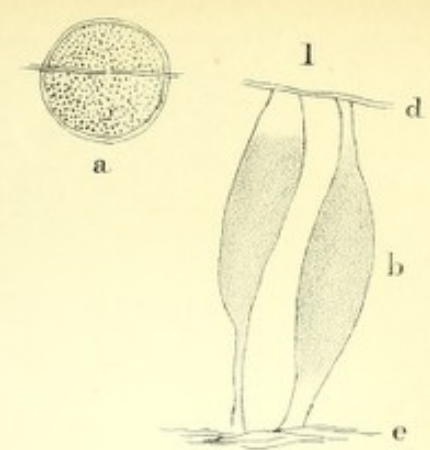
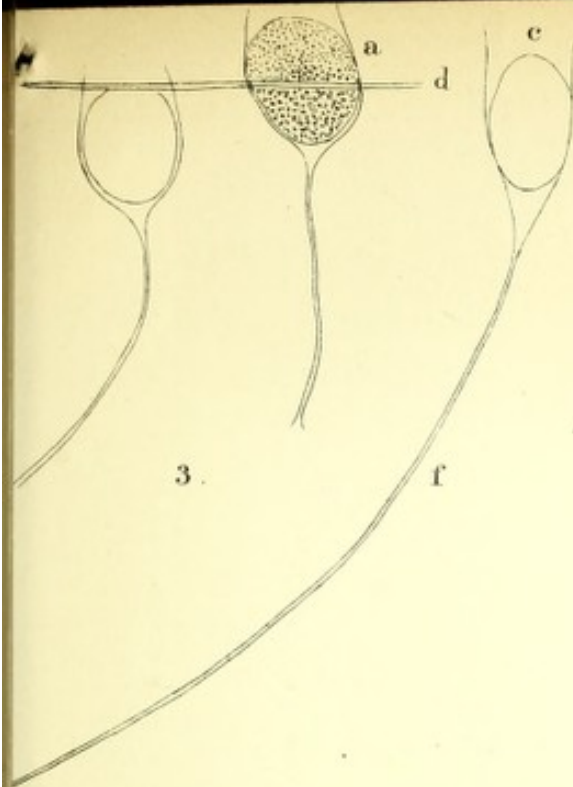
a, the choroid hiding the cone-shafts; *b*, the cone-appendages; *c*, membrana limitans externa; *d*, outer-granules; *e*, vertically radial connective tissue-fibres arising in *f*, a thin stratum of connective tissue constituting the smaller part of the inter-granule layer, and ending in *c*. These fibres form long spaces in which are seen *g*, the cut ends of the bundles of the nervous plexus which composes the principal part of the inter-granule layer.

Fig. 3. A vertical section through the centre of the chameleon's fovea, $\times 20$. *c*, choroid; *b*, bacillary layer; *o*, outer-granule layer; *i*, inter-granule layer; *i'*, inner-granule layer; *g*, granular layer; *n*, optic nerve and ganglionic layers; *f*, fovea.

Owing to a slight folding of the section the cones appear shorter at the centre of the fovea instead of longest, as they actually are.







5

