

## **The histology of the eye / by John Whitaker Hulke.**

### **Contributors**

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these spaces occur in the portion enlarged at Fig. 2 *b*, which was accurately drawn with the aid of the camera lucida. In the longitudinal section (Fig. 4), made at right angles to the radius, several of these openings are shown. There is an apparent approach at regularity in their arrangement, which induces me to suppose that they may be the openings through which the vascular bundles passed to the leaves. They may, however, be only cracks produced in the desiccation of the tissues.

Beyond this cylinder no structure is preserved, until we reach the surface of the stem with the impressions of the leaves and the series of larger scars. The parts preserved agree so nearly in regard to the nature and arrangement of the tissues with what I have described in *Lepidodendron selaginoides* (Sternb.), that there cannot be any doubt as to the close affinities of these two stems. The structureless space represents the portion occupied with the delicate parenchyma, the more thickened and larger parenchyma beyond, and the elongated cells of the outer portion, together with the true bark. The proportion between the scalariform cylinder and axis and the external layers of parenchyma is the same in both stems. In the *Lepidodendron selaginoides*, figured on Plate XXVII. in the October number of this Journal, the cylinder measures  $\frac{1}{4}$ th of an inch, and the whole stem is an inch in diameter, while in the *Ulodendron minus*, figured on Plate XXXI., the scalariform structures are  $\frac{1}{3}$ ths of an inch in diameter, and the stem in its original cylindrical form measured 4 inches. The proportion of the axis in both is  $\frac{1}{3}$ th of the whole stem.

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II.—*The Histology of the Eye.* By JOHN WHITAKER HULKE, F.R.S., F.R.C.S., Assistant-Surgeon to the Middlesex Hospital, and Surgeon to the Royal London Ophthalmic Hospital.

THE eye is a *microcosm*—a very compendium of all the tissues. True *cell-tissues*, *connective tissue* in several forms, *muscular*, *vascular*, and *nervous tissue*, are all represented here; and there is not another part of the whole human body which offers such facilities for direct clinical observation, and for the anatomical investigation of the minute tissue-changes produced by disease.

*Cornea.*—The cornea is composed of three distinct structures: an *outer* or conjunctival layer, which, at the circumference, passes into the loose conjunctiva covering the sclerotic; a *middle* layer, the proper or lamellated cornea, which is uninterruptedly continued into the sclerotic; and a very delicate *inner* layer, having complex peripheral relations with the sclerotic, ciliary muscle, and iris.



The *conjunctival layer* consists of an *epithelium*, underlaid by a *homogeneous stratum*, known as "Bowman's membrane," or the "anterior elastic lamina."

The *epithelium* is composed of four or five superposed rows of cells, the aggregate thickness of which averages  $\frac{1}{430}$ th of an inch. The deepest cells are subcolumnar. Their inner ends are straight, and they rest directly on Bowman's membrane. Their outer ends are convex; and they form generally a crenated line, which interlocks with the cells immediately external to it. These intermediate cells have a jagged inner border, and a convex outer contour. The outermost cells are large flat scales.

The structural and chemical distinctions which so sharply separate the horny from the mucous stratum of the epidermis are wholly absent from this epithelium, all the cells of which, the outermost as also the deepest, are nucleated, and are capable of manifesting every endowment of cell-life proper to them; and this alone would be enough to throw great doubt on the commonly assumed parallelism between the manner of the renewal of the corneal epithelium and that of the epidermis. The common idea, that the deepest epithelial cells constitute a sort of matrix, from which there is a constant progression of nascent cells towards the outer surface to replace the loss by exfoliation, has been lately challenged by Dr. Cleland, who, from a study of the corneal epithelium in the ox, concludes that not merely the external waste, but also the internal decay of the deepest cells, is made good by new cells evolved out of those of the middle tier. My own observations lead me to believe that an outward progression of cells from the innermost tier really does take place, but that all the superficial cells are not directly referable to this source, since proofs of cell-multiplication are met with at every depth in the epithelium.

But the formative energy may take another direction, and produce from the epithelium a progeny unlike the parent. Wounds and ulcers, again, afford us abundant illustrations of this perversion. Around these we find the epithelial cells enlarging; their nuclei, or masses of germinal matter, dividing and subdividing until the parent cell is filled with a brood which we cannot optically distinguish from the corpuscles of granulation, or lymph, or pus, and which, when set free by the deliquescence of the parent capsule, we recognize as the formed elementary constituents of granulation-tissue, of lymph, or of pus. (Fig. 1.)

*Bowman's Membrane: Anterior Elastic Lamina.*—Beneath the anterior epithelium, between it and the lamellated cornea, is the structureless stratum first particularly described by Mr. Bowman, and named by him the *anterior elastic lamina*. In several early human foetal eyes I found that this stratum was

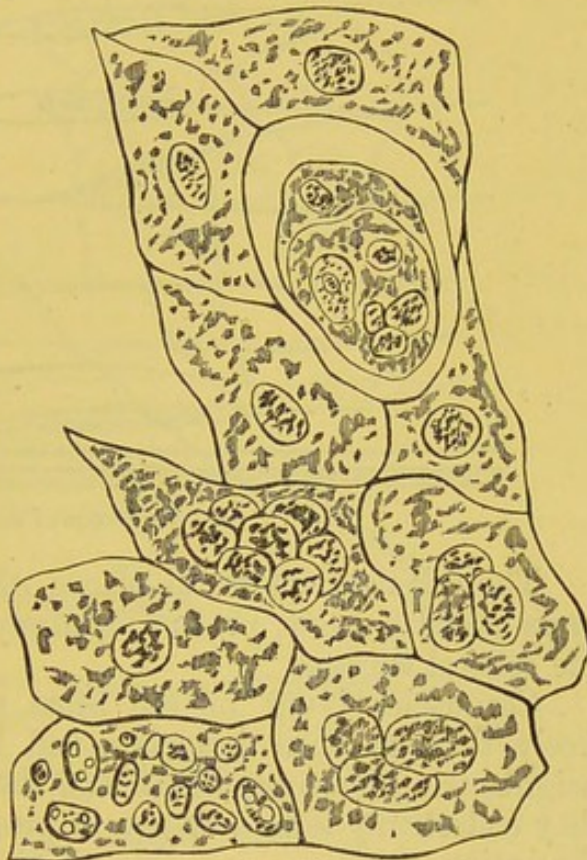


not yet differentiated; but at full term it is very distinct. In the adult cornea, in which its average thickness is about  $\frac{1}{1500}$ th of an inch, it is always remarkably conspicuous by its transparent structurelessness, which marks it off from the epithelium in front and the lamellated corneal tissue behind it. The front of the lamina bearing the epithelium is perfectly even; while the posterior surface is slightly irregular, owing to the production of fibres which pass slantingly from it into the lamellated tissue, and tie the lamina to this so closely that it is inseparable from it by dissection, except in very minute pieces. These *tie-fibres*, originally described by Mr. Bowman, are, I believe with him, of the same nature as the lamina—a modified connective substance; and they are perfectly distinct from the nerve-fibres, the tracks of which a recent author supposes them to be.

The peripheral relations of the anterior elastic lamina are very simple. It becomes suddenly thinned at a short distance in front of the foremost conjunctival vessels, and thence runs backwards over the loose submucous tissue as the basement-membrane of the conjunctiva bulbi.

The next structure is the *lamellated cornea*, one of the group of connective substances. It is mainly composed of two elementary tissues—one cellular, the other a modification of common connective or white fibrous tissue. Their microscopic characters and the proportions in which they occur are not the same at all ages. At its first appearance, the cornea, embryology teaches, is purely a cell-tissue; and, in the earliest human foetal cornea which I have examined (at the fourth month), the cell or corpuscular tissue has greatly preponderated. At full term, the disproportion is less: the cells have still simple shapes; but they are separated by a larger quantity of interstitial tissue, which is very distinctly fibrillated. In the adult's cornea, the fibrous tissue dominates; and the corpuscles are large-branched cells, cohering in nets of variable sizes,

FIG. 1.

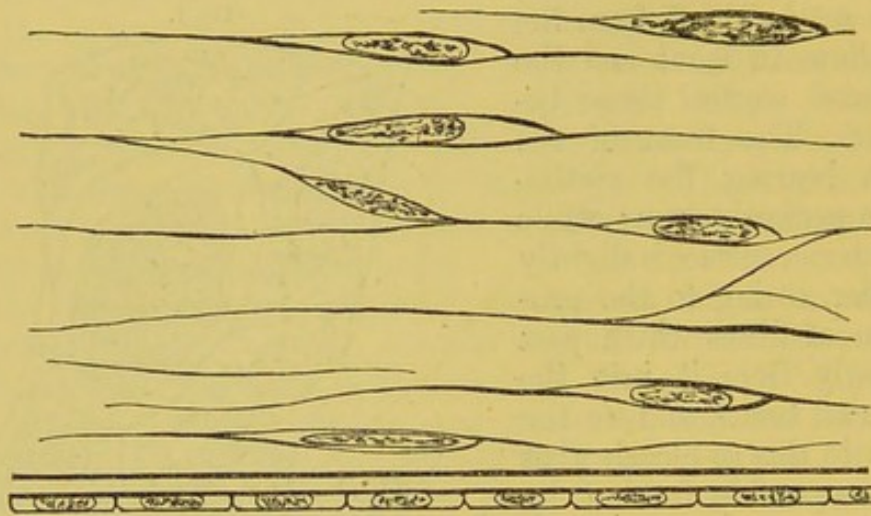


Suppuration of Anterior Corneal Epithelium.



but never co-extensive with more than a very small fraction of the entire corneal area. (Fig. 2.)

FIG. 2.



Vertical Section of the Cornea.

The cell-nets extend in planes which intersect one another at every possible angle, preserving always more or less parallelism to the corneal surfaces.

Corpuscles lying in the same plane intercommunicate very freely through their branches, and less freely with those in the neighbouring more superficial and deeper planes; and in this way they collectively form a system of plasmatic canals, which pervades the entire cornea.

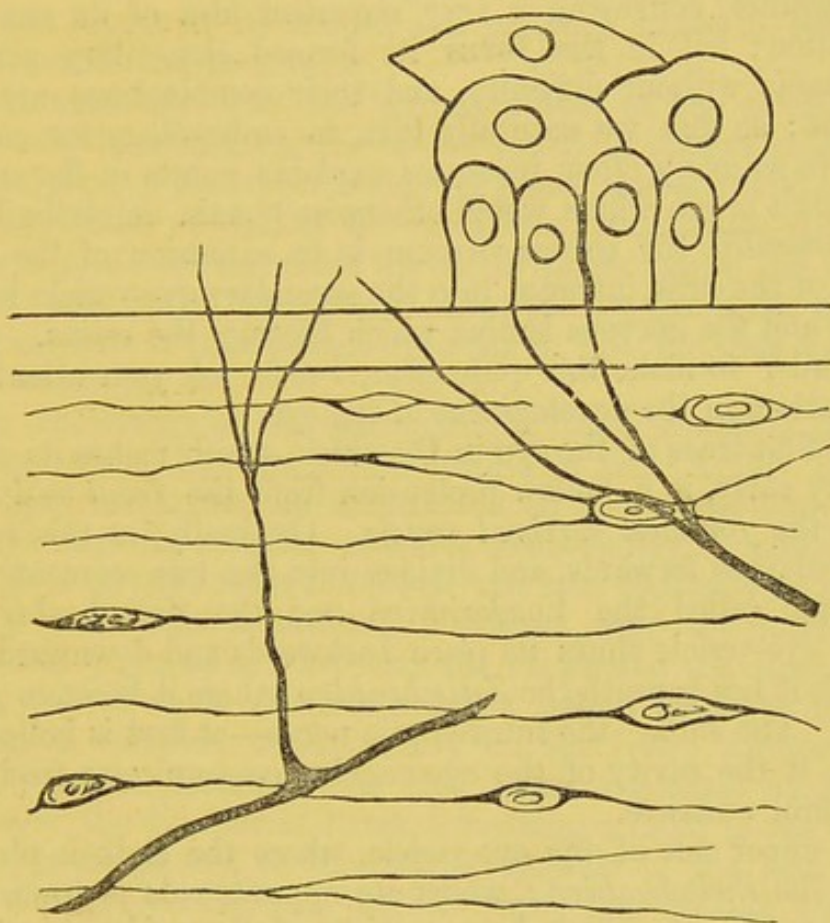
The *interstitial fibrous tissue* consists of broad flat lamelliform bundles, interwoven with the cell-nets, necessarily also in planes more or less parallel to the corneal surfaces—an arrangement of the tissues which gives the quasi-laminated appearance observable in vertical sections of the cornea. In the foetus, the fibrillation of the bundles is very distinct; and in the adult it is also evident.

*Blood-vessels* are entirely absent from the healthy adult cornea, the nutrition of which is wholly carried on by the corpuscular system, which draws its plasma from the vessels of the sclerotic and conjunctiva. Its *nerves*, however, are numerous. The distribution of the coarser bundles is easily demonstrable. They enter the circumference of the cornea, and converge towards its centre, repeatedly dividing and uniting in a plexus, most of the bundles of which tend towards the anterior surface. Near here they recombine in a plexus of very fine bundles, from which minute branches are detached towards the anterior elastic lamina, which they perforate, and reach the anterior epithelium. (Fig. 3.) The exact relation of the nerve-fibres to the epithelium is so delicate a subject of inquiry, that it cannot surprise us that different opinions have



been arrived at respecting its nature. The passage of the perforating nerve-fibres quite through the epithelium, and their free termination at the outer surface of this, described by one observer

FIG. 3.



Corneal Nerves perforating the Anterior Elastic Lamina.

(Cohnheim), requires, I think, confirmation. I have not myself succeeded in tracing these fibres beyond the middle tier of epithelial cells; nor have I yet been able to demonstrate their ultimate distribution.

The only remaining corneal tissue is the *delicate membrane* which lines the posterior surface of the lamellated tissue, called after *Démours and Décémet*, and sometimes also named the *posterior elastic lamina*. Its thickness is only about one-third of that of the anterior elastic lamina. It is perfectly homogeneous, without the slightest trace of structure. It is separable from the lamellated tissue by careful dissection in pieces of large size.

A single layer of *delicate pavement-epithelium* lines the inner surface of the lamina. Its cells poliferate in some forms of keratitis, and produce minute opaque dots upon the back of the cornea, recognizable when illuminated by an oblique pencil of light.



*Vitreous Humour*.—This, in a perfectly healthy state, is a clear, colourless mass of gelatinous consistence, enclosed in a hyaloid membranous capsule.

In the *adult*, the traces of structure perceptible in it are scanty and indistinct, conveying a very imperfect idea of its anatomical composition; but in the *fœtus* its formed elementary parts are recognizable without difficulty, and their combinations are easily made out; so that we naturally turn to embryology for aid; and this, as in so many other instances, explains points in the anatomy of the adult organ which would otherwise remain unintelligible.

*Genetically*, the corpus vitreum is an extension of the deeper stratum of the cutis, intruded into the secondary eye-vesicle between the lens and the nervous lamina which becomes the retina.

In order to make this quite clear, I must ask your attention to some matters in the development of the eye.

The first trace of the eye in the chick, which makes its appearance very early, is a hollow protrusion from the *front and lateral part* of the *foremost cerebral vesicle*. Gradually, as this cerebral vesicle enlarges forwards, and divides into the two segments which Von Baer called the *Vordernhirn* and the *Zwischenhirn*, the primary eye-vesicle shifts its place backwards and downwards until at length it lies beneath the *Zwischenhirn*; there it becomes *pedunculated*. The *stalk*—the future optic nerve—at first is hollow, and through it the cavity of the eye-vesicle communicates freely with the cerebral ventricle.

The upper side of the eye-vesicle, where the stalk is placed, is towards the *Zwischenhirn*; whilst its opposite side is towards the external tegument, which here consists of the epidermal stratum only, as Remak thought, or which includes, as Kölliker believes, a part of the cutis. At this spot the epidermis thickens; and an *inbud* of it, pressing on the summit of the primary eye-vesicle, pushes this inwards, so changing the *globular* shape of the vesicle into a *cup* consisting of an inner and an outer plate, separated by an interspace, the remnant of the original cavity of the first vesicle, which continues for some time longer to communicate with the brain-ventricle through the still hollow eye-stalk.

The cup thus formed, distinguished as the *secondary eye-vesicle*, is incomplete below; and through this gap—the *fœtal cleft*—the deeper stratum of the cutis intrudes between the epidermal inbud, which is the matrix of the lens, and the anterior plate of the secondary eye-vesicle, which is the foundation of the retina.

It will be perceived that this intruded portion of cutis fills the space in the secondary eye-vesicle which corresponds to that in the completed eye occupied by the vitreous humour. So long as the fœtal cleft remains open, the intruded portion of cutis (which we may now call the vitreous humour) is directly continuous through





it with the exterior cutis, and nutrient blood-vessels enter the vitreous humour through this channel. At a later stage, the foetal cleft closes, which perfectly isolates the internal corpus vitreum from the external cutis. Von Ammon says that the closure of the foetal cleft begins at its middle, and proceeds hence in both directions, forwards and backwards.

Simultaneously with the transformation of the primary eye-vesicle into the secondary, the hollow eye-stalk became solid by the approximation of the upper and lower plates, and acquired the form of a flat ribbon. Next, by the inbending of its edges, the ribbon became a gutter, along which the blood-vessels gained the inside of the eye; and, lastly, the gutter, closing in the eye-stalk, takes the cylindrical form of the perfect optic nerve, and includes the blood-vessels within it.

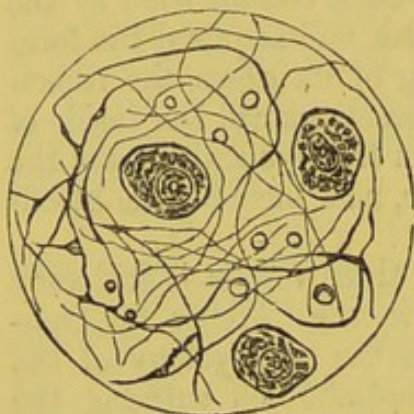
Our knowledge of the distribution of these vessels is still very imperfect. Von Ammon, whose articles in the 'Archiv für Ophthalmologie' are a fund of information on the embryology of the eye, says that the *arteria centralis*, immediately on entering the globe, gives off *fine twigs to the sclerotic and choroid*; next it detaches several *lateral branches to the retina*, upon the inner surface of which they spread out and form the *membrana vasculosa foetalis retinae*; then it sends off a second set of lateral branches, from five to seven in number, which ramify on the outer surface of the hyaloid capsule, forming here the *discus arteriosus hyaloideus*; and, finally, the diminished trunk, traversing a canal in the vitreous humour, is distributed to the vascular capsule of the lens. Thus Von Ammon describes *two vascular nets*—one *retinal*, the other belonging to the *vitreous humour*; but this has not been confirmed by later observers. The late H. Müller distinctly says that there are not any other vessels on the outer surface of the corpus vitreum than the retinal ones; and he also mentions that the retina continues long without blood-vessels—a fact which I have myself verified in the human foetus, the moment of their appearance being apparently determined by that of the obliteration of the *arteria hyaloidea capsulae lentis*. In the human foetus of the fifth month, in which all the retinal layers except the bacillary were distinctly recognizable, I found the retina still quite devoid of blood-vessels; the axial vessels going to the lens-capsule were still pervious; and I failed to detect the vascular net on the hyaloid capsule described by Von Ammon.

Absolutely fresh human embryos are so rarely obtainable that the structure of the human vitreous humour in the earliest stages of development is unknown. Before and after the fifth month it consists of a web of delicate fibres, the meshes of which contain a viscid colourless substance. Throughout this tissue, in chromic acid preparations, numerous minute bright globules occur, which,



mingled with the fibres, give, under a moderate enlargement (a quarter of an inch) some resemblance to a stellar tissue. This resemblance is, however, only superficial, and disappears under a higher magnifying power which makes it evident that the bright globules have not any definite relations to the fibres, since some of them lie free in the meshes of the web, and others cohere singly or

FIG. 4.



Foetal Vitreous Humour.

in groups to the sides of the fibres or at their intersections. Examined with one-twelfth or one-twenty-fifth objective, these bright globules do not exhibit any trace of structure; and I am disposed to conjecture that they are artificial products, resulting from the action of the chromic acid on the interstitial albuminous substance. (Fig. 4.)

But, besides the formed elements just described, there occur in the foetal corpus vitreum *other elementary parts of the highest physiological importance*—large nucleated cells, which are most

abundant upon and near the hyaloid capsule and around the central canal, but which are also found throughout the whole organ. Most of them have a simple round or roundly oval shape; some are fusiform and branched. All are distinctly nucleated. Their diameter ranges between  $\frac{1}{300}$ th and  $\frac{1}{800}$ th of an inch.

In the human adult's vitreous body, the foetal fibrillary net steps into the background; but it does not wholly disappear, for portions of it persist even to old age; and it is replaced by delicate membranes of such extreme tenuity, and differing so little in their refraction from that of the fluid substance of the organ, that they would elude detection, but for the presence of folds and the adhesion of minute impurities to them. The arrangement of these membranes is not yet certainly known; and, in truth, their very existence is doubted by some anatomists.

Beyond all doubt, the most important constituents in the adult's corpus vitreum are the large nucleated cells which I mentioned as occurring in the foetus. These embryonal cells persist throughout life, and they are the starting-point of many of the morbid changes to which this organ is subject.

They are endowed with an extraordinary formative energy, normally latent, but promptly responsive to an appropriate stimulus, the nature of which determines the dynamical direction this energy takes. Anatomically, this excessive formative energy principally manifests itself in two ways—one marked by a remarkable extension and fission of the cell-wall and contained protoplasm; the other characterized by inordinate proliferation of the nucleus. The

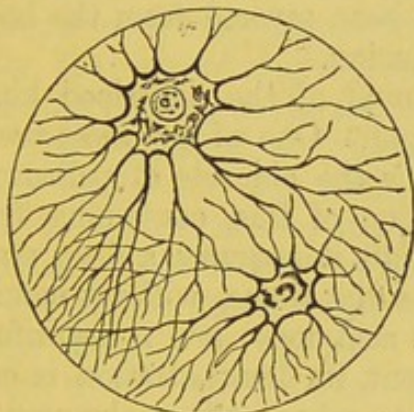


first produces, in its most complete form, very finely fibrillated tissue. (Fig. 5.)

Where the fission of the cell-wall is carried to a less degree, it produces open fibre cell-nets of coarser texture, which are often combined with corrugated hyaloid membranes.

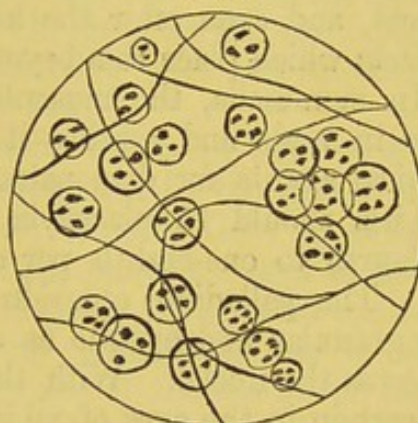
Proliferation of the nucleus in a minor degree is common in association with chronic irritative affections of the vascular coats—*e. g.* chronic glaucoma and the late stages of posterior staphyloma, in which we find the cells larger than normal, but still retaining

FIG. 5.



Fibrillation of Cells of Vitreous Humour.

FIG. 6.



Proliferation of Cells of Vitreous Humour.

their simple forms, and containing two, three, or several nascent cells, instead of a single nucleus. But it is in suppuration that proliferation is carried to its highest development. Advanced cases, where the entire corpus vitreum is changed into a tough yellowish substance, are not suitable for the demonstration of this; but, before its metamorphosis is complete, at an earlier stage, in which the opacity due to the presence of pus diminishes from the exterior towards the still transparent centre of the organ, all the intermediate phases between the simple mononucleated embryonal cell and perfect pus are easily traceable. (Fig. 6.)

The *Tunica Uvea*, so named from its resemblance to a grape or large berry, *uva*, consists of two segments—the iris and the choroid—which differ in their principal anatomical constituents and in the offices which they subserve in the physiology of vision, and agree mainly in both of them containing numerous blood-vessels and much pigment.

The *Choroid* corresponds to the coat of lamp-black with which we line the interior of the camera obscura, and serves the same purpose, absorbing the incident rays, and so lessening dispersion in proportion to the intensity of its pigmentation. But, the eye being a living camera, the choroid has additional functions of another kind. It directly ministers to the nutrition of the bacillary stratum of the retina in man, as also to that of all the retinal strata in those animals whose retinae are devoid of blood-vessels.



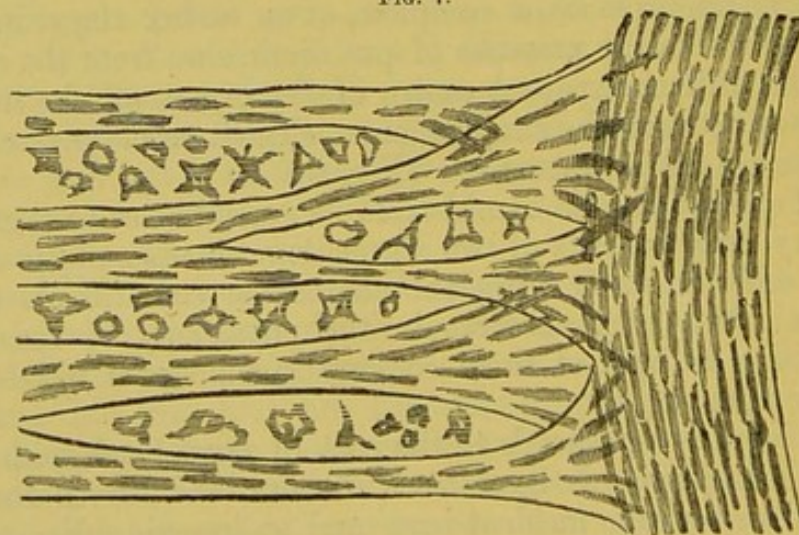
The *Iris* corresponds to the diaphragm in the cornea. Stretched across the anterior chamber, it stops out the most peripheral rays, which, in its absence, would pass through the edge of the lens, and in this way it lessens spherical aberration; then, by varying the size of the pupil, it regulates the quantity of light admitted to the retina; and, finally, it is an accessory of the apparatus of accommodation, although not in man an actual factor.

The iris is essentially a *muscular organ*. The contraction and dilatation of the pupil are due to muscular irritability, and not to vascular erectility. Their continuance after the heart has ceased to beat, and even after the head has been severed from the body, are facts which place this beyond discussion.

In mammalia, the muscular tissue is of the unstriped kind; while in birds and reptiles it is striped. One of the most useful chemical agents for demonstrating it is the chloride of palladium. The iris should be placed in a solution of this, containing from one-fourth to one-eighth per cent., until it acquires a deep straw tint. The palladium chloride hardens the tissue, without making it so granular and opaque as chromic acid does; and it beautifully preserves the nuclei. With this reagent, its demonstration is easy and certain in the eyes of white rabbits, where it is unobscured by pigment which conceals it in human eyes.

The cells, which are not easily individually isolated, are long spindles containing a rod-like nucleus. They resemble closely the cells of the larger organic muscles. The cells cohere in small flat bands, and these again combine in larger bundles. In man, I believe also in

FIG. 7.



Iris of White Rabbit, prepared with Chloride of Palladium, to show the disposition of the Muscular Tissue.

mammalia generally, in birds, and in reptiles, the muscular bundles are disposed in two sets, which have a radial and a circular direction, and constitute a sphincter and a dilator muscle of the pupil. (Fig. 7.)



In the white rabbit, the muscular bundles of the sphincter pupillæ are disposed with great regularity in lines concentric with the pupil, at the edge of which they form a very distinct band upon the anterior surface. On the back of the iris, the outer border of the muscular ring is less distinct; and here, intersecting the radial bundles of the dilator, a thin layer of circular fibres is traceable for some distance towards the great circumference of the iris.

The dilator pupillæ consists, in this animal, of slender bundles running along the posterior surface of the iris from near the great circumference towards the pupil, separating and combining again in a plexus with long narrow meshes. On nearing the sphincter pupillæ, they spread slightly, and, intersecting with one another and with the bundles of the sphincter, are lost.

The peripheral relations of the radial muscular bundles are less easily made out. The difficulty is occasioned by the greater thickness of the iris, and by the parallel direction of the very muscular arteries. I am inclined to think that the bundles attach themselves to the elastic fibres, which the ligamentum pectinatum iridis prolongs inwards to the iris. This very remarkable net of elastic tissue, which fixes the great circumference of the iris to the margin of the anterior chamber, is derived from the posterior elastic lamina of the cornea, which in my last lecture I mentioned as having peripheral relations with the ciliary muscle, iris, and sclerotic. These I shall now explain. The lamina at the circumference of the cornea resolves itself into fibrous tissue. This dehiscence begins first on its anterior surface, and goes on until the whole membrane is converted into fibres, which take three principal directions. One set passes backwards and outwards to the sclerotic, behind the *circulus venosus* in Schlemm's canal; another set goes directly backwards to the ciliary muscle; and a third set springs across the margin of the anterior chamber to the great circumference of the iris, on the anterior surface of which they form a network remarkable for its hard stiff outlines, from which fibres are produced upon the front and in the substance of the iris for a considerable distance towards the pupil.

The *blood-vessels* of the iris are very numerous. Its arteries come from the arterial circle formed by the inosculation of the two long posterior ciliary arteries, and known as the *circulus arteriosus iridis*. The mode of formation of this arterial circle is very variable; but the ordinary plan is, that each of the two long posterior ciliary arteries divides upon the outer surface of the ciliary muscle, near its front, into a couple of primary branches, which separate and encircle the iris, and meet the corresponding branches of the other long ciliary artery. The arterial circle thus made sends branches backwards to the ciliary muscle; others inwards to the ciliary processes; and a third set run forwards to the iris through



the ligamentum pectinatum. These latter have, as Leber notices, very thick muscular walls. They run from the great circumference of the iris towards the pupil with a straight or wavy course, detaching branches to the capillary net, which is very abundant, especially at the anterior surface of the iris. On reaching the lesser circle of the iris (the little circlet of minute irregularities on the front of the iris near the pupil, which marks the attachment of the foetal pupillary membrane), the now greatly diminished arteries join here in a second arterial ring, the *circulus arteriosus minor iridis*. From the inner border of this, capillaries extend inward, encroaching slightly upon the sphincter, but not quite reaching the edge of the pupil.

The veins of the iris lie nearer its posterior than its anterior surface. They pass backwards, and, joining the veinlets of the ciliary processes, convey the venous blood from the iris to the *vasa vorticosa*.

The iris receives its *nerves* from the ciliary plexus—that exquisite net on the outer surface of the ciliary muscle. I can strongly recommend osmic acid for their microscopical demonstration. If the iris be placed in a solution of this acid holding about one-fourth to one-half a grain per cent. for about twenty-four hours, we get the nerves blackened, and the muscular tissue only slightly stained. Stronger solutions are not so useful as the weak ones, because they blacken more, and less discriminately; and, if the preparations are left a little too long in them, everything is black alike, and indistinguishable. (Fig. 8.)

The nerves of the iris, most easily studied in white rabbits and guinea-pigs, are numerous. The larger bundles, containing several fibres, converge from the great circumference of the iris towards the lesser circle, forming, in their hitherward course, an open plexus, the larger meshes of which are occupied by a finer net. At the lesser circle, the nerves combine in a circular plexus, from which single fibres are traceable inwards in the sphincter nearly to the edge of the pupil. The coarser bundles have a very abundantly nucleated neurilemma. The nerve-tubules vary greatly in size, ranging between  $\frac{1}{3375}$ " and  $\frac{1}{7000}$ ". All such tubules have a medulla; they are dark-edged fibres; while the smallest pale fibres which I have traced were not more than  $\frac{1}{14000}$ " in diameter.

The interstices between the muscular bundles and the meshes of the vascular and nervous nets are filled with a homogeneous connective substance, in which simple, jagged, and very large, irregular, and much branched connective-tissue corpuscles, plentifully occur. Many of these contain a granular pigment, which, by its quantity and distribution, produces the different colours of the iris.

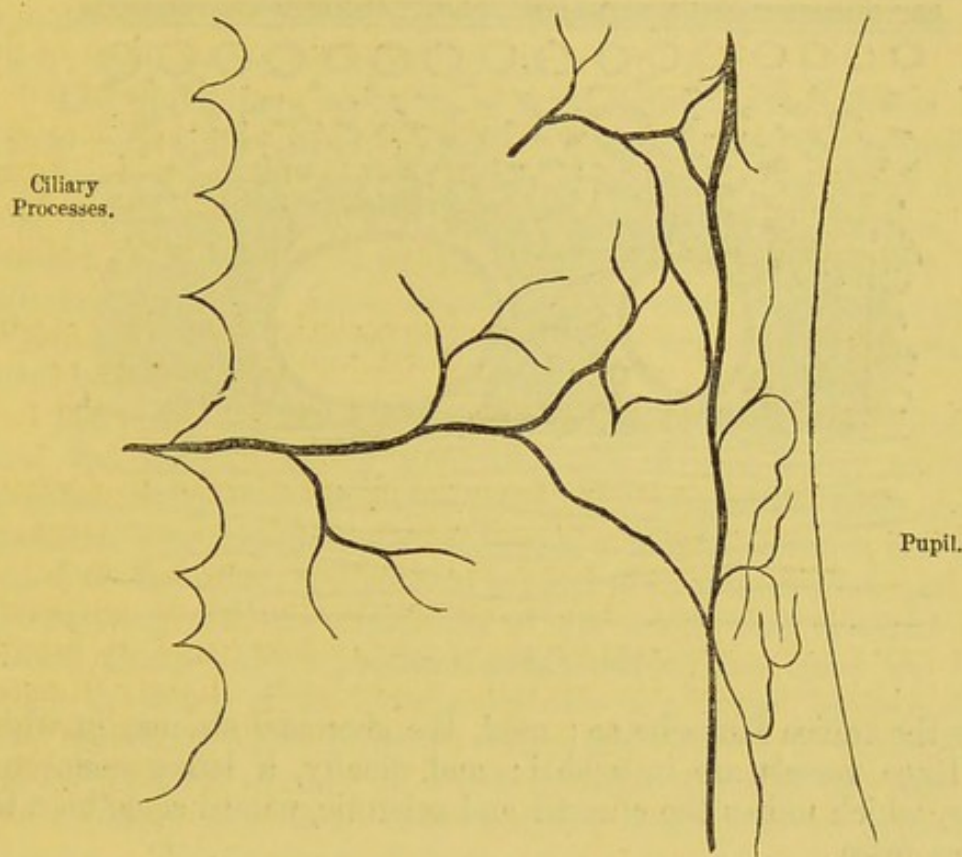
The back of the iris is overlaid with a coat of pavement-epithelium, loaded with granular pigment, which is sometimes called the



uvea or uveal surface. The cells are less regular in size and shape than those of the corresponding epithelium of the choroid.

FIG. 8.

Nervous Circle.



Nerves of Iris, prepared with Osmic Acid.

The front of the iris also has an epithelium. It is much more delicate than that on the back, and more difficult to demonstrate. Weak solutions of nitrate of silver are useful for this purpose.

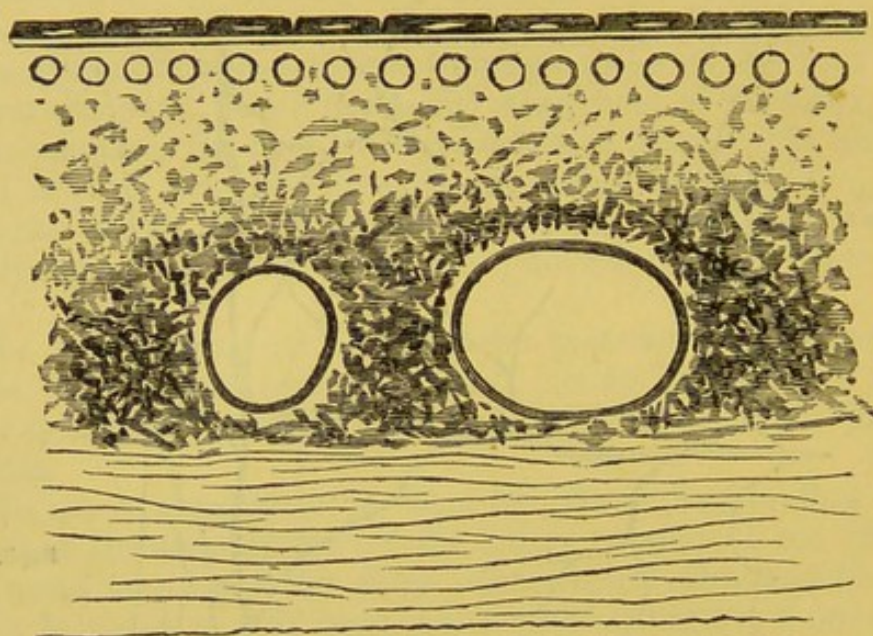
In the *Choroid* we recognize two subdivisions—a larger posterior portion, reaching from the optic nerve forwards as far as the jagged line which marks the termination of the nervous retina, ora serrata; and a smaller anterior portion, lying between this and the iris, which we call the ciliary body. So much of this latter as belongs properly to the apparatus of accommodation, it is not my purpose to describe in this lecture. My present remarks will relate more particularly to the posterior segment. Its principal characteristics are, its pigmentation and its great vascularity. This latter much exceeds that of the iris; and, further, there is a peculiarity in the arrangement of the blood-vessels—the capillaries lie apart from the large vessels.

Enumerating the different tissues in the order in which they occur in passing from the inner to the outer surface of this coat, we first meet with a pavement-epithelium, borne upon a structureless



membrane, the elastic lamina of the choroid (Fig. 9); then the capillary net, called the chorio-capillaris, and by the older anato-

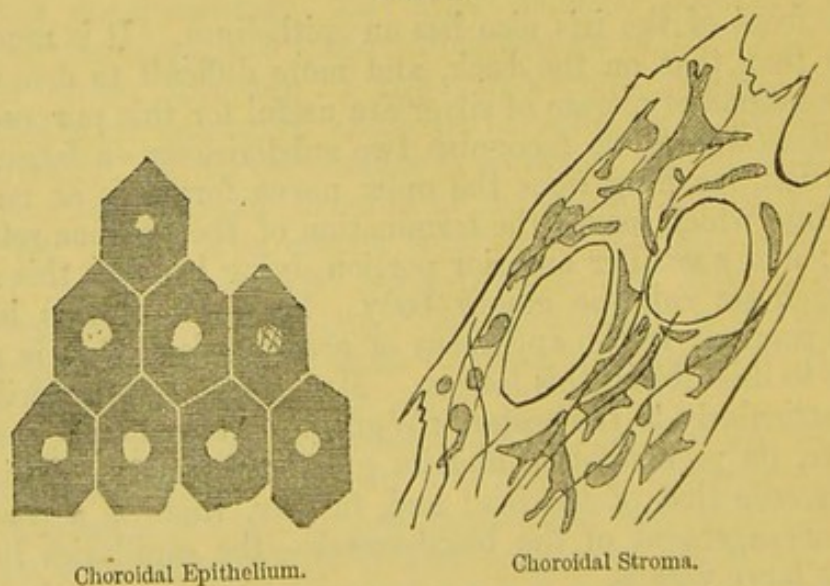
FIG. 9.



Vertical Section of Choroid.

mists the tunica Ruyschiana; next, the choroidal stroma, in which the large vessels are imbedded; and, finally, a looser connective tissue, which unites the choroid and sclerotic, named sometimes the lamina fusca.

FIG. 10.



Choroidal Epithelium.

Choroidal Stroma.

The choroidal epithelium is formed of a single layer of flat polygonal, mostly hexagonal cells, containing a nucleus and some brown granular pigment. (Fig. 10.) In Albinos, in the white choroid of



cetaceans, and upon the glistening silvery portion of the choroid, called the *tapetum lucidum* in ruminants, solipedes, and carnivores, the epithelium is also present, but it is devoid of pigment. In birds, reptiles, fish, and amphibia, brushes of pigmented tissue pass inwards from the epithelial cells between the retinal bacilli. In man, the diameter of the cells ranges between  $\frac{1}{1400}$ th and  $\frac{1}{2150}$ th of an inch; their average is about  $\frac{1}{1450}$ th.

The epithelium rests on a very distinct structureless membrane—the *elastic lamina*. This is often the seat of circumscribed thickenings, which begin as little elevations of the inner surface, and grow into knobs, and globes, and glandiform masses, large enough to be seen, in a strong light, with the unaided eye. The affection is one of those degenerations common in old age, but which also occurs in young persons as a sequel of long-continued local inflammation.

The choroid is supplied with arterial blood by the short posterior and the anterior ciliary arteries. The former, about twenty in number, pierce the posterior segment of the sclerotic, some near the posterior pole, others farther forwards. The hindermost are distributed to the sclera and choroid around the optic nerve: and, here inosculating with the capillaries of the nerve, they establish a collateral channel, through which a little blood can enter the retina when the trunk of the *arteria centralis* is plugged by an embolus. The remaining short posterior ciliary arteries run forwards with a straight course, sending off short branches through the stroma to the capillary net, where they break up quickly in an arborescent manner. The foremost of these arteries inosculate in front of the equator with the anterior ciliary arteries (branches of the muscular), which supply this region of the choroid. The capillaries form a net immediately at the outer surface of the elastic lamina, the meshes of which are smaller and less regular in the posterior segment of the choroid than in the anterior, where they are wider and longer. The vessels are large; and in all situations the interstices of the net are relatively narrow, less broad than the diameter of one of the overlying epithelial cells. We can recognize the collective effect of the capillary net, but not the individual vessels composing it in the living eye. (Fig. 11; p. 242.)

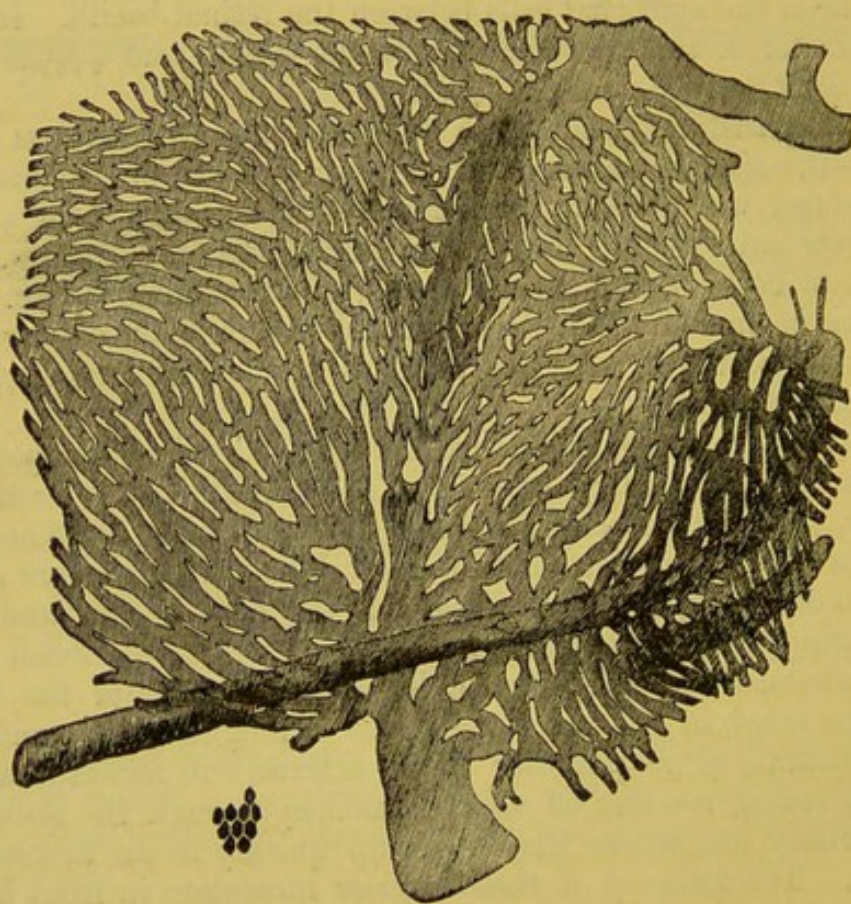
The blood of all the choroidal capillaries is collected by the well-known venus whorls, *vasa vorticosa*, which empty their contents by four short wide trunks which pierce the sclerotic very obliquely a little behind the equator. The valvular form of these sclerotic canals has been noticed by Leber, who adds the remark that it would tend to hinder the exit of the venous blood whenever there is an increased pressure on the inner surface of the eye-ball.

The *stroma* in which all the larger arteries and veins are bedded is a modified connective substance. It contains, like that of the



iris, branched pigmented corpuscles, which hang together in nets and membranes, and send off long and very fine elastic fibres. The

FIG. 11.



Chorio-capillaries.

thin layer of looser tissue external to the large vessels—the lamina fusca—has an essentially similar structure.

Besides the branched and irregular pigment-cells, the stroma always contains many pale, inconspicuous, roundly oval, and round cells and nuclei, of about the size of lymph-corpuscles, which increase considerably in number in inflammation, and which are, I think, the tissue out of which the formed elementary products of inflammation are evolved.

The *nerves* which we meet with in the choroid come from the ciliary ganglion; they lie quite on the outer surface, often in grooves in the inner surface of the sclerotic; and they all pass forwards to the plexus on the outer surface of the ciliary muscle. Whether any are distributed to the choroidal tissues has not yet been made out with certainty; but there is this in favour of it, that in the posterior segment very fine bundles of fibres, as well as single tubules, occur.

In both the choroid and in the ciliary plexus, pale as well as



dark edged nerve-fibres occur. In both situations, ganglion-cells are present. These latter were, I think, discovered first by H. Müller and by Schweigger. Their demonstration is not always easy, or even a certain matter.

In front of the ora serrata, the inner surface of the choroid exhibits a circle of vascular plaits. First rising gently above the surface, and then projecting freely, these compose the pars striata of Zinn and the familiar ciliary processes. They are covered with a pigmented pavement-epithelium, the cells of which are less uniform than those of the posterior segment of the choroid. Each ciliary process is a vascular plait, composed of large capillaries, which receive their arterial blood by two or three branches, which come off directly by a short trunk from the circulus arteriosus major iridis, or which arise nearly as often together with one of the arteries proceeding to the iris. The little arteries enter the outer surface (or rather edge) of the processes; and small veinlets run along the inner or free border; and they form a long meshed venous capillary plexus, which conveys the venous blood backwards to the vasa vorticosa. This venous capillary plexus not only transmits all the blood from the ciliary processes, but it also receives veins from the iris, as also some from the ciliary muscle.

In all vertebrates (except the lowest fishes, *e. g.* myxine and lancelet) a section vertical to the surfaces of the retina shows the following superposed layers.

First, there is a layer of columnar bodies, the rods and cones abutting against the choroid—the bacillary layer, known also as Jacob's membrane. To this succeeds the layer of corpuscles called the outer granules. Next follows a fibrillated stratum—the inter-granule layer; then another layer of corpuscles, the inner granules; next to this the layer, called by some the granular layer, by others the grey vesicular or grey nervous layer; then a stratum of ganglion-cells; and, finally, a stratum of optic nerve-fibres, bounded internally by a thin membrane, the "*membrana limitans interna retinæ*."

In all these layers, nervous and connective tissues are intimately commingled; and it is just this interpenetration of the two tissues which constitutes our principal difficulty whenever we attempt to decide the nature of a particular retinal element.

Before proceeding to a detailed account of its tissues, a few words on the best methods of studying the retina may be useful to some readers. First, it is absolutely essential that the eyes be perfectly fresh—the lapse of half-an-hour after the circulation has ceased, or even of a few minutes if the eye have been opened, makes differences in the appearance of the bacillary elements. Next, the outer surface of the fresh retina should be carefully scrutinized, in order to learn if both rods and cones are present. The latter will be known by their greater stoutness, and by their outer ends lying



in a deeper level than those of the rods; while in birds, in some reptiles, and in the batrachians, they are immediately betrayed by their bright-coloured beads.

But there are many things which cannot be made out in the fresh retina, or which can only be recognized by a practised observer already familiar with their characters when they have been artificially hardened and stained. The fresh retina is also too soft to allow us to cut vertical sections sufficiently thin without greatly disturbing the tissues. The most useful agents are chromic and osmic acids. Of the former acid, solutions of about a half per cent. are most useful; they have a pale straw tint; small eyes may be placed in them entire, but large ones should be cut in two before immersion. After remaining during three or four days in this solution, the retina will be hard enough to allow sections to be cut sufficiently thin for study with  $\frac{1}{25}$ -inch object-glass. The usefulness of chromic acid lies chiefly in its hardening the retina well, with little alteration in the shapes of most of its elementary tissues, and enabling us to cut our sections in any given direction we choose—for instance, through the fovea, or tangential to it. But it has the disadvantage of distorting the elements by distending them, when the solution is too weak, or by shrinking them when it is too concentrated. It also renders them granular and proportionately opaque. Sections so prepared may be still stained with carmine.

Osmic acid is, in some respects, more useful than chromic. It was first brought into notice by Max Schultze of Bonn, whose labours have thrown much light on retinal histology. Solutions of from a quarter to a half per cent. are best. It not only blackens the transparent nervous tissues, making them distinct, but it enables us, with a couple of fine needles, to split the retina in vertical planes, which afford us beautiful sections much thinner and clearer than any that the most practised hand can cut with the sharpest knife. Another advantage is, that it does not make the tissues so granular as chromic acid; but it has this drawback, that with it we cannot run the section in any direction we choose. It is of greater service in those vertebrates whose retinæ are devoid of blood-vessels, because their presence seriously interferes with clean cleavage. The retina, stained and hardened by osmic acid may be kept for use in distilled water without undergoing any further change during several weeks. It is best mounted in glycerine for microscopic examination.

To return from this digression to the description of the retinal layers; in the outermost or bacillary there are two sorts of elements, distinguished as *rods* and *cones*.

Every rod and every cone consists of two segments—an outer one, the bacillus or shaft; and an inner one, the appendage or body. The shafts of both rods and cones are highly refracting conspicuous



microscopic objects; whilst the appendages are pale, have a low refractive index, and are less evident.

The inner and the outer segment are separated by a sharp transverse line, where the slightest violence snaps them asunder.

The rod-shaft is a long, slender cylinder—in profile, a narrow rectangle. The ends are truncated; the outer rests on the choroidal epithelium, and the inner joins the appendage. In the perfectly fresh shaft I cannot discern any differentiation of parts, except an external outline, indicative of a containing membrane, and a homogeneous contained substance; but very soon after death the shafts begin to alter. The fresh perceptible change is, I think, a very faint longitudinal striation, and this is followed by the appearance of cross lines, which divide the shaft into light and dark segments; at the same time the shafts swell and bend and lose their rectilinear figure. This segmentation, which must have been familiar to every one since Hannover first wrote on the retina, I have never seen in absolutely fresh shafts examined instantly after death; so that, in common with others, regarding it as a *post mortem* change, I did not attach much importance to it. Professor Schultze, however, has founded upon it the ingenious view that the shafts are built up of discs of alternately nervous and connective substances.

The inner segment or rod-appendage has commonly the shape of a slender triangle or spindle; and one of the outer granules, as I shall shortly show, is always associated with its inner end. In its outer end, immediately inside the line which marks it off from the shaft, there may often be seen, particularly in the large rods of amphibia, a small hemispherical body of the same refractive index as the shaft to which it sometimes remains attached when the shaft and appendage separate. It was long ago described by the late H. Müller, whose loss every histologist deplores, and I figured it myself in a communication to the Royal Society in 1862. Schultze, who has lately called attention to it, suggests that it may act as a collecting lens.

The outer segment of the cones—the cone-shaft—is usually shorter than the rod-shaft, and it commonly tapers slightly outwards, the outward end being slightly narrower than the inner. The cone appendage is usually flask-shaped or bulbous; and, like the corresponding part of the rod, its inner end always has its associated “outer granule.” In the outer end of the appendage in birds, in some reptiles, and in batrachians, lies the well-known coloured bead which forms so exquisitely beautiful a microscopic object in the retina of these animals.

The interstices between the bacillary elements are occupied by a soft, homogeneous connective substance, which in all vertebrates below mammals contains a granular pigment. This extends inwards from the choroidal epithelium around and between the shafts as



far as their line of union with the appendages. It completely insulates the shafts, and would have the effect of absorbing any pencil of light which, making a relatively small incident angle, might escape laterally outwards through the shaft-wall, and in this way the escaped pencil would be prevented from entering a neighbouring shaft.

In mammals, the greater slenderness of the shafts probably renders such a provision unnecessary, because the incident pencil, to enter the shaft, must nearly coincide with its axis; and, as regards the side of the shaft, the angle of incidence would be so large that the pencil would probably be totally reflected.

The inner ends of the rods and cones pass through apertures in the connective membrane, called the *membrana limitans externa retinae*, and are produced inwards amongst the outer granules as slender bands or fibres. The *membrana limitans externa* is the sharp, hard line, always perceptible in vertical sections between the bacillary and the outer granule layers.

That the rods and cones are the percipient elements in the retina is now universally received, so that it needs hardly be mentioned; but it may be well to adduce the chief considerations on which this presumption rests. First, they alone of all the retinal tissues are so arranged as to be capable of receiving separate and distinct stimuli from small incident pencils of light. Next, their absence entails absence of perception. Mariotte's experiment proves this as regards the optic nerve disc, and the increase of the size of the blind-spot in myopia from posterior staphyloma, proportionately to the extent of the white atrophic crescent—a fact which is easily roughly verified—is another proof of the same thing; because here, together with the disappearance of the choroidal epithelium and chorio-capillaris, I have had opportunities of proving microscopically the absence of the cones and rods.

When we endeavour to press our inquiries farther, and try to ascertain what may be the respective functions of the outer and the inner segment of the rods and cones, and in what respect the functions of the rods and cones differ, we meet with difficulties which have yet to be overcome.

As regards the first part of this inquiry, the high refractive index of the shafts, and their insulation by a coat of pigment in many animals, points to a physical optical rôle; while the association of a nucleus (an outer granule) with the appendage, suggests a more vital dynamical share. If this be so, then the junction between the shaft and appendage marks the line where, so to say, the physical vibrations of light are converted into nerve-force.

Towards the solution of the second point of the inquiry, Schultze contributes the important fact that nocturnal mammals, as the mouse, bat, hedgehog, have no cones; and that in owls, they want



the bright orange and ruby beads of diurnal birds; and from this he conjectures that the cones may be concerned in perception of colour.

The *outer granules*, to which I must now pass on, are not minute, angular, solid particles, as their name implies, but cells or nuclei of very appreciable dimensions. Their numbers are directly proportionate to those of the rods and cones: and it is very probable—I may say certain—that each outer granule is associated with a rod or cone, and this in one of two ways. When the rod or cone-appendage is large enough to hold it, the outer granule lies inside the appendage in the plane of the *membrana limitans interna*, or at its inner surface; but, when the appendage is too slender to contain the granule, it is joined to the granule by a communicating fibre, the length of which is determined by the distance between the inner end of the appendage and the granule. In either case, the appendage is prolonged inwards in the form of a band or fibre beyond the “outer granule” towards the next stratum. This fibre I call the primitive bacillary fibre, or the primitive rod or cone-fibre, when I wish to distinguish it more particularly.

The *intergranule layer*, which, as its name conveys, lies between the outer and the inner granules, is a fibrous stratum. Some of its component fibres are nervous, passing between the outer and inner granules, and others are connective tissue. Of the latter set of fibres, those which traverse the layer vertically belong to the system of connective radial fibres, known by the name of their discoverer, H. Müller. The others, which extend parallel to the direction of the layer, constitute its proper substratum; and amongst these lie imbedded small nuclei, and in some of the lower animals, *e. g.* chelonians and fishes, large branched corpuscles of very considerable dimensions.

The *inner granules*, like the outer ones, are also cells or nuclei. According to their sizes, which vary much, they fall into two sets—smaller granules, everywhere numerous; and larger ones, most abundant near the inner surface of the layer, which I cannot distinguish from ganglion-cells. On the one side, the inner granules receive the fibres sent inwards towards them through the intergranular layer from the outer granules; and, on the other side, they send fibres inwards into the granular layer towards the ganglion-cells.

The *granular layer*, as Schultze correctly pointed out, is resolved, by a sufficiently high magnifying power, into a very finely fibrillated spongy web, which manifestly hangs together with, and is in great part a derivative of, the connective radial fibres entering it. The only nervous elements occurring in it are the internuncial fibres which traverse it, and the outermost ganglion-cells bedded in its inner surface. The term granular, which simply expresses its



appearance under a low power, is therefore preferable to that of grey vesicular or grey nervous layer, which gives a wrong idea of essential composition.

The cells of the ganglionic layer possess a very distinct roundish nucleus, imbedded in a pale and very soft protoplasm, about which there is not generally any distinct cell-wall perceptible. I believe that all the cells are branched. The outer branches, which are the more numerous, run outwards into the granular layer to join those coming inwards from the inner granules, while their inner branches join the bundles of optic nerve-fibres.

These last radiate in a plexiform manner from the optic nerve entrance. Where there is a fovea centralis, as in men, apes, some birds, and reptiles, the nerve-bundles are so distributed that those only destined for the fovea and its surrounding maculæ pass directly to it; while those bundles going to more distant parts beyond the fovea arch around it. With some exceptions, the nerve-fibres are devoid of medulla. In our own eyes, this ceases at the lamina cribrosa; and only pale fibres, equivalent to axis-cylinders, with perhaps an investment of the sheathing membrane, are produced into the retina.

The connective-tissue frame, which supports and holds together the nervous elements, consists of three segments. First, there are the two membranes;—the outer limiting membrane, which I have already described; and the membrana limitans interna, which some identify with the hyaloid capsule of the vitreous humour, but which I regard as a distinct membrane. This distinctness cannot be always demonstrated at pleasure; but I believe it to be a fact, because I have found the two membranes separated by inflammatory effusions, and because in the eyes of a Burchell's zebra, for which I was indebted to the liberality of the Zoological Society, I found a beautiful pavement of epithelium on the outer surface of the capsula hyaloidea. The second member of the connective substances is a system of stout pillar-like fibres, which arise by expanded wing-like roots from the outer surface of the limitans interna, and traverse vertically all the layers in a direction radial from the centre of the eye-ball. These are the fibres which, when originally discovered by H. Müller, were believed by him to link the percipient elements on the outer side of the retina—the rods and cones—with the conducting optic-nerve fibres at the inner surface of the retina, an error which he himself was one of the first to correct. They form a frame, which mechanically binds together the several layers in their order. Lastly, the retina contains a large amount of interstitial connective tissue, which is accumulated in larger quantity between the inner and outer granules, and between the inner granules and ganglionic layer, but which also pervades, in smaller quantity, all the nervous layers except the bacillary.



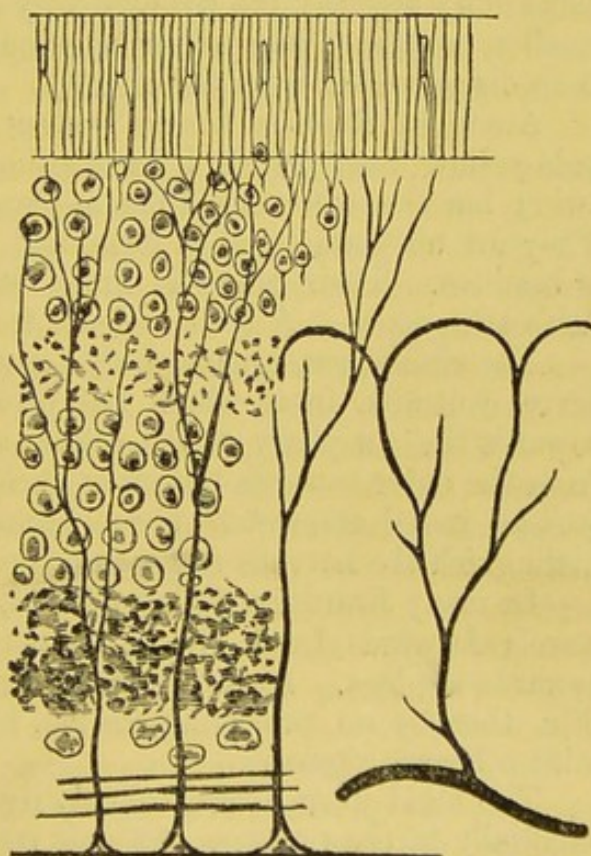
Spinning an excessively fine web around the cells and fibres, it maintains them all in position, and it supports the blood-vessels when these are present. To sum up, the connective tissue occurs in three forms—membranous, as the *membrana limitans externa* and *interna*; fibrous, as Müller's radial fibres; and as an excessively finely-fibrillated interstitial web.

It is a remarkable circumstance that the retina in the greatest number of vertebrate animals does not contain any *blood-vessels*. A retinal vascular system is confined, I believe, to *mammalia*; and amongst these there are great differences in the distribution of the vessels. In man, the whole extent of the retina, from the optic nerve entrance to the *ora serrata*, is vascularized; and the same obtains, I believe, in the ox, sheep, deer, and antelope; while in the hare the vessels are restricted to the area of the opaque nerve-fibres; and in the horse they form a narrow zone around the optic nerve entrance.

In the human retina no capillaries penetrate farther outwards than the intergranule layer or the inner surface of the outer granule layer. In consequence of this arrangement, the rods and cones are nearer to the chorio-capillaris than to the retinal capillaries. This alone would make it probable that they derive their nourishment from the capillaries; and morbid anatomy abundantly confirms this, for it is an established fact that atrophy of the chorio-capillaris, entailing atrophy of the hexagonal pigment epithelium, is also followed by atrophy of the rods and cones.

In the common hedgehog I have observed a peculiar disposition of the vessels, which is intermediate between the typical distribution in man and most other mammals I have examined, and that which obtains in the lower vertebrates; *viz.* the larger vessels, arteries, and veins, channel the *capsula hyaloidea*, while capillaries only pierce the retina.

FIG. 12.



Vertical Section of Retina, to illustrate the Distribution of the Vessels.



In fish, batrachia, and reptiles, the vascular net which pervades the capsula hyaloidea represents the retinal vascular system of mammals, but in birds this hyaloid net is wanting; and the great development of the pecten was thought by Müller to be a compensatory provision for both its absence and that of retinal vessels.

I will now pass on to notice—and I can only do so very briefly—the characteristic modifications which the retinal elements undergo in the five vertebrate orders.

In *Fish*, the retina is distinguished by the occurrence of cones of a peculiar kind—double or twin cones, as they are commonly called—by the large quantity of connective tissue it contains, and by the presence of very large branched connective tissue corpuscles in the intergranule layer.

The twin-cones have distinct outer segments or shafts. Their symmetrical appendages are joined together down one side, and at their inner end they sometimes appear to be actually continuous. Each twin has, I think, its own outer granule, and detaches a separate fibre inwards.

The *Batrachian* retina is distinguished by the large size of its elementary tissues: the rods are very large. The cones, which are smaller, contain a pale yellow or colourless bead. Twin-cones have been discovered in it by Schultze.

Amongst *Reptiles*, lizards possess cones only; these contain a pale yellow bead (in all I have examined). They are single and twin; but the twin-cones differ in many respects from those of fish. They are unsymmetrical in form, and one is beaded while the other is beadless. Their union is much less intimate than that of the fish's twin-cones. A little violence frequently disassociates them.

The chameleon, iguana, gecko, and many other lizards, have a fovea centralis, from which the primitive bacillary fibres radiate towards the periphery of the retina, and pursue an oblique course from the outer towards the inner surface of the retina, crossing the vertical radial connective tissue fibres, which enables us easily to distinguish the nervous and connective tissue fibres in this region.

In many lizards, a well-developed, conical, or sword-like pecten stands forwards from the optic nerve in the vitreous humour towards the lens. In the common alligator, and in the Nile crocodile, there is no projecting pecten, but the optic disc is marked with a brown pigment.

The blind worm's retina closely resembles that of typical lizards, especially in the presence of a pale cone-bead.

A cone-bead is wanting in snakes. In other respects, their retina resembles that of lizards.

The common English snake has no pecten: the viper has a rudiment of one; and the boa's optic nerve has a minute globular one.



The *Chelonian* retina agrees very closely with that of birds. Both are distinguished by bright cone-beads, and by twin-cones, the structure of which, particularly in chelonia, resembles that of lizards, and differs in the same way that this does from that of the fish's twin-cone. Each twin has certainly its own outer granule, and its separate primitive cone-fibre, which, as in lizards, takes an obliquely radial direction from the posterior pole of the globe. The cone-beads are of three colours—ruby, which are the largest; and orange, passing through pale yellow into pale green: the orange and green beads are the most numerous. The intergranule layer contains large branched connective tissue corpuscles, resembling those occurring in the same layer in the fish's retina.

The *Bird's* retina, as I have just said, agrees in several particulars with that of the chelonia. It has cones with beads of three colours, except in the case of nocturnal birds, *e. g.* owls, in which, as Schultze first showed, all the beads are pale, almost colourless, a light yellow. It has also twin-cones, like those of reptiles. In many birds there exists a very distinct fovea, and in some H. Müller discovered two, one at the posterior pole and the other near the ora retinæ, the former being affected by the incident pencils in monocular vision, the latter coming into use in vision with both eyes. The primitive bacillary fibres radiate obliquely from the fovea, as in man and reptiles.

The *Mammalian* retina is marked by the absence of twin-cones and of cone-beads. Its elements are smaller than those of the lower vertebrates. That of man has a macula lutea, in which is a distinct fovea centralis. The macula lutea occurs also in certain apes. The bat, mouse, hedgehog, and certain other animals, chiefly of nocturnal habits, have rods only; in most others cones and rods are both present, as in man. The retina is vascular; the distribution of the vessels, however, varies in different families.

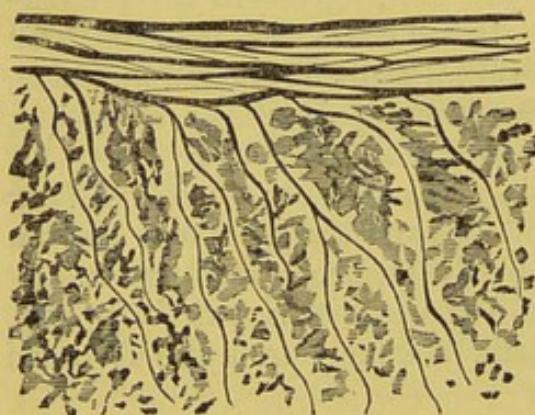
There are two situations where the structure of the retina in man and some other vertebrates which I have particularized is peculiar; these are the macula lutea and the ova retinæ. The macula lutea is an oval spot, at the posterior pole, of a yellow colour: the coloration is not produced by granular pigment, as in that of the choroid, but it is a diffuse stain of the elementary tissues. In the centre of the macula is the minute pit—not a perforation—the fovea centralis. This pit is produced by the radial divergence of the primitive cone-fibres from a central point, and by the thinning and outward curving of all the retinal layers (except the bacillary) as they approach this point. In the fovea and the macula, except at its periphery, cones only occur, and they are more slender and longer than in other parts of the retina. The greater length is chiefly due to the elongation of the cone appendage. The slenderness of the cones does not allow their appendages to include the



outer granules, so that these latter lie, all of them, at the inner side of the *membrana limitans externa*. Owing to the radial direction of the primitive cone-fibres, the outer granules belonging to the central cones lie peripherally, so that the outer granular layer is absent from the foveal centre.

At the inner surface of this layer the cone-fibres combine in a plexus the bundles of which, near the centre of the macula, are directed obliquely towards the inner surface of the retina; between the centre and the circumference of the macula they assume a direction nearly parallel to the retinal layers, and at the circumference of the macula they run nearly vertically.

FIG. 13.



Primitive Bacillary Fibres, from the innermost  
Bundles of the Cone-fibre-plexus, traversing the  
Intergranule Layer.

At its inner surface, the cone-fibre-plexus breaks up into primitive fibres, which pass through a thin connective tissue stratum, the intergranule layer, and enter the inner granule layer. This latter, at its beginning in the centre of the fovea, is not separate from the ganglionic layer. The nerve-fibres pursue in it the same direction as in the outer granule layer.

The ganglionic layer, at the periphery of the fovea, contains three or four tiers of cells;

these become fewer towards the foveal centre, but even here they lie in a double or treble series, bedded in a granular tissue.

The *ora retinæ* is the other situation to which I referred as having a peculiar arrangement of its tissues. Being less important than the fovea, I can notice it only very briefly. Towards the *ora* the nervous elements gradually become fewer, the layers thin out, the beads and cones shorten and become stouter. With this decrease of the nervous tissues, the connective tissues predominate, and they are prolonged beyond the *ora* as the *pars ciliaris retinæ*, the radial fibres becoming, according to Kölliker's observations, the columnar, epithelial-like bodies which line the *pars striata*.







