VI. *On the Anatomy of the Fovea Centralis of the Human Retina.* *By* J. W. HULKE, *F.R.C.S., Assistant Surgeon to the Middlesex and Royal London Ophthalmic Hospitals. Communicated by* WILLIAM BOWMAN, *F.R.S.*

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THE following account of the fovea centralis is chiefly drawn from a study of this part in a perfectly healthy eye excised during life (in order to allow the extirpation of a tumour) and *instantly* put into a solution of chromic acid. By *instantly* hardening the retina, the formation of the *Plica* and the resulting disturbance of the fovea were prevented, and it was possible to make extremely regular sections.

The fovea centralis is a minute circular pit in that central spot of the retina called, from its yellow colour, the macula lutea—yellow spot. This colour proceeds from a diffuse stain of the retinal tissues, and not from the presence of granulated pigment as in the choroid. It is most intense at the centre of the spot, and fades towards the circumference of the spot, where it ceases gradually without a distinct margin, so that neither in the fresh retina nor in that which has been artificially hardened in chromic acid (which destroys the colour) can we use this as a measure of the extent of the spot. The size of the spot is, however, more certainly fixed by the extent of certain anatomical peculiarities which do not occur in any other part of the retina.

The ophthalmoscopic appearance of the spot in the living eye is that of an ellipse, the major axis of which is horizontal. It is rather larger than the disk of the optic nerve, and comes into view when the eye under observation looks directly at the sight-hole in the mirror. It is distinguished from the parts around by its deeper colour and by a certain dullness, difficult to describe but readily appreciated when seen, which proceeds from the faintness or absence of the reflection occurring at the inner surface of the retina elsewhere. In children, particularly in those of dark complexion, the retinal reflection ceases at the periphery of the macula with such a definite edge that the macula appears as a dull, dark-coloured spot encircled by a bright ring. In the middle of the macula lutea a bright dot marks the position of the fovea centralis.

According to HELMHOLTZ the *visual line* (the straight line which joins the most sensitive part of the retina and the object directly seen) does not coincide with the axis of the eyeball, as is commonly thought, but includes an angle with it; and the most sensitive point in the retina (the fovea) lies slightly outwards, and usually a little below the posterior end of the axis of the globe*.

In an artificially hardened normal eye, in which the relations of the parts were undis-

* CORNELIUS, 'Die Theorie des Sehens und räumliches Vorstellens.' Halle, 1861, Abth. 1. S. 250.

turbed, I found the distance of the fovea from the centre of the optic nerve exactly equalled $1\frac{5}{6}'''$.

In vertical sections through the artificially hardened macula the fovea centralis is seen to be produced by the radial divergence of the cone-fibres from a central point, and by the thinning and curving of the inner retinal layers towards the outer surface of the retina as they approach this point. The thickness of the retina decreases in a rapid uniform curve from the edge to the centre of the fovea, and very slowly from the foveal edge towards the ora retinæ. Since the maximum thickness coincides with the edge, and the minimum with the centre of the fovea, the former is the most elevated, the latter the most depressed part in the macula.

At the centre of the fovea, where the retina is thinnest, passing from the outer to the inner surface, we meet with the following structures:—the bacillary layer, the outer limiting membrane, a thin band of areolated connective tissue which transmits a few cone-fibres, the inner granule and ganglionic layers represented by scattered cells and not separated by a distinct granular layer, optic nerve-fibres, and lastly, the inner limiting membrane.

Minute Structure.

1. The bacillary layer (Plate VII. fig. 1, $_1$) in the fovea contains cones only; and rods first appear midway between the centre of the fovea and the outer border of the macula*.

The foveal cones (figs. 2 & 3) are longer and more slender than those distant from the macula, and there is a similar difference in the length and stoutness of the rods. In both rods and cones an outer and an inner segment are observable; the outer in profile is a slender rectangle; the inner is flask-shaped, and is in the cones much stouter than the outer segment, while in the rods it only slightly exceeds the outer segment.

The inner segment is always associated in the usual manner, by inclusion or by a communicating fibre, with an "outer granule" (figs. 2 & 3). Connexion by a fibre obtains (1) with the central cones whose associate outer granules are peripherally displaced, (2) with all cones associated with a distant outer granule, and (3) always with the rods whose smaller diameter does not allow them to include their granule.

There is a definite outer limiting membrane which has the same relations to the bacillary and outer granule-layers as in other situations.

Outer Granule-layer (fig. 1, $_2$).—Owing to the peripheral situation of the outer granules belonging to the central cones, this layer is absent from the centre of the fovea. It begins at a short distance from this latter, attains its maximum thickness near the foveal edge, then decreases gradually, and again increases towards the border of the macula. This variation is due to the presence, at the margin of the fovea, of the granules belonging to the central cones in addition to those connected with the cones of this part, and to

* Kölliker says there are no rods in the macula (Handbuch der Gewebelehre, Aufl. iv. S. 664). This difference perhaps proceeds from the difficulty in fixing the exact extent of the macula in chromic-acid preparations, in which the colour of the spot is destroyed.

the increase of outer granules connected with the occurrence of rods towards the border of the macula.

The relation of the outer granules to the cones and rods (figs. 2 & 3) (mentioned in the description of the bacillary layer) indicates them to be nuclei of the inner segments of these. In fresh specimens they are roundly oval bodies. I have not been able to distinguish any constant difference between those associated with cones and those with rods. The lozenge-shape of some granules in chromic-acid preparations results, I suspect, from their compression by the sheathing membrane of the rod or cone which shrinks under the action of the acid, or from traction exerted upon them by the cone- or rod-fibre.

The fibres produced from the inner segments of the cones and rods—primitive bacillary fibres (some of which connect these with the outer granules, fig. 1, 2)—traverse the layer obliquely from its outer to its inner surface, and radially from the centre of the fovea towards the ora retinæ. At the inner surface of the layer they combine in a plexus (fig. 1, 3, *Cone-fibre plexus*), which at the centre of the fovea (where the outer granule-layer is absent) lies between the bacillary and inner granule-layers, but at the margin of the fovea between the outer and inner granule-layers. The thickness of this layer (which in the chameleon I termed the cone-fibre plexus, H. Müller's intergranule-layer) at the margin of the fovea equals or slightly exceeds that of the combined outer and inner granule-layers. The general direction of the bundles of the plexus coincides with that of the primitive bacillary fibres in the outer granule-layer; it becomes, however, less oblique in the inner part of the plexus, where the bundles run nearly parallel to the surface of the inner granule-layer.

These inner bundles midway between the centre of the fovea and the edge of the macula form a stratum parallel to the surface of the inner granule-layer. Beyond this point, with increasing distance from the centre of the fovea, the obliquity of the bundles increases until at the margin of the macula their direction is vertical.

At its inner surface the bundles of the plexus (fig. 4) resolve themselves into primitive fibres which enter the inner granule-layer (fig. 1, 4) through a granular stratum of finely areolated connective tissue. At the edge of the fovea and at the border of the macula, where the bundles of the plexus are very oblique or nearly vertical, the primitive fibres pursue the same direction for a short distance in the inner granule-layer, but where the bundles are parallel to the surface of the inner granule-layer, the resultant fibres pass off nearly vertically into this layer*.

* An oblique fibrillation has long been known in the intergranule-layer of the human macula lutea. Bergman seems first to have described it as a natural appearance[1].

H. Müller and Kölliker originally regarded it as a post-mortem or an accidental change; but subsequently Müller, having discovered the oblique fibres in the chameleon's macula, saw their correspondence to the oblique fibres in the intergranule-layer of the human macula, and acknowledged the oblique direction of these to be natural[2].

Kölliker a year later described two forms of fibrillation in the human macula, and left it undecided which

[1] Bergman, Ztsch. f. rat. Med. N.F. V. S. 245.

[2] H. Müller, Würzb. Naturwiss. Ztsch. Bd. iii. S. 31.

Inner Granular Layer (fig. 1, 5).—At the centre of the fovea this layer is very thin, and its innermost granules are not clearly separated from the outermost cells of the ganglionic layer (fig. 6); but at the margin of the fovea it has already a considerable thickness, and the granular layer, now a distinct band, separates it from the ganglionic layer. The granules are roundly oval nuclei of ·000465″ diameter, and larger cells of ·000697″ diameter, in some of which a nucleus is discernible. The layer also contains obliquely and vertically radial fibres. The latter are connected on the one side with the membrana limitans interna, and on the other with the thin granular band lying between the cone-fibre plexus and the inner granule-layer; they are manifestly a modified connective tissue, and form conspicuous objects when examined with an $\frac{1}{8}$″ objective.

The oblique fibres are much more delicate, and require the highest magnifying powers for their demonstration (fig. 5). With $\frac{1}{25}$″ object-glass I traced their identity with the fibres which enter the layer from the cone-fibre plexus (fig. 4), and I have also seen the smaller inner granules or nuclei intercalated in the oblique fibres, and observed these connect themselves with the larger granules or cells.

The Granular Layer (fig. 1, 6).—This does not exist as a distinct layer at the centre of the fovea, but appears at a short distance from it in the angle between the inner granule and ganglionic layers. At the margin of the fovea it has a thickness of ·001627″, which it keeps with little variation throughout the macula. It transmits the connective tissue and nerve-fibres which pass between the inner granules and the ganglion-cells.

The Ganglionic Layer (fig. 1, 7).—At the centre of the fovea the ganglion-cells do not lie in a continuous band, but are scattered in a double or treble series through a finely areolated matrix of connective tissue. At the margin of the fovea they lie closer together, four or five deep, in the spaces between the vertically radial connective-tissue fibres. Throughout the fovea and macula the cells are separated from the membrana limitans interna by a narrow granular band. This latter is structurally identical with the granular layer; throughout the macula and fovea it contains optic nerve-fibres.

Connective-Tissue Structures.—The origin and distribution of the vertically radial

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was natural: one, in which he says "the fibres in the intergranule-layer had an oblique and horizontal curve (as BERGMAN saw them);" another, in which "they had a generally vertical direction broken by a double almost rectangular band"[1].

It does not, however, appear in their writings that BERGMAN, MÜLLER, or KÖLLIKER actually demonstrated the connexion of the oblique fibres of the intergranule-layer of the human macula with the elementary tissues of the other layers. KÖLLIKER says that he saw processes from the cones (which he calls MÜLLER's fibres) in the intergranule-layer throughout the macula, even in the fovea itself, adding "they can be easily followed to the inner granule-layer;" yet as he subsequently disputes SCHULTZE's[2] statement—that the oblique fibrillation in the human macula occurs in the inner part of the outer granule-layer (a layer which lies between the bacillary and the intergranule-layer)—he leaves the subject, even so far as his own observation goes, very ambiguous.

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[1] KÖLLIKER, Handb. der Gewebelehre, iv. Aufl. S. 674.

[2] SCHULTZE, Sitzungber. der niederrhein. Ges. in Bonn, 1861. I regret that this paper has not been within my reach. The reference I take from KÖLLIKER's 'Handbuch.'

fibres agree with that which obtains in other parts of the retina, only their branches are with difficulty traceable through the granular band lying between the cone-fibre plexus and the inner granule-layer, in which most of them appear to end. They are also structurally connected with the finely areolated tissue composing the granular layer, and, further, with the interstitial tissue which pervades all the layers.

Blood-Vessels.—In none of my sections have I found blood-vessels at the centre of the fovea; at the margin, however, capillaries occur, and small arteries are not uncommon within the limits of the macula. The vessels nowhere penetrate beyond the outer surface of the inner granule-layer.

Deductions.

1. Since the total of the effects of light upon living tissue will be greater as the extent of tissue traversed by it is greater, and since the relative common sensitiveness of a surface varies with the number of distinct sentient elements it contains, it follows that the greater length of the cones and rods, and their greater slenderness, which allows a larger number of them to the superficial unit, are in harmony with the greater sensitiveness of the retina at the macula lutea. Inasmuch, however, as the foveal cones are stouter than the rods, a superficial unit at the centre of the fovea contains fewer sentient (*i. e.* percipient) elements than the same unit near the periphery of the macula lutea; and on this ground the sensitiveness of the retina at the fovea should be less than that of the retina near the periphery of the macula. On the other hand, the extreme thinness of the inner layers of the retina at the centre of the fovea, places the bacillary layer here most favourably for receiving incident light.

2. The division of the rods and cones into an outer and an inner segment is natural. The facts in support of this are, the presence of the division in perfectly fresh specimens; its sharpness and constant occurrence at a definite place; the constantly rectilinear figure of the outer, and the curvilinear figure of the inner segment; the different refractive powers of the segments; and their different behaviour towards staining and chemical solutions.

3. From these structural differences it is a fair inference that the segments have different physiological meanings.

The higher refractive power, straight sides, and slender cylindrical or prismatic figure of the outer segment may be adaptations for confining within the segment light incident upon its end, and for preventing the lateral escape of light through the sides of the segment into neighbouring cones and rods. These considerations incline me to adopt the opinion that this segment has an optical function, an opinion which derives further support from the fact that, in those animals in which the segment is so wide a cylinder that a ray might be incident upon the inner surface of its sides at a small enough angle not to be reflected but to pass out, the segment is insulated by a sheath of black pigment.

The inner segments of the cones and rods are the specially modified peripheral terminations of the optic nerve-fibres; and at their junction with the outer segment the conversion of light into nerve-force may take place.

4. The outer granules being the nuclei of the inner cone- and rod-segments, probably maintain the integrity of these as living tissues, and are not directly concerned in their specific functions as organs of perception.

5. The primitive bacillary fibres are the link by which the cones and rods communicate through the inner granules and ganglion-cells with the optic nerve-fibres.

6. The smaller inner granules are nuclei of the oblique bacillary fibres in the inner granule-layer; or they may be small bipolar ganglion-cells, and act specifically on the forces transmitted through the oblique fibres from the cones and rods. The larger inner granules not being distinguishable by any definite structural characters from the smaller cells of the ganglionic layer, may agree with these latter cells in function.

7. Since the ganglion-cells (of the ganglionic layer) are fewer than the inner granules, and much fewer than the cones and rods, and since it is probable that these latter communicate with the optic nerve-fibres only through the ganglion-cells, it follows that one ganglion-cell probably is in correspondence with more than one inner granule and with several cones and rods. From this it is not an improbable conjecture that the cones and rods are disposed in groups*, each of which is represented by one or more ganglion-cells, the function of which is to connect or coordinate the individual action of the separate bacillary elements in their groups in a manner analogous to that attributed to the ganglion-cells of the spinal cord by V. der Kölk.

8. There is a close general resemblance between the human fovea and that of the chameleon†.

Description of the Plate.

PLATE VII.

Fig. 1. A vertical section through the centre of the fovea centralis in the vertical meridian, extending about halfway towards the periphery of the macula lutea, ×240.

1. Bacillary layer.
2. Outer granule-layer.
3. Cone-fibre plexus.
4. A granular band between the latter and the inner granule-layer.
5. Inner granule-layer.
6. Granular layer.
7. Ganglionic layer.

a. Centre of fovea; *b*, membrana limitans externa; *c*, membrana limitans interna; *d*, section of a blood-vessel.

* I have an impression that I have seen this in a German author, but have not been able to find the passage again.

† H. Müller, "Ueber das Auge des Chamäleons," Wurzb. Naturw. Zchr. Bd. iii. S. 36.

Fig. 2. Three cones from the centre of the fovea, with outer granules lying in their diverging primitive fibres, ×1300.

Fig. 3. Cones and outer granules from near the margin of the fovea. The inner segments of the cones are coarsely granulated; three include outer granules, and all produce a fibre which runs obliquely inwards through the outer granule-layer, ×1300.

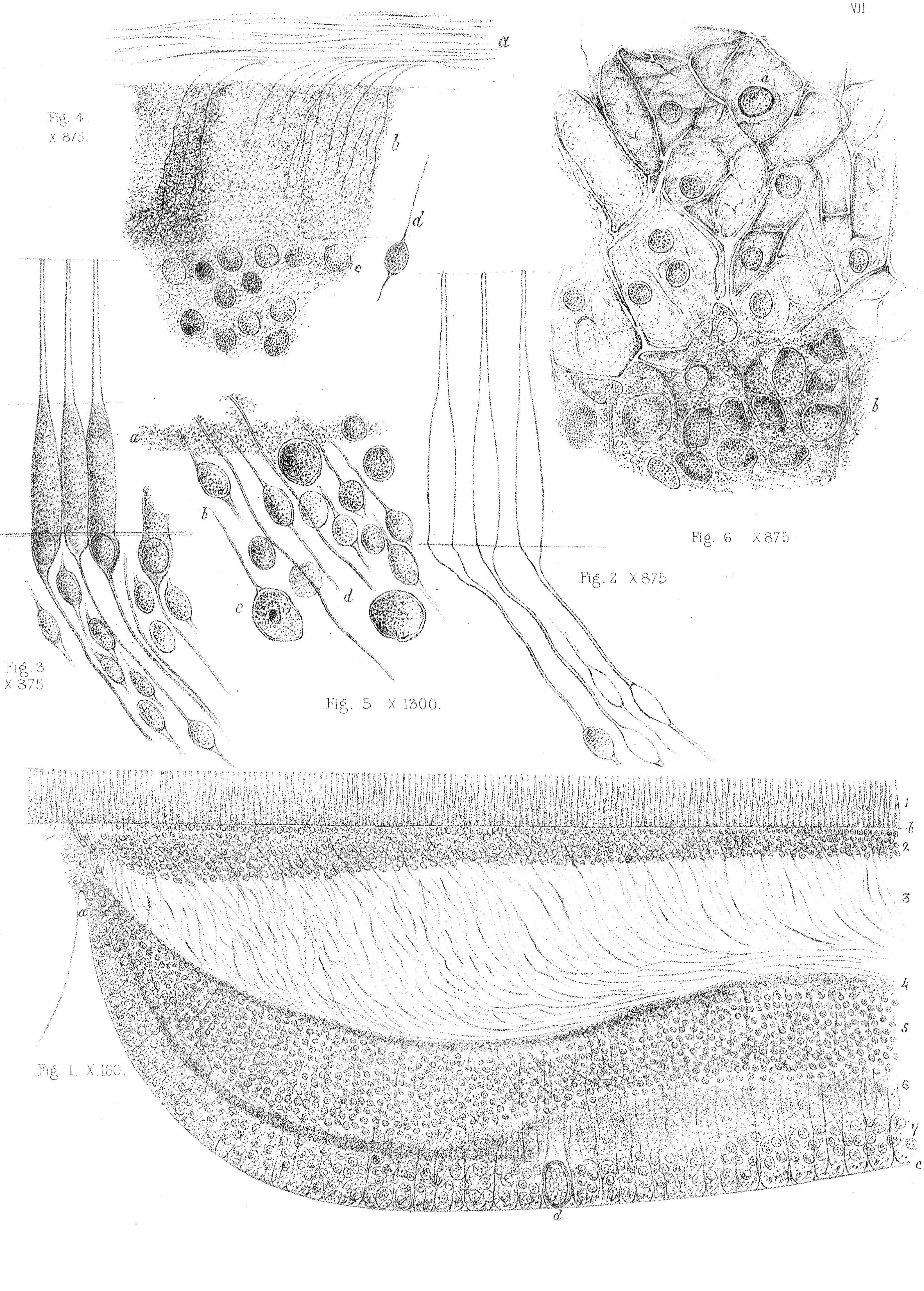
Fig. 4. A vertical section showing the passage of the primitive fibres of the cone-fibre plexus into the inner granule-layer midway between the centre of the fovea and the margin of the macula lutea, ×1300: *a.* horizontal band of inner bundles of the cone-fibre plexus detaching fibres which traverse *b*, a finely areolated band lying between the plexus, and *c* the inner granule-layer; *d*, an inner granule in one of these fibres.

Fig. 5. A vertical section through the inner granule-layer near the edge of the fovea, ×1300: *a*, the granular band marked *b* in the preceding figure; *b*, the smaller granules; *c*, the larger granules; *d*, obliquely directed bacillary fibres with which the granules are connected.

Fig. 6. A vertical section through the inner layers at the centre of the fovea, ×1300: *a*, inner granules imbedded in areolated connective tissue; *b*, ganglion-cells.

Note.—In order to include these figures in one Plate they have been much reduced from the size of the original drawings, the fine outlines and delicacy of which can scarcely be reproduced by lithography.

VII



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