Observations on the structure of the central fovea of the human eye / C. H. Golding Bird and E. A. Schäfer.

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rend bekanntlich noch bis vor wenigen Jahren, als Samelsohn seinen Fall publicirte, kein solcher existirte.

Während unsere beiden letzten Fälle also in Betreff des Verlaufes der papillomaculären Opticusfasern die früheren Angaben bestätigen, lehrt uns unser erster Fall von Tabes (Hoepfner), wie 1/4 aller Opticusfasern, welche den äusseren-unteren Netzhautquadranten versorgen, im Sehnervenstamm bis zum Chiasma verlaufen. Die Configuration und die Lage des Herdes lehrt, wie sich die Fasern des äusseren - unteren Netzhautquadranten nach aussen-unten zwischen die papillomaculären Opticusfasern und die Sehnerven-Peripherie einschieben, und wie sie im Verlauf des Opticus weiter nach hinten ihre Configuration ändern und allmählig an die Unterfläche rücken, also eine leichte spiralförmige Drehung beschreiben. Glauben Sie nun, m. H., dass es zu gewagt ist anzunehmen, die übrigen 3/4 der peripheren Nervenfasern machten einen ähnlichen Verlauf durch? Ich bin eigentlich davon überzeugt, und somit würden wir im Sehnervenstamm einen leicht zusammengedrehten Strang vor uns haben, wo die peripheren Opticusfasern einen leicht spiraligen Verlauf nehmen, während das papillomaculäre Faserbündel im hinteren Theil des Opticus die Axe bildet, sich jedoch weiter nach vorn allmählig nach aussen zieht und in der Papille gerade keilförmig nach aussen liegt, die Spitze des Keils den Centralgefässen zugerichtet.

Für die Längsschnitte durch die Papillen bei den verschiedenen Patienten bin ich Herrn Collegen Siemer-

ling zu grossem Dank verpflichtet.



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Observations on the structure of the central fovea of the human eye

by

C. H. Golding Bird, F. R. C. S. and E. A. Schäfer, F. R. S.

(With pl. I and 4 figs. in the text.)

In his classical dissertation "On the Retina of Man and Vertebrates" Heinrich Müller 1) gives a minute account of the structure of the macula lutea and of its contained central fovea. Long previous to that time the view which held that the central fovea was a hole in the retina had been given up and it had been described by Michaëlis as a fossa from $\frac{1}{10}$ " to $\frac{1}{5}$ " (0.2 mm. to 0.4 mm.) in depth, a measurement which Müller acquiesces in. The latter further describes the depression as measuring about 0.2 mm. in diameter in the vertical meridian and as dipping in at first gradually afterwards more steeply. He states that it appeared to him to have an elongated form (we presume in the horizontal meridian). Although the various layers are described by Müller as diminishing greatly in thickness at the fovea, he states that only the inner molecular layer seems entirely to disappear and that "certainly the inner granule layer does not constantly fail in the middle of the fovea". Müller further makes the pregnant remark "Es ist nur indessen mehr als wahrscheinlich, dass in der Conformation der Grube und damit auch in der Anordnung der Netzhautelemente daselbst nicht unerhebliche individuelle Verschiedenheiten vorkommen, welche mit Entwickelungszuständen zusammenhängen mögen".

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¹) Anatomisch-physiologische Untersuchungen über die Retina des Menschen und der Wirbeltiere. Zeitschrift für wissenschaftliche Zoologie. 1856. p. 1—122.

Müller gives no figure of the fovea in man, but in another paper 1) he describes and figures the structure of the same part in the chameleon and from this and the comparisons which he draws between the two it is clear that he fully recognises the many points of similarity which they exhibit. In the figure of the chameleon's fovea a dipping inwards of the membrana limitans externa which is covered by long slender cones, is distinctly represented; and the cone-nuclei are shown to be here removed from the limitans externa instead of being closely applied to that membrane as is the case over the rest of the retina.

The measurements given by Müller would give the human fovea the form of a small horizontally extended pit with steep sides, somewhat like the figures given by Hulke and Krause (see fig. 2). Henle 2) figures a broadly open fovea which he states to be only 0.2 mm. diameter but calculated from the magnification of the figure it must be at least double this. He gives the thickness in the middle as about 0.1 mm. but the figure again represents it as somewhat greater (0.123 mm. without the pigment layer). There is no distinct depression of the external limiting membrane. The retinal elements are evidently so ill-preserved as to render it extremely difficult to determine their relations at this part.

Hulke 3) gives a description of the yellow spot and central fovea which is in many respects different from that of H. Müller. He figures the fovea as a deep pit with steep sides terminating in a point, opposite the very middle of which there are no recognisable retinal elements except the cones; this most central part is however quite narrow, almost linear, and the retinal layers with the exception of the nervefibre layer are all represented as extending quite up to the centre. The limitans externa is a plane, without any depression; the cones opposite the centre of the fovea are not delineated as longer than elsewhere in the macula; the cone-nuclei are absent opposite the very middle of the fovea, which appears occupied below the cones by a blending of the inner granules and ganglion cells. Near the

¹⁾ Würzburger naturwissenschaftliche Zeitschrift. 1862. Bd. III.

²) Handbuch der system. Anatomie. 1866. — Eingeweidelehre. Fig. 512. p. 662.

³⁾ Phil. Trans. 1867.

middle the cone-nuclei are shown as somewhat removed from the limitans externa, but traced to the side they very soon come to lie up against that membrane. The ganglion-cells are spherical. The oblique direction of the fibres of the inner granules (bipolars) is clearly indicated. Although no measurements are given of the diameter of the fovea depicted, to judge by the stated magnification of the figure its width is about 0.75 mm. and its depth about the same. The section is expressly stated to be in the vertical meridian. The close resemblance between the human fovea and that of the chameleon, which has also been described by Hulke 1) is specially insisted on.

F. Merkel²) gives a figure and description of the central fovea which seems to be based upon specimens so ill-preserved as to be of

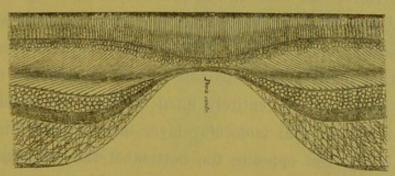


Fig. 1. Diagram of central fovea (M. Schultze).

little use towards the elucidation of its structure. It is noteworthy however that he also like Hulke, represents the external limiting membrane as flat and the cones of the same length throughout. It is here that we first find the ganglion-cells described as bipolar.

The diagram of the structure of a section through the macula lutea and fovea centralis of a human retina which was given in 1872 by Max Schultze in his article upon the retina 3) is almost too well-known to need description, for it has been copied into nearly all text

¹⁾ Journ. of Anatomy and Physiology. 1867. Vol. I.

²) "Ueber die Macula lutea des Menschen etc." Leipzig 1870.

³⁾ Stricker's "Handbuch der Lehre von den Geweben". Leipzig 1872. This diagram has a general similarity to two diagrammatic figures of sections through the fovea, described by Schultze in Bd. II of the Arch. f. mikr. Anatomie, and is evidently adapted from them; but it shows more than one not unimportant modification, as will subsequently be noticed.

books. In this diagram the fovea is represented as a broad and deep depression of the internal limiting membrane, shapen like an oldfashioned wide tea-cup, having the sides at an angle of 45° and the bottom nearly flat, and occupying about one-fourth of the whole section of the fovea. This depression of the internal membrane nearly abuts against a shallower but well marked pit formed by a depression inwards of the external limiting membrane, upon which are set the cones. These diminish in diameter towards the centre but show an increase in length exactly corresponding to the depression upon which they stand, so that the line of pigment cells is maintained at an even plane without any depression of the external surface of the retina being produced corresponding to that of the limitans externa 1). This diagram therefore, like that of the chameleon's fovea given by Müller, shows two depressions or foveae, inner and outer, with their convexities directed towards one another. The interval between the two membranes at this place is very narrow and is represented in Schultze's diagram as being almost entirely filled by the cone-nuclei and by an extension of the internal molecular layer, none of the other layers of the retina being seen opposite the bottom of the cup, that is to say, over one quarter of the diameter of the fovea. The cone-nuclei are represented as forming a layer two or three deep, close to the limitans externa. They appear as oval bodies and the fibres which are prolonged from them (cone-fibres) are delineated as very fine filaments diverging obliquely towards the sides of the fovea. The inner granules are shown as closely packed, round nuclei, forming a layer gradually diminishing towards the middle of the fovea but sharply marked off up to its point of disappearance from the strata above and below it; whilst the nerve-cells of the ganglionic layer are represented as elliptical or spindle-shaped bipolar cells with their axes parallel to the sides of the fovea.

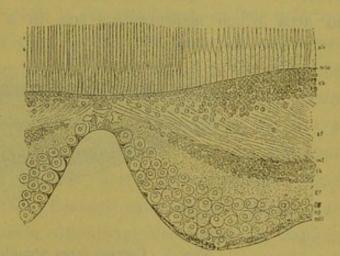
W. Krause²) also gives a representation of a section "durch

¹⁾ It is noteworthy that in the original drawings in the Arch. f. mikr. Anatomie Bd. II the cones which are set on this depression are not exactly vertical but their outer ends tend to converge somewhat towards the centre so as to be more closely packed where they abut against the pigmentary layer.

²⁾ Allgemeine Anatomie. 1876. p. 168.

das wirkliche Centrum der Fovea." This does not profess to be a diagram but an actual representation of a frozen section. In general form it closely recalls the representation given by Hulke. The fovea is shown as a conical depression, deep, with steep convex sides; the apex or bottom of the fovea is rounded; the limitans externa dips slightly towards it, much less than in Schultze's diagram. The cones over this depression are longer in the middle than at the sides, so much so that the line joining their outer ends is even somewhat bulged. This author agrees with Müller, Schultze and nearly all other observers in representing the cones as more slender over the middle

of the fovea than elsewhere, but he makes them pass abruptly into thicker cones about half way up the declivity of the external depression. Here also cone-nuclei are represented throughout close to the limitans externa, but the deeper ones are less closely packed at the fovea than at its margin. The cone-fibres are again delineated



than at its margin. The cone- Fig. 2. Central fovea according to W. Krause.

as mere lines. The inner nuclear layer is seen to be separated everywhere by a thick inner molecular layer from the ganglionic layer and it also terminates sooner than the last mentioned layer, which is represented as if continued nearly to the centre of the fovea. The ganglion-cells are represented large and round. At the very bottom of the fovea "the inner retinal layers are replaced by hyaline stellate cells and radial fibres (fibres of Müller); besides these there are here present only the cone and cone-fibre layers." To this it may be added that the cone-fibre layer in Krause's figure is at this part nothing but a small mass of cone-nuclei.

Kuhnt (1881)1) made a special study of the fovea in three normal

¹⁾ Sitzungsbericht der ophthalmol. Gesellschaft in Heidelberg. 1881.

eyes, but the detailed description of only one of these is given. Kuhnt has not published figures of his preparations nor does he say in what meridian his serial sections were taken. He describes the dip of the fovea as beginning 0·135 mm. from the middle which would give a diameter of only double this amount (0·27 mm.) for the whole fovea. In another place however he states that the nerve fibres end as a distinct layer 0·4 mm. from the centre. As according to the testimony of all observers they unquestionably end within the dip this would give a total diameter of nearly 1 mm. for the fovea. We do not know how the discrepancy between these statements is to be explained. He describes the bottom of the fovea (over an area which measures 0·2 mm. in a horizontal by 0·15 mm. in a

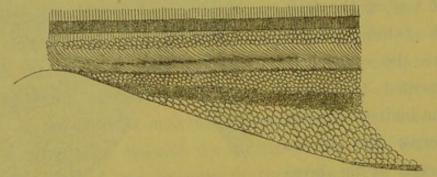


Fig. 3. Central fovea according to Schwalbe.

vertical direction) as quite flat, and reduced to the cone and fibrous layer. In the middle of this flat bottom (fundus foveae) is a minute depression (foveola) which has only five or six cones over it in a single plane of the section. Kuhnt further states that at the very centre the cone-nuclei lie close to the limitans externa and in a single layer and that their fibres radiate from this centre in a nearly horizontal direction to either side (or rather to all sides).

The illustrative deficiency of Kuhnt's paper is filled up by Schwalbe 1) who represents a section through the central fovea and states that he owes the figure and description to a preparation sent him for the purpose by Kuhnt. He adds "Leider zeigte sich an denselben das Centrum der Fovea nicht genau getroffen, so dass ich Kuhnt's Angaben

¹⁾ Sinnesorgane. Erlangen 1887. p. 112.

über den Fundus Foveae und seine Foveola nicht näher prüfen konnte. Als neu füge ich der im Wesentlichen der Kuhnt'schen entsprechenden Beschreibung Angaben über das Verhalten der Limitans externa zur äusseren Grenzlinie der Zapfenkörner hinzu."

The semi-diagrammatic representation given by Schwalbe shows a broad depression of the limitans interna gradually sloping towards the centre, which is rounded. As noted above by Schwalbe the figure shows nothing of Kuhnt's flat fundus with its central foveola. There is no depression of the limitans externa and the cones appear of exactly the same size and length over the whole extent of the fovea. The cone-nuclei, which are oval, are three deep at the edge of the fovea and are here seen to be close to the membrana limitans externa; nearer the centre of the fovea they become less numerous and somewhat removed from the limitans externa. With regard to this Schwalbe makes the following remarks "Dieselbe ist aber nicht nach innen convex eingebogen, wie dies Max Schultze aus dem Gebiet der Fovea beschreibt und abbildet, sondern wie im übrigen Teile der Netzhaut vollkommen geradlinig, worin ich mit Merkel übereinstimme. Eine solche Einbiegung der Membrana limitans externa wird leicht vorgetäuscht durch eine eigentümliche Anordnung der Kerne der Zapfenzelle innerhalb der Fovea. Sie liegen nämlich nicht unmittelbar an der Innenseite der Membrana limitans externa, sondern beginnen erst in 12 \mu Abstand nach innen von der genannten Membran, so dass dadurch in den centralen Partien der Fovea eine kernfreie Zone entsteht, die sich peripher allmählich verschmälert und schliesslich unter Anlagerung der Zapfenkörner an der Membrana limitans externa schwindet. Die äusserste Grenzlinie der Zapfenkörner convergiert also peripher zur Membrana limitans externa und ist wohl, da man stets von einer inneren Anlagerung der äusseren Kerne an die limitans externa geredet hat, in unserem Falle mit letzterer verwechselt worden." That is to say that previous observers (e. g. Max Schultze) have been deceived by the shifting of the outer granules from the membrana limitans externa into thinking that that membrane was depressed over the fovea, whereas according to Merkel, Kuhnt and Schwalbe no such depression exists.

With regard to the elements of the other layers as figured by Schwalbe, both the inner granules and ganglion-cells are represented as oval, obliquely disposed cells, the former ceasing near the middle of the fovea, the latter some little distance from the middle. At the middle of the fovea only the cones and cone-fibres are represented, with a very thin layer of molecular substance. The cone-fibre layer is thicker than the cone-layer, and is moreover represented as being quite as thick here as at the periphery of the fovea; in fact like the cone-layer itself, it is drawn of the same thickness throughout the section. In most other points the diagram is like that of Max Schultze.

Finally we may mention a figure by Cadiat¹) which has been copied into some text books of Physiology. In this representation the fovea is a broad depression of the inner surface and there is a corresponding depression of the external limiting membrane. The cone-nuclei are shown to be removed from the latter near the middle of the fovea. But there has been no attempt to depict with accuracy the number, size and relations of the retinal elements, so that the figure, although correct in certain general features, is inaccurate as regards the details, being rather the expression of a general impression that an exact reproduction of the appearance of a specimen.

The preparations upon which the observations to be recorded in this paper are mainly based are from the retina, apparently perfectly normal, of a lad of 15, from whom the eye had been removed in consequence of anterior staphyloma.

After separation of the anterior part of the globe and the removal of the vitreous humour from the posterior part, the latter was filled with 1/6 0/0 solution of chromic acid and placed in a quantity of the same solution for three days. The preparation was then transferred to a mixture of one part of glycerine to seven of methylated spirit in which it remained for some days, it was then preserved in a mix-

¹⁾ Anatomie Générale.

ture of 1 part of glycerine to sixteen of spirit. The effect of this treatment was to obviate the brittleness to which chromic acid preparations are otherwise liable. An oblong piece of the retina including the macula and fovea was then carefully cut out and after having been stained in bulk with haematoxylin it was placed in gum and cut by aid of a Wiliams' freezing microtome into a series of sections each of which was mounted separately. The sections extend from the edge of the macula lutea to just beyond the middle of the central fovea; one section of the series passing, so far as we can judge, exactly through the middle of the fovea. The sections vary in thickness, some being fairly thin, others not very thin; but they are sharply stained and perfectly transparent, so that it has been possible not only to make out with great distinctness all the details which such specimens are able to show, but also to obtain sharp micro-photographs of the most important parts (Zeiss' apochromatic objectives having been employed for this purpose). The actual specimen from which the photographs which accompany this paper have been taken, is one which as before said passes through the very middle of the fovea. The reasons for considering that this section passes through the centre are:

- 1. The depression of the external fovea (which as will be subsequently seen is in this retina more acute than that of the internal) passes its deepest point in this section 1).
- 2. The vertical course taken by the central cone-fibres and the manner in which these and the more laterally situated cone-fibres can be followed along their whole length from the limitans externa to the outer molecular layer. It is obvious when we consider the oblique course which the more peripheral cone fibres take, radiating as they do from the middle, that they could only be followed out in this way in a section which passes exactly through the centre.
- 3. The fact that the cone-nuclei, which, from the edge of the fovea, have been gradually leaving the limitans externa and appro-

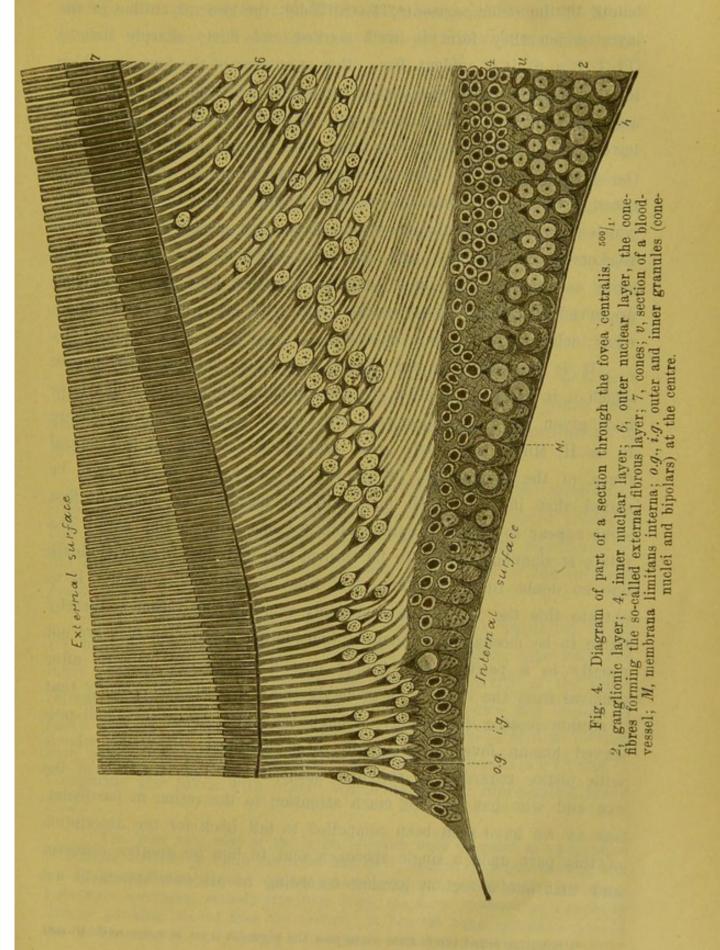
¹⁾ The line of the membrana limitans interna is distorted in this section by a slight injury a little to one side of the centre so that it is not possible to draw any inference as to the position of the section from the depth of the internal fovea. This fovea is, moreover, so gradually curved that it would in any case be difficult to say at which section the greatest curvature is reached.

aching the outer molecular layer, reach the lowest part of the fibrous layer in the middle of this section, being here actually sessile upon the outer molecular layer.

4. The place of cessation of the ganglion-cell layer is at about the same relative distance from the middle of the fovea as is shown by all previous authors who have described the region, excepting W. Krause. In sections which do not pass accurately through the middle this layer approaches the middle of the dip much more closely than is the case in the section we have selected for representation.

The appearance of the nerve-fibre layer on either side of the fovea in this section is characteristic. On the one side, presumably the inner, or that which is directed towards the entrance of the optic nerve, the nerve-fibres are cut exactly longitudinally, upon the other, or outer, exactly transversely. This may be taken to show that the section passes precisely in a horizontal meridian or at least in the meridian which includes the point of entrance of the optic nerve.

Besides photographs (see Pl. I), which are of varying degrees of magnification, we give a drawing from the central section which represents the middle and the adjoining part of the fovea magnified about 500 diameters (Fig. 4. p. 11). The drawing has been made in the first place from a microphotograph, most of the elements of the several layers as well as the general outlines having been directly traced from the photograph. The figure is so far schematized that where the retinal elements are obviously artificially distorted they have been represented in the drawing as if not thus distorted, but their number, their position, and as much as possible their actual size have been rendered as accurately as possible so far as they were visible in a single optical plane under the microscope. If the diagram is compared with the photograph which is the most magnified of the four (Pl. I. Fig. 4), it will be seen that the main difference between them is in the representation of the cones, especially of their outer segments, which for some reason were not well preserved over the very middle of the fovea photographed, and which were therefore copied for the diagram from other preparations. On this account the photographs themselves could not be taken as guides to the actual



length of the outer segments, for although the general outline of the layer which they form is well marked and fairly sharply defined (Pl. I. Fig. 2), it is evident, from other specimens of the fovea in which these structures have been better preserved, that the outer segments are much longer than there shown. If they are to be assumed to have been in the unaltered condition long enough to compensate for the dipping in of the external limiting membrane at the fovea, the cones would have to measure in total length no less than 0·133 mm. which is much longer than any that have been measured by previous workers¹). In diameter also the outer segments are nearly if not quite as thick as the inner segments, so that they appear in well preserved specimens closely packed and with their outer ends somewhat inclined towards the centre.

It is obvious from this figure and from the photographs upon which it is based that either the accounts and delineations which have been given by former observers are largely erroneous or that there is, as H. Müller supposed, great individual variation in the central fovea of the human eye. Whatever be the explanation it must be stated that it is a much more difficult matter than would at first sight appear to obtain irreproachable sections through this part. The retina is singularly liable to be thrown into folds just here after death due no doubt to its imbibing fluid from the vitreous humour. If to obviate this the vitreous is completely removed the retina is thereby liable to be mechanically injured. Considering that histologists are not usually in a position to obtain a normal human eye instantly after removal from the body, it is probably therefore only very rarely that a section passing indubitably through the very centre of a well-preserved human fovea has actually been obtained. Schwalbe, who is with justice regarded as the first authority on the structure of the eye and who has devoted much attention to the retina in particular, has as we have seen been compelled to fall back for the description of this part upon a single specimen sent to him by another observer and that one a section passing according to his own statement not

¹⁾ Schultze found the central cones plus the pigment layer to measure 0.118 mm.

through the very centre; and M. Schultze based his description of the general structure and arrangement of the part largely upon abnormal specimens 1).

We have ourselves examined three other normal foveae, besides the one here described: all three were fixed and hardened with osmium-bichromate mixture. Two of these were cut in serial sections by the paraffin-method and the third was imbedded in celloidin. In nearly all points these three specimens agree with the one we have selected for description but in one the dip of the inner fovea is sharper than in the others and its diameter is somewhat less. The depth of both foveae but especially of the outer, shows considerable variation. In all however the outer fovea is very marked and the cones upon it are very much longer than those on the rest of the retina.

In drawing attention to the chief points which our specimens illustrate it will perhaps be most instructive if on these points they are compared in detail with the statements and representations of previous authorities.

1. As to the shape and size of the depression of the membrana limitans interna which is commonly known as the fovea centralis but which (as there certainly exists a corresponding depression of the external limiting membrane) we may distinguish as the internal fovea.

In the specimen figured this is a basin-shaped depression about 1·1 mm. in horizontal diameter and with the margins, especially the inner one, slightly raised beyond the general concavity of the inner retinal surface (Pl. I. Fig. 1). The slope of the sides and bottom is fairly uniform and there is no sign of a flat fundus or central foveola such as Kuhnt describes. The total depth of the depression is 0·13 mm. 2). Comparing this fovea with others which have been represented, those

¹⁾ Two from eyes most of the layers of which were atrophied in consequence of tumours and one in which the fovea was partly spoiled by a post mortem fold.

²⁾ Its surface appearance was not recorded, but in two well-preserved osmiumbichromate specimens, entirely free from folds, the fovea appeared as a perfectly circular pit when viewed from the surface. It has the same appearance also in the monkey.

of Hulke and Krause are much more limited in diameter and their sides much steeper. Krause states regarding this point "doch erschien die Grube an den Rändern der Fovea selbstverständlich weit flacher, nicht mit so steilen Rändern abfallend wie in der Figur". The fovea of Schultze is also steeper than ours but the difference is less marked than with those previously mentioned 1). Schwalbe's figure gives nearly the same curve of the internal fovea as is shown in our preparation, as do also those of Henle and Cadiat, and a meridional section of the fovea of a foetus of 8½ months which is represented by Chievitz 2) has nearly the same general outline. The fovea of the chameleon as shown by H. Müller and recently by W. Krause 3) has a very similar general sectional outline to ours.

2. As to the existence of an external fovea due to the cupping in of the limitans externa.

On this point the sections and photographs are explicit. cupping of the limitans externa may be even sharper and steeper than that of the limitans interna. Its centre is almost angular in section in the specimen figured, tapering to a blunt point and having a sectional angle of about 120°, whereas, as we have seen, the curve of the internal fovea is quite gradual. In our other specimens the curve of the outer fovea is more gradual but always present and well marked. The external fovea in fact so far from being absent and the result of misinterpretation of the position of the outer granules, as Schwalbe in the passage above quoted (p. 7) has suggested, is a most distinct formation; far more so in fact in our specimen than could be supposed from the diagrams of previous observers. Its horizontal width is not much less than that of the internal fovea, viz 0.8 mm.; but the dip is at first very gradual and afterwards steeper. The depth of the external fovea, measured along a line passing vertically from the middle to meet another line joining the margins of the dip, is 0.1 mm.;

one of Schultze's original drawings gives a curve of the internal fovea wery much like that we have represented (Arch. f. mikr. Anat. Bd. II. Pl. XII. Fig. 2).

²) Chievitz, Intern. Monatsschrift f. Anat. u. Physiol. 1887. Bd. IV.

³⁾ W. Krause, Intern. Monatsschrift. Bd. X.

but it is slightly more (0.133 mm.) if reckoned to a line following the general curve of the outer surface of the retina.

3. As to the relative size of the cones over the fovea.

A point which is apparently shown by our specimens and photographs, viz. that the dip of the external fovea is not fully compensated by the extra length of the cones as we approach its centre, cannot, for reasons which we have already entered into (p. 10) be regarded as settled satisfactorily. The appearance however of a general cupping in of the external surface is so very well marked (Fig. 1), and the cones would have to be so enormously long to compensate for the depression, that we are of opinion the general external surface including the pigmentary layer must also have been somewhat cupped in. 1) We are unable however to offer satisfactory evidence on this point against the positive statement of Max Schultze 2) that the dip of the limitans externa is fully compensated by the elongation of the cones. In any case there is certainly some compensation, for the outer segments of the cones unquestionably become gradually longer towards the centre of the fovea. But on the other hand the inner segments are decidedly shorter, measuring 0.020 mm. as compared with a length of 0.028 mm., at a distance of 0.3 mm. from the centre. At the very edge of the external fovea they are again reduced to 0.021 mm. The total length of the cones at the centre we are for the before-stated reasons unable to give, but at 0.3 mm. from the centre, where the outer segments are fairly well preserved, the length of these is 0.05 mm. and at the edge of the external fovea 0.03 mm. The diameter of the inner segments at the centre of the fovea we find to be 0.0021 mm. which is almost exactly the measurement obtained by H. Müller. At the edge of the external fovea the diameter of the inner segments is somewhat greater viz 0.0028 mm. Schultze was of opinion that the measurement given by H. Müller was smaller than it should be in consequence of a shrinkage of the retina from the mode of preparation, but there is no evidence of shrinkage of the retinal elements in our preparations,

¹⁾ If this is the case the choroid is probably slightly bulged opposite the fovea.

²) Archiv f. mikr. Anatomie. Bd. II.

and indeed the method of preparation employed would, we believe, not have tended to produce this effect. The outer segments measure slightly less than the inner. We are therefore inclined to think that a measurement of 0.002 mm. represents as nearly as possible the diameter of the outer segments at the very centre

4. As to the position of the cone-granules in the fibrous layer (outer nuclear layer) of the fovea.

The cone granules, which are packed close against the limitans externa in other parts of the macula lutea, are at the very centre of the fovea placed in the inner part of the fibrous layer, almost as far as possible from the external limiting membrane. They begin to leave their position close to that membrane at the edge of the external fovea (Fig. 2) and at the same time acquire a less closely packed arrangement; and they gradually increase their distance from the membrane as we approach the centre. The cone-granules are more numerous opposite the margin of the fovea than anywhere else in the retina, being at least five or six deep here; and in consequence of their looser arrangement they occupy even relatively to their number a greater part of the thickness of the fibrous layer than in the adjacent macula. As they attain in approaching the centre a deeper position in the layer they very gradually diminish in number and towards the centre of the fovea they are only two or three deep.

It will have been noticed in the introductory account which we have given, that more than one previous observer has described or pictorially represented the cone-nuclei as being less closely applied to the limitans externa within the fovea than elsewhere. For the most part, however, their position as given in Max Schultze's diagram has been accepted. Schwalbe is the only one who has laid stress upon the fact that they are no longer applied to the membrana limitans externa in this region; but even he does not nearly approach the truth as regards the position of the cone-nuclei at the centre of the fovea, for in the first place he represents them there as only one deep and secondly as still lying nearer to the limitans externa than to the molecular layer. Our specimens through the foveal centre show them here to be almost resting upon the outer molecular layer.

5. As to the thickness of the fibres of the fibrous layer.

In the greater part of the retina the nucleated bodies of the cones are placed close below the limitans externa and are continuous with the inner segments, the two forming, as is well shown in teased preparations of an osmic retina, a continuous structure of uniform diameter, except where the cone tapers externally. From the inner pole of the nucleated cone body the cone-fibre passes through the outer nuclear layer to end within the outer molecular layer. In the macula lutea just outside the central fovea the inner segments of the cones have become more slender while the cone-nuclei retain about the same size as in other parts of the retina and the part of the cone-body which contains the nucleus is bulged out by the latter. The cones, moreover, being not only more slender but also more numerous here, there is no longer room for all their nucleated bodies in one row, hence we find them at first two or three and ultimately five or six deep, but still forming a nucleated layer close to the limitans externa. The rest of what in the remainder of the retina is the outer nuclear layer is occupied by the cone-fibres as they pass to the outer molecular layer, as well as by the few rod-fibres which are still present. Since some of the nucleated cone bodies are thus removed from the limitans externa it necessarily follows that the part of the cone-cell between the nucleus and the cone-proper is elongated in proportion to the extent of removal of the cone nucleus from the limitans externa. The outer part of the cone-element, which extends from the cone-nucleus to the external limiting membrane, although it may now be drawn out more or less to the appearance of a fibre is really in direct continuity with and, except for the line formed by the limitans, histologically indistinguishable from the inner segment of the cone proper, with which it forms a continuous structure. The same considerations apply exactly to the cone-elements in the central fovea so that we may describe these as possessing as we approach the centre always longer and longer peripheral portions and shorter and shorter proximal portions; until at the very centre the nucleated bodies are almost sessile upon the external molecular layer, owing to the shortness or practical absence of the proximal portions, and the

elongation of the peripheral portions of the cone-element. Now it is noticeable in the specimens and well brought out in parts of the photographs that these portions of the cone-elements are of exactly the same size as the cones with which thay are continuous. They are just as closely packed and are stained to precisely the same extent, and there can be no doubt that they form morphologically single structures. On the other hand the proximal parts of the cone fibres have not the same uniformity of thickness. They are however by no means the extremely fine linear fibres which they are represented to be in all the figures which we have above considered; that of Cadiat alone excepted.

6. As to the direction of the fibres in the fibrous layer of the fovea and the relative thickness of this layer at different parts.

In our specimens the most central fibres — those which are continuous with the cones which rest on the umbo of the external fovea and which are really as above shown prolongations of the cone-bodies run perfectly vertically towards the outer molecular layer, upon which, as we have seen, their nucleated bodies are almost sessile; the fibres expand slightly as they pass to the nuclei. The opposite side of the nucleated enlargement in those which are thus sessile, forms a kind of triangular base from which fibres appear to diverge into the outer molecular layer. A very short distance (some six or eight cones width) from the centre the fibres begin to diverge obliquely outwards as they pass towards the outer molecular layer, the obliquity being at first slight but afterwards extreme, so that the outer ends of the fibres are nearly horizontal. The fibrous layer is thinnest opposite the centre of the fovea and from here gradually expands to the margin of the fovea, where it is thicker than anywhere else in the retina. Its depth from within out at the very centre, measured from the limitans externa to the external molecular layer, is 0.064 mm., whereas at the edge of the fovea it amounts to as much as 0.145 mm. We are unable to understand how it is that in Schwalbe's specimen it should have been of the uniform thickness which is depicted in his diagram.

As to the vertical direction of the central fibres of this layer,

this is a point which we have not found noticed by any previous observer. Kuhnt indeed goes so far as to describe the most central fibres as immediately diverging from their nuclei in an almost horizontal manner, and Hulke and M. Schultze (in one section) also depict them as at once diverging to either side. This also we are quite unable to understand unless there is a vast difference of structure in different foveae.

7. As to the form, size, and appearance of the cone-nuclei in the fovea.

In our chromic acid specimens the cone-nuclei throughout all parts of the retina are nearly spherical and differ in this point from the rod-nuclei, which are somewhat oval in form. They all have a distinct nucleolus and punctated appearance, apparently due to a network. At the edge of the fovea they have a diameter of about 0.0071 mm., while the rod-nuclei measure 0.0057 mm. in length but only about 0.0043 mm. in breadth. The nuclei belonging to the most central cones are smaller than the others, the diminution however not occurring abruptly; those at the very centre only measure about 0.0057 mm., that is to say about the same as the length of the rodnuclei at the edge of the fovea. They are interpolated at different levels in adjacent fibres, no doubt for convenience of packing here and there one is seen at an entirely different level from the rest. They have usually been represented as oval in this part of the retina but Krause has given their spherical shape and general appearance fairly accurately.

8. As to the inner granule layer (layer of bipolars) and the molecular layers at the fovea.

The layer of inner granules becomes gradually reduced in size and in the number of its constituent granules from the edge of the fovea inwards; more rapidly as the middle third is approached so that they soon become not more than two or three and finally not more than one deep. Here they appear to be imbedded in what looks like a blending of the two molecular layers, but since the

¹⁾ Cajal however represents a similar condition of the cone-fibres in the centre of the bird's fovea. La Cellule. T. IX Pl. VI. Fig. 15.

specimens show nothing of the structure of these layers we are unable to say how far such blending may actually occur. Both molecular layers appear however still to be represented quite at the centre; and this is also the case with the bipolars, which here seem exactly to correspond in number with the cones and cone fibres 1).

The nuclei of the bipolars (inner granules) are at the fovea decidedly smaller than the cone-nuclei (outer granules) and are stained more darkly and uniformly; they are round or oval, and tend, especially a short distance from the centre, to be placed somewhat obliquely. On one point viz. the presence of inner granules at the centre of the human fovea we are in disagreement with most, if not all, previous observers²). Nevertheless our specimens seem clear upon this point and to judge from the figures given by Cajal of the fovea in the bird and the chameleon they are also present in a similar situation in those animals.

9. As to the size and form of the ganglion-cells and the extent of the ganglion-cell layer at the fovea.

The ganglion-cells are six or seven deep at the edge of the fovea, whence they gradually diminish in number as we trace them inwards; and with this there is a corresponding diminution in the thickness of the layer which they form. They are not however smaller at the fovea than for some distance on either side of it, nor are they obliquely disposed, elliptical, bipolar cells as might be supposed from the diagram given by M. Schultze³) and that of Schwalbe; but are of a rounded or somewhat pyriform shape; with a peripheral process directed almost perpendicularly outwards towards the inner molecular layer, within which no doubt they form stratified arborisations

¹⁾ In the fovea of the bird and in that of the chameleon it has been shown by Ramón y Cajal that the bipolars exactly correspond in number with the cone-fibres, against the bases of which their peripheral processes abut each against each (Op. cit.).

²⁾ Compare however the statement of H. Müller quoted above on p. 1.

³) With reference to this it is noteworthy that in the original of this diagram (which is to be found in Bd. H of the Archiv f. mikr. Anatomie. Plate 13) the ganglion-cells are correctly represented as spherical bodies. For some reason which does not appear in the text Schultze seems to have had the figure modified for the article in Stricker's Histology.

similar to those which Cajal has described in the fovea of the bird and reptile.

There are in our sections a very few large cells, not more than one in each section (Figs. 3 and 4), resembling in size and general appearance the ganglion-cells, but placed amongst the inner granules, near to but not quite at the centre of the fovea; whereas the ganglion-cells as a layer have thinned off and ceased altogether some little way (0.086 mm.) from this point. Since in several of these isolated nervecells it is possible to see a stalk-like peripherally directed process like that of the ganglion cells we are constrained to regard the cells in question as "dislocated" nerve-cells. We have not been able to determine the existence of basal or horizontal cells or of "amacrines" at this part, but the methods we have employed are not adapted for displaying these. The same may also be said regarding the connections of the concatenated elements of the retina.

10. The hydloid membrane of the vitreous humour is gradually thinned out as it passes over the fovea. At the periphery of the depression it is about 0.003 mm, in thickness but at the very centre it is a mere film too thin to be measured. As elsewhere in the retina it is entirely separate and detachable from the limitans interna, which as in other parts is apparently formed entirely of the conjoined inner extremities of Müllerian fibres. The form of these fibres at this part and their exact relations to the retinal elements are not apparent in our sections.

We append some measurements showing the thickness in millimeters of the retinal layers, taken respectively (1) from the macula lutea, 1.5 mm. mesial and lateral to the edge of the fovea; (2) from the edge of the fovea (also mesial and lateral); and (3) from the very centre of the fovea.

Thickness of retinal layers.

	1.5 mm. f	from fovea	At edge	At centre	
THE RESIDENCE PROPERTY.	mesial	lateral	mesial	lateral	of fovea
Pigment-cell layer	0.015	0.015	0.016	0.016	0.0161)
Rod and cone layer	0.045	0.040	0.040	0.040	0.090 2
Fibrous layer	0.130	0.105	0.145	0.140	0.064
Outer molecular layer	0.005	0.005	0.005	0.005)	Constitution of
Inner nuclear layer	0.050	0.050	0.075	0.070	0.022
Inner molecular layer	0:025	0.030	0.025	0.020	State of the last
Ganglionic layer	0.025	0:035	0.070	0.055	absent
Nerve fibre layer	0.025	0.015	0:020	0.010	absent
Total thickness	0.396	0.356	0.320	0.295	0.192

Other measurements at fovea.

Diameter of outer segments of cones at extreme centre.	0.0020 mm.
Diameter of inner segments of cones at extreme centre.	0.0021 "
Diameter of cone nuclei at extreme centre	0.0057 "
Diameter of nuclei of bipolars	0.0043 mm.
Diameter of ganglion cells	0.0140 "
Diameter of "dislocated" nerve-cell close to centre	0.0130 "
Extreme width of internal fovea	1.1 "
Extreme width of external fovea	0.8 "
Depth of internal fovea	0.130 ".
Depth of external fovea (measured to prolongation of re-	
tinal curve)	0.133 %

The figures on Plate I are photographs from a section passing horizontally through the middle of the fovea. In all the figures, the nasal side of the section is to the left and the inner surface looks downwards. The limitans externa is very distinct but the limitans

¹⁾ The measurement of the pigment-layer in the centre is adopted from H. Müller as the layer was detached just here in our specimens.

²) This is taken not from the specimens which are photographed, in which these structures were ill preserved, but from another (osmium-bichromate) preparation in which they were very well kept. But even here the pigment layer was detached and with it the ends of the outer segments so that probably the cones should be somewhat longer than this.

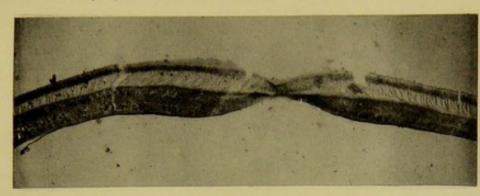


Fig. 1.

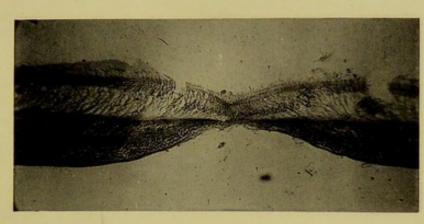


Fig. 2.

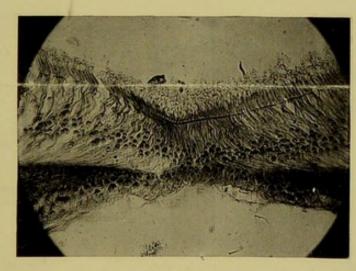


Fig. 3.

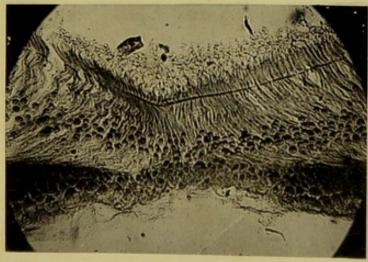


Fig. 4.

Golding-Bird and Schäfer.

FOVEA CENTRALIS.



interna is not well marked, owing to the fact that the inner surface has become slightly frayed near the centre. The photographs are not as clear as might be desired and fall short of the sections from which they are taken, but most of the statements in the text can be verified upon them. Their details may be followed out more easily if they are compared with the diagram on p. 11. The magnification is as follows:

Fig.	1					24	diameters
Fig.	2					42	diameters
Fig.	3					130	diameters
Fig.	4					180	diameters.

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Addendum to the article "on the Structure of the Fovea centralis"

by

C. H. Golding-Bird and E. A. Schäfer. 1)

On the account which we have given of the literature of the Fovea a paper by A. Schaper (Archiv f. mikr. Anat. 1893. Bd. XLI. p. 147) has escaped our notice. This author gives a representation of a section through the middle of the Fovea in which the outer granules are correctly represented as approaching close to the molecular layer and the inner granules are shown to be present even at the centre of the Fovea. Schaper appears however not to regard this as a constant condition and he entirely denies the existenc of the dip in the membrana limitans externa (external fovea) which is characteristically present in all our preparations. The details of structure are not well shown in Schaper's figure and the description is correspondingly scanty, but the author agrees in the main with the account given by Kuhnt — an account the details of which we ourselves have been entirely unable to confirm.

We may further take the opportunity of remarking regarding the assertion of W. Krause 2) that our figures represent sections, not

¹⁾ This Journal. Bd. XII. Heft 1.

²⁾ This Journal. Bd. XII. Heft 2.

through the middle but half way through the fovea, that such an assertion is not only unfounded but preposterous! For we possess three complete series of sections through the whole foveae of perfectly freshly prepared and normal retinae — from operative-cases, not from the cadaver — and we have selected for a photographic representation the section which in our judgment passes most exactly through the centre.

BEITRÄGE

ZUR

PHYSIOLOGIE.

EWALD HERING, DR. MED. PRIVATDOCENT DER PHYSIOLOGIE.

VON DEN IDENTISCHEN NETZHAUTSTELLEN.

LEIPZIG,

VERLAG VON WILHELM ENGELMANN

1862.

