Everett Franklin Phillips

STRUCTURE AND DEVELOPMENT OF
THE COMPOUND EYE OF THE
HONEY BEE

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Structure and Development of the Compound Eye of the Honey Bee.

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From the Proceedings of The Academy of Natural Sciences of Philadelphia, February, 1905.

Issued May 4, 1905.

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CONTENTS.

I.—INTRODUCTION.

The morphology of the compound eye has puzzled zoologists for years, and much work has been done on the subject, but so diverse are the views held by the various investigators in the field that we are far from a final solution of the problem. With a view to adding some evidence from the embryological point of view this work was begun, in the belief that a detailed examination of this one insect eye would throw some light on the adult morphology.

The eye of the common honey bee, *Apis mellifera*, is particularly favorable for embryological work, since its growth is gradual and the steps of development well marked out. The material is also easily obtained, and the various stages of growth can be distinguished by the external appearance of the larvæ and pupæ. It is also favorable for a comparison with the development of the eye of *Vespa*, which was described by Patten, since it is desirable to find how far his results can be verified on a closely related form. The large number of ommatidia in each eye make the preparation of sections an easier matter, since it was not necessary to cut so many eyes.

The adult ommatidium of the bee was briefly described and figured by Grenacher in his celebrated work, *Sehorgan der Arthropoden* (1879), and has been figured in works on apiculture, but has never been fully worked out in the adult condition, and no work has been done on the development of the eye. Bütschli (1860) in his work on the embryology of the bee discusses the formation of the eye, but does not go into the subject of the development of the ommatidium.

This work was taken up with a view to getting, first of all, a complete description of the development and structure, and in addition to get some light on certain problems which are of especial interest from a theoretical standpoint. The innervation of the ommatidium, the method of formation and fundamental plan of the ommatidium, the method of modification of numerical plan and structure in the evolution, the arrangement of ommatidia, the homology of various cells in different ommatidia, and the comparison of ommatidia with other sense-organs are questions which have been much discussed, and in this work an effort has been made to apply the observations made to the solution of these problems. This is done not without the realization that some of these things can be settled only from wide comparisons, but with the thought that a piece of work which takes in the whole course of development is of more value than superficial observations of a large number of forms. Some of the theories are merely matters of interpretation rather than of direct observation, and must remain so until decisive observations are made, but in matters of this kind the accumulation of evidence is of decided value.

The formation of the optic lobes and the course of the nervous elements through them are problems which have not been taken up for investigation in this work. Kenyon has worked out the structure of the optic lobes for *Apis* in detail with nerve methods. The technique used in the present work not being suitable for the tracing of nerves, only on matters concerning the nerve endings of the retinula has any investigation been made in this work, and that was not done by Kenyon.

In the matter of nomenclature an effort has been made to avoid the use of new names or of some of the names which have been proposed by some workers who have special theories to uphold, such as calyx, lentigen, corneagen, etc. In the case of the cells which surround the cone I have used the name corneal pigment cells, since they have a double function. In other cases I have used generally accepted names.

The plan followed in this paper is to give, first, a brief description of the adult eye, so that further discussion will be more intelligible, and then to take up the development of the entire eye and ommatidium, followed by a detailed description of the adult conditions, since that was the plan followed during investigation, and is, perhaps, the order which will be most clear to the reader.

This work was taken up at the suggestion of Dr. Thos. H. Montgomery, Jr., now Professor of Zoology in the University of Texas, and was completed under the supervision of Professor E. G. Conklin. To both I am indebted for many valuable suggestions and for help throughout the work.

II.—METHODS.

Larvæ and pupæ were fixed in Flemming's fluid, Hermann's fluid, picro-sulphuric, picro-acetic and picric acid saturated in 50 per cent. alcohol, but of these the Flemming and Hermann preparations yielded the best results. For the smaller larvæ it was not necessary to dissect before fixation, but for older larvæ and pupæ the head was removed to make penetration easier. For adult material, where penetration is difficult, the best fixative was acetic acid, generally a 10 per cent. or 20 per cent. acetic solution in 80 per cent. to 100 per cent. alcohol. Kleinenberg's picro-sulphuric and picric acid in 50 per cent. alcohol were also used with fair results when the head was cut in two.

The material was all cut in paraffine, and it was found that for adult material long embedding was necessary, four to eight hours, to get the paraffine all through the tissues. Some material was embedded for a shorter time to see whether the heat had produced any artifacts in the other material which was embedded for the longer period, but in such cases the lens invariably separated from the retinular layer; no difference was observed in the internal tissues due to long heating.

In staining, the best results were obtained in the use of Heidenhain's iron hæmatoxylin, with the use of a strong mordant for a long time. For material of this kind there seems to be no better stain. It was found that by destaining to different degrees the various parts of the eye would show differences in color, the rhabdome, for example, staining an intense black in rather deeply stained material. The nerve fibrils of the retinula cells also stained black with this stain. Other stains, such as Delafield's hæmatoxylin and eosine or Bordeaux red, were employed with very good results.

For depigmenting Grenacher's solution with a somewhat greater per cent. of acid was used. Parker's solution was also used, though the former gave the better results.

ganglia. During the larval growth the eye increases greatly in size and mitotic figures are abundant, the mitosis always dividing the cells lengthwise, so that the one-layered condition is retained until the close of the larval period.

During the semipupa stage, after the larva is sealed up by the workers of the hive but before it assumes the true pupa form, the one-layered epithelium gives place to a condition in which all the cells do not extend all the way from the outer surface to the basement membrane. This is brought about by the lengthening of some cells, the shortening of others and by the rearrangement of the cells in a manner to be described later. By the time the head has attained the size and shape of the adult, the cells have arranged themselves so that the ommatidia are completely formed and no more mitoses occur. The development of the ommatidia from now on consists of the differentiation of the cell elements until they assume their adult form. The development of the eye as a whole consists of a thickening of the organ and the laying down of a chitinous lens over the surface.

At the sides of the eye of the young pupa the appearance is as shown in text fig. 2, and the cells which correspond to the corneal pigment cells around the ommatidia are quite numerous and shade off gradually into the cells of the hypodermis over the rest of the head. As the eye increases in thickness by the lengthening of the ommatidia there appears a dipping in of the cells of the border, so that there is an invagination all around the eye where the secreting surface of the hypodermis is pulled down. This is shown by a thin sheet of chitin which runs around the eye (seen in section, text fig. 1) in the late pupa and adult eye. This chitin is similar to the chitin of the body proper, but not like that over the eye. This invagination must not be confused with such an invagination as is described by Patten for the formation of the lens layer, for the ommatidia are here completely formed and the corneal pigment cells have moved to their place at the proximal end of the cone before the dipping of the cells here described takes place.

In the formation of the optic ganglia, which takes place by the invagination of cells of the hypodermis, there is formed a brain sheath —a sheath of cells covering the ganglia and still continuous with the hypodermis at the edge of the eye. This layer of cells runs along proximal to the basement membrane and very close to it in the pupa stage. As the retinular ganglia take on their final shape these cells are pushed away from the basement membrane, and are seen in the adult eye as strands of cytoplasm woven in among the nerve fibres between the basement membrane and the retinular ganglion. The nuclei of these cells are smaller and are easily distinguishable from the retinular ganglion nuclei which lie near them (see text fig. 3). On the edge of the nerve bundle this layer is continuous with the brain sheath in the adult. The strands of protoplasm of which this layer of cells is composed after it is perforated by the nerve fibres often run up close to the basement membrane and might easily be mistaken for nerve fibres to the outer pigment cells, but their origin indicates that they are not nerves and there is no indication of any nervous connection for the pigment cells.

Kenyon recognized this layer of cells, which he describes as follows:[1] "The outer mass (first fibrillar mass) presents a lunar appearance in frontal sections (see fig. 1 of this paper), and lies close inside the basement membrane of the retina, being separated from it by sufficient space for the entrance of large tracheal sacs and a thin layer of cells commingled with the fibres from the retina." It will be seen that working with nerve methods this author did not recognize them as nerve fibres, nor did he describe any nervous connection with the pigment cells. Frequently these strands of protoplasm run close to the basement membrane and there spread out as a pyramidal protoplasmic mass lying between the nerve fibrils. This is particularly noticeable in pupa stages before this layer of cells is so greatly distorted.

The basement membrane is made up of a fusion of the proximal ends of the outer pigment cells with the pigmented portion of the retinular cells. This makes a sheet of cytoplasm, perforated where the nerve fibres pass from the retinular cells, which can easily be macerated away from the other elements of the eye and is easily distinguishable on account of its deeply pigmented condition. The nerve fibres from the retina pass through this and are seen as more or less separated on a section through that region (fig. 18). This basement membrane is continuous with the basement membrane of the hypodermal cells. Fig. 10 shows diagrammatically the structure of the base of an ommatidium and the elements which compose the basement membrane, but does not show the separation of nerve fibrils, since that is seen clearly only in cross sections through that region.

There are no tracheæ distal to the basement membrane in the compound eye of the bee such as have been described in other eyes, especially among the Diptera. Exception must be taken to the statement of Hickson[2] that "no spirally-marked tracheæ penetrate the optic tract at any part of its course in Hymenoptera." Between the basement

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[1] P. 369.

[2] P. 223.

membrane and the retinular ganglion tracheæ with spiral markings occur in all specimens examined (see text fig. 3), but the statement of Hickson holds good for all other parts of the optic tract as far as has been observed. Kenyon also mentions the presence of tracheæ in this region.

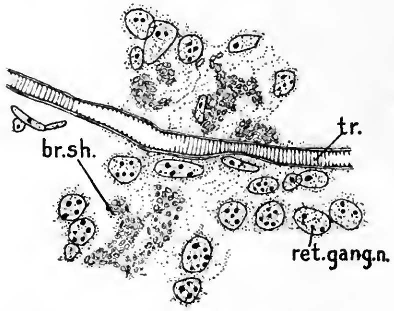

Fig. 3.—Section below basement membrane, showing retinular ganglion cells and nerve fibrils from ommatidia.

2. *Arrangement of Ommatidia.*

The facets of the lens are arranged in hexagons, as is true for so many insect eyes, but this is probably not a primitive condition. Hexagonal arrangement is what is produced whenever any circular objects are closely pressed together, just as the cells of the honeycomb are hexagonal, and this undoubtedly explains the shape and arrangement of the facets. Parker (for Crustacea) looks upon unfaceted eyes as primitive, and probably this is true for insects also. We have, however, in the proximal portion of the eye a different arrangement which is perhaps more primitive than the hexagonal method. At any level proximal to the cone cells the ommatidia are arranged in parallel rows, and the nearer we come to the base of the ommatidia the clearer is this arrangement, until on a section at the level of the basement membrane (fig. 18) we see this parallel arrangement very marked. Since here we get a condition in which the ommatidia are not pressed together and therefore are not modified mechanically, it probably represents a more primitive condition than that found in the lens region. In the pupa, even the facets do not have as marked a hexagonal arrangement as they have later, and in the larva we get an arrangement identical with that of the bases of the adult ommatidia.

The numerical plan and shape of the parts of the ommatidium may have something to do with the arrangement. The retinular cells are eight in number, but four of these are wider than those which alternate with them, and as a result a cross-section of the retina is roughly a square. The outer pigment cells are twelve in number when their arrangement is unmodified by hair cells, and this number readily arranges itself into a square with three on a side, or into a hexagon with two on a side. Since the outer pigment cells are simply strands of cytoplasm they readily accommodate themselves to any change of arrangement and are not, as a rule, without some bend, so these cells could scarcely modify an ommatidial plan of arrangement. The basement membrane is considerably smaller in area than the lens chitin, and as a result the room provided for each ommatidium is considerably decreased, so that in contrast with what has been stated, that the ommatidia are not so crowded proximal to the cone, it might be supposed that the converse would be true. However, the fact is that in cross-section a larger proportion of space is occupied by outer pigment cells, the interommatidial spaces, near the base of the ommatidia than near the lens; and since, as above stated, these cells are flexible and not crowded, it scarcely seems to follow that this parallel arrangement is due to crowding.

The hexagonal arrangement is undoubtedly the common plan, at least as far as the lens is concerned, and the tetragonal arrangement may be derived from it as held by Parker, and his arguments for such an origin seem good; but, on the other hand, the hexagonal arrangement could scarcely give rise to the tetragonal unless preceding the hexagonal facets the ommatidia were in squares, so that the secondary crowding would bring about the primitive arrangement again. Taking again the case of the honeycomb, no additional crowding could possibly make the cells square, for the more the circular walls (the primitive cells) are crowded the more truly they become hexagonal. However, if the walls were made of four parts, as is the cone, and if they were fastened at their bases in parallel rows, then additional crowding might cause the lens to lose its circular outline and become square, in which case the hexagonal arrangement of the lens would be lost. It seems probable that the cone determines the arrangement rather than the lens-secreting cells, and Parker's figures of *Gonodactylus* (Parker, 1890, Pl. VIII, fig. 93), in which the tetragonal arrangement is found in the large ommatidia and not in the small ones, lend support to this view.

To sum up, it seems probable that the arrangement of ommatidia, where they are sufficient in number to be said to have any plan at all, is normally the tetragonal plan. If the cones are somewhat compressed, as they generally are on account of the way in which a compound eye is made up, a hexagonal arrangement of the distal parts of the ommatidia results; but if the pressure is sufficient to cause the cone to lose its circular form then it becomes a square, and the facet plan again becomes tetragonal.

3. *Hair Cells.*

The entire lens of the eye of the bee, especially in the younger individuals, is covered with large hairs, unlike those of the rest of the body in being unbranched. These hairs are secreted by large hair-mother cells which lie among the outer pigment cells between the ommatidia, and their development is of interest on account of the presence in them of an intracellular duct and because of their binucleated condition. In the larval eye these hair cells cannot be definitely located, but there are certain large cells with peculiar nuclei

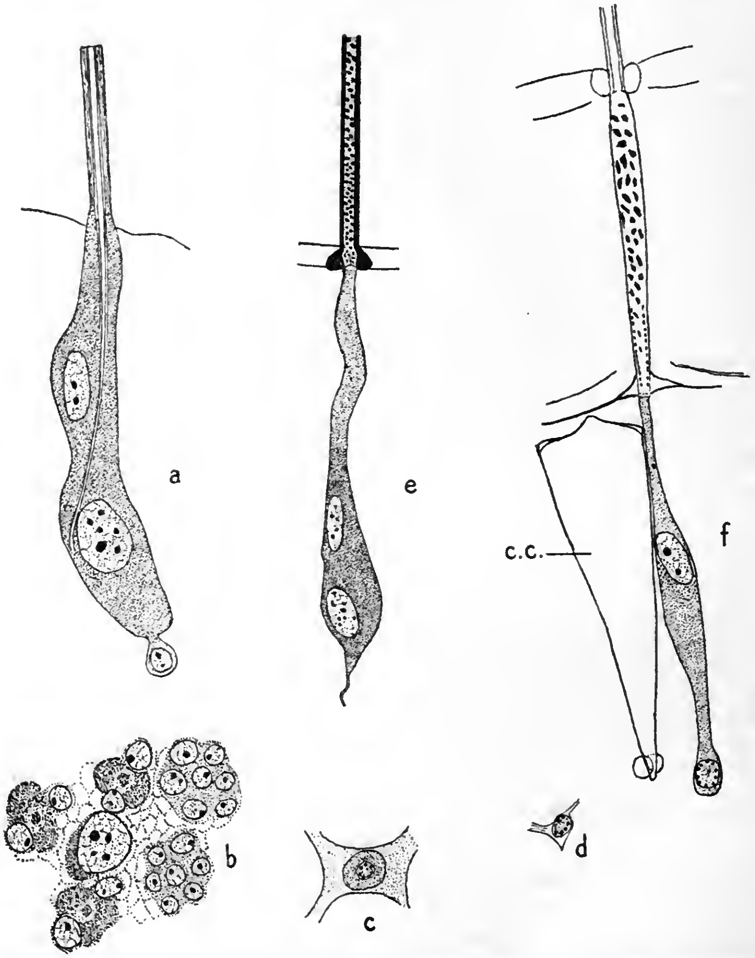

Fig. 4.—*a.* Hair cell of young pupa, showing three nuclei and intracellular duct. *b.* Cross-section through pupal retinulæ, showing one hair cell. *c.* Cross-section through hair just at level of cones, showing structure of intracellular duct. *d.* Cross-section distal to *c* and beyond surface of eye. *e.* Older pupa hair cell. *f.* Hair cell of adult, showing relation to cone and lens.

which are probably hair cells. In the early pupa these cells are large and have two, or sometimes three, nuclei, but when a third nucleus is present it is considerably smaller than the two more distally placed ones. In the early stages this polynucleated cell contains an intracellular duct which opens into the tubular hair, and through this duct passes the secretion products of the cell for the formation of the hair. The hair proper is tubular and in material stained in iron hæmatoxylin darker lines appear in the walls, and these structures extend for a short distance down into the cell proper around the duct. The duct has well-marked boundaries, does not branch, and generally coils around the second nucleus (text fig. 4).

As the lens increases in thickness the hairs elongate by the secretion of the hair cells, and as this goes on the cytoplasm of the cell is used up, until finally, in the adult eye, the cell has about one-sixth the volume it had in the early pupal eye. In the intracellular duct and in the hair duct the products of secretion may be observed in fixed material as darker bodies of irregular shape.

These hairs and hair cells have no nerve connection, as far as I can observe, and are therefore not sensory hairs. Just why the entire eye should be covered by hairs is hard to explain, for they must undoubtedly obscure vision, and since such a hindrance is present we should expect to find it compensated for by some sensory function on the part of the hair. I can find no indication that such is the case. It is worthy of note that the older bees have lost most of the hairs both on the eyes and on the body by the time they need the eyes for prolonged flight. The younger bees, up to nearly three weeks of age, leave the hive but rarely, and then for short distances only, but the older bees which take long journeys have the eyes much more bare. It is also noticeable that all the bees, but especially the drones, brush the hairs so that they all point down toward the mouth just before leaving the hive entrance. No doubt, in the hive, the head, which is so frequently put into the cells, becomes soiled with honey and pollen, and this action of brushing may be merely to remove dirt; but, on the other hand, the arranging of the partly transparent hairs in one direction may produce certain results of refraction which are favorable.

In *Vanessa*, Johansen describes hair cells as running the length of the ommatidia without an intracellular duct and with but one nucleus. He is able to locate these cells at an earlier stage than has been possible for the bee on account of the proximal position of the nucleus. From the figure of a cross-section of the cornea it would appear that these cells are not so abundant as in *Apis*. Patten figures hair cells for

Vespa very similar to those here described, but I am unable to find the nerve connections which he describes. Semper and Breitenbach also describe such hair cells for Lepidoptera.

The number of facets in the different kinds of individuals of the colony differs considerably. The drones (males) have an extremely large number of ommatidia, the eyes meeting on the top of the head, and as a result the three ocelli are crowded down to the front of the head. The workers and queens have a considerably smaller number, about one-third as many, and the ocelli are located at the top of the head. It is not clear why the drones should have a larger number of ommatidia than the females of the colony, since they do not seem to need so much larger range of vision. The only reason which might be suggested from a knowledge of the habits of the two sexes is that at the time when the queen takes her "mating flight" she flies almost directly upward, after a preliminary circle or two near the hive, and then often flies to some distance from the hive; this manner of flying making more probable a mating with a drone from some other colony than her own. Drones do not, as a rule, fly as high as does the queen, and it would be advantageous to have the eyes extending to the top of the head in order to follow the queen's flight. As soon as a queen starts upward any drones which are flying near at hand start upward after her, the eyes on the top of the head making it possible for them to see her.

To say that this difference has arisen on this account scarcely seems justifiable, for it would seem easier for natural selection, sexual selection, or whatever other factor is potent here, to modify the habits of flight rather than to enlarge an organ so much as in this case. This much may, however, be said with a good deal of surety: two things which would be likely to be acted on by selection in the bee are acuteness and range of vision and the power of flight.

V.—Retinular Ganglion.

In the early larval stages the optic ganglia are clearly marked out, but the retinular ganglia are not. The only indication of the retinular ganglia is a number of cells which lie near the basement membrane of the eye, principally at the posterior margin. During the larval growth the nerve fibres from the ommatidia grow in from the retinular cells, and as this growth goes on the cells of what are to be the retinular ganglia are pushed farther away from the basement membrane and assume their more definite position. Finally, in the adult animal the nerve fibres from the ommatidia form a relatively compact mass and the retinular ganglion cells are scattered through the fibres in such a way as to have the appearance of a definite ganglion. The nuclei of the retinular ganglion are no longer nearly in one plane, but are scattered for a considerable distance between the basement membrane and the outer fibrillar mass due to the crowding of the nerve fibres.

The question naturally arises as to the number of cells of the retinular ganglion as compared with the number of ommatidia. A count is, of course, impossible, but careful examination reveals that there cannot be many more than one to an ommatidium, certainly not one to each retinular cell. The eight nerve fibres from each group of retinular cells are entirely separate, but lie close together, so that probably one and only one retinular ganglion cell receives the impulse carried from the retina on eight nerve processes, and consecutive cross-sections indicate that the eight nerve fibrils surround the thick part of the retinular ganglion cell where the nucleus is located and transmit the impulse by contact.

In his description of this region Kenyon says:[3] "The elements from the retina terminate each in a small tuft of fine branches in the outer fibrillar body, and come in contact with the fine lateral branchlets given off in the same region by fibres originating from the cells of Berger's granular layer (retinular ganglion)." The tuft of fine branches here mentioned are the separate nerve fibres from the retinulæ. I have been unable to see the fine branches of the retinular ganglion cells.

The retinular ganglion cell in turn sends in its fibre through the first fibrillar mass, and then through the outer chiasma to the opposite side of the group of ganglia, where the impulse is given over to a cell of the first optic ganglion. From here on the tracing of the fibres requires special nerve methods which were not employed in this work. However, this much is evident: the cells of the first optic ganglion send their fibres through the second fibrillar mass and through the inner chiasma to the second optic ganglion, where the impulse is probably again transferred to another cell which, in turn, carries it to the brain. The course of these fibres has been worked out in detail by Kenyon (1897), and in my work I find nothing to contradict his results, although the methods used in my work were not such as to warrant either a positive denial or confirmation of his work.

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[3] P. 374.

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[3] P. 374.

VI.—THE OMMATIDIUM.

1. *The Larva.*

In the larva, just after being hatched from the egg, I have been unable to find any indication of the grouping of cells which are later to go together to form a single ommatidium. The eye at this time is a simple layer of the thickened hypodermis with the nuclei arranged one above the other. At this time, and throughout the entire larval period, mitotic figures are abundant, the spindles always having their axes at right angles to the length of the cell and dividing the cells lengthwise.

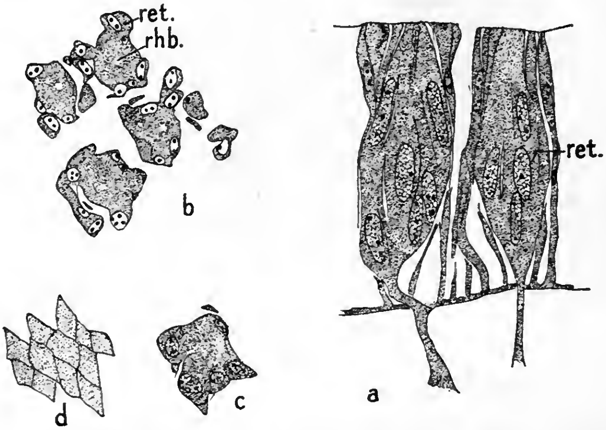

Fig. 5.—*a.* Longitudinal section of larval ommatidia. *b.* Cross-section near surface of eye, showing first differentiation of rhabdome (rhb.) as a clear space in the retinula (ret.). *c.* Cross-section at a lower level. *d.* Cross-section of a very young larva, each division line representing a complete ommatidium.

The division figures seem to be more abundant near the outer surface of the epithelium.

About one day after leaving the egg, when the larva has about doubled in size, a tangental section of the eye at right angles to the long axes of the cells at the outer surface reveals a grouping of cells as represented in text fig. 5*d*. The lines in this figure do not represent cell boundaries but are the boundaries of groups of cells; each group contains four or five cells at this time, the nuclei of these cells being directly one above the other. The cell groups are tetragonal and are arranged roughly in parallel rows. In longitudinal section these groups appear as made up of long strands with superimposed nuclei about the diameter of the entire width of the group of cells. That these are the beginnings of the ommatidia is evident since they can be traced through all the larval stages to the pupa, where the ommatidia are definitely marked. This is further indicated by the fact that they are arranged in the same way as are the proximal ends of the ommitidia, even in the adult eye. It should be borne in mind that this epithelium is strictly one-layered, and this is true all through the larval period.

During the larval period, as above stated, mitotic figures are abundant, and as a result of these divisions the groups come to be composed of more and more cells, but it is not until a late larval period (about four and a half days from the hatching of the egg for worker larvæ) that any further differentiation is observable, except possibly that the nuclei of some of the cells are larger than others in the same group. At this late larval period the cells arrange themselves as a spindle-shaped mass surrounded by smaller cells whose smaller nuclei lie in the space left at the outer end of the spindle. Mitotic figures are now absent except an occasional one in the smaller cells, but so far none have been observed in the larger centrally placed cells of the group. The number of cells in the spindle is hard to determine, since the nuclei are at different levels and the cell boundaries are not visible. All the nuclei of the central bundle of cells are some distance below the surface. There are certainly, however, not more than eight or nine, the number of retinular cells of the adult ommatidium. At the distal end of this spindle a differentiation of cytoplasm takes place, and a clear space is formed in the centre of the cells in the very granular protoplasm, and this I believe to be the beginning of the rhabdome. A cross-section near the outer surface of the cell mass shows this clear space surrounded by granular cytoplasm of the spindle cells, and this in turn surrounded by nuclei arranged around the central bundle. These outer nuclei are not as yet differentiated, so that their future fate cannot be determined. The cells of the spindle by this time have sent out protoplasmic processes toward the optic lobes which become the nerve fibres of the ommatidium, so that at any rate some of the spindle becomes the retinula.

Several facts seem to indicate that the spindle-shaped centre of the ommatidium goes to form only the retinula: (1) There are no nuclei near the outer surface, as one would expect were crystalline cone cells to be formed from any of the cells; (2) there are not enough cells to form both retinula and crystalline cone cells, and since no mitotic figures have been observed they have undoubtedly ceased division; (3) a clear space is formed at the distal end of the spindle by a differentiation of the cytoplasm, possibly the beginning of the rhabdome, since it is in this portion of the retinula that the rhabdome is seen in the youngest pupal eye observed (just after the semipupa stage). The number of nuclei around the spindle throws no light on this, since they are still dividing occasionally and their number in the adult is not fixed.

Considerable stress has been laid on the fate of this spindle-shaped mass of cells, since the determination of this fact alone is of such great importance in the consideration of the morphology of the ommatidium. That the outer pigment cells are morphologically peripheral to the crystalline cone and retinula no one would deny. The position of the corneal pigment cells might be a doubtful point if they were derived from a separate layer of cells formed by invagination of the entire eye, but as no such invagination occurs in the bee, and as at an early pupa stage they are clearly outside the cone, I think there can be no doubt as to their morphological position. The question as to the relative morphological position of the crystalline cone cells and the retinular cells is, however, not so clear.

According to Grenacher the ommatidium is two-layered, and the lens and cone are morphologically distinct from the retina. If this view is held, then the question stated above does not exist; but such an interpretation can no longer be held on comparative anatomical or embryological grounds, as has been shown so well by numerous investigators, the evidence for which it is not necessary to give here. Suffice it to say that, as has been shown previously, the ommatidium of *Apis* arises from a one-layered epithelium, and all the cells are morphologically equivalent. Taking into consideration, then, only such views as are based on such interpretations, we find two opposing theories.

According to Patten, Kingsley and others, the crystalline cone is sometimes continuous with the rhabdome; these two would therefore be the morphological centre of the ommatidium, while the retinula must arise from cells outside this. When the crystalline cone is not continuous with the rhabdome, Patten still considers the cone as the centre, since he describes processes running from each cone cell around the rhabdome but inside the retinula (as in *Vespa*). To this interpretation those investigators who consider the crystalline cone as the terminus of the nerve fibres would probably agree. On the other hand, Watase holds that the ommatidium is a morphological invagination of which the retinula is the centre, and the cone cells, lens cells (homologous with the corneal pigment cells of *Apis*) and pigment cells follow in the order named. By this interpretation the rhabdome, cone substance and lens are homodynamous. These two views seem in no way reconcilable, and more investigation is necessary to decide between them, since it scarcely seems probable that both plans exist, since all ommatidia are probably the result of one kind of development.

Patten bases his view on the fact that the cone cells are continuous with and part of the rhabdome, but surely in *Apis* there is no such continuity, since all through the development they are separate, and in the adult eye there is a sharp line of demarcation between them, and they also react very differently to stains. In *Vespa,* Patten admits that the rhabdome is not continuous with the crystalline cone cells, but in this case he describes processes between the rhabdome and retinula which correspond to the processes which form the rhabdome in other forms. Since, as will be discussed later, the rhabdome is really part of the retinula, being formed as an intracellular secretion, any such process from the cone cells would have to pierce the retinula cells to occupy such a position. No such processes occur in *Apis.* If such a view be held because it is necessary in some way for the nerve fibres to reach the crystalline cone, on the assumption that the nerves end there, such a necessity disappears, for, as will be shown under a discussion of the innervation of the ommatidium, the cone is in no way a nerve terminus. Such a theory of innervation does not seem justified for any ommatidium, and therefore the necessity for this conception of the morphology disappears.

On the other hand Watase based his view largely on the eye of *Limulus.* This view commends itself on account of its extreme simplicity, since all ommatidia readily lend themselves to the plan of diagrammatic representation used by Watase with this interpretation. Watase seems to have advanced this theory rather for the purpose of giving some explanation for the existence of the rhabdome than for the morphology of the entire ommatidium. There is, I think, no reason to believe that the rhabdome was ever a chitinous substance, and in that sense it is not homologous with the lens. In the ommatidium, as we now know it, the rhabdome is an intracellular secretion full of nerve fibrils, and is far from being a hard chitinous growth. To that extent, then, Watase's conception seems an error. If, however, we look on the lens, cone substance and rhabdome as secretions (non-living protoplasmic differentiations), of which the lens only is an extracellular secretion, then the homology may hold. Acording to this view, then, the ommatidium did not arise as a pit filled with chitin, but rather the sinking in of certain cells, with a corresponding retention of the secretion inside the cell, has taken place with the assumption of new functions. Parker has argued that the retinular cells cannot be considered as homologous with the lens secreting cells, since the lens cells secrete on their distal surface while the retinular cells secrete on their lateral surfaces. My observations show that both cone cells and retinular cells form their secretions intracellularly and from their very positions they could not secrete on their distal surfaces, but this does not seem to me to be any objection to the theory of Watase, since in the invagination of the cells and the taking on of new functions new forms of metabolic activity might easily be acquired.

Since, however, in the embryonic development of the ommatidium of the bee we find a stage in which the retinula is formed without cone cells on the distal end and with the rhabdome partly formed, the only inference, it seems to me, is that the cone arises from lateral cells, and the corneal and outer pigment cells are, of course, still more peripheral. From this, then, it seems to follow that the conception of Watase concerning the morphology of the ommatidium is the correct one. There is, so far as has been observed, no real invagination, but such a thing would scarcely be expected in so compact an organ; neither have I observed the actual overgrowing of the cone cells, but the conclusion seems inevitable that the retinula is the centre of the ommatidium.

Some compound eyes have been described in which, in the adult eye, the retinular cells extend outside the cone to the lens. Such cases are found when the number of pigment cells is reduced or when they are entirely wanting, and it is safe to assume that the distal lengthening has taken place secondarily, late in development. From the migration of the corneal pigment cells of the ommatidium of the bee, to be described later, we see that a late rearrangement is possible, and it seems more plausible to assume that such cases are a secondary modification rather than that there are two ground plans of ommatidia, one of which has its retinula centrally placed, the other has the cone cells inside the retinula as the axis.

The retinular spindle of the larva resembles in appearance various sense buds throughout the animal kingdom, such as taste buds and lateral line organs of vertebrates, the æsthetes of Chitons, etc. These sense buds often have some marked differentiation of the cytoplasm internally to enable the peripheral organ to perform its function. This similarity is more than superficial, however, for the method of innervation which will be described in detail later is from the sense cell toward the central nervous system, and this is the method for many of these sense buds, although the opposite direction of fibres is described for some (*e.g.*, taste buds).

It is safe to assume that these sense buds are accumulations of single sensory cells, such as are widely known (*e.g.*, sensory epithelial cells of *Lumbricus*, epithelial sensory cells [Flemming's cells] of Molluscs), giving greater efficiency at a certain spot, and that the internal differentiations are but secretions or cytoplasmic differentiations due to the specialized condition of the cell. Granting these facts, then, sense buds are homologous of necessity only in their origin from an epidermal tissue, although the homology may be greater. Since sense buds are known which are sensitive to touch, taste, smell, sight and vibration waves, it seems entirely unnecessary to assume that a light-perceiving organ, such as an ommatidium, has arisen as a modification of some other kind of sense bud, rather than that it arose as an accumulation of epithelial cells already sensitive to light.

Since we know that single cells are acted upon by light waves (*e.g.*, Protozoa), and that epidermal cells often give rise to nervous impulses when acted upon by light (*e.g.*, skin of the earth worm), there seems no reason for assuming that the ommatidium has arisen other than by an accumulation of such sensitive cells and then by invagination a light-refracting organ has been formed over it. Such a view is directly opposed to the view of Patten that the ommatidium is a hair-bearing sense organ. As will be shown later, his theory is untenable on account of the absence of the essential structure for such a homology—the hair. There is not only no indication of such an organ for the eye, but no need for such a complicated theory of the origin of these organs, since easy transition steps from a single cell sensitive to light to the ommatidium are obtainable and such an origin seems far more probable.

Johansen (1893), in his description of the development of the eye of *Vanessa urticæ* L., figures and describes a spindle-shaped mass of cells which is the ommatidium of the pupa when two days and one hour old. He has also observed the same spindle mass in the young pupa of *Sphinx euphorbiæ*. This differs from what I have described for *Apis* in that the corneal pigment cells and cone cells lie distal to the retinula, and I am led to conclude that he has observed a stage just after the sinking in of the retinula, a stage which I am unable to describe for *Apis*. At any rate his conception of the morphology agrees with mine, since the retinula is in the centre of the ommatidium and the cone cells and corneal pigment cells are lateral to it.

2. *Pupa.*

During the so-called semi-pupa stage, just after the larva is sealed up by the workers of the hive, and before the bee is a complete pupa, very rapid growth takes place, and the eye increases still more in size and becomes more and more differentiated until at the beginning of the pupa stage proper the ommatidia are completely formed. The exact method by which this differentiation takes place is difficult to learn, since the growth at this time is so very rapid that it is practically impossible to get all the stages. The head of the insect grows very rapidly and the eyes keep pace with it. The retinular cells become longer and broader, and the retinulæ lie closer together. The cone and corneal pigment cells come to lie at the distal end of the retinula by the method previously described. When the pupa stage proper is entered upon, the area of the eye is practically that of the adult eye.

The various stages of the pupa period are easily distinguishable externally, and this fact is of great value in the selection of material. The eye is first white, like the rest of the body, then pink, then brown, and finally, as the other parts of the body take on their adult colors, black. These changes of color are due to the deposition of pigment in the various cells of the ommatidium, pigment in the corneal pigment cells being red in color, giving the first color externally, and the darker pigments of the other cells obscuring this color at a later period. These changes enable one to choose the desired material by simply uncapping the cells containing pupæ without removing the bee from its cell, since the head is always toward the outside.

From this stage on it becomes necessary to discuss the various parts of the ommatidium separately. Such a method tends to give the impression of a lack of continuity in mode and time of development, but the drawings which accompany the description are made of the entire ommatidium, and these will show the relative size and degree of development at various stages. The order followed is from the retinula to the more lateral cells.

a. The Retinula.—The retinula cells are eight in number normally, but numerous ommatidia are observed in which nine cells are present. In the earliest pupa stage (fig. 3) these cells extend from the proximal end (apex) of the cone cells to the basement membrane, and each cell has a protoplasmic process extending through the openings in the basement membrane toward the optic lobes, which later functions as the nervous connection of these cells with the cells of the retinular ganglion. At this time the only indication of the rhabdome is the clear space at the distal end which was described for the larval ommatidium; its differentiation has gone on little, if any, during the rearrangement of cells. The cytoplasm at the distal end of the cells is more granular than elsewhere, and by the time the eye has reached the stage figured pigment is laid down around the forming rhabdome. This is the first pigment laid down in the ommatidium, but at almost the same time the corneal pigment cells acquire pigment. The spindle shape of the retinula so marked in the larval condition is still retained, the retinula being widest at about one-third of the distance from the cone cells to the basement membrane. The relatively large nuclei of the retinula at this time are near together, and in no definite arrangement in the thickest portion of the cell group. The cytoplasm of the cells is uniform except as described for the distal end, and the cell membranes between the various cells are not visible. The outside boundaries of the retinula group at this time and all through development mark off the retinula from its surrounding pigment cells very sharply, and the difference in the appearance of the protoplasm makes it impossible to confuse the various cells.

The portion of the retinula which lies between its thickest part and the basement membrane is a strand of protoplasm circular in cross-section and without any signs of differentiation. As the basement membrane changes its position, by a process to be described later, coming to lie near the optic ganglion, this portion of the retinula becomes longer, and the changes which take place in the retina consist of the making over of this strand of protoplasm into the retinula cells proper. This change progresses proximally and consists in the widening out of the cells with its accompanying rhabdome formation. The nuclei shift as the retinula enlarges and elongates until we reach a condition (fig. 2) in which two of them are at one level and the other six (or seven) are at a lower level and arranged in a rosette.

At the time when the nuclei are arranged in this manner, the most distal portion of the retinula becomes arranged in a definite rosette, caused by each of the cells forming a projection which shows its distinctness from the others in the group in cross-section. This arrangement also progresses proximally until in the adult condition it is found throughout the length of the retinula. At the same time the inner portion of the mass becomes still more differentiated, and in the stage just mentioned the axis of the distal end is occupied by a strand of protoplasm which takes the iron hæmatoxylin stain (the future rhabdome) surrounded by a clearer protoplasm. Outside of this clear area the protoplasm is granular and pigment deposition takes place here, keeping pace with the inner differentiations, and these changes also progress toward the basement membrane. The rhabdome formation precedes slightly the formation of the clear protoplasm around it, and the proximal end of the forming rhabdome shades off gradually into the surrounding undifferentiated cytoplasm.

The nuclei gradually move inward as the cells assume their adult form until they come to rest at about one-third of the distance from the cone to the basement membrane, which on account of the tapering of the retinula is at about the centre of the cell, as far as mass of cytoplasm is concerned. One of the nuclei, however, moves proximally until it lies about half-way between the other nuclei and the basement membrane. Where a nucleus is present, the retinula cell is slightly pressed out, encroaching on the outer pigment cells, and the upper nuclei are not all at the same level. The one nucleus which occupies a more proximal level is separated by some distance from any of the others, however, and, owing to the regularity with which it is found, cannot be considered as due merely to a mechanical shifting. In the older stages of development it becomes difficult to count the nuclei of the retinula since they are at different levels, but I have been unable to see anything which would lead me to suspect that this proximal nucleus was other than one of the retinular nuclei. Neither is there any indication that the presence of this nucleus is accountable for the presence of nine retinular cells in some ommatidia, for it is found in all ommatidia and the nine-celled condition is comparatively rare.

The rhabdome differentiation proceeds until it reaches the distal surface of the basement membrane where it ends abruptly. In the pupa stages I am unable to find the nerve fibres which in the adult eye run parallel with the rhabdome and send fine fibrillæ into it. It will be noticed, however, that in the pupa the rhabdome is wider and not so definite in outline as it is in the adult eye, and the nerve fibrils are no doubt included in this darker central body which I have identified as the rhabdome. Both rhabdome and nerve fibrillæ are but differentiations of the cytoplasm of the retinula cells and their development takes place together. The rhabdome is probably not a uniform structure, but no doubt contains a mass of fibrillæ, the endings of the nerve fibres. I am unable to see any such structures, however.

The development of the retinula consists, then, in the changing of the sense-bud-like spindle of the larval eye into a long column of cells with a clear shaft through the centre, through which light can pass to reach the nerve endings in it. From the previous description it will be evident that the rhabdome is not formed by processes from the cone cells, which are present from the beginning of ommatidial development, but is an intracellular differentiation of the retinula, there being a sharp line of demarcation between the cone cells and rhabdome throughout their development.

b. The Cone Cells.—The cone cells are four in number, and in the early pupa stage (fig. 3) the cone is spindle-shaped and lies directly distal to the retinular spindle. The nuclei are large and spherical, and lie slightly distal to the centre of the cell. The cytoplasm is granular, especially in the distal portion of the spindle, and the cell membranes are well marked.

Very soon the cytoplasm begins to be differentiated, and by the time the pupa has reached the stage figured (fig. 2) vacuoles begin to appear in the proximal end of the spindle, which marks the beginning of the formation of the clear cone substance. The cells now increase in size considerably, and at the same time the number of small vacuoles increases. Later these vacuoles unite, and finally a condition is reached in which the proximal end of each cell is occupied by one large clear vacuole. The cell boundaries remain distinct and a thin layer of granular protoplasm remains surrounding the vacuole, so that it is strictly an internal secretion and not to be interpreted as a secretion poured out on the inner face of each of the cells. This process of differentiation or intracellular secretion goes on until the nuclei, which decrease in size and become long and narrow, are pushed to the distal and lateral portion of the cell, where they remain in the adult eye. These nuclei are filled with fine chromatin granules. The cone in the meantime becomes wide at the distal end, and elongates very much to assume its true cone shape, and all that remains of the original cytoplasm is an extremely thin sheet all around the cone. I am inclined to attribute the descriptions by some authors of nerve fibrils on the cone to the shrinking of this thin film under certain fixatives. There is no nervous connection with the cone, nor does it appear to have any function save transmitting light rays to the sensitive retina.

There is no indication of any prolongation of the cone proximally, either to form the rhabdome, as previously described, or to form protoplasmic processes surrounding the rhabdome inside the retinula cells, such as Patten describes for *Vespa*. Such fibres could not exist unless they were to pierce the retinula cells, since the rhabdome is really a part of the latter; and since the cell boundaries of the cone and retinula are so well marked I feel sure that no such ingrowth occurs.

Equally unsuccessful has been a search for any additions to the cone at the distal end. In his work on the embryology of the eye of *Vespa*, Patten describes a layer of cells distal to the cone which arose by an overfolding of the sides of the entire eye, and which gave rise to the lens. In a later paper (1890) he disposes of his invagination theory, but describes a pouring out of chitin from the distal end of the cone, which secretion he mistook for the layer of nuclei at an earlier time. From my examination of *Apis* material I am unable to find anything which could be mistaken for nuclei in that position (unless it be the corneal pigment cells which are lateral to the distal end of the cone) or for chitinous secretion of the cone; and for this insect eye, at any rate, I am led to doubt the validity of his homology of such a structure with the pseudocone of ommatidia of the "pseudocone type," since the distal end of the cone is perfectly well defined at every stage observed.

The differentiation of the cone consists in a transformation of a cone without any refractive secretion into one in which this secretion fills all the cells proximal to the nuclei, or, in other words, a modification of an acone condition into an eucone condition, to use terms introduced by Grenacher for adult conditions of some eyes. There can be no doubt that this was the course taken during the evolution of the eucone ommatidium. Similarly, Hickson has shown that the so-called pseudocones described for many insect eyes are but instances in which the secretion has accumulated in the distal end of the cone rather than in the proximal end. While the distinction drawn between these three kinds of cones is justifiable, yet there seems nothing to oppose the view that they are but modifications of one primitive type. The acone ommatidia have no clear refractive substance differentiated in the cone cells, and are considered as the primitive type of eye. The pseudocone cones with the differentiation of clear cone substance distal to the nuclei and the eucone cones with a proximal secretion are but modifications of the primitive type.

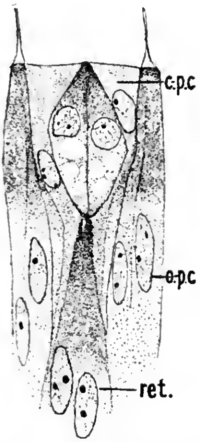

Fig. 6.—Young pupal ommatidium at time of migration of corneal pigment nuclei.

c. The Corneal Pigment Cells and the Lens.—The lens is secreted by the two cells which have been designated corneal pigment cells. In the very earliest pupa stage these cells lie distal and lateral to the cone cells, and since they are thus placed at this time, and since their secretion product is distal to the cone, they are next in order in going out from the axis of the typical ommatidium.

Before these cells begin their secretion, however, the nuclei migrate down the sides of the spindle-shaped cone and come to lie around the apex of the cone. The cause of this migration is probably purely mechanical, viz., the enlargement laterally and distally of the cone; at the same time the nuclei are thus brought nearer to the source of nutriment. As this shifting takes place the nuclei, originally ovoid, become crescent-shaped, and finally almost encircle the apex of the cone. Strands of cytoplasm connect the nucleated portion of the cell with the distal portion, which remains at the point where secretion is to take place. As the cone enlarges and the cell substance of the corneal pigment cells is used up in the secretion of the lens, the portion distal to the cone becomes reduced until in the adult eye it is almost entirely absent.

Almost immediately after pigment is first formed in the retinula cells, it begins to be deposited in these corneal pigment cells. Owing to the fact that the retinula pigment is at first small in quantity, and since there is none in the outer pigment cells at this time, the pigment of these distal pigmented cells, which is red, gives a pink color to the entire eye in the early stages, rather than the brown or black color possessed by the other pigment, as is true in late stages.

The granules of pigment are large and red in color, and when treated with depigmenting mixtures do not disappear, but become somewhat lighter in color.

The lens is secreted by these cells in much the same way as is ordinary chitin over the entire body of the bee. This chitinous covering is deposited in layers which are easily visible in the adult lens. In addition to these cells the outer pigment cells also seem to enter into this. In the pupal eyes before any chitin is deposited by the corneal pigment cells thin sheets of chitin extend out from the outer pigment cells, and since these cells are arranged at their distal ends in a nearly hexagonal manner a cross-section of these plates shows the future boundaries of the facets. In the adult eye the portion of the cornea which directly overlies the outer pigment cells differs slightly from the part directly over the cone in refractive index and in general appearance, so that I think it probable that the space between these sheets of chitin in the larva is filled by a secretion of the outer pigment cells. If this be true, then every cell which enters into the formation of the compound eye has to do with some sort of secretion, either intra- or extracellular.

The structure of the chitin laid down by the corneal pigment cells is not uniform, the outermost layer being more dense than the rest, with a decided tendency to take up an iron hæmatoxylin stain, the middle or main portion being arranged in alternating layers of different density, and the inner portion taking a protoplasmic stain, such as eosine or Bordeaux red.

From this description it will be seen that the corneal pigment cells (Hauptpigmentzellen, pigment cells of the first order) are homologous with the corneal hypodermal cells of the crustacean and apterygote insect eyes. In all crustacean compound eyes small nuclei are described as lying distal to the cone cell nuclei (or Semper's nuclei), and these are the nuclei of the cells which secrete the lens. When the ommatidia are arranged in facets, two such cells are present. In the Apterygota, *e.g.*, *Lepisma saccharinum*, *Orchesella*, etc. (Hesse, 1901), these two cells are present and occupy a similar position or may be placed slightly more laterally. These two cells are characteristic of these two types of compound eyes. On the other hand, the compound eyes of most pterygote insects have the two pigment cells of the first order (corneal pigment cells), and do not have the corneal hypodermal cells. Hesse (1901) concluded that these two kinds of cells are homologous from an examination of adult eyes, and considered his point strengthened by the fact that Johansen had described these pigment cells as being distal to the cone cells at an early stage. Johansen did not describe them as homologous, however, and derived the lens from another source. From an examination of *Apis* I am convinced that Hesse was correct in his deductions, for in this case the cells are not only homologous, but the pigment cells here have identically the same function as have the corneal hypodermal cells of the other eyes.

As mentioned above, Johansen failed to see this homology and describes and figures the lens as being secreted by the cone cells. It has been pointed out with sufficient detail that no such interpretation is tenable for *Apis* at least, and we may well doubt its occurrence in *Vanessa*. In Pl. 23, fig. 11, he figures the secretion of the lens by the cone cells and shows the corneal pigment cells extending to the distal margin, and I am led to conclude that he has overlooked the position of the pigment cell which remains distal to the cone.

d. The Outer Pigment Cells.—These cells from the earliest larva to adult stages extend the entire length of the ommatidium, and are what are known as accessory cells in many eyes. They, like all the other cells of the eye, are of ectodermic origin, there being no cells from the mesoderm in the eye of *Apis*, such as are described in some eyes. These cells are, normally, twelve in number, but when hair cells are present between the ommatidia, which is very frequently the case, this number is increased so that any definite enumeration is impossible; and since these cells serve merely to fill the interommatidial spaces and to prevent reflection inside the lens, no more definite arrangement is required. The nuclei of these cells lie proximal to the cone in pupal stages, but in the lengthening of the cone they come to lie at about its middle.

Pigment is deposited in these cells quite early, but not until after it has appeared in both the retinular and corneal pigment cells, and is most abundant at the two ends of the cell. It will be noticed that of all the cells of the eye which contain pigment none acquire this until they have begun to form the secretion to which they give rise. The rhabdome is the first secretion formed, and pigment first appears in the retinula; later the lens secretion appears, and then pigment appears in the secreting cells, indicating, it seems to me, that this pigment is of the nature of a by-product, although it is of itself of value. From one point of view, pigment itself is a secretion, but the accumulation of pigments often accompanies other secreting activities. Concerning any possible movements of the pigment under different light conditions, no observations have been made.

In the region where the basement membrane is formed these cells are deeply pigmented, and the line of demarcation from the cell below is very marked. At this point, also, and only here, the cells are fused with the retinular elements. This intimate union can exist only when the retinular elements have filled out to that point, since in the pupal stages that portion of the retinula is a thin strand. The retinular cells here are also deeply pigmented.

3. *The Adult Ommatidium.*

In the discussion of the changes which take place during the pupal period many of the details of the adult ommatidia are given, and to avoid unnecessary repetition only such things as have been omitted will be discussed here.

a. The Retinula.—The adult retinular cells are extremely complicated structures, due to the fact that each cell has so many differentiations internally. The central part of each cell is differentiated into a sector of the rhabdome, which is possibly a dead secretion, but of this there is room for some doubt. Outside the rhabdome is an area of clear protoplasm in which the nervous elements of the cell are found, and still outside of this is the granular portion of the cell in which pigment granules are found. Each of these cells then secretes part of the rhabdome, acts as a pigment cell by the accumulation of pigment on its outer surface, and is, in addition, a nerve-ending cell.

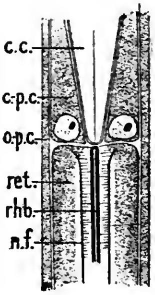

Fig. 7.—Diagram of part of ommatidium, showing apex of cone and distal end of retinula.

The innervation of the ommatidium is a question over which there has been much discussion, and various views have been put forth. The views can, however, be classed into two groups: those which make the cone cells the nerve-ending, and those which find the terminations in the retinula. It has been shown conclusively by numerous investigators that the cone has nothing whatever to do with receiving light stimuli, and it would be useless to take up the arguments against this view, any more than has been done in showing that in the development the cone and rhabdome are separate.

Those who hold that the retinula is the nerve-ending of the ommatidium have not always been able to show in a satisfactory manner just how this innervation takes place. On this point two views have been held: (1) that the retinula is innervated by nerve fibrils from the retinular ganglion which run into the retinular cells or rhabdome, or (2) that the retinular cells are themselves ganglionic epidermal cells which send in nerve fibres to the retinular ganglion. From the description which has preceded it is evident that the second of these views is the one here held for the eye of the bee. Before going into a detailed descripton of the nervous elements in the cells concerned, let us first examine the problem.

In the first place, it seems reasonable to assume that during the course of the evolution of light-perceiving organs the first condition was that in which certain cells of the hypodermis became sensitive to light, or possibly heat, through the accumulation of pigment or some other change in the cytoplasm. Such cells would arise before there were any cells in the central nervous system to receive their nerve stimuli, and it may be assumed without danger that such cells would send in processes to the centrally placed nerve cells, when the time for nerve connections arrived, rather than that the nerves arose from the central nervous system. In other words, the peripheral nervous system is older than the central nervous system which elaborates the impulses, and on hypothetical grounds, a basis which is rather unsafe in zoology unless backed up by observations, we may assume that the innervation is centrad.

From the standpoint of embryology, we find that the eye epidermis is formed and even the ommatidia are differentiated before the retinal ganglion cells have assumed their adult position or are connected with the optic ganglia. Not only that, but the strands of cytoplasm which become the nerves of the ommatidia arise from the retinula cells and grow centrad.

In the adult condition we find that the nerve fibres are continuous with the cytoplasm of the retinula and run to the retinular ganglion, where they surround the nuclei of the ganglionic cells. There is no indication of long nerve processes from the ganglion cells toward the eye.

The nervous elements of the retinular cell proper consist of a differentiated portion of the cytoplasm inside the clear area which lies outside the rhabdome. This nerve fibre can be seen best in sections stained in iron hæmatoxylin, where it stains black. From this fibre, which starts at the distal end of the cell and runs parallel to the rhabdome, smaller fibrils are given off which run into the rhabdome where they all end. More properly speaking, these fibrils are further differentiations of cytoplasm which lies between the main fibril and the centre of the retinula. These fibrils extend from the fibre to the rhabdome along the whole length of the retinula proper, so that the nerve-endings are very numerous. Below the basement membrane these main fibres can be traced as dark lines in the centre of the protoplasmic processes to the retinular ganglion. All of these fibres are best seen on cross-sections where they stand out as black dots, but they can also be seen on longitudinal sections. It is probable that the cause of the black color of the rhabdome in sections stained with iron hæmatoxylin is the presence of these numerous nerve fibrils. Concerning the distribution of these fibrils inside the rhabdome, I am unable to say anything definite, but they probably extend almost straight to the centre. In material fixed in Kleinenberg's picro-sulphuric fixing fluid the rhabdome sometimes appears as a tube, and this may indicate that these fibrils do not run all the way to the centre. While the innervation of the ommatidium is under discussion, it might be stated that there is no indication of nervous connection with any of the other cells peripheral to the retinula.

The significance of the single retinular nucleus which lies at a lower level than the others of each ommatidium, is somewhat hard to explain. Hickson held that some of the retinular cells of *Musca* had more than one nucleus. In this form there are three layers of nuclei in place of two, as in *Apis*. Hesse, on the contrary, homologizes these lower nuclei, only one of which is present in *Apis*, with the proximal retinular cells of the apterygote insect eyes. In these forms the retinula is divided into two parts, one distal to the other, each of which acts alone in the formation of rhabdome structure, and both have nerve fibre connections with the optic ganglia. A similar condition is found in some pterygote insect ommatidia. Of these two views the one of

Hesse seems more probable. As Hickson says, there is nothing morphologically wrong with the supposition that certain cells are multinucleate; but since the explanation of Hesse helps us to complete the homologies of the cells of the ommatidia of the various groups, it seems to have more weight.

The question as to the method of modification in number of retinular cells during the course of evolution is an interesting one, but it must be admitted that as yet very little is known concerning it. It seems not unlikely that the ommatidium of the bee is changing either from eight to nine retinular cells, or from nine to eight, since it is rather rare for the number of these elements to be variable. The thought has suggested itself that possibly this one proximal nucleus was one which was in the process of delamination from the ommatidial epidermis, and was therefore tending toward a reduction of retinal elements, but this does not seem to be as probable an explanation as that of Hesse. It may be said, however, that Johansen describes the ommatidium of *Vanessa* as having seven retinular cells and two retinal ganglion cells, while in *Apis* there is probably but one retinal ganglion cell to each ommatidium and at least one more cell in each retinula.

VII.—Homologies of Component Parts.

The question of homologies of the various eyes of the invertebrates has excited much discussion, but since only compound eyes have been investigated in this paper, this problem will not be taken up here. The question of the homology of the different kinds of compound eyes is worthy of consideration. Such eyes occur in crustacea and insects,[4] and a comparison of the groups indicates that there is here either uniformity of origin and plan or one of the most remarkable cases of convergence known in the animal kingdom. The essential part of the ommatidium is the retinula, and this may be considered as a sense bud, formed by the accumulation of cells sensitive to light, which has been modified internally to aid in light perception. Since such groups of cells occur throughout the whole animal kingdom and associated with all the senses, there is nothing remarkable about the similarity so far. In addition to the retinula, an ommatidium consists of a cone and a

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[4] No account of the so-called compound eyes of myriapods and arachnids is taken here, since their plan is so different that they cannot readily be homologized with those of crustaceans or insects. Until we know more of the comparative embryology of these forms it may be as well to suspend judgment. I do not feel qualified to include these in the present discussion, but evidently from the researches of numerous investigators we may conclude that the homology is not as close as in the forms under discussion.

chitinous covering which may be faceted, and possibly accessory cells occur between ommatidia which act as pigment cells. In order that the light rays may be centred on the retinular nerve fibres, some refractive organ must be present above it (the cone) and the whole organ must be covered by chitin, as is the rest of the body. This chitin in turn may assist in the refraction, as it does in many cases, or may even secondarily assume the functions of the cone entirely if no cone substance is differentiated (acone eyes). For the occurrence of these parts there are but two explanations: either they are differentiations of cells which formerly lay outside the retinula group, and have been placed distal to it to assist in collecting light rays to form a more perfect image, or they have been placed distal to the retinula by the differentiation of some other cell layer which has been superimposed.

The various cells of the ommatidium seem to lend themselves to homologies very readily. The retinulæ of the various ommatidia are groups of cells which are the nerve endings of the eye, and all ommatidia agree in this respect. Retinulæ of apterygote insects, some crustacea and a few pterygote insects have two layers of retinular cells, while others have but one, but, as was pointed out for *Apis*, the position of nuclei at different levels in the higher insects may indicate a remnant of a former two-layered condition for these retinulæ also. In other words, the morphological invagination by which the insect eye has arisen may be carried farther in some cases than in others. Hickson has shown that acone, pseudocone and eucone cones are probably homologous, and the fact that some cones are composed of but two cells while others have four seems a matter of small moment. The probable homology of the corneal hypodermal cells of apterygote insects and crustacea with the corneal pigment cells of most pterygote insects has been dwelt on sufficiently and is held on comparative anatomical grounds by Hesse. The accessory pigment cells are undoubtedly but undifferentiated cells of the layer of epidermis from which the retinulæ arise, and their presence or absence is of small importance in homologizing the different ommatidia. The fact also that mesodermal cells may migrate to a position between ommatidia, as is held for some eyes, is also of small consequence. As far, then, as the component parts of the ommatidia are concerned there is no difficulty about establishing a very close homology, and this similarity is considerably strengthened by showing that the corneal pigment cells are not only similar in function to the corneal hypodermal cells, but that at an early stage they actually occupy the same position.

The whole question seems, then, to be one which must be settled from embryological evidence. The problem is, which of the two methods of formation previously mentioned is the method which actually exists in ontogony, and are all compound eyes formed by the same method? From this work on *Apis* and that of Johansen on *Vanessa* it is evident that the differentiation of cells outside the retinula to form cone and lens layers is what occurs in insects, and the whole question hinges on the development of the crustacean eye. Reichenbach and Kingsley describe the eye as arising by an invagination; and if either of these investigators is right, although they differ as to the fate of the three layers formed, then the compound eyes of these crustaceans are not homologous with the compound eyes of insects. On the other hand, Herrick insists that the compound eye of *Alpheus* arises from a single layer of epidermis, and according to this view the homology holds. Herrick's view, that even if an invagination does occur it is of no importance, does not seem tenable, for if an invagination occurs then cone and retinula do not come from contiguous cells, and that I believe to be a matter of great importance.

From the striking similarity in position and function of the parts of the ommatidium, and from the observations of Herrick, we are safe in concluding that the eyes of the various groups under consideration are distinctly homologous, and there must be some other explanation for the invaginations observed by the other writers mentioned.

The interpretation of the formation of the ommatidium which is held from an examination of the eye of *Apis* makes possible a very close homology of the elements of the compound eye with the ocelli of insects, such as was held by Grenacher; and this homology seems materially strengthened since an homology can be shown between the corneal pigment cells of insect ommatidia with the chitin-secreting cells of the ocelli. An objection that might be raised is that the vitreous body of the ocellus arises from cells which are all to one side of the retina rather than from all sides, but since they are adjoining cells this might be a secondary change. From sections of ocelli of the pupæ of the bee which have been examined, it is evident that the middle ocellus arises from a double invagination, indicating a fusion of two organs, while the lateral ocelli arise from single invaginations.

VIII.—SUMMARY.

The primitive arrangement of ommatidia is tetragonal (p. 130).

The hairs over the lens are secreted by bi-nucleated hair cells with intracellular ducts which lie between the ommatidia (p. 131).

The ommatidium arises as a group of cells with superimposed nuclei, which later become arranged as a spindle surrounded by smaller cells (p. 136).

This spindle is the retinula, and the cone cells and pigment cells assume a distal position by a morphological invagination (p. 137).

The retinula is the centre of the ommatidium, and the cone cells, corneal pigment cells and outer pigment cells follow in the order named (p.141).

The ommatidium is composed of eight or nine retinula cells around the rhabdome, four cone cells, two corneal pigment cells and about twelve outer pigment cells (p. 126).

The rhabdome and cone are intracellular secretions, while the lens is an extracellular secretion of the pigment cells (p. 144).

The corneal pigment cells are homologous with the corneal hypodermal cells of crustacean and apterygote insect ommatidia (p. 147).

The innervation of the ommatidium is by a differentiation of part of the retinular cells into nerve fibrils, and these extend to the retinular ganglia (p. 149).

The lens is secreted by the corneal pigment cells which early in the pupa stage lie distal to the cone, and possibly also by the outer pigment cells (p. 148).

Pigment is formed inside all the cells of the ommatidium, except the cone cells, by a cytoplasmic differentiation (p. 149).

The ommatidium arises from a strictly one-layered epidermis, which passes directly from the larva to the pupa without the loss of any cells or additions from other tissues (p. 136).

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ABBREVIATIONS.

l., lens.
c. p. c., corneal pigment cell.
o. p. c., outer pigment cell.
b. m., basement membrane.
l. ret. n., lower retinular nucleus.
ch., chitin.
f. b., facet boundary.
ret. gang. n., nucleus of retinular ganglion.
br. sh., brain sheath.
int. d., intracellular duct.
c. c., crystalline cone.
rhb., rhabdome.
ret., retinula.
pgm., pigment.
n., nucleus.
h. c., hair cell.
tr., trachea.
n. f., nerve fibre.

EXPLANATION OF PLATES VI, VII, VIII.

PLATE VI, Fig. 1.—Section of entire eye and optic lobes. The heavy lines show the course of the nerve fibres as worked out by Kenyon (diagrammatic).

PLATE VII, Fig. 2.—Ommatidium of young pupa before rhabdome is differentiated and at time of first pigmentation of retinula cells.

Fig. 3.—Ommatidium of older pupa, showing differentiation of rhabdome and lens formation.

Fig. 4.—Cross-section through distal end of cone of pupa of same age as fig. 2, showing corneal pigment cells.

Fig. 5.—Cross-section through cone of older pupa.

Fig. 6.—Cross-section through proximal end of cone of pupa (same stage as figs. 3 and 5).

Fig. 7.—Cross-section through cone of young pupa.

Fig. 8.—Cross-section through retinula of young pupa before rhabdome formation.

Fig. 9.—Cross-section through distal end of retinula of young pupa, showing first traces of pigment.

PLATE VIII, Fig. 10.—Entire ommatidium (somewhat diagrammatic). Adult.

Fig. 11.—Entire ommatidium, as if dissected out, without outer pigment cells (diagrammatic). Adult.

Fig. 12.—Section of entire ommatidium, showing distribution of pigment. Adult.

Fig. 13.—Cross-section just proximal to lens, slightly oblique.

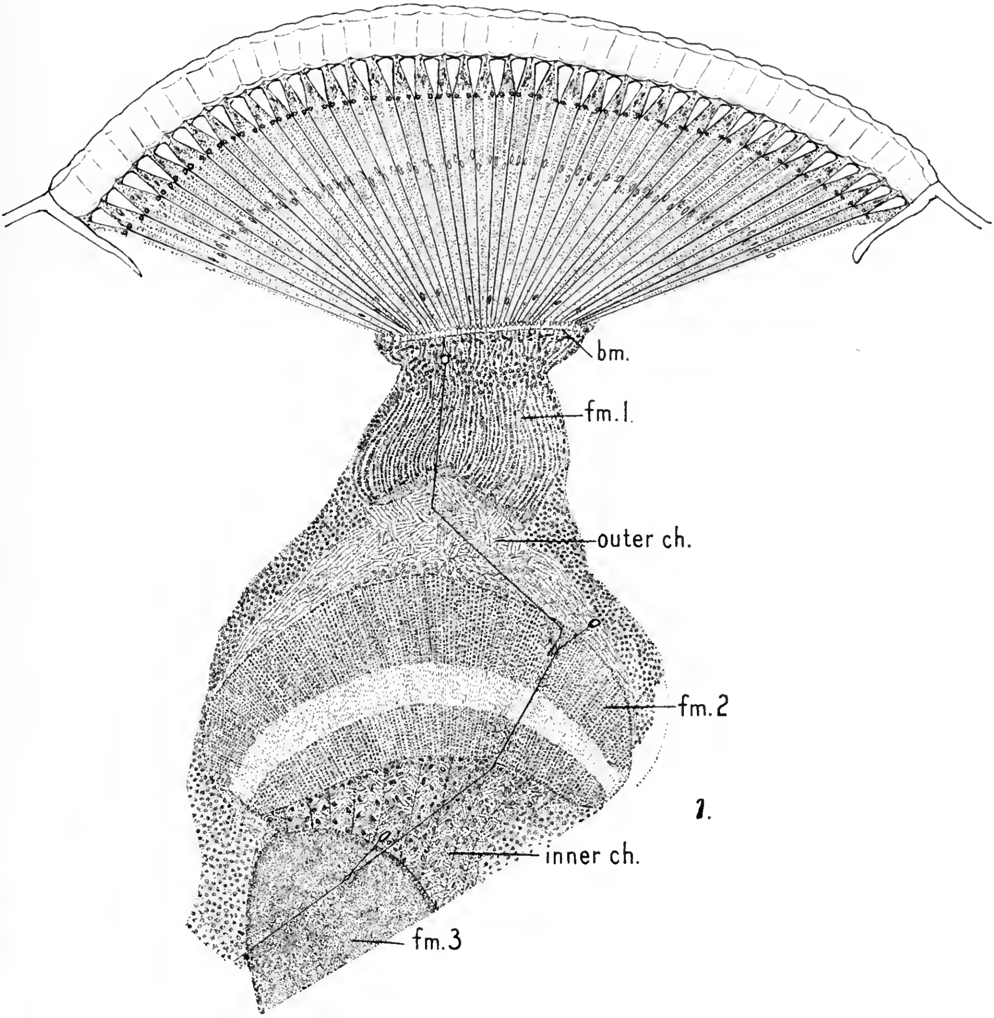
Fig. 14.—Cross-section through extreme distal ends of retinulæ and proximal ends of cones, slightly oblique.

Fig. 15.—Cross-section through retinulæ, showing relation of outer pigment cells in this region.

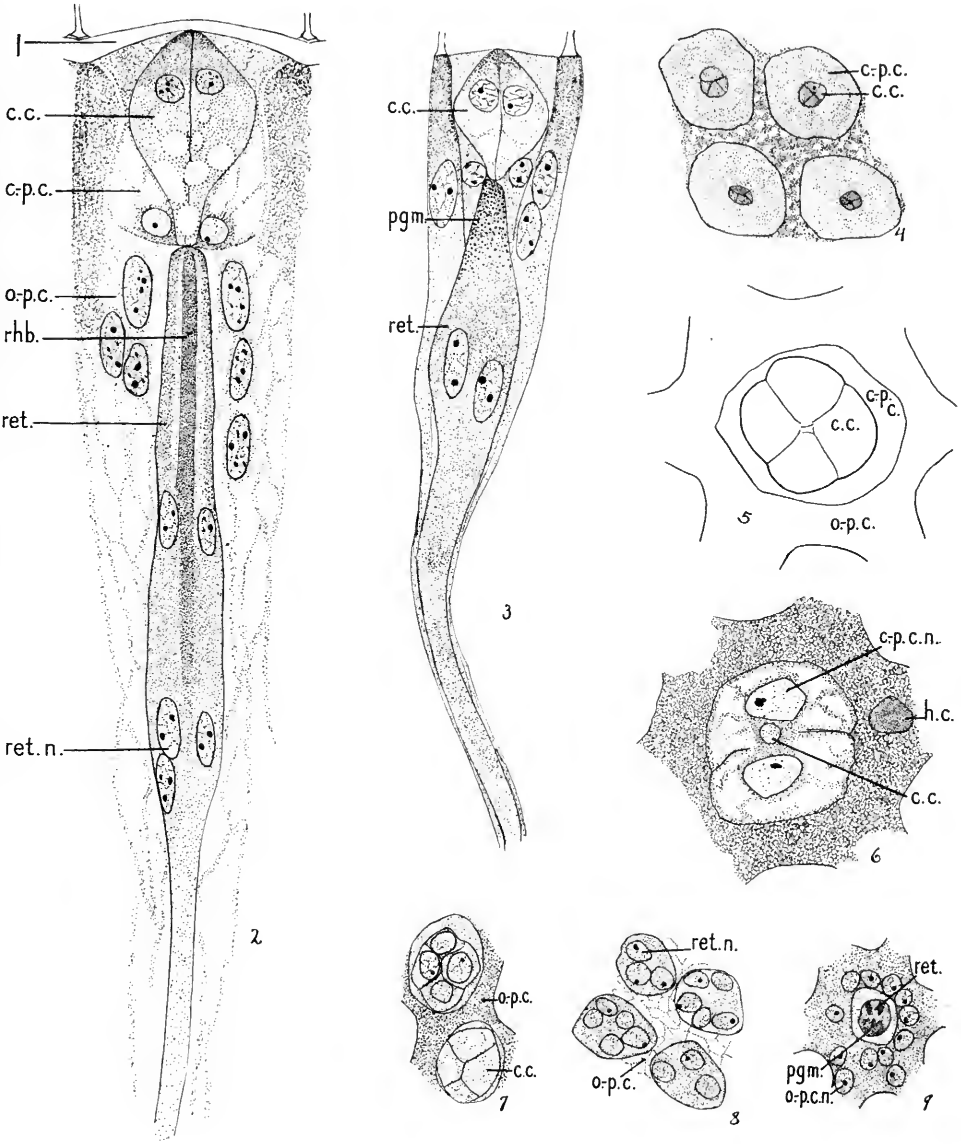
Fig. 16.—Cross-section through retinulæ in region of nuclei.

Fig. 17.—Cross-section through retinulæ in region of proximal nucleus.

Fig. 18.—Cross-section of eye, cutting basement membrane parallel. The distinctness of nerve fibres of each ommatidium is shown.



PHILLIPS. EYE OF THE HONEY BEE.



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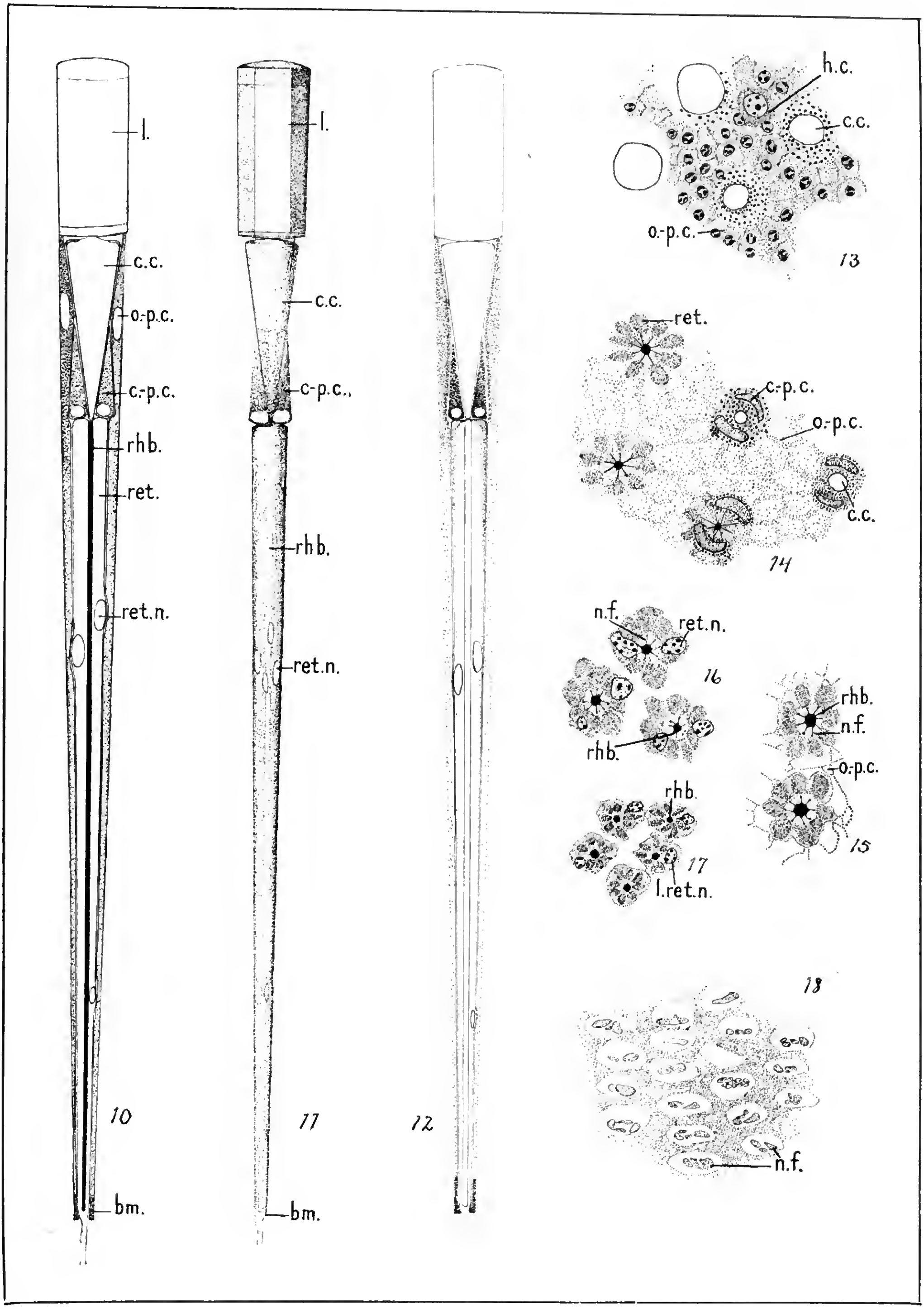

PHILLIPS. EYE OF THE HONEY BEE.