XVII. *On the Modifications of the Simple and Compound Eyes of Insects.*

By B. Thompson Lowne, *F.R.C.S., Lecturer on Physiology at the Middlesex Hospital Medical School, Arris and Gale Lecturer on Anatomy and Physiology in the Royal College of Surgeons, &c.*

Communicated by Prof. W. H. Flower, *F.R.S.*

Received February 27,—Read March 28, 1878.

[Plates 52–54.]

Although the compound eyes of the Arthropoda have been examined and described with great care in former times by J. Müller,* Leydig,† Gottsche,‡ and Claparede,§ and more recently by Max Schultze|| and Dr. R. Grenacher,¶ the improved methods and instruments of the present time have enabled me to add considerably to the published descriptions of the eyes of insects.

My attention was first directed to this subject by a paper from the pen of Dr. Grenacher. My observations do not accord well with the observations of this author, but I think this is chiefly from the fact that he has used the eyes of immature insects, which differ greatly from those of the mature insect, and from the difficulty there has hitherto been in preparing sections of sufficient thinness to allow the minute structure of the pigmented portion of the eye to be observed. I have been enabled to overcome this difficulty by imbedding the head of the insect in cocoa butter, in the manner first devised by Mr. Schafer, and used by him in the investigation of the early conditions of the mammalian ovum; in this way I have been enabled to obtain sections of the requisite thinness.

In the present communication the principal types of eye are described which I have found in the class Insecta. Reserving the distribution of these types in the class for a future communication, I shall merely indicate the Orders in which each type is found; and in so doing would especially draw attention to the fact that the number of species and genera which I have at present examined is far too small to enable me

* Verg. Phy. der Gesichtssinnes, 1826.

† Müller's Archiv., 1855. Lehrbuch der Histologie, 1857.

‡ Müller's Archiv., 1852.

§ Kol. Zeitsch., band viii.

|| Archiv., band iii., 1867.

¶ Zehender Monatsblatt, 1877.

to state that the eyes described are typical examples of the structure in the Order in question.

I shall conclude with some remarks on the function of the compound eye.

All the preparations, except where the contrary is stated, were prepared from insects hardened in a 2 per cent. solution of chromic acid. I have not found the peroxide of osmium so good in their preparation, and have only used it in a few instances.

I. *On the Structure of the Stemmata of* Eristalis tenax. (Plate 52, fig. 1.)

I have but little to add to what is already known of the structure of the simple eye. I have at present only examined it in a few of the Diptera, but have found such complete accordance between the descriptions of the authors already named and my observations, that I shall only briefly describe the structure of the ocellus of this insect, as it affords the best starting point for the correct interpretation of the structure of the compound eye.

Fig. 1 represents the ocellus. It consists of a very convex lens, rather more convex on its inner than its outer surface. Immediately behind the lens are the recipient structures, rods (fig. 1, *a*), consisting of an outer and an inner segment. The outer segment (*a*), which is next the lens, is a cylindrical, highly-refractive rod; the inner (*b*) is a fusiform nucleated cell. The inner segments are surrounded and separated from each other by an orange-coloured granular pigment.

The outer segment of each rod is from $\frac{1}{1000}$th to $\frac{1}{500}$th of an inch in length, and $\frac{1}{6000}$th of an inch in diameter; it is finely striated in the longitudinal direction. These rods are not closely packed together, but seem to lie in a fluid; this may, however, be a *post-mortem* change. Those at the periphery of the eye appear to be twice as long as those at the centre. I have not found them to be doubly refractive, nor have I ever observed any transverse division into disks.

The inner extremity of each rod-cell is connected with a fusiform cell (fig. 1, *c*), or with several fusiform cells arranged one beyond the other, and these are connected with the central nervous ganglion by fine nerve fibres. The fibres are surrounded by a few minute granules of a highly refractive substance. The nerves of the three ocelli unite into a single trunk.

The principal fact to which I would draw special attention is the apposition of the recipient elements of the retina with the lens, and the entire absence of anything like a vitreous body. In the young eye, the percipient structures are separated from the lens by a layer of cells. I have not observed this condition in the present species, but it is seen in the ocellus of the larva of *Dyticus, Acilius,* &c.

The great convexity of the lens in the ocellus of *Eristalis* must give it a very short focus, and it is manifestly but ill adapted for the formation of a picture. The comparatively small number of rods must further render the production of anything like a perfect picture, even of very near objects, useless for purposes of vision. I strongly suspect that the function of the ocelli is the perception of the intensity and the direction of light rather than vision in the ordinary acceptation of the term.

II. *On the Structure of the Compound Eye in* Tipula. (Figs. 2 to 5.)

The eye in *Tipula oleracea* is intermediate in structure between a true compound eye and a collection of ocelli.

The curvature of the common cornea is nearly hemispherical. It is divided into a number of strongly convex hexagonal facets, each of which is $\frac{1}{1000}$th of an inch in diameter, and $\frac{1}{2000}$th of an inch in thickness in its thinnest part. The outer surface is more strongly curved than the inner. The axes of the adjacent lenses make an angle of from four to five degrees with each other. Each lens is surrounded by a deeply pigmented portion of the cornea, which forms a black hexagonal framework between the lenses.

Beneath each lens there are sixteen rod-like cells (a''), which are easily distinguished in the immature imago.

In the mature imago these cells are so strongly pigmented with deep black pigment, that even in the thinnest sections I have been unable to detect the divisions between them; neither do they exhibit any transparent openings in transverse sections. I have found this to be the case both in specimens hardened in chromic and osmic acids.

Between each of these opaque cells and the facet of the cornea is a minute highly-refractive globule (a'), of a bright purple colour. These cells bring to mind the highly pigmented retinal cells of the Pigeon.*

Beneath the rod-cell layer is an elongated chamber containing a very remarkable structure, the "retinula" of Dr. GRENACHER, which I shall name the facellus (f). The facellus consists of seven fusiform cells, the outer extremities of which terminate in fine hair-like points, which appear to pass into the rod-like cells of the more superficial layer. The points of the cells of the facellus are the extremities of fine highly-refractive threads, which pass through the fusiform cells of which it is composed, and are prolonged through the long cylindrical organ which connects the facellus with the ganglionic retina. These axial threads are easily distinguished in transverse sections through the facellus (figs. 4 and 4a).

The cells of the facellus appear to become chitinous in the fully-formed imago, and are yellow in specimens hardened in chromic acid; like all the highly-refractive structures of the eye, including the cornea, they resist the action of solutions of caustic alkali for a considerable time. In the immature imago they are slightly granular, especially near their surface, but they contain no pigment.

A strong chitinous membrane (m) separates the parts already described from the

* MAX SCHULTZE, Archiv., bd. iii.

deeper structures of the eye, but it is perforated beneath each facellus, so that the latter is in continuity with the deeper structures.

A membranous flask-like sac extends from the inner extremity of each facellus to the edge of the corresponding facet of the cornea; this is lined with deep black pigment cells.

Between each facellus and the ganglionic retina is a long compound rod, larger at its outer extremity than at its inner extremity. It is usually spoken of as the rod of the compound eye, but I shall call it the stemon (*st*), as I think I shall be able to show that it cannot be considered as the homologue of the rod-like structure of the true compound eye.

The stemonata, corresponding to the outer facets of the eye (fig. 5), are very short and conical, being very much larger at their outer than at their inner extremities. In the immature imago the stemon can be seen to consist of seven cells, but in the mature insect, and especially in the centre of the eye, these are so perfectly fused together that the component cells of the stemon can be no longer recognised.

The stemon is surrounded at its outer extremity by a very dense sheath of pigment, but this is deficient at its inner end. The stemon contains minute black granules of pigment, and these are arranged in four thread-like lines, which, with comparatively low powers, have an appearance which induced LEYDIG* to describe them as muscular elements; beside these, minute scattered black pigment granules are seen in the protoplasm of the stemon.

Some of the stemonata remain distinct throughout their whole course, but others unite with each other, so that three or four are fused at their inner extremities into a single thread. At their inner extremities all the stemonata branch, and are connected with pigmented stellate cells.

The highly refractive threads of the facellus are seen in transverse sections at the outer end of the stemon, but I have been unable to distinguish them at the inner attenuated extremity.

The stellate cells already alluded to are situated between two fine chitinous membranes. The outer of these (m^1) sends delicate sheaths over the stemonata; the inner (m^2) is perforated by the fine processes of the stellate cells, which communicate with the round cells (g) within the second membrane. The round cells are supported in a fine network of neuroglia, also apparently given off from the inner surface of the second membrane. Beneath the round cells are several layers of fusiform cells (c), which appear to be situated at the outer extremity of the optic nerve, and to be in continuity with its fibres.

III. *On the Compound Eye of* Vespa vulgaris *and* Vespa rufa. (Figs. 7 and 8.)

I have used these two species indiscriminately in the investigation of the compound eye, as I have found no difference in its structure.

* *Loc. cit.*

The type of the compound eye in the Wasp is the same as that of the eye of *Tipula*, but the two differ in the following points :—

The curvature of the general cornea is so slight that the visual axes of adjacent facets in the centre of the cornea only make angles of 8′ with each other. The facets are only $\frac{1}{2000}$th of an inch in diameter, but they are $\frac{1}{1000}$th of an inch in thickness, and consist of numerous layers. The approximate radius of curvature of the outer surface of a facet is $\frac{1}{1500}$th, and that of the inner surface is $\frac{1}{2500}$th of an inch.

The refractive index of the material of which the compound cornea is formed does not differ materially from that of Canada balsam: this is easily seen in specimens mounted in fluid balsam. In order to determine the index of refraction with the greatest accuracy, I found the focal lengths of the lenticular facets of the cornea of a Hornet first in air and then in water, thus eliminating the radii of curvature. By this means I calculated the refractive index to be 1·53. The great difficulty is the determination of the real focus with sufficient accuracy, but the results are sufficiently accurate to give an approximate idea of the position of the focus in the eye. These results give $\frac{1}{200}$th of an inch as the distance of the focus behind the inner surface of the cornea, so that the rays may be considered as approximately parallel to the axes of the rod-cells.

As in *Tipula*, there are sixteen rod-cells (a'') behind each facet. There is also a small highly refractive globule of a dark purple colour, and a facellus (f) very similar to that in the eye of *Tipula* behind the rod-cells. All these structures are surrounded by so much deep violet pigment in my preparations that the details can only be observed with considerable difficulty.

IIIA. *On the Compound Eye of* Formica rufa. (Figs. 6, 7*a*, and 8*a*.)

My description and figures of the eye of this insect are taken from the eye of the mature female imago.

The eye of this Ant differs but little from that of the Wasp. The corneal facets are larger, measuring $\frac{1}{1500}$th of an inch in diameter, but are not more than $\frac{1}{2000}$th of an inch in thickness. The spherules beneath the cornea are colourless. The rod-cells (a'') are imbedded in a large quantity of deep violet pigment (fig. 7*a*); they are $\frac{1}{10000}$th of an inch in diameter. The facellus (f) is shorter and wider, and consists of more rod-like cells than I have observed in the facellus of any other insect: there are at least twelve cells; it is surrounded by a layer of deep purple pigment. The chamber in which the rod-cells lie is lined by deeply pigmented rod-like cells which differ from those in the centre of the chamber in the extent of their pigmentation and in not being connected with the facellus, so that in some of my sections in which the facellus and the deeper parts have been torn away the pigmented rods of the periphery of the chamber alone remain. Under these circumstances the eye appears to be provided with a chamber like the eye of a true dipterous insect, surrounded with palisade-like rods of pigment.

The stemon (*st*) is much shorter than that of the Wasp. Each has four elongated cells attached to its surface; these, as well as the stemon itself, are coloured with violet pigment. This pigment is in fine granules, and, like that of the rods in the eye of the Lobster, according to KUHNE,* and that of the eye in all the insects which I have examined, is unaffected by light. The transverse section of the stemonata (fig. 8*a*) shows that they are cylindrical and not prismatic; they exhibit four or more bright spots on their periphery, and are surrounded with granules of purple pigment. I am at a loss to understand the bright spots, but am inclined to view them as the result of molecular change; they may, however, be the indications of highly refractive threads. I have not, however, been able to detect any such threads in the vertical sections.

The stemonata rest on a limiting membrane of chitin (*m*).

I have been more fortunate in the examination of the ganglionic retina of the Ant than in that of the Wasp. The stemon is connected with the nuclear layer by a single thick nerve fibre (*n*); but from what I have seen in the Lepidoptera I have no doubt that by appropriate preparation this would be found to consist of a large number of component fibrillæ. My preparations of the eye of this insect were made from specimens which were killed some two or three years ago by immersion in spirit, and which had been put away and forgotten. The ganglionic retina (*g*) consists exclusively of small nuclei, or perhaps of very small round cells: these are connected with the deeper ganglia by bundles of nerve fibres.

I have not detected any stellate cells, nor have I found the fusiform cells so universally present; but I have not obtained sections of the deeper ganglia; neither have I as yet, in any of the insects which have a semi-compound eye like the Ant, detected the presence of any decussation of the fibres of the optic nerve. I have not, however, obtained a thoroughly satisfactory section of all the parts of the nervous structures connected with the optic tract, owing to the difficulty of getting a section in the plane which includes them all, if such a plane exists, as it certainly does in many of the Diptera and Lepidoptera. I am inclined to believe, however, from what I have seen, that no such decussation occurs in these insects.

IV. *On the Structure of the Compound Eyes of* Eristalis tenax, Syrphus, Musca vomitoria, Stomoxys, *and* Tabanus. (Figs. 9 to 20.)

The eyes of all the Brachycerous Diptera which I have examined are formed on one type, which differs entirely from that on which the eyes hitherto described are formed. They all have a cavity beneath each facet of the cornea containing a slightly coagulable fluid. At the inner extremity of this cavity, which is conical, there is a body consisting of four nuclei or small cells, and beyond this a rod-like structure which apparently differs but little from the stemon. I shall, however, distinguish it

* *Loc. cit.*

by the term rhabdion, as I think that there is evidence that it does not in any way correspond to the structure which I have named the stemon. I am rather inclined to regard it as the representative of the rod-like cells in the eyes hitherto described. If a facellus exist at all, it is placed beneath this structure—a fact that is clearly indicated by the position of the facellus in the eyes of the Lepidoptera, in which there can be no doubt of its presence. As will be seen, there is a structure in the nervous retina of the flies which resembles the facellus very closely, but a true facellus is entirely wanting.

Eristalis. (Figs. 9 to 13.)—The eye in *Eristalis* does not differ in any way that I have been able to discover from that of *Syrphus,* but the parts of the latter are often more easily made out from their greater transparency. I shall describe the eye of the former insect, and refer to that of the latter when I have found the parts more distinct in it.

The cornea is about $\frac{1}{1500}$th of an inch in thickness, and the facets average $\frac{1}{800}$th of an inch in diameter. In the centre their adjacent axes make an angle of about 1° with each other. Those in the centre of the cornea are hexagonal and small: usually $\frac{1}{1000}$th of an inch in diameter; those at the edges are square, and as much as $\frac{1}{750}$th of an inch across. The facets in the immature imago and at the periphery of the cornea are surrounded by nuclei of a bright brown tint (the so-called nuclei of SEMPER) (fig. 9 *a*). These appear to be adherent to the substance of the cornea. In the mature imago and in the centre of the cornea the facets are surrounded by a framework of deep black pigment which conceals the nuclei, and is probably developed in or around them. Immediately beneath each corneal facet is a deep cup-like cavity (fig. 9) surrounded by flat cells filled with bright orange-coloured pigment; at the bottom of this cup there are four nucleated cells (a') which rest upon the extremity of a quadrangular rod (figs. 10 *a* and 10 *b*). These parts attain a very high development in *Acridium* and in the Diurnal Lepidopterà. I shall call the four cells the tetrasome, and the quadrangular rod on which they rest the tetraphore.

Between the tetrasome and the nervous retina is the rhabdion (a''). This consists of a protoplasmic sheath, containing a bundle of four fine highly-refractive threads, which are united together at the outer end of the rhabdion into an apparently single axial thread, which enlarges to form the tetraphore. I have been unable to make out the fourfold nature of this structure, but suspect that it consists of four elements. The outer extremity of the rhabdion is cylindrical, and is surrounded by a number of pigment cells (*p*), forming a structure which has been called the iris. I shall speak of these cells as the outer pigment cells of the rhabdion. In this region the rhabdion is seen to be grooved longitudinally, the grooves being filled by prolongations of the pigment cells (fig. 10 *e*). These details are best seen in sections of the eye of *Syrphus.* Beyond the region of the outer pigment cells the rhabdion is triquetrous, or more rarely quadrangular (figs. 10*f*, and 11); a double bundle of fine moniliform pigmented fibres lies at each angle. These pigmented fibres are partly derived from the outer pigment cells of the rhabdion, and partly from four pigmented nuclei which are situated at the inner extremity of this structure (fig. 12). These pigmented fibres become very tortuous when they are acted on by water, and apparently produce the contorted conditions of the rhabdion which have been attributed to the elasticity of its axial structure. The interspaces between the prismatic portions of the rhabdia are occupied by large sac-like tracheal tubes. These are, so far as I can tell, confined to the Diptera, and are quite characteristic in this group.

The inner extremities of the rhabdia rest on a strong chitinous membrane (fig. 12, *m'*), which is perforated for the rhabdia to communicate with the nervous retina beneath, and for the tracheal tubes. The rhabdia appear to be continuous with the thick outer processes of the large stellate cells of the nervous retina (fig. 12). In a few cases I believe I have seen two rhabdia connected with one cell. I have been unable to trace any continuation of the axial structure of the rhabdion into the nerve cells of this region, but in some specimens I have seen four fine processes continued from the rhabdion into the region of the nervous retina, but in these the cells had disappeared in the preparation, so that I cannot state whether these were mere connective elements, or whether they belong to the proper structure of the nervous apparatus.

Fig. 12 shows the inner extremity of the rhabdia and their relation to the nerve structures beneath them. The oval cells are probably embryonic, as I have not found them in the adult imago. The drawing is from the eye of a small species of *Syrphus*, from which I succeeded in getting a very beautiful series of preparations.

The rhabdia of the two peripheral rows of facets are united into bundles at their inner extremities, four or more forming a compound structure, which is surrounded by elongated pigment cells (fig. 10 *l*). These compound rhabdia have six or more pigmented nuclei at their inner extremities. The form of the transverse section of the rhabdia is very variable (fig. 10, *d* to *i*).

The Nervous Retina of Eristalis *and* Syrphus.—As my most successful investigations of the nervous retina have been made in these insects, and as the modifications of the other parts are best understood when the nervous retina is included in the description, I shall describe the nervous retina in these insects, and afterwards state the points in which the same part appears to differ from it in other insects.

Fig. 13 represents this structure. From without inwards there are (*g'*) two layers of ganglion cells, (*n*) a layer of small round cells, (*f'*) a very remarkable layer of bundles of fusiform cells, so like the cells of the facellus in the eyes of the insects already described that it can hardly be regarded as anything but its physiological representative; and (*g''*) a third layer of stellate ganglion cells. These structures form the outer ganglionic retina, and are connected by a decussating optic nerve (*n'*) with a still deeper layer of staff-shaped cells, or, rather, with several layers of fusiform cells (*c*) superimposed one on the other. This inner ganglion is connected with the supraœsophageal ganglion by a distinct peduncle.

The intercommunication of the elements of the external ganglion or ganglionic retina is very difficult to determine, but I have no doubt, from the examination of many hundred preparations, that the ganglion cells of the outer layer are continuous with the protoplasm of the rhabdia by their outer processes, and that the stellate cells of the two outer layers form a complex network with each other by their lateral processes. I have been unable to determine whether the inner processes of these cells pass into the small round cells of the third layer, but I suspect they do; they certainly communicate with the fusiform cells of the fourth layer.

Figs. 10, *k*, and 13, *f'*, represent the bundles of cells in this layer. The first is a transverse section through a bundle from a stained specimen. I shall call this the facelloid layer of the retina. The bundles of cells consist of five or six cells. (I am at a loss to explain this deviation from the number of structures in the rhabdion, but it will be remembered that the number of cells in the facellus of *Tipula* is not the same as the number of rod-like elements.)

The innermost or fifth layer of the ganglionic retina (*g''*) is formed of stellate nerve cells like those of the outer layer. These rest on a membrane of extreme tenuity: the inner limiting membrane. This is connected with the outer or basal membrane on which the rhabdia rest by a fine connective network, or neuroglia, in the spaces of which the elements already described are situated. The number of layers of elements is very much reduced in those portions of the retina which correspond to the peripheral portions of the eye. The outer ganglion cells are reduced to a single layer, and the facelloid layer exhibits fewer sets of cells.

The optic nerve (*n'*) consists of clear, often varicose fibres. These unite the inner and outer ganglia, and form a complete decussation from above downwards, as well as from behind forwards. The inner half of each of these fibres is surrounded by a vast number of minute nuclei, which refract light highly. I have been unable to satisfy myself of their connection with the fibres, but I am inclined to the belief that they are united with them, as they move with them when the glass cover is shifted, and are only separated from them with great difficulty. The inner ganglion (*c*) consists of five or six layers of fusiform cells of granular protoplasm.

Musca vomitoria (figs. 14 to 17).—In this insect the chamber of the eye (fig. 14) is shorter than in *Eristalis*, and the tetrasome (*a'*) is placed in a small ovoid cavity at its inner extremity, surrounded by a dense layer of pigment, so that only its apex is exposed to the light. The segments of the tetrasome are finely striated in a longitudinal direction.

The cornea has the curvature of an epicycloid in section (fig. 51, page 596). The facets are $\frac{1}{1000}$th of an inch in diameter; the radius of curvature of the outer surface is $\frac{1}{1000}$th of an inch, and that of the inner surface is $\frac{1}{750}$th of an inch. The focal length of the lens is $\frac{1}{400}$th of an inch, measured in air. The distance of the outer extremity of the tetrasome to the inner surface of the cornea is as nearly as possible $\frac{1}{1000}$th of an inch. The focal length of the lens is given from the same surface of the cornea, so that the tetrasome lies considerably within the focus of the lens.

The rhabdia are less regular in size and structure than those of the Syrphidæ, as they intercommunicate with each other in the manner represented in fig. 15. The axial threads vary from four to twelve after the intercommunication of the rhabdia. The communicating branches contain only two axial threads, and the rhabdia near the tetrasomes contain four axial threads (fig. 15*a*). I do not think the axial threads intercommunicate. Fig. 16 represents the rhabdia and axial threads in transverse section.

Beside the pigmented moniliform fibres of the rhabdia, which are like those in the eye of *Syrphus*, there is a network of stellate pigment cells between the rhabdia, which contain a brilliant rose-coloured pigment; this becomes darker as the age of the insect advances.

A quantity of granular orange-coloured pigment is collected at the inner extremity of each rhabdion in a small spherical mass (fig. 17). The inner extremities of the rhabdia seen *in situ* have the appearance of a layer of polygonal epithelium.

Stomoxys calcitrans.—The only difference that I have been able to observe in the eyes of this insect as compared with those of *Musca vomitoria* is that the corneal facets are smaller: a condition which appertains in all small insects. They are only $\frac{1}{1600}$th of an inch in diameter.

Tabanus bovinus.—I have only examined the eye of *Tabanus* in dried specimens, so that I can only speak of the chitinous framework by which the various parts of the eye are supported. This attains a very remarkable development in *Tabanus* (figs. 18, 19, and 20). Not only are the chambers surrounded by chitinous hexagons, but the rhabdia are invested by chitin, and are connected by membranous septa, which divide the spaces from each other in which the trachea lie. These septa are strengthened by transverse thickenings. The most remarkable deviation from the ordinary structure of the dipterous eye is seen in the structure of the rhabdion, which appears to consist of two separate halves divided from each other by a fissure, each having its own sheath. I have found nothing like this in any other insect; but the structure needs investigation in the recent insect. It is apparently identical with a condition described by Dr. GRENACHER as existing in the rhabdia of some Coleoptera.*

V. *The Structure of the Eye in* Agrion puella. (Figs. 21 to 24).

In *Agrion puella* the type of the eye does not differ greatly from that in the Diptera. The chamber is much deeper and is filled with a gelatinous fluid. It is prismatic in form, and has a ring of four very transparent cells immediately under the cornea (fig. 21*a*); but in *Æschna* there are from eight to twelve cells.† The walls of the chamber (fig. 21) are not surrounded by pigment cells, but sixteen are found around the tetrasome. Long, exceedingly fine processes are given off from

* *Loc. cit.*

† CLAPAREDE.

these cells which line the chamber. They are moniliform, with small granules of dark brown pigment. The walls of the chamber are chitinous.

The rhabdia are hexagonal in transverse section in their outer extremity (fig. 23, *a*), and in the young imago at least are easily seen to be made up of six cells surrounding the central highly refractive threads. The inner portions of the rhabdia are round in transverse section (fig. 23, *b* and *c*); these organs are everywhere pigmented with fine black pigment. In many of my preparations they contain bright globules like oil; I suspect this is due to degenerative changes during the preparation of the specimens. I have observed the same in the stemonata of *Formica*.

The rhabdia are surrounded by a network of stellate cells containing black pigment (fig. 22).

The trachea of the rhabdia form a network in the spaces between them; but there is nothing like the large blind tracheal sacs found in the same region of the eye in the Diptera.

The external ganglionic retina (fig. 24) differs from that of the Diptera in the large quantity of black pigment developed in it: this is contained in the stellate cells of the neuroglia. The granules or round cells (*n*) are more numerous than in the Diptera, and form several layers, and the place of the facelloid layer of the Dipterous eye is occupied by a triple layer of large prismatic cells (*f* and *n′*). These also contain a large amount of pigment. I have not been able to make out the structures of this portion of the eye with the same clearness as in the Diptera, owing to the pigment in the cells of the neuroglia.

VI. *On the Structure of the Eye in* Acridium (Stenobothrus). (Figs. 25, 26, and 27.)

The cornea is not divided into facets in this insect, but both its surfaces are continuously curved. Beneath the cornea is a framework of chitinous chambers like the cells of a honeycomb; these are $\frac{1}{1000}$th of an inch in diameter. In each chamber there is an exceedingly complex tetrasome; this consists of two parts, which I shall call the tetrasome (*t*) and the tetraphore (*t′*) (figs. 25, 26, and 27).

The tetrasome is placed immediately beneath the cornea. In the young *Acridium*, just before the development of the wings, it consists of four transparent nucleated cells (fig. 25); but in the adult insect these are developed into four spherical highly refractive bodies containing numerous minute vacuoles* (figs. 26 and 27). They are supported on the sides of a square rod-like body formed of four segments, which are enlarged below into the body of the tetraphore.

The tetraphore in the adult insect consists, like the tetrasome, of a highly refractive substance, probably chitin; but in the immature insect it consists of four cells, which first become chitinous where they are in contact with each other, or they develope a

* Similar vacuoles exist in the tetraphore of *Vanessa;* these have been described by CLAPAREDE, *loc. cit.*

rod-like chitinous structure between them, which gradually takes their place. I am entirely inclined to the former view, and regard the segments of this organ as modified cells.

The inner extremity of the tetraphore rests on the outer extremity of the rhabdion, which is swollen into an ovoid enlargement (a). The highly refractive continuation of the tetraphore is plainly seen to be continued as a thread-like process in the axis of the rhabdion (a'). In transverse sections this is easily seen to be composed of four separate fibres. The thread-like axis of the rhabdion is enlarged into two fusiform swellings at the outer extremity of the organ.

The outer extremity of the rhabdion is surrounded by a number of pigment cells; these send fine moniliform pigment threads over it. The pigment is of an olive-brown colour. The rhabdia are cylindrical and straight.

I have at present been unsuccessful in the investigation of the ganglionic retina in this insect.

VII. *On the Structure of the Compound Eye in* Vanessa atalanta. (Figs. 28 to 34.)

The eyes of this insect are similar to the last-described form, but present important differences in the presence of lenticular facets to the cornea, in the structure of the tetraphore, and in the presence of a distinct facellus upon which the rhabdion rests.

The corneal facets are strongly convex on their outer, and slightly concave on their inner, surface; they are $\frac{1}{1000}$th of an inch in diameter.

The tetrasome consists of four nucleated cells in the immature, and of four highly refractive spheres (t) containing vacuoles in the mature insect. It is placed immediately beneath the cornea. The tetraphore consists of an outer very transparent globe (t''), enclosing an ovoid highly refractive body (t') containing vacuoles. An exceedingly fine prolongation of this body connects it with the rhabdion, and the whole floats in the fluid of the chamber (figs. 28 and 30). The chamber is prismatic, as in the last form; its pigment cells are arranged in two sets: eight surround the edge of the corneal facet, and a second set is situated at the inner extremity of the chamber. Numerous fine moniliform pigmented processes are given off from these cells, those from the outer set interdigitating with those of the inner, and so forming the pigmented lining of the chamber, as in the eye of *Agrion*.

The rhabdia are quadrangular in section, and are of smaller diameter at their outer than at their inner extremities. In transverse section some of these rhabdia appear to consist of five cylinders, but in the majority four of these are fused into a single investing sheath, enclosing an axial structure (fig. 31). Each of the external portions has a pigmented thread, which is easily separated from the rhabdion; it is connected with a pigmented nucleus at its inner extremity.

At the inner extremity of each rhabdion (figs. 32 and 33, a'') there is a cylindrical cavity (a''') formed by a membranous sheath from the basal membrane; the walls of these cavities are deeply pigmented. Between these cylindrical cavities are others of smaller diameter. Each of the larger cylinders contains seven rod-like cells; the smaller ones transmit tracheal tubes. I suspect the rod-like cells represent the facelli in the eye of *Vespa* and *Tipula*—a view strengthened by, and indeed entirely resting upon, the condition of the eye in the Crepuscularia. (See fig. 36.)

Immediately beneath the basal membrane there is a grouping together of the nerve-fibres into bundles, which are deeply pigmented with dark brown pigment. Amongst these bundles are a number of large stellate cells (*p*),* all more or less strongly pigmented, but bearing a very close resemblance to the stellate nerve-cells of the outer ganglion or nervous retina; together with small round and stellate nerve cells (*g*). Beneath these are numerous elongated fusiform cells (*c*), arranged in bundles like those of the facelloid layer in the retina of the Diptera, but more nearly resembling the fusiform cells of the deep ganglion of those insects. The fibres of the decussation of the optic nerve, which unite the outer and inner ganglia, are arranged in bundles which have the appearance of large nerve-fibres.

VIII. *On a Modification of the Eye in the Diurnal Lepidoptera.* (Fig. 35.)

The only modification I have observed in the Diurnal Lepidoptera is one in which the tetraphore is placed near the bottom of an elongated chamber; this appears to occur in *Pieris, Colias,* and *Gonepteryx:* the only three genera in which I have examined the eye, except *Vanessa.* Eight very delicate transparent cells (c' and c'') appear to fill this chamber (fig. 35). The lens of the corneal facet has a much less curve on its outer surface in this form of eye. Owing to an accident in the process of preparation, I regret that I am unable to determine from which of these three genera the figure is taken, but they are all very much alike in structure. I believe, however, that it is a drawing from the eye of *Colias.*

CLAPAREDE represents a semi-diagrammatic section of the partially developed eye of the pupa of *Vanessa;* it shows the original condition of the chamber of the eye filled with eight cells, in the interior of which the hard structures of the tetrasome are developed. The researches of CLAPAREDE on the development of the eye in this genus are very complete, and throw great light on the morphology of the compound eye.†

IX. *On the Structure of the Eye in the Sphingidæ.* (Fig. 36.)

I have not been able to examine the eye in the recent insect, but Prof. FLOWER placed at my disposal a very fine pupa of a *Sphinx* which had been many years preserved in spirit, from which I obtained some very excellent preparations.

* These cells are figured by CLAPAREDE (*loc. cit.*) in a drawing of the parts in the mature pupa. Judging from his figure, they are probably nervous elements.

† *Loc. cit.*

The eye in *Sphinx* is quite intermediate in structure between that of the Nocturnal and of the Diurnal Lepidoptera.

Immediately beneath the cornea, which was still in an undeveloped state in the pupa examined, are four small cells containing nuclei (a'); these rest upon a hard cone, consisting of four segments (a). This structure is characteristic of the eyes of the Nocturnal Lepidoptera, and it is perfectly clear in recent specimens. It persists in the dried insect, like the other chitinous structures. It had assumed an amber colour in the *Sphinx* pupa from which this description is taken (fig. 36, a). Immediately beneath the cone, as I shall call this body, is the rhabdion (a''). This differs in no way from that of *Vanessa,* except in its greater length, and in the fact that its outer end was much contorted. Beneath the rhabdia is a layer of undoubted and true facelli (f): one to each ocellulus. Each facellus consists of seven cells, the slender prolongations of which pass into the corresponding rhabdia. The facelli are surrounded by nucleated pigment cells and are continuous with the nerve-fibres. These are gathered together into bundles and unite into nerve-trunks (st); the fibres from thirty or forty facelli being united into a single trunk. They are deeply pigmented with violet-coloured pigment. At their inner extremity the bundles of nerve-fibres branch, and are connected with stellate nerve-cells. The other structures of the retinal ganglion were not distinguishable. The nerve-fibre bundles appear to represent the stemon of the semi-compound eye of *Vespa* and *Tipula.*

X. *On the Structure of the Eye in the Noctuid Moths.* (Figs. 37 to 42.)

At present I have only examined the eye in the true Noctuids. As in the Crepuscularia, there are four cells (a') immediately beneath the cornea, but in some species these cells each contain one or two bright highly-refractive nuclei, which appear to be formed of the same material as the deeper cone (figs. 38 and 42). The nuclei are rod-like, and have their long axes at right angles to the corneal facet. These cells rest upon a cone (a) formed of four segments, like that in the eye of the Crepuscularia. In some Moths this cone is surrounded by pigment cells which form four lines, one adjacent to each segment of the cone (fig. 38), and give off numerous moniliform fibres, which entirely surround the cone; in other species the cells are reduced to the magnitude of minute granules, from which the pigment fibres of the chamber are given off (fig. 37).

The inner extremity of the cone is continued inwards, in the form of four exceedingly fine, highly refractive threads (a''). These are, I believe, always surrounded by a protoplasmic sheath in the recent condition; but in a great many of my preparations the sheath has disappeared, and nothing is left but the highly refractive axial threads. They form the rhabdion. It is not uncommon to find these rhabdia united into bundles which form a network, and in some species the rhabdia are united into complex bundles, which are enclosed in chitinous sheaths surrounded by a large amount of pigment (figs. 39 and 40).

In the eye of the Herald moth (fig. 38) I have found some very remarkable drop-like appendages at the inner extremities of some of the cones (a'''), but I have not been able to make out their nature. I almost suspect they are the result of the rupture of the axial threads of the rhabdion, and are produced by the contraction of these threads, which, if such is the case, are viscous in the recent condition.* The thread-like prolongations of the cone are seen to end at their inner extremities in very long fusiform cells (c), which like the rhabdia are sometimes contained in tubular sheaths of chitin (fig. 41). The inner extremities of the fusiform cells are connected with stellate ganglion cells; but the whole of the deeper structures in the few species I have examined are so deeply pigmented that I am not able to give any satisfactory details concerning the ganglionic retina.

XI. *General Remarks on the Morphology of the Eyes of Insects.*

Three forms of eye have been recognised in the Arthropoda since the time of J. MÜLLER'S investigation of the subject: the simple, the aggregate, and the compound eye.

In the simple eye there is no difficulty in recognising the signification of the rod-like elements which are situated beneath the cornea, or their epithelial origin.

There can be little doubt but that we have the highest development of the aggregate eye in the so-called compound eye of the Nematocerous Diptera and of the Hymenoptera.

As far as the cornea is concerned, these eyes do not differ from the true compound eyes of other insects and of many crustaceans; but as I have shown, the deeper parts are similar to those of the simple eye in a high condition of differentiation. This form of eye is therefore to be regarded as a highly developed form of a connecting link between the simple and compound eye.

I am at present unable to point out in a satisfactory manner the nature and morphological relations of the facellus. Although this structure is present in the eyes of many Lepidoptera, it is apparently absent in the true Diptera, unless the facelloid layer of the retina can be regarded as its representative. The morphological representative of the facellus is more probably found in the pigmented bundles at the inner extremity of the compound rhabdia of the periphery of the eye in these insects.

A comparison of the parts in the aggregate eyes of the Nematocerous Diptera and Hymenoptera with the structures in the true compound eye is not difficult, but it can only be made in a tentative manner until the development of the aggregate eye has been more thoroughly worked out and a comparison has been made with the

* A similar contraction has been observed by MAX SCHULTZE in the inner extremities of the rods of Vertebrates, as a *post-mortem* condition. (Archiv., band iii., p. 220.)

development of the compound eye: a task which I shall hope to commence at least next summer.

CLAPAREDE's paper, which is most accurate, gives very valuable details on the development of the true compound eye.* He has also described and figured the various stages of the development of the eye of *Formica*, but he has neither detected the rod-cells of the chamber nor the facellus: I cannot help thinking that this has been from the manner in which the stemon separates from the facullus. I strongly suspect that CLAPAREDE's preparations represent only a part of the eye, and that in the more advanced stage the chamber is only partially represented. Unless this is the case, the remarkable deviation in the Hymenoptera from the more usual form of the eye in insects is developed from an eye which differs in no important particular from the compound eye in its simplest condition.

The true compound eye of insects is seen in three very different forms in the fully developed insect; but the observations of CLAPAREDE show that in the undeveloped condition of the eye these are all most probably identical, or nearly so. In this condition each segment of the eye consists of thirteen principal cells: eight form the cone (Krystalkegel) and five represent the rhabdion. Beside these there is a variable number of pigment cells.

The highly refractive structures of the axis of these parts are probably formed by the deposit of chitin in the substance of the primitive cells; but I think that further investigation of the whole subject is needed. Although my observations on the development of the compound eye agree in the main with those of CLAPAREDE, I have yet to work out the subject with the increased knowledge which I now possess.

The view that the hard and highly refractive parts of the cone or chamber are formed in the interior of the primitive cells is borne out, however, by the condition of the cone in the Nocturnal and Crepuscularian Lepidoptera, and according to LEYDIG† in the eye of *Cantharis melanura, Elater noctiluca,* and *Hyperia,* where the whole of the large cells of the primitive cone are replaced by the hard scleral cone.

I shall call the form of eye typical of the Nocturnal Lepidoptera the conic eye: and shall speak of the conic eye as proto-conic in its embryonic condition, and sclero-conic in the form it assumes in the Nocturnal Lepidoptera, and many other insects.

At present I have not found the proto-conic form of eye in any fully developed insect, but I have not yet examined the eyes of the Coleoptera, in which the writings of previous observers render it highly probable that such eyes exist, at least amongst the Pentamera. The work of LEYDIG shows that it exists in Melolontha.

Starting from the conic eye as the nearest approach to the primitive eye, there are two very remarkable and opposite deviations. In one, the cone is replaced by fluid, and the recipient structures are reduced to their simplest condition, as in the eyes

* *Loc. cit.*

† *Loc. cit.*

of the Brachycerous Diptera, and the Dragon-flies. I shall speak of this as the hydro-conic eye.

In the other form the cone is highly modified, and appears as a very complex tetrasome and tetraphore. I shall speak of this as the tetraphoric eye.

I shall conclude this portion of the subject by indicating very briefly the probable distribution of the three forms of compound eye, as well as that of the highly complex semi-compound eye, which for brevity may be called micro-rhabdic.

I have at present found the micro-rhabdic eye in the Nematocerous Diptera, the Hymenoptera, and Hemiptera, although I have only examined the eyes of a few members of the Order, and these far from exhaustively. I believe that it will also be found in the eyes of many Coleoptera, such for instance as Bryaxis.

The conic eye is the usual form of the compound eye in the Crustacea: at least it is found in the Lobster, Palæmon, and Hyperia. As already stated, it is found in the Nocturnal Lepidoptera, in the Sphingidæ, and probably in all the Pentamerous Coleoptera at least.

Judging from LEYDIG's descriptions, it is also found in the Cursorial Orthoptera.

I have at present found the tetraphoric eye only in *Vanessa, Colias, Pieris, Gonepteryx*, and *Acridium*; but I have not examined any other species of the Orthoptera and Diurnal Lepidoptera. The hydroconic eye occurs in all the Brachycerous Diptera and in the Dragon-flies.

XII. *On the Theory of Mosaic Vision.*

The structure of the compound eye appears to favour the view long ago expounded by JOH. MÜLLER. This view is supported by the absence of lenticular facets in many species of Arthropods; by the relative sharpness of vision, not only in different species, but in different parts of the field of the same eye, as well as by the behaviour of a beam of light in passing through a highly refractive rod immersed in a less highly refractive medium, or surrounded by black pigment.

It is, further, the only theory which has been hitherto advanced that is competent to explain the phenomena when we bear in mind the relation of the recipient structures of the compound eye to the nerve elements beneath them.

On the passage of a ray of light through a highly refractive rod of small dimensions.—In order to arrive at some knowledge of the manner in which light passes through the highly refractive rods of the eye in the Arthropoda, I made the following experiments.

I took a capillary glass tube about $\frac{1}{100}$th of an inch in diameter, and placed it upright in a small transparent trough under the microscope, and filled both the vessel and the tube with water. The tube was an inch in length and was examined with an inch objective. I found that no light passed through the lumen of the tube, but that the section of the wall of the tube was brilliantly illuminated. I next placed a few fine glass threads, drawn from glass rod, in the interior of the capillary tube; these were as nearly as possible the same length as the tube, and measured $\frac{1}{1000}$ of an inch in diameter. The end of each of these fine rods appeared as a small bright disk in the deep black lumen of the tube, and when the light was shut off from the rest of the field reminded me of the appearance of the disk of a planet seen through a telescope, although the illumination was not by any means powerful, but was obtained from an ordinary gas burner ten feet from the microscope. When the focus of the microscope was altered so that the ends of the rods lay beyond it, the circles of light enlarged, showing that the rays left the rod in a divergent direction.

The same phenomena were observed when the diameter of both the rods and the containing tube was somewhat increased, but they were not so brilliant. In some cases when the ends of the rods were beyond the focus of the object glass, the central spot of light was surrounded by grey rings from interference. When the extremities of the rods were lenticular, as well as when the lower end of the rod was enlarged by fusing it into a globule of glass, or when it was drawn into a cone, the same phenomena occurred; so the brilliancy of the upper extremity of the rods was increased when the light, falling on the lower extremity, was convergent, so long as the axis of the ray was in the same direction as the axis of the rod, although oblique pencils produced only very feeble illumination of the upper extremity of the rod, even when the obliquity was only slight—at most, three or four degrees from the axis of the rod.*

It appears pretty evident that the appearances described are due in some way to total internal reflection.

In order to estimate the effect of the pigment I used glass rods, covered, except at their ends, with a layer of black varnish; and I found that even with rods $\frac{1}{500}$th of an inch in diameter, and only half an inch long, it was very difficult to transmit any light at all, unless the rays were absolutely parallel with the axis of the rod. With longer lengths of rod, or rods of smaller diameter, no light was transmitted, and the ends of the rods appeared quite black.

From these facts I think the inner extremities of the fine rod-like structures of highly refractive material which extend from the cornea, or from the inner end of the chamber into the deeper structures of the eye, may be regarded in the light of luminous points, illuminated by the light of the central pencil transmitted through the lens, and having as their function the excitation of the nerve ending in which they are embedded.

The focus of the lenticular facet in all the insects which I have examined lies considerably deeper than the outer extremity of the rhabdion in the true compound eye, and much below the surface of the rod-like recipient structures in the micro-rhabdic eye, so that for objects removed only the tenth of an inch or less from the

* OSCAR SCHMIDT has since recorded some similar experiments with glass rods in KÖLLIKER, 'Zeitsch. für Wissensch. Zoo.', Bd. 30. Beiblatt.

facet, we have to do with convergent rays and not with the focal point. This points to some mode by which the stimulation of the nerve ending is brought about, other than the union of homocentric pencils in a point beneath the compound cornea. In *Hydrophilus piceus*, however, according to EXNER,* the focal point for parallel rays lies within the crystal cone.

Whether each facet in the compound eye corresponds to one or to four distinct luminous impressions must at present, at least, remain a matter of doubt. I think, however, there can be no doubt that several distinct luminous impressions are transmitted from each facet in the micro-rhabdic eye of *Tipula* and *Vespa;* and there can be no doubt that a number of distinct luminous impressions are received by the ocellus or simple eye. I cannot, however, believe that the ocelli of insects can produce anything worthy of the name of an image, in the Diptera and Hymenoptera at least. The few retinal elements, their near approach to the lens, and the strong curves of the surfaces of the latter, are but ill adapted for more than the perception of light and the direction in which it is most intense.

In the compound eye the curvature of the cornea and the number of facets agree well with MÜLLER'S theory. It is true that CLAPAREDE has expressed the opposite opinion, but I think I shall be able to show that this is based on an incorrect assumption.

CLAPAREDE has stated that if MÜLLER'S theory were true, a hive Bee should be unable to perceive objects of less than eight or nine inches in diameter at a distance of 20 feet as distinct; but he comes to this conclusion by assuming that the acuity of vision is the same over the entire field. This is far from being the case in any insect which I have examined, with the single exception of *Tipula*, where it is approximately so, perhaps. In all the other insects which I have examined, the axes of vision for adjacent facets make a very small angle with each other in the central portion of the visual field, and a much larger one at its circumference. And although I have not had the opportunity of examining the cornea of the hive Bee critically, in the humble Bee, the Wasp, Tabanus, and the great Dragon-flies, the angles made by the axes of adjacent facets are not more than from eight to fifteen minutes: a condition which would enable objects of from half an inch to an inch in diameter to be seen as distinct at a distance of twenty feet—an acuity of vision quite sufficient to account for all the observed phenomena of vision in insects.

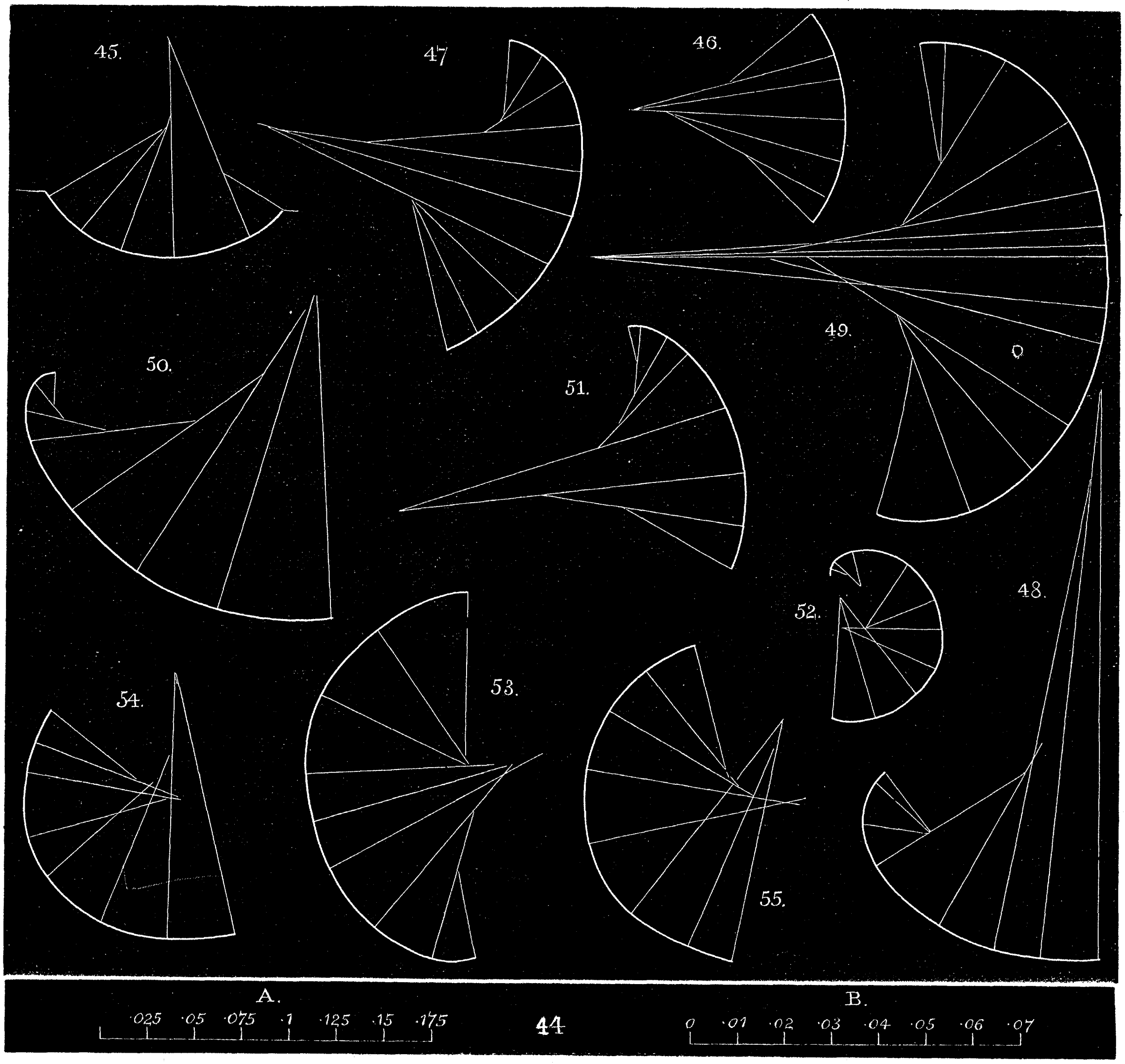
The method which I have adopted in calculating the acuity of vision is as follows:—

A magnified image of the entire cornea is thrown upon a sheet of paper by means of a camera lucida attached to the microscope. By using low powers and appropriate illumination, the error from distortion of the image can be reduced to a minimum. The profile of the various meridians was then sketched. By drawing tangents to the curve, the radii of curvature of different parts of the curve are readily found. The ratio of the diameter of the facets to these radii gives the sine of the angle subtended

* Wien Sitzungsberichte, 1876.

by each facet. It will be seen by the accompanying figures (figs. 45 to 55)* that the curves of the meridians of the compound cornea approach more or less closely to an epicycloid.

The average angles subtended by the facets in the region of most distinct vision in different insects are given in the following table, in which I have added the greatest angles subtended by the facets at the periphery, the diameter of the corneal facets and



the acuity of vision, both in the centre and at the periphery; according to SNELLEN'S system, the unit of vision being the power of perceiving an object at twenty feet, which has a diameter corresponding to an angle of five minutes: an angle of one minute being taken as the mean size of a visual perception in man. The signification of the fraction in the fourth and fifth columns is, that an object appears in the same detail to the insect as it does to man, when the distance of the object from the eye is

* See description of plates, p. 602.

measured by the denominator of fraction for man, and by the numerator for the insect. Thus a Dragon-fly would see an object 20 feet from its eye in the same detail that a man would perceive if it were seen at a distance of 160 feet.

	Least angle.	Greatest angle.	Diameter of facets.	Greatest sharpness of vision.	Least sharpness of vision.
Æschna grandis	8′	30′	$\frac{1}{750}$	$\frac{20}{160}$	$\frac{20}{600}$
Vespa rufa, worker	8′	85′	$\frac{1}{2000}$	$\frac{20}{160}$	$\frac{20}{1700}$
,, *vulgaris*, worker	8′	85′	$\frac{1}{2000}$	$\frac{20}{160}$	$\frac{20}{1700}$
Bombus muscorum, female..	8′	30′	$\frac{1}{1000}$	$\frac{20}{160}$	$\frac{20}{600}$
Tabanus bovinus, male	18′	12°	$\frac{1}{1000}$	$\frac{20}{360}$	$\frac{20}{14400}$
Syrphus, sp.	1°	4°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{4800}$
Musca vomitoria	1°	6°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{7200}$
Colias edusa..	1°	2°	$\frac{1}{1000}$	$\frac{20}{1200}$	$\frac{20}{2400}$
Noctua, sp.	2°	12°	$\frac{1}{1000}$	$\frac{20}{2400}$	$\frac{20}{14400}$
Tipula oleracea	4°	5°	$\frac{1}{1000}$	$\frac{20}{4800}$	$\frac{20}{6000}$

The region of the most distinct vision extends from the visual line or the perpendicular to the centre of the least curved portion of the cornea, to a distance of from twelve to fifteen degrees in the horizontal, and from twenty to thirty degrees in the vertical meridian; so that the region of the most distinct vision for each eye is approximately half an ellipse, with its long axis vertical in front. But when the two eyes are taken it is approximately a circle in front of the insect; the two fields do not overlap in this direction.

It will be seen that the acuity of vision, according to MÜLLER's theory, must vary directly with the radius of curvature of the surface of the cornea, and inversely as the diameter of the corneal facets. In many of the Diptera, as in *Tabanus*, the facets of the peripheral region of the cornea are three times the diameter of those in its centre.*

The size of the corneal facets varies in different insects from $\frac{1}{750}$th to $\frac{1}{2000}$th of an inch. They seem to bear a relation to the size of the insect, as the largest are found in the largest and the smallest in the smallest insects; but I have found none less than $\frac{1}{2000}$th of an inch, although I have examined the eyes of many Diptera, of a line or less in length. As the radii of curvature in very small insects are also very short, the vision of such insects is less distinct than that of larger insects; at least, the distance at which objects can be seen distinctly must be very small.

J. MÜLLER has pointed out that the flight of insects depends on their power of vision, and this will account for the distances which large insects sweep through when

* In the genus *Æschna* the facets of the upper third of the compound cornea are twice the diameter of those of the lower two-thirds; there is apparently no difference in the other part of the eye, except a proportionate increase in size.

disturbed, whilst the smaller species are confined, as a rule at least, to short flights, and remain hovering around a single branch or twig, unless carried away by currents of air.

The direction of the visual line is also a point of considerable importance. The fields of most acute vision are so combined in *Tabanus* that the visual line is directed forwards in the horizontal plane of the insect. In the pollen-feeding Diptera, and in most Lepidoptera, the visual lines diverge from each other to the extent of from fifteen to thirty degrees, and are directed downwards at an angle of thirty degrees, instead of lying in the horizontal plane.

In the Wasp the line of vision is directed forwards; in a species of *Noctua* it is directed almost directly downwards; and in the great Dragon-flies, where a very large field exists in which the visual power must be very great, the visual lines are directed forwards in the plane of the insect, diverging from each other to the extent of about thirty degrees.

In all the Coleoptera which I have examined, although the corneal facets are small, the radii of curvature of the cornea are very short; so that they cannot see objects distinctly in detail at any great distance. The same is true of the ants.

J. MÜLLER has stated that the vision will be the same for distant as for near objects, and this is true if measured by the angle under which the smallest object is seen as a distinct visual impression; but it will make a great difference in the details which can be perceived whether the object, as for instance another insect, subtends an angle of only one degree, or of from fifty to sixty degrees. By means of the fourth column in the table given above we may also estimate the distinctness with which near objects are seen by the species of insects in question. I have often been struck with the fact that the mimicry of the Diptera to the Hymenoptera is only sufficiently close when the insects are seen at a distance to be likely to afford any protection to the Diptera; but if the view of MÜLLER is the true one, and the acuity of vision is expressed in the above table, it would be sufficiently close to deceive the majority of other insects even at close quarters. I have frequently observed that Flies give place to both Wasps and the Syrphidæ which resemble them.

Under the supposition that MÜLLER'S theory is the true one, I was for a long time much puzzled to account for the lenticular facets of the cornea. That they are not essential to the vision of insects is apparent from the frequent absence of such facets both in insects and crustaceans, which give the strongest evidence of very considerable acuity of vision. My experiments, however, with glass rods seem to point to the explanation that these facets enable a larger pencil of rays to reach the inner extremity of the highly refractive parts of the eye; for instance, when a cone exists, the axial cone of light entering the rhabdion will be much larger with a lenticular facet than when no lens exists.

There are some very interesting facts with regard to the distribution of lenticular facets in the Insecta. Thus some Noctuids have practically no lenticular facet, or, at least, a very feeble one, whilst others have a very convex lens. The same is true in the Diurnal Lepidoptera. In Hydrometra the corneal facets are composed of two parts of different refractive powers. The outer portion of the cornea is more strongly refractive than the inner portion ; it is also more convex on its inner surface than the inner surface of the corneal facet, so that it presents the condition of a very powerful bi-convex lens in apposition with a second lens, which is concavo-convex, the two fitted together like an achromatic object glass. In *Dyticus* there is also a remarkable arrangement: the corneal facets have a scleral cone adherent to their inner surfaces. I have at present examined only dried specimens, but hope to continue the investigation.

The region of binocular vision.—In most insects the field of vision in the two eyes has a common portion in the peripheral region in the vicinity of the mouth ; in this region the radius of curvature of the cornea is very short. It is, therefore, only adapted for the acute vision of very near objects. It is chiefly developed in predaceous insects. It probably serves the insect in judging of the distance of objects from the mouth.

J. MÜLLER, in his classical work 'On the Comparative Physiology of Vision,' states that no portion of the compound eye in any of the insects he examined corresponded in the direction of the axis of the facets with the eye of the opposite side ; but he does not appear to have examined the eyes with sufficient minuteness to have been able to detect the slight overlapping of the two fields which I have described.

Description of the Plates.

PLATE 52.

Fig. 1. The ocellus of *Eristalis.*

Fig. 1*a.* One of the rod cells of the same.

Fig. 2. A vertical section of a portion of the compound eye of the common Crane-fly.

Fig. 3. A vertical section of a portion of the chamber of the compound eye of an immature Crane-fly, showing the rod cells and the facellus.

Fig. 3*a.* One of the facets of the same eye seen from without, showing the extremities of the rod cells beneath.

Fig. 4. A transverse section through the middle of the facellus.

Fig. 4*a.* A section through the lower extremity of the facellus.

Fig. 5. The stemon and nervous retina of the same.

Fig. 6. A vertical section of a portion of the compound eye of the female of *Formica rufa* (from a specimen preserved in spirit).

Fig. 7. The rod cells, facellus, and stemon of the eye of the Wasp.

Fig. 7*a*. A transverse section immediately below the cornea of the eye of *Formica rufa.*
Fig. 8. Transverse section through the rod cells of the eye of the Wasp.
Fig. 8*a*. A transverse section through the stemonata of the eye of *F. rufa.*
(Figs. 9 to 13, inclusive, are in Plate 53.)
Fig. 14. The chamber from the eye of the Blowfly.
Fig. 15. The rhabdia of the same.
Fig. 15*a*. A portion of one of the rhabdia of the same.
Fig. 16. Transverse sections through the rhabdia of the same.
a and *b*. Compound rhabdia.
c and *d*. Simple rhabdia.
Fig. 17. The inner extremities of the rhabdia and the nuclear masses of pigment seen from the retinal surface of the rhabdia.
Fig. 18. The rhabdia and chambers of *Tabanus*, from a dried insect.
Fig. 19. A portion of two rhabdia from the same.
Fig. 20. The chambers of the eye of *Tabanus.*

The details in all the figures are drawn with a Nachet $\frac{1}{16}$th immersion.

PLATE 53.

Fig. 9. Section through one of the elements of the compound eye of *Eristalis.*
Fig. 9*a*. Four facets of the cornea, showing SEMPER's nuclei.
Fig. 10. Details of the compound eye of *Eristalis.*
a. Transverse section through the tetrasome.
b. Transverse section immediately below the tetrasome.
c. Section through the lower end of one of the rhabdia from near the periphery of the eye.
d. Section just above the pigment cells of the rhabdion.
e. Section just below the pigment cells.
f, *g*, and *i*. Sections through the rhabdia.
h. Lower end of one of the rhabdia, with six pigmented nuclei from near the periphery of the eye.
k. Section through a facellus from the facelloid layer of the retina.
l. Lower end of a compound rhabdion from near the outer edge of the eye.
Fig. 11. A portion of one of the triquetrous rhabdia.
Fig. 12. Lower end of the rhabdia to show their connexion with the nervous retina.
Fig. 13. The nervous retina of *Eristalis.*
Fig. 21. Two chambers from the eye of *Agrion virgo.*
Fig. 21*a*. Four facets from the same eye seen from the outer surface.
Fig. 22. A portion of one of the rhabdia.

Fig. 23. Transverse sections of the rhabdia.

a. Section throughout the outer extremity of a rhabdion.

b and *c*. Through the middle of the rhabdion.

Fig. 24. The ganglionic retina of the same insect.

(For figs. 25, 26, and 28, see Plate 54.)

Fig. 27. The tetrasome of *Acridium* seen from the surface of the cornea.

Fig. 29. The tetrasome of *Vanessa atalanta*.

PLATE 54.

Fig. 25. The chamber of the eye of the nymph of *Acridium*.

Fig. 26. The same, from an imago of the same.

Fig. 28. Two chambers from the eye of *Vanessa atalanta*.

Fig. 30. Four chambers seen from the surface of the cornea. For the sake of clearness, all the parts are only represented in one of the segments.

Fig. 31. The rhabdion of the same.

Fig. 32. Transverse section through some of the facelli of the same eye.

Fig. 33. The ganglionic retina.

Fig. 34. Vertical section through one of the facelli of the same eye.

Fig. 35. The chamber of the eye of *Colias*.

Fig. 36. A vertical section of a portion of the eye of a Hawk Moth from the pupa.

Fig. 36*a*. One of the cones of the same.

Fig. 37. One of the cones of the compound eye of a Noctuid.

Fig. 38. A vertical section of a portion of the eye of another species of Noctuid.

Fig. 39. A similar portion of the eye of a third species of Noctuid.

Fig. 40. A transverse section through the compound part of the rhabdion, from the same insect as the last preparation.

Fig. 41. A transverse section through sheaths of the rhabdia of a Noctuid Moth.

Fig. 42. The cones seen from the cornea, from the same specimen as fig. 38.

Fig. 43. An outline of the eye of *Vespa* to show the direction in which the principal meridians were drawn.

DIAGRAM. (Page 596.)

Fig. 44. Scales of fractions of an inch to which the succeeding diagrams are drawn.

(For figs. 44 to 54, see page 596.)

Fig. 45. The principal horizontal section of the cornea of *Vespa* (scale A).

Fig. 46. The vertical meridian of the same eye (scale A).

Fig. 47. The curvature of the principal vertical meridian of a species of *Syrphus* (scale B).

Fig. 48. The curvature of the principal horizontal meridian of *Æschna grandis* (scale A).

Fig. 49. The principal vertical meridian of the same (scale A).

Fig. 50. The horizontal meridian of *Tabanus bovinus* (scale A).

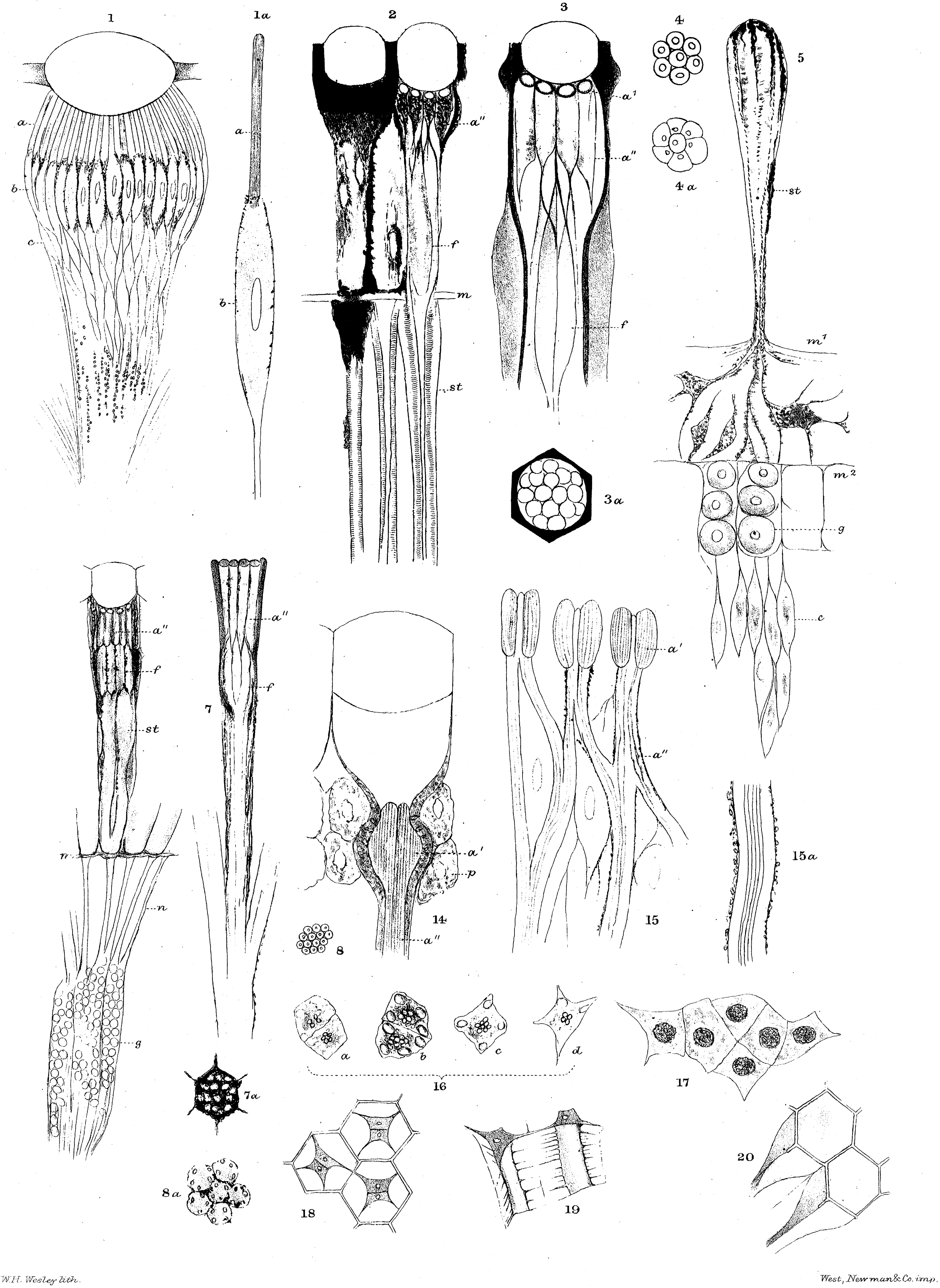
Fig. 51. The principal vertical meridian of *Musca vomitoria* (scale B).

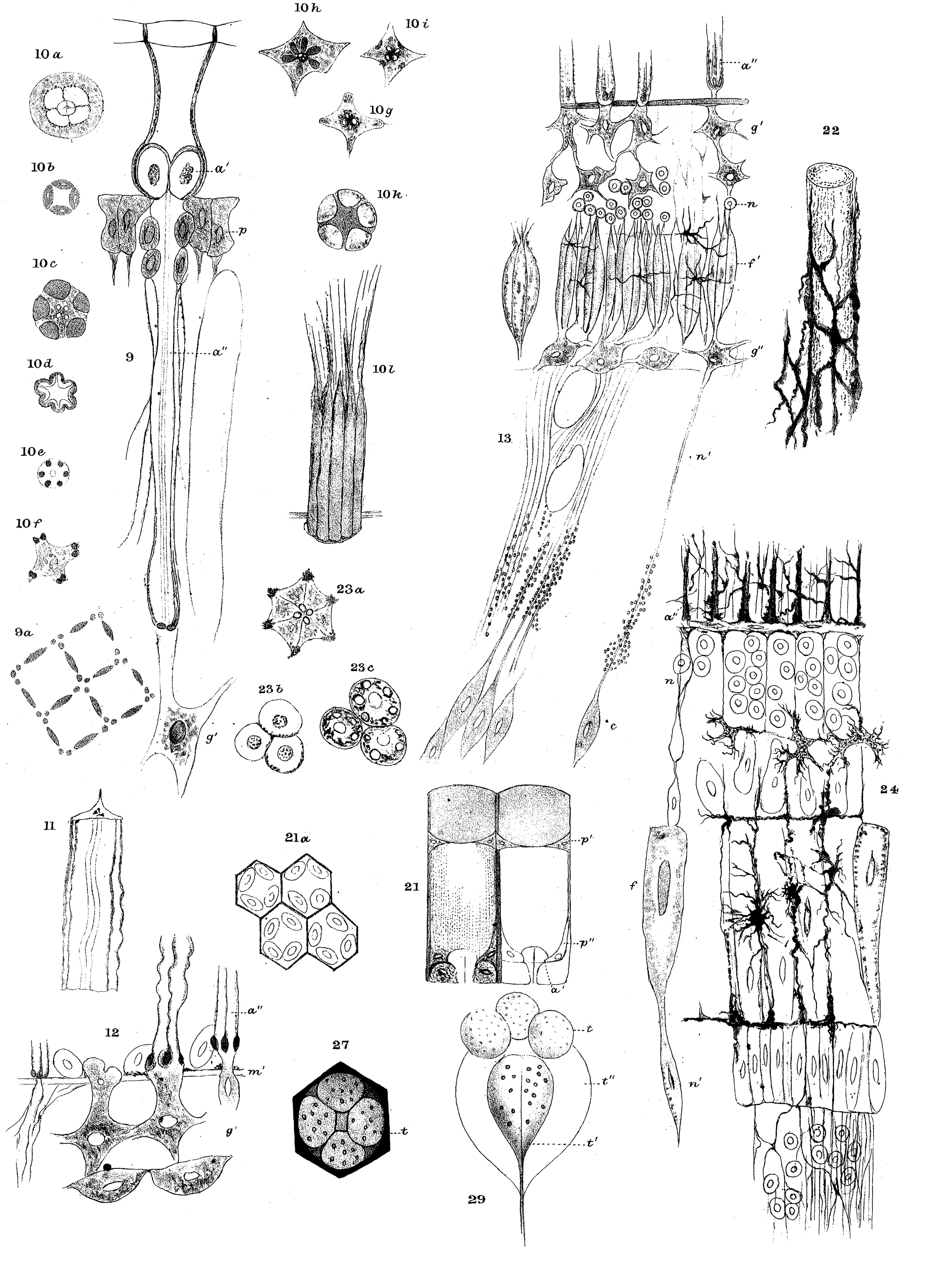
Fig. 52. The vertical meridian of the eye of a Noctuid Moth (scale B).

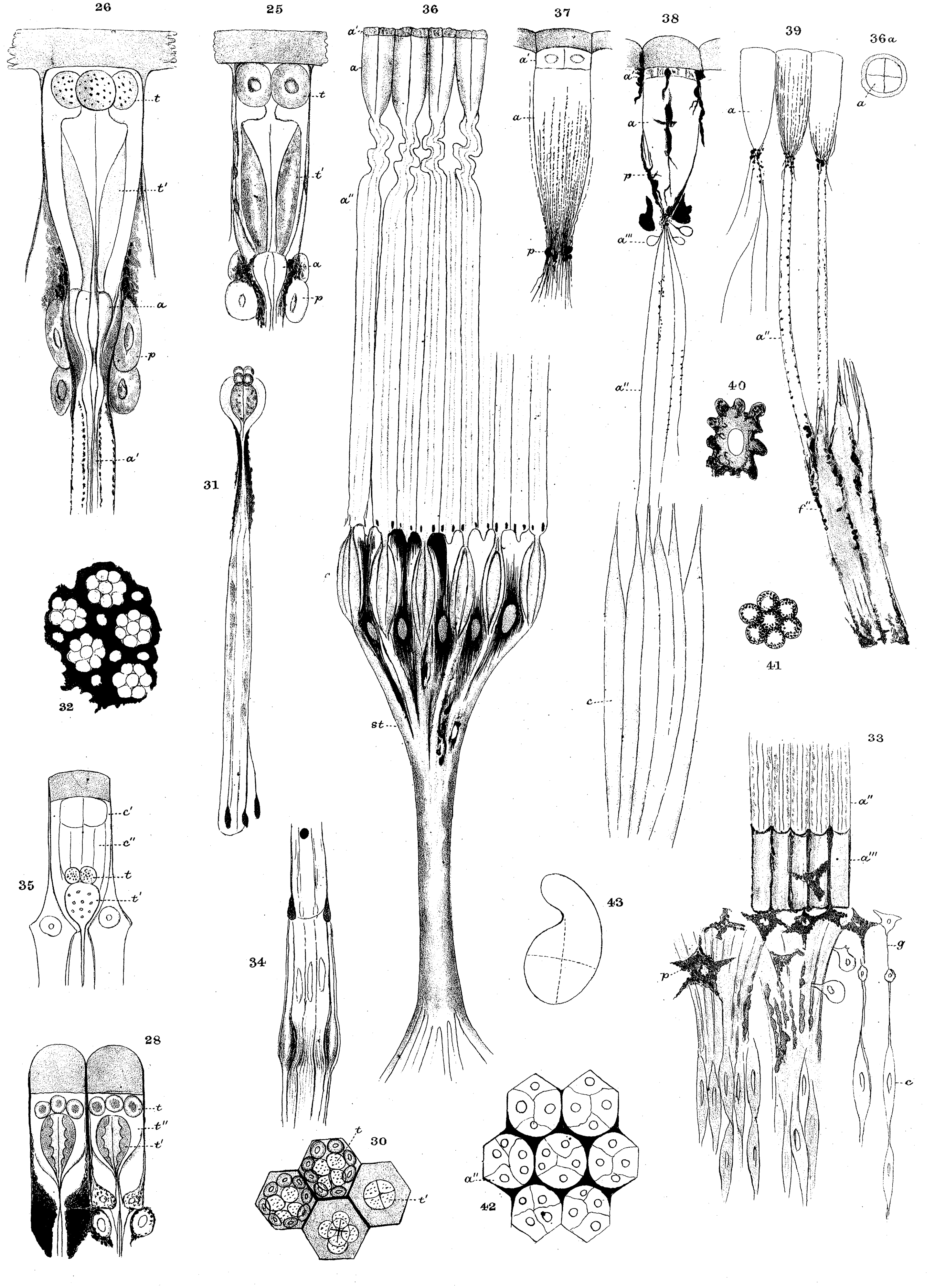
Fig. 53. The principal vertical meridian of the eye of *Colias edusa* (scale B).

Fig. 54. The same, a meridian 30° from the last (scale B).

Fig. 55. The same, a meridian at right angles to the last (scale B).


1
a
b
c
1a
a
b
2
a''
f
m
st
3
a'
a''
f
4
4 a
5
st
m'
m2
g
c
3a
a''
f
st
m
n
g
7
a''
f
14
a'
p
a''
8
15
a'
a''
15a
16
a
b
c
d
17
7a
8a
18
19
20


10 a
10 b
10 c
10 d
10 e
10 f
9
9 a
a'
p
a''
g'
10 h
10 i
10 g
10 k
10 l
23 a
23 b
23 c
13
g'
n
f'
g''
n'
c
22
a''
24
11
21 a
21
p'
p''
a'
12
m'
27
t
t''
t'
29
f


26
25
36
37
38
39
36 a
31
32
40
41
33
35
34
43
28
30
42
t
t'
t''
a
a'
a''
a'''
p
c
c'
c''
st
f''
g