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HISTOLOGY AND DEVELOPMENT OF THE DIVIDED EYES OF CERTAIN INSECTS.

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EXNER, 1891, Zimmer, 1897, and Kellogg, 1898, 1900, and 1903, have discussed the divided-eye condition of certain crustaceans and insects. It is the purpose of the following paper:

1. To describe the histological structure of the divided compound eyes of *Sympetrum corrupta*, *Anax junius*, *Bibio hirtus*, two species of Blepharoceridæ and two species of *Callibætis*.

2. To describe the development of the large-facetted area of the eye in *Callibætis* and *Sympetrum corrupta*.

3. To refer briefly to the significance of the divided-eye condition in these eyes.

This investigation was made in the Entomological Laboratory of Stanford University, under the direction of Prof. V. L. Kellogg. I wish here to thank Professor Kellogg, Mr. Doan and Miss McCracken for help in the laboratory; also Professor Aldrich, Dr. Needham and Mr. Grinnell for identifying some of the material used.

SYMPETRUM CORRUPTA Hagen.

The compound eyes of *Sympetrum corrupta*, as shown in Fig. 1, Plate XXIV, are divided by a curved line into almost equal upper and lower parts. The lower half of the eye is dark and a good hand lens shows it to be made up of very small facets. The upper half is lighter in color and made up of larger facets. Longitudinal sections of the ommatidia of both these parts of the eye may be obtained by making vertical cross-sections, or by making longitudinal sagittal sections of the head. Fig. 2 shows a vertical section passing through both the upper and the lower portions of the eye. Most of the eye elements are cut longitudinally. A few in the region *a*, of the upper part of the eye are represented in diagonal cross-section. A glance at the figure makes clear the deeply pigmented condition of the narrow eye elements of the lower half as contrasted with the less pigmented larger elements of the upper half of the eye. There is no gradual transition in the pigmentation or in the size of the eye elements. The line of division is as sharp within the eye as it appears in the outside facet view. No septum marks the division; but with the first larger ommatidial element, passing toward the upper part of the eye, the deep black iris pigment stops and a brownish less dense iris pigment begins. This is true also of the deeper seated pigments, but these are a little darker in color in the large element half of the eye than in the iris pigment in the same part. Figs. 3 and 4 show some of the details of structure of the upper and lower parts of the same eye. The corneal region is made up of hexagonal lens-like segments each of which may be called a corneal lens. In vertical section each lens is seen to consist of a thin cuticular portion and a thicker stratified layer just beneath. The cuticular portion takes and retains nuclear stains well. The under portion takes stains readily enough but gives them up easily. No hypodermal cells or nuclei have been observed in the eye, but the bases of the pseudocones lie close to the under portion of the lens. The cells which compose these pseudocones have lost their identity entirely in the lower portions, and nearly so in the upper, outer, larger portion of the cones. However, in the extreme upper ends, the cone cells have each secreted a denser curved plate-like body within itself, and this stains deeply. Four of these may be found in each pseudocone. Two are shown in the longitudinal sections at *cn*. Each plate appears to surround a cell nucleus. In the case of the pseudocones of the small ommatidial elements, cross-sections made just below the little plates mentioned show four cells as represented in

Fig. 3, *B*. Two of these cells are always larger than the other two. Two of the plates of the pseudocones are always larger when four are seen — sometimes only 2 can be found. The pseudocones of the large ommatidia are wider, longer and farther apart than those of the small ommatidia. Both have relatively the same shape. The inner portion of each pseudocone tapers nearly but not quite to a point. Each inner end is really truncate and appears to have a funnel-like opening. Extending along the line of the longitudinal axis of the pseudocone and beginning immediately beneath the truncate cone tip is the retinula. This has a darker rhabdome portion along the axis from the tip of the pseudocone to the basement membrane. The axis itself, however, is occupied by a very narrow light band. Often, if the sections are jammed a little in the cutting, the rhabdome portion takes a wavy form as shown in the fragment at *w* (Fig. 4, *A*). The retinulæ of the large ommatidia are wider, but no longer than those of the small ommatidia.

Immediately beneath the basement membrane, in all parts of the eye is a network of tracheal vessels, 2 of which are shown in cross-section at *tr* (Figs. 3, *A*, and 4, *A*). Under the tracheal network is a narrow layer of retinular-like bodies *rb* (Figs. 3 and 4, *A*). These bodies have their long axes parallel with each other, but not always exactly parallel to the retinular axes above them. Some sections show a definite fibrous or continuous cell connection between the ends of the retinula at the basement membrane *bm*, and the upper outer ends of these retinular-like bodies. These connecting strands are always narrower than either the retinula or the retinular-like bodies, and they curve around the tracheæ, often, in order to make the connection. It seemed impossible to demonstrate the presence of retinular nuclei satisfactorily in old adult eyes used, but they were easily shown at *rn* (Fig. 4, *A*), in the eye of a young insect dissected from an old nymph case when the adult was just ready to issue.

Here and there along the upper part of some cells of the retinular-like bodies large nuclei have been found (*n*, Figs. 3 and 4, *A*). These nuclei appear larger than the ordinary pigment cell nuclei. Whether they have any special significance has not been determined. Cross-sections of the retinular-like bodies under the large ommatidia are shown in Fig. 4, *B*. Regularly, they appear as shown, with 4 cells — one large, 2 smaller and 1 very small cell. Cross-sections of the corresponding retinula above show that the separate cells there have almost lost their identity in the adult eyes; but in the very young teneral adult 4 nucleated cells may be seen (Fig. 4, *C*) in cross-section. From the lower part of the retinular-like bodies extend branching tree-like nerve fibers which break up into brushes of fibrils at their inner ends.

The pigment of the region of the small ommatidia may be described under 4 heads:

1. That grouped in dense black masses around the pseudocones and already named the iris pigment. It is contained in 2 kinds of cells called by Grenacher, 1879, primary and secondary pigment cells. The secondary cells are long, narrow and closely packed around and among the pseudocones — their axes lying parallel with the cone axes. Around cross-sections of the upper parts of the cones 20 to 22 of these pigment cells may be counted in a circle touching the outer boundary of the cone (Fig. 3, *B*, *sip*). In the sections near the inner tapering tip of the cone as few as 14 pigment cells have been counted touching the cone. Below that the separate cells could not be counted, but they are packed all the way between the different pseudocones, being densest on the middle plane of the cone. There are 2 chief pigment cells for each eye element. They are short and thin and the 2 encircle the cone tip (Figs. 3 and 4, *A*).

2. Pigment occupies the retinula and the cells between the retinula from the apex of the cones to the basement membrane. Beginning near the distal ends of the retinula this pigment becomes denser and denser toward the basement membrane until a plane (*ee*, Fig. 3, *A*), is reached a little below the middle of the retinula. From this plane to the basement membrane the pigment is again less dense.

3. A band of dense black pigment lines the basement membrane and on the inner side of this membrane, extends down to the distal ends of the retinular-like bodies. It is densest immediately beneath the basement membrane, around the trachea and

in a thin band, *i*, which marks its lower boundary along the distal ends of the retinular-like bodies.

4. A black pigment similar to that along the retinula surrounds the retinular-like bodies, and ends at the proximal ends of these bodies in a narrow densely black band of pigment, *gp* (Figs. 3 and 4, *A*). This in *Sicyonia sculpa*, has been named the pigment or tapetum sheath of the optic ganglion by Exner, 1891.

The same description of pigment holds for the large ommatidial part of the eye except that the iris pigment and retinular pigment in this case are brownish yellow and everywhere in this part of the eye the pigment is very much less dense than in the small ommatidial region.

ANAX JUNIUS Drury.

The facets of the compound eyes of the male of *Anax junius* are not all of the same size. Facets may be found that differ as much in size as those of the different areas on the eye of *Sympetrum*, but no line divides the eye of *Anax* into 2 regions. In this case the larger facets are found on the upper and inner surfaces of the eyes, and the smaller facets on the outer lower margins. The 2 sizes grade into each other. It was not until sections were made of the eye that this condition was noticed. Fig. 12 was made from a cross-section of the head of a male *Anax*, cut in a plane passing through the ocellus and perpendicular to the facet area of the compound eye. The figure shows clearly this gradation of the large facets on the upper inner part of the eye into the smaller ones at the outer margin. As is shown also, along with this gradation in the size of facets, the elements of the ommatidia pass through a like gradation in size and length. Moreover, a similar but reverse condition holds for the pigmentation in this eye. Around the smaller shorter elements at the outer margin of the eye the pigment is densest and occupies the whole length of the retinulæ. Passing toward the inner part of the eye, the pigment becomes less and less dense around the proximal ends of the retinulæ until in the region of the largest ommatidia almost no pigment is present except the iris pigment. Other than this difference in size and pigmentation, the large and small ommatidia are very similar as may be seen in Figs.

13, *A*, and 14, *A*. Beneath the corneal lenses and lying above the distal ends of the pseudocones is a distinct hypodermal layer. In longitudinal section, two apparent nuclei are present above each pseudocone, *sn* (Figs. 13 and 14, *A*). The pseudocone itself has a structure similar to that of *Sympetrium*, its upper part showing still the boundaries of 4 cells which may be seen in cross-section (Fig. 13, *C*).

Each retinula is made up of 4 retinular cells which enclose a single rod-like rhabdome, *rb* (Figs. 13, *A* and *B*, and Figs. 14, *A* and *B*). The retinular cells of the ommatidia from the 2 extreme parts of the eye described vary, somewhat in shape (as seen in Figs. 13, *B*, and 14, *B*) but there are always the 4 cells present, each with its nucleus (Fig. 13, *B*). Extending up between the different retinulæ and lying parallel with them are many open spaces or lumina (Fig. 13, *A*, *l*). The smaller ends of these extend even between the distal parts of the pseudocones and their surrounding pigment cells (Fig. 13, *C*, *l*). The iris pigment of this eye occupies cells of 2 types called by Grenacher and others the primary or chief pigment cells and the secondary pigment cells. Two primary pigment cells surround the small proximal end of each pseudocone (Figs. 13 and 14, *A*, *cip*). These cells are shown as they appear in cross-section in Fig. 13, *D*, *cp*. The nuclei of these cells have not been satisfactorily seen although the nuclei of the retinular cells and secondary pigment cells in the same sections were deeply stained and easily seen. Eight to 10 pigment cells have been counted around each pseudocone. They are longer and more slender than the primary cells around which they lie, and they extend down a little between the distal ends of the retinulæ (Figs. 13 and 14 *A*, *nsp*). As has already been said, the pigmentation of the smaller outer elements of the eye occupies the whole length of the retinulæ. This pigment lies in the retinular cells themselves, and it is densest always in the distal half of the cells.

BIBIO HIRTUS Goef.

The compound eyes of the male *Bibio* are much larger than those of the female. They nearly touch along the narrow front and occupy almost the entire head. The whole facet area is thickly covered with slender hairs[1] and the remarkable double character of the eyes may be easily overlooked.

Indeed, it is only upon careful observation that the densely black, small, facetted area is seen at all. If the head of the fly is tilted back by lifting up the proboscis, a hand lens will show the narrow black small facetted area on the extreme ventral surface of the compound eye. This area is scarcely one sixth that of the entire eye and is separated from the large facetted upper surface by a narrow groove or offset. Fig. 11 shows the position of the small facetted part of the eye. Fig. 8, perhaps, shows better the relative extent of the 2 kinds of elements as seen in longitudinal sagittal section. As shown in this Fig. 8, the elements beneath the small facetted region are little more than half the length of those under the large facets. Moreover, the part occupied with small elements is densely pigmented. The rest of the eye has but little pigment.

The elements of a large ommatidia consist of a thin cuticular hexagonal facet, a pseudocone, a retinula, and iris pigment cells surrounding the pseudocone. The cells of a pseudocone cannot be distinguished from each other in the outer large part of the cone. The lower truncate or slightly rounded apex of the cone is a little denser than its upper part and this denser portion stains more readily. Here the 4 cells making up the cone can be distinguished, each having its nucleus (Figs. 9 and 10, *cn*, and Fig. 9, *B*). Cross-sections of the distal ends of 3 neighboring retinulæ are shown in Fig. 9, *C*. Each retinula is made up of 6 cells arranged in a circle around a seventh cell in the center. The inner borders of each of the 6 cells has a rounded deeply stained rhabdomere (as this part of the eye was named by Grenacher, 1879). The rhabdomere of the seventh cell occupies the axis of the retinula. At their distal ends the 6 retinular cells overlap entirely the rounded denser apex of the pseudocone, *d* (Figs. 9, *A*, and 10). The seventh cell, together with its rhabdomere and those of the other 6 cells, stop snugly against the inner end of the pseudocone. Near the middle part

[1] Whether these apparent tactile hairs, which cover the eye of *Bibio* so densely and are found on the eye of *Blephorocera* less abundantly, are really supplied with tactile sense organs has not been determined by me.

of the retinula this seventh cell, which is entirely surrounded at its distal end, is found squeezed out between the other 6 retinular cells and is not here completely surrounded by them (Fig. 9, *E*). This condition holds for the retinula for its entire proximal half. It is true also that this seventh cell crops out in every case on the same side of the retinula, namely, on that side of the retinula turned toward the inner ventral angle of the eye. Fig. 9, *D*, shows 3 adjacent retinulæ in cross-section in the region of the nuclei. These nuclei are long-elliptical in shape (Fig. 9, *A*, *rn*), and in cross-section they are not all the same size, since some are cut near the middle and some near their ends. In the cross-section of every retinula, however, the nucleus of the narrow seventh cell may be found near its outer margin (Fig. 9, *D*, *7n*). The rhabdomeres are all smaller at the proximal end of the retinula, but they are always 7 in number, the odd one occupying the axial position at the inner part of the narrow seventh cell. These facts, taken with that of the constant presence of the seventh nucleus, make it certain that this peculiar seventh structure is truly a retinular cell whose distal end is entirely surrounded by the corresponding ends of its 6 companions. The proximal ends of the retinulæ are bounded by a very thin basement membrane, *bm* (Figs. 9, *A*, and 10). A little beneath this membrane spreads a somewhat thicker granular tapetum, *tp* (Figs. 9 and 10), and immediately under this is a network of tracheæ, *tr*. Leading from the inner proximal end of each retinula through the basement membrane, the tapetum, and between the tracheæ is a narrow bundle of nerve fibers, which are soon lost in a fine granular layer, *gr* (Figs. 9, *A*, and 10), just within the trachial network.

The iris pigment of the large element part of the eye is comparatively slight. It is contained in narrow pigment cells, *nsp* (Figs. 9 and 10), which surround the pseudocones and extend a little way down between the retinulæ. Fig. 9, *C*, *sip* shows the arrangement of these cells between the retinulæ. The proximal three fourths of the retinulæ have no pigment cells around them at all and the retinulæ themselves touch each other (Fig. 9, *D*).

The conditions described above also hold for the small eye elements with the following exceptions. The cuticular facets of this portion of the eye are much denser than those above the large elements. The iris pigment is black and extremely dense. A heavy black pigment occupies the retinular cells throughout their entire length. Drawing 10 was made from a section that had been depigmented with conc. nitric acid and absolute alcohol, equal parts. The tapetum and the basement membrane in this part of the eye are always a little farther apart than in the large element region. Under the trachea and between the nerve strands that lead down from the retinulæ of both the large and the small elements are numerous large round or oval nuclei which stain deeply (*gn*, Figs. 9 and 10, *A*). No pigment is present around these nuclei. It might be added here that cross-sections of the retinulæ of the small ommatidia did not show the number of retinular cells present so clearly as those cut across the large ommatidia. Judging from the number of retinular nuclei however, the number of retinular cells is the same in the retinulæ of both regions of the eye.

[1]BLEPHAROCERA CAPITATA Loew.

Kellogg, 1903, has called attention to the fact that both males and females of the Blepharoceridæ have divided compound eyes. In all the genera described by Kellogg the large facetted area of the eye is dorsal, and the small facetted deeply pigmented area of the eye is lateral. Moreover, the dorsal area of the female eye is greater than that of the male. Males and females of species representing 2 genera (*Blepharocera capitata* and *Bibiocephala elegantulus*) were studied by me. The histological structure of the eye elements in the 2 genera and in both sexes is practically the same. The description and drawings given here are taken from *Blepharocera capitata*. Fig. 30 is a microphotograph showing the optic ganglion, as well as the dorsal and the lateral eyes of the right side of the head of this species. It will be convenient hereafter to speak of the two areas as the dorsal and the lateral eyes since they are separated from each other by a narrow but distinct groove and the outer lobes of the

[1] I am glad to make reference to a recent preliminary note on the "Morphology and Development of the Divided Eyes of *Blepharocerca tenuipes*" by Dr. Wm. A. Riley, in *Science*, Sept. 7, 1906.

optic ganglion beneath each area are distinct. The corneal lenses over the greater part of the dorsal eye have been torn from this section. The remaining 2 entire elements, however, show the ommatidia in this dorsal eye to be about two and a half times the length of those in the lateral eye. The lens and the pseudocone of a dorsal ommatidia are continuous. That is, the inner surface of the corneal lens is not noticeably separated from its adjoining cone beneath. This is easily seen in microphotograph 29 and Fig. 15. The rounded apex of each of the pseudocones is denser than the rest of the cone and stains readily. Cross-sections through this denser apex show the cone to be made of 4 cells and the nucleus of each cell is found in this denser part (Fig. 15, *A*). In the outer larger part of the cone the cell walls cannot be distinguished. Surrounding the tip of each one are 2 very thin primary iris pigment cells (Fig. 15, *A*, *cip*). Outside of these, sheathing the distal part of each cone and extending down between the retinulæ are 22 to 24 slender secondary pigment cells (Fig. *A*, *sip*, and Fig. 29, *sip*). A retinula in this eye is composed of 7 cells — 6 entirely surrounding the seventh for its entire length. The rhabdomere of each cell is distinct (Fig. 15, *C*, *rb*). The distal ends of the retinular cells abut closely against the rounded cone tip and in their extreme proximal ends just above the basement membrane, lie the 7 large retinular nuclei (Fig. 15, *A*, *rn*). A definite bundle of nerve fibers leads from the base of each retinula through the basement membrane (Figs. 15, *A* and 29, *nf*).

The number and position of the cells in the ommatidia of the lateral eye of this fly is the same as that just described for the dorsal eye. The corneal lenses of the lateral eye are more distinctly formed and the retinular cells as well as the iris pigment cells (primary and secondary) are densely packed with pigment. In the dorsal eye the pigmentation in the iris is very slight and it is absent in the retinular cells of this eye.

CALLIBÆTIS HAGENI Etn.

Several references have already been made by different investigators to the condition of the compound eyes of certain mayflies (Pictet, 1845; Ciaccio, 1880; Carriere, 1893; and

Zimmer, 1897). The large facetted dorsal eyes have been called turban eyes and the smaller deeply pigmented eyes, the lateral eyes. The females have only the small lateral pigmented eyes. Zimmer, 1897, has given the histological structure of the eyes of 7 genera of mayflies according to Pictet's classification and he discussed also the physiological significance of the turban eyes of these insects.

The structure of the eyes of *Callibætis hageni* differs in only a few points from that given by Zimmer for *Cloe fuscata* Pict. It will be well, however, to describe briefly the structure of the eye in the adult male of *Callibætis hageni* before taking up the development of the turban eye in that species. Microphotograph 24 (a cross-section through the head) shows the relative size, position, pigmentation and the general structure of the right turban and lateral eyes. The large and small eye elements are entirely separated here by a deep, rather wide, groove. A single partly divided optic ganglion lies beneath the right turban and lateral eyes and a similar ganglion beneath the left eye *opg* in Figs. 23, 25 and 26. Drawings in Fig. 16 show more clearly the structure of 2 entire elements of the turban eye. The light-gathering or dioptric apparatus consists of a corneal lens, 16 *Ac*, a cone, *Aco*, and a hypodermal space between the lens and the cone, 16 *Ahs*. The cornea is made up of rather distinct convex lenses, *Ac*, which are continuous with each other. The outer third of each of these lenses appears to be denser than the inner two thirds. The cone is composed of 4 crystaline bodies so closely associated along their inner faces that they appear in all except cross-sections as one solid cone body with its slightly convex base facing the cornea. This is the *eucone* type of Grenacher, 1879. The outer faces of each crystaline body are surrounded by the less dense protoplasm of the mother cone cell and in this protoplasm just distal to the base of the cone are the cone cell nuclei (Fig. 16, *A*, *cn*). The cross-section made just distal to the cone base *B*, shows the 4 cone cells and their nuclei. The hypodermal space contains no nuclei, and it is filled by transparent fluid only. Zimmer demonstrated 2 nuclei in this space for *Cloe*. He did not figure the nuclei in this space for the eye of *Bætis cerea* Pict., or for that of *Chiro-*

tonetes ignotus Walk., but speaks of the space nevertheless as being formed by 2 hypodermal cells.

Closely surrounding the entire length of the cone cells and the hypodermal space are 20 to 22 secondary pigment cells (Figs. 16, *A*, *nsp* and *B*, *sip*). No primary pigment cells are present. The distal ends of the secondary pigment cells touch the cornea and their proximal ends are in contact with the outer or distal retinula (Fig. 16, *A*, *drn*). It is proper to speak of a distal retinula in this eye because there is also an inner or proximal retinula *prn* in each ommatidia — the 2 retinular parts being connected by a very delicate strand (*rs*, Fig. 16, *A*). Both proximal and distal retinulæ are composed of 7 retinular cells. Fig. 16, *C*, shows the 7 short distal retinular cells and their nuclei. These cells surround the tip of the cone rosette fashion. The proximal retinula is of about the same length as the connecting strand. Fig. 16, *D*, shows the 7 nucleated cells of this part in cross-section, and Fig. 16, *E*, is a similar section near the middle part of a proximal retinula. The rhabdome in its cross-section here is seen to be a 7-pointed star within a circle which bears on its circumference 7-knobbed projections, *w*, radiating along the same lines as the points of the star and lying between the boundaries of the retinular cells. The knobbed parts, *w*, are the *secondary rods* of Zimmer, 1897. This large surfaced rhabdome terminates a little short of the outer end of the proximal retinula in a single blunt rod tip as shown in Fig. 16, *D*. The outer end of the retinula therefore appears filled with transparent liquid. Zimmer has described these transparent ends in *Cloe* as "bladder trachea," and he figures no nuclei in them. My sections of the turban eye of *Callibætis* show the 7 nuclear structures present always, as represented in Fig. 16, *D*. The inner faces of the distal retinular cells bear an extremely thin rhabdome plate next to the tip of the cone (Fig. 16, *C*, *drb*). Near the distal ends of the proximal retinula the connecting strand, *rs*, breaks up, Fig. 16, *A*, into smaller strands which seem to be continuous with the 7 secondary rods, *w* of Fig. 16, *E*. The connecting rods may be seen in the photograph no. 27. The space around the rods, between the distal and proximal retinulæ, appears to be filled with an almost transparent liquid —

tiny pigment granules being present in some sections. But these may have been carried there by the razor. Upon the basement membrane are short pigment cells which are sometimes above the membrane between the proximal ends of the retinulæ; sometimes beneath the membrane between the nerve fibers, *nf*; and sometimes partly above, partly beneath the membrane. A second delicate membrane *k* marks the lower limit of migration of this pigment.

Fig. 17, *A* and *B*, show the structure of two ommatidiæ in the lateral pigmented eye of *Callabætis*. One of the elements is represented in its normal pigmented condition, the other depigmented so that the position of nuclei may be seen. The corneal lenses in this eye are thin as compared with the turban eye and their inner faces fit snugly upon the distal bases of the cones. These cones are not as dense as those of the large elements just described. They are 4 in number, however, and appear to have the same density throughout. The cone cell nuclei *cn*, are found in the extreme distal base of the cone. In depigmented sections the nucleated distal ends of the retinular cells may be seen touching the tip of the cone. There are 7 of these retinular cells surrounding the rod-like rhabdome as represented in Fig. 17, *B*. No primary iris pigment cells are present, and there are but half the number of secondary pigment cells found in the turban eye. The 11 cells (Fig. 17, *B*), which are present, however, are densely pigmented, and they overlap the cones and the upper retinulæ. The retinular cells are deeply pigmented through their entire length. Just beneath the basement membrane is a narrow almost transparent granular tapetum and under that an irregular broader band of pigment. So far, this pigment has not been observed above the basement membrane in the lateral eye. Nerve fibers *nf* (Fig. 17, *A*) lead from the inner ends of the retinula through the tapetum and the underlying pigment.

Another species of *Callibætis* (probably *californica*) was studied in connection with *hageni*. The latter is the larger of the 2 species but the eye structure of the male of this smaller form differs from that just described for *hageni* in but two particulars that are worth attention:

1. The cornea of the turban eye of the smaller species is thinner and its lenses less convex than those in *C. hageni*.

2. The retinular connecting strands in the eye of the smaller species are about one and one third times longer than the proximal retinulæ. That is, the strands in this species are relatively a third longer than they are in the eye of *C. hageni*.

DEVELOPMENT OF THE LARGE FACETTED EYE AREA (TURBAN EYE) IN CALLIBÆTIS Etn., AND IN SYMPETRUM CORRUPTA Hagen.

As is well known, the young of dragonflies and mayflies pass through incomplete metamorphoses in their post-embryonic development, and the young of both live in fresh water. Young nymphs of both species of *Callibætis* and of *S. corrupta* were collected from still or slowly running water near Stanford University in March and reared to the adult stage in the laboratory. In this way material was obtained representing different stages in the development of the large facetted-eye areas. Carriere, 1886, first briefly called attention to the origin of the elements of the turban eye of mayflies from elongated epithelial cells near the dorsal edge of the lateral eye. His observations in the main agree with the following account.

All nymphs of *Callibætis* under 4 mm. in length have only lateral pigmented eyes. When the nymphs are 4 to 5 mm. long however, the lateral eyes have about completed their development. Then a narrow yellowish or light brown band appears above the dorsal edge of each lateral eye of the male nymphs. This marks the first noticeable beginning of the large facetted eye, and cross-sections made of the head of such a nymph show the hypodermis, just beneath the light brown band, to be made up of modified long slender hypodermal cells with a second layer of much shorter cells lying against their inner bases. Already 2 membranes very close together are forming here. One of these membranes (Fig. 21, *A*, *k*), marks the inner boundary of the second layer of cells *A*, *2hn*. The other membrane *A*, *bm*, marks the inner boundary of the outer layer of modified long hypodermal cells. The nuclei of some of the cells of the second layer are above the membrane *A*, *bm*, and some are below it. These 2 membranes were found also beneath the developing unpigmented ommatidia in the upper eye of young *S. corrupta* (Fig. 7, *A*, *bm* and *k*, and Fig. 6). The upper membrane is found throughout the further development of the eye and corresponds to the basement membrane of the adult. The lower membrane, *k*, seems to be identical with the limiting membrane, *k*, of the lower pigment cells in the adult eye (Fig. 16, *A*). This second layer of cells (Fig. 21, *A*, *2hn*), then, appears to be that from which developed the lower pigment cells of the adult eye. If that is true, it is clear how it is possible for those pigment cells to migrate up and down through the basement membrane in the adult eye since that membrane is formed, in the beginning, at the inner ends of the outer hypodermal layer of cells (Fig. 21, *A*, *1hn*), around these developing pigment cells *A*, *2hn*, not as an entire or closed membrane above them.

In cross-sections of the head made at a little later stage of development, cells of this upper modified hypodermal layer just described are found to be differentiating into an outer and an inner layer so that 2 rows of nuclei may be seen above those which lie along the basement membrane (Fig. 21, *B*, *1fa*). Long undivided hypodermal cells may still be seen, however, at the edges of this developing turban eye, Fig. 21, *B*, *x*, next to the normal hypodermis, and at *y*, next to the dorsal edge of the lateral pigmented eye. In a still later stage of development (Fig. 22) the cone cells and the secondary iris pigment cells are found occupying the position of the outer row of nucleated cells described in Fig. 21, *B*, opposite *x*. The retinulæ, each already definitely formed of its 7 cells occupies the position of the second row of nucleated cells in Fig. 21, *B*, opposite *o*. Here again the elements in the middle of the developing eye (Fig. 22, *1fa*) are easily recognized as the older elements. Younger elements at the edges, *x* and *y*, are seen much below the cornea. At each molt of the growing nymph these newer elements at the margin of the eye rise to their normal position under the cornea and thus increase the size of the eye. Fig. 22 represents the stage of development of the turban eye when the nymph is 8 to 9 mm. long. The pigmented eye has practically the same size as that in the 5 mm. nymph.

None of the sections offers definite proof as to how the group of 7 retinular cells or, of the 4 cone cells, in a single element arise — whether by multiplication of a single mother cell to form each retinula for example, or by association of the original mother cells into groups of cells. The secondary pigment cells however, seem to be homologous or identical with some of the original long hypodermal cells of the first upper hypodermal layer (Fig. 21, *A*, *1hn*). The evidence for this is very strong at least, in the young nymph eye of *S. corrupta*. Fig. 7, *A*, shows a single developing ommatidia from the unpigmented area of the eye of a young nymph. In this eye, some of the cells of the first hypodermal layer separate into upper and lower parts, the latter giving rise to the retinular layer as in *C. hageni*. The upper part then becomes two-layered again and cells of the lower of these layers (Fig. 7, *A*, *npc*) become chief pigment cells; the upper, gives rise to the cone cell layer *A*, *cn*. Other cells of the first hypodermal layer appear simply to elongate. They grow very little and are seen surrounding the cone, chief pigment cells and retinular elements at *A*, *nsp*. These elongated dormant cells lie in the position of the secondary pigment cells in the adult eye. Fig. 7, *B*, shows 2 elongated hypodermal cells from the developing margin of the eye (Fig. 6, *x*). They are almost identical in size and shape with what are evidently secondary pigment cells in Fig. 7, *A*, *nsp*. As development goes on, the young short retinulæ lengthen rapidly.

In the 9 mm. stage of development of the *Callibætis* nymph, the rhabdomes are found as round rod-like bodies in all the older middle retinulæ. By the time the sub-imago is ready to issue, the cones have all practically finished development. A few very small undeveloped cones are found around the outer margin, but most of these remain still undeveloped in the adult.

Photographs 23 and 25 are made from cross-sections of the heads of sub-imagoes. The turban and lateral eyes are so definitely formed here that one might suppose development complete. Fig. 18, *A*, shows the structure of 2 ommatidia in a turban eye of a sub-imago of *C. hageni*. The corneal lens is definite but thin. The retinulæ are slightly constricted just beneath the tips of the cones. In the cross-section (Fig. 18, *B*) the rhabdome is seen to be star-shaped with the "secondary rods" beginning to develop between the boundaries of the retinular cells. Fig. 19 shows the structure of the turban eye elements of an old sub-imago of *C. californica*—*i. e.*, just before time for the adult to issue. The cornea is still thin, but the secondary pigment cells have pushed it up a little and the distal ends of these cells may be seen overlapping the bases of the cones between *c* and *cn* (Fig. 19). The retinula is now more nearly pinched into two. I was unable however, to demonstrate the presence of any nuclei in this retinula of the sub-imago below the constriction (*d*, Fig. 19) as might perhaps be expected. Otherwise the preparation for the separation of the distal and proximal retinulæ and for the formation of the hypodermal space seems complete in this stage of the development.

It is wonderful to see the rapid enlargement of the turban eyes as the adult issues from its sub-imago stage. Sub-imagoes issue from the nymphs in less than 3 seconds. The process for the adults is longer—40 to 60 seconds—but the head enlarges immediately upon breaking through the chitin, and the turban eyes expand almost to bursting with a liquid. When photographs 24 and 26 of the adult eye are compared with 23 and 25 of the sub-imago or drawing 16, *A*, with drawing 19, it is clear what happened to permit the enlargement. The secondary pigment cells which overlapped the bases of the cones have straightened up. The cornea has been lifted to permit this and thus the hypodermal space is formed—being bounded by the cornea, the cone and the surrounding secondary pigment cells. The liquid contents of this space and the secondary pigment cells together, undoubtedly secrete the thicker corneal lens of the adult eye. That is to say, the hypodermal space is analogous to a cell in this eye, but it is in no sense homologous to a cell as is shown by its origin. Furthermore, the space between the distal and proximal retinulæ is to be directly associated with the rapid expansion of the eye of the issuing adult. The narrow connecting portion of the retinula of the old sub-imago (Fig. 19) has been stretched to form the connecting strands of the adult. It must be observed here also that the proximal retinulæ outnumber the distal in the old sub-imago and in the adult. The extra retinulæ are found in a ring around the outer margin of the eye. This has been noted by Pictet, and figured by Zimmer, 1897, and named by them the "abkonical ring" in the adult eye.

Fig. 20 shows the structure of 2 ommatidia from the turban eye of an unidentified mayfly. It has primary pigment cells. No adults of this species were reared, but the development of the eye up to the sub-imago stage is, in general, identical with the development of the eyes just described.

TABLE OF MEASUREMENTS OF DIVIDED-EYE ELEMENTS.

	Small pigmented Ommatidia.			Large Ommatidia.		
	Length. mm.	Greatest Diameter. mm.	Greatest Thickness. mm.	Length. mm.	Greatest Diameter. mm.	Greatest Thickness. mm.
1. *Sympetrum corrupta* Hagen.						
Corneal lens			0.546			0.728
Pseudocone	0.728	0.273		1.82	0.546	
Retinula	4	0.395		4	.5	
2. *Anax junius* Drury.						
Corneal lens			0.32			0.36
Pseudocone	1.09	0.205		1.5	0.45	
Retinula	4.5			6		
3. *Bibio hirtus* Goef.						
Lens and pseudocone	0.348	0.19		0.507	0.327	
Retinula	0.65	.18		1.54	0.3	
4. *Blepharocera capitata* Loew.						
Lens and pseudocones	0.3	0.2		0.7	0.42	
Retinula	.507	.18		1.33	.39	
5. *Callibætis hageni* Etn.						
Corneal lens			0.07			0.158
Hypodermal space	measured along the cone axis.					0.19
Cone	0.348	0.095		0.44	0.125	
Entire retinula	1.268	.07		2.73		
Proximal retinula				1.18	0.12	
6. *Callibætis californica* Banks.						
Cornea			0.07			0.09
Hypodermal space	measured along the cone axis.					.126
Cone	0.35	0.9		0.368	0.124	
Entire retinula	1.23	.05		3.8		
Proximal retinula				1.26	.11	

In an eye like that of *Anax* where the large elements in one part of the eye pass gradually over into smaller elements in another part of the eye, both kinds of elements seem to develop from the same center — the smaller elements being the last formed.

As has been shown in the 2 divided eyes studied (*Callibætis* and *Sympetrum*) the large ommatidial elements begin development after the pigmented lateral eye is complete. In this case the optic ganglion which has already been formed for the pigmented eye appears to bud or enlarge to receive the nerve fibers of the new eye elements. To support statements already made and for further reference the accompanying table of measurements of the eye elements of the different eyes studied is given.

SIGNIFICANCE OF THE DIVIDED EYE CONDITION.

Exner, 1891, has shown that an eye with a structure like that of the turban eye of *Callibætis* (adult) is capable of forming an image of superposition upon the proximal retinulæ as well as an image of apposition upon the distal retinulæ. By means of this repeated formation of images upon the retina, the eye with the superposition image is enabled to see, even if somewhat indistinctly, in dim light where the small facetted deeply pigmented eye could not see at all. Zimmer has shown that this is of advantage to the mayflies in mating, since the males seek the females on the wing in the twilight.

In the case of all the other large facetted eyes discussed in this paper, an image of superposition would be impossible, since the retinulæ in every case lie rather close together and are not divided into proximal and distal parts. In every eye however, the increase in the size of the dioptric apparatus accompanies the decrease in pigmentation. Both of these conditions favor the admission of more light. This would admit of a better apposition image being formed in dim light. The small dioptric apparatus and dense pigmentation accompany each other and both favor the formation of a distinct apposition image in extremely bright light. Whatever the *special* adaptation then, the divided condition of the eyes may be regarded as an adaptation of different parts of the eye to suit different intensities of light.

Moreover, it would be of as much advantage to increase the sensitive receiving surface (rhabdome surface) in the eye used in dim light as to increase the dioptric or light gathering surface. The complicated rhabdome surface of the turban eye of *Callibætis* shows this increased sensitive surface and furthermore, the retinulæ of the "abkonical ring" each have well developed rhabdomes. The rhabdomes of the larger ommatidia of all the divided eyes are larger than those of the small ommatidia.

STANFORD UNIVERSITY,
April 28, 1906.

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EXPLANATION OF FIGURES.

The sections from which the following drawings and microphotographs were made were cut 3 to 6 microns in thickness. They were stained either with Haedenheim's iron hæmatoxylin or by a modified Weigert's hæmatoxylin method. Some sections were cross-stained with good results by safranin in analin. Depigmentation was done with absolute alcohol and C. P. nitric acid, equal parts, mixed. Killing of live material was done with best results in hot Gilson's fluid. The drawings were outlined with a camera lucida.

Abbreviations not found in the following list are explained in the text itself.

c. Corneal lens (cornea).
cn. Cone-cell nucleus.
tr. Trachea.
Bm. Basement membrane.
rn. Retinular nucleus.
nsp. Nuclei of secondary iris pigment cells.
sip. Secondary iris pigment cell.
lfa. Large facetted area (dorsal eye).
sfa. Small facetted area.
tp. Tapetum.
opg. Optic ganglion.
cip. Chief iris pigment cell.
up. Dorsal part of the head.
rb. Rhabdome (rhabdomere).
sn. Semper's nuclei in hypodermis.
co. Cone or pseudocode.
nf. Nerve fibers leading from retinula.
hs. Hypodermal space.
drn. Distal retinula nuclei.
prn. Proximal retinula nuclei.
rs. Connecting retinular strand.
h. Tactile hair.
œ. Œsophagus.
tb. Turban or dorsal large facetted eye.
la. Lateral pigmented eye.
tls. Transparent liquid space around the connecting strands.
drb. Rhabdome of the distal retinula.

PLATE XXIV.

FIGS. 1 to 7. Male of *Sympetrum corruptum* Hagen.

FIG. 1. Head of adult showing relative size and shape of the large and small facetted areas, × 8.

FIG. 2. Cross-section of the right eye of adult, × 34.

FIG. 3. *A*. A few elements from the small facetted deeply pigmented part of the eye (adult), × 141.

B. Cross-section of a cone and its surrounding secondary pigment cells from *A*, × 500.

FIG. 4. *A*. Ommatidia from the large facetted part of the eye of *S. corrupta*, × 141.

B. Cross-section of three of the rhabdome-like bodies, *rb* of 4, *A*, × 500.

C. Cross-section of the retinula in the region of the nuclei from Fig. 4, *A*, × 385.

FIG. 5. Head of a male nymph *S. corrupta*, showing the triangular large facetted area forming.

FIG. 6. Cross-section of one eye of Fig. 5.

FIG. 7. *A*. A single ommatidial element from the developing large facetted area of a nymph of *S. corrupta*, × 385.

B. Two of the upper modified hypodermal cells from the margin *x* of Fig. 6, × 385.

FIGS. 8 to 11. Eye of male *Bibio hirtus* Goef.

FIG. 8. Longitudinal sagittal section of right eye, × 41.

FIG. 9. *A*. Three ommatidia from the large facetted area, × 205.

B. Cross-section of cone tip through cone nuclei and surrounding secondary pigment cells.

C. Cross-section of three retinulæ near their distal ends.

E. Cross-section of a retinula near its middle.

D. Cross-section of three retinulæ in region of retinular nuclei.

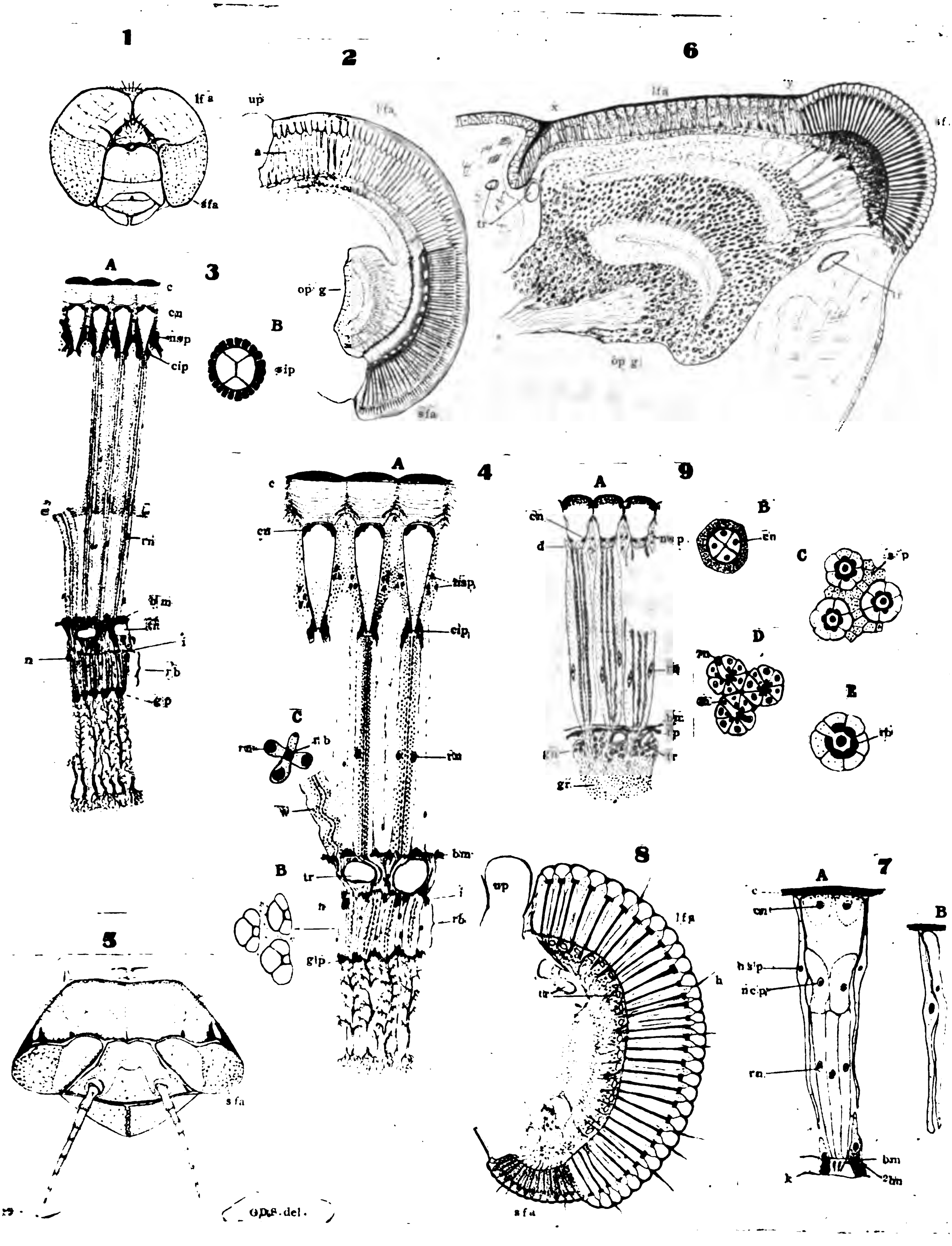
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PLATE XXV.

FIG. 10. Ommatidia from the small facetted pigmented area of male *Bibio* eye, $\times$ 900.

FIG. 11. Head of male *Bibio hirtus*.

FIGS. 12 to 14. Eye of *Anax junius*, Drury.

FIG. 12. Cross section of a single eye of adult, $\times$ 41.

FIG. 13. *A*. Two ommatidia from the upper largest facetted part of the eye, $\times$ 102.

B. Cross-section of the retinula through the nuclei.

C. Cross-section of cone and surrounding secondary pigment cells and lumina.

D. Cross-section of cone tip showing surrounding primary or chief pigment cells and secondary pigment cells.

E. Cross-section of three retinulæ and enclosed lumina.

FIG. 14. Two ommatidia from the smallest facetted part of the eye, $\times$ 102.

FIG. 15. Eye of *Blepharocera capitata* Loew.

A. Two ommatidia from the large facetted division of the eye (dorsal), $\times$ 205.

B. Cross-section through tip of cone showing four cone cells with their nuclei and the surrounding secondary pigment cells.

C. Cross-section of a retinula showing the rhabdomeres.

FIG. 16. Adult eye of a male *Callibætis hageni* Etn.

A. Two entire ommatidial elements from the turban or dorsal eye and parts of two proximal retinulæ whose corresponding cone elements are not shown, $\times$ 385.

B, *C*, *D*, and *E*. Cross-sections of corresponding parts of Fig. *A* as indicated by the lines.

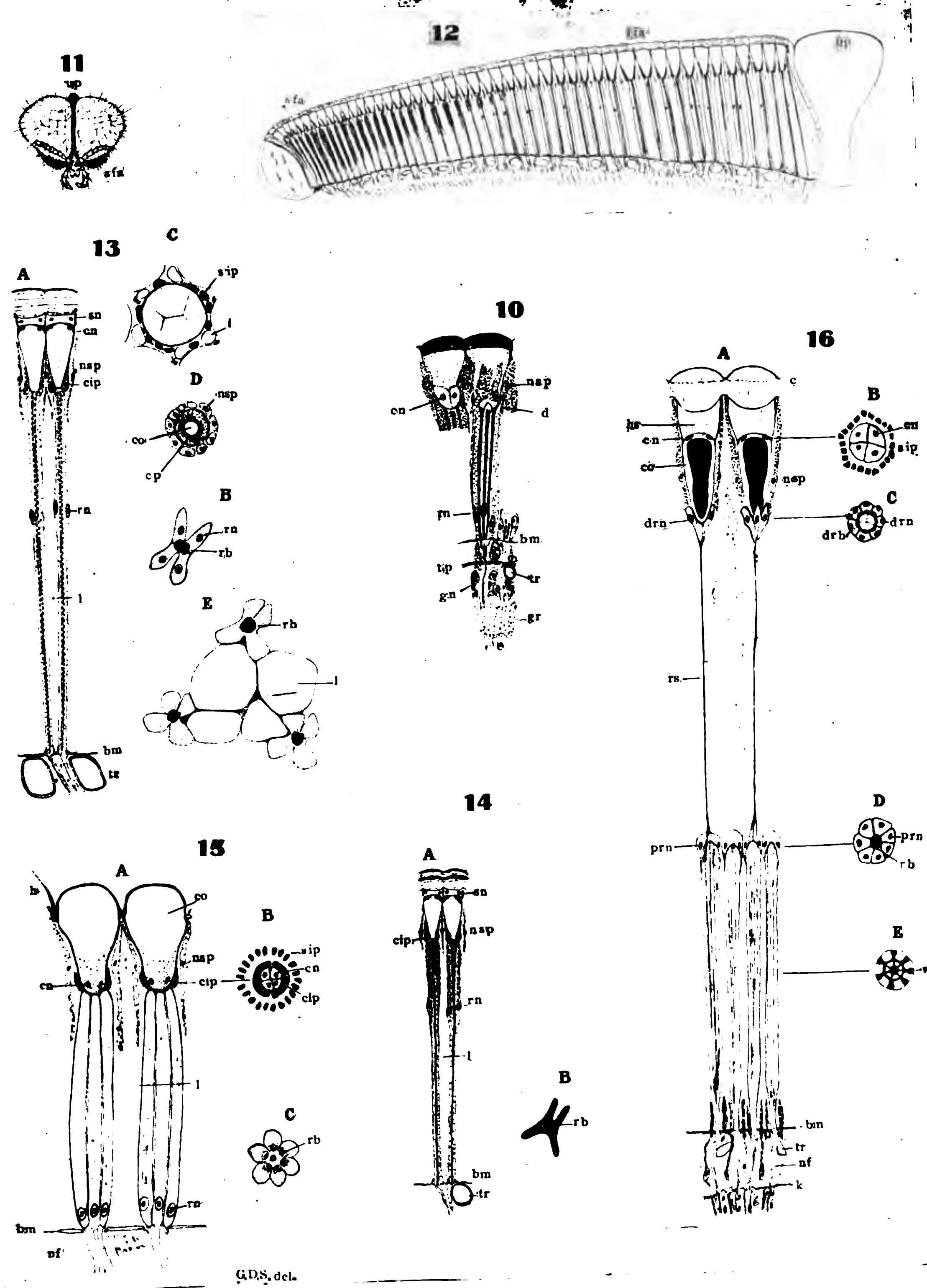
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PLATE XXVI.

FIG. 17. *A*. Two ommatidia from the lateral pigmented eye of adult male *C. hageni* Etn. One element is represented as depigmented, $\times$ 385.

B. Cross-section of retinula of *A*.

FIG. 18. *A*. Two ommatidia of a turban eye of a male subimago of *C. hageni* Etn.

B. Cross-section of retinula of *A*.

Fig. 19. Two ommatidia from the turban eye of a male subimago of *C. californica* Banks. An old subimago just before adult was ready to issue, $\times$ 385.

FIG. 20. Two ommatidia from the turban eye of male subimago of a mayfly of unknown species showing chief pigment cells. Adult of this species was not reared.

FIGS. 21 to 22. Eye of nymph of *C. hageni* Etn.

FIG. 21. *A*. A small part of the earliest developmental stage of the turban eye of *C. hageni* observed.

B. Entire eye of a young male nymph at a little later stage of development than *A*, *i. e.*, nymph 5 mm. long, $\times$ 120.

FIG. 22. Entire eye (turban and lateral) of a male *C. hageni* nymph 8 to 9 mm. long, $\times$ 120.

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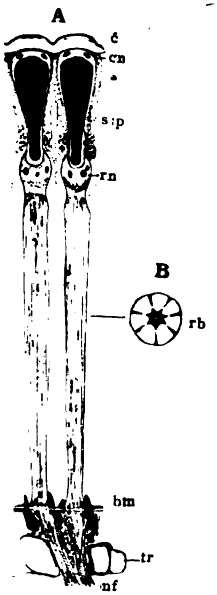

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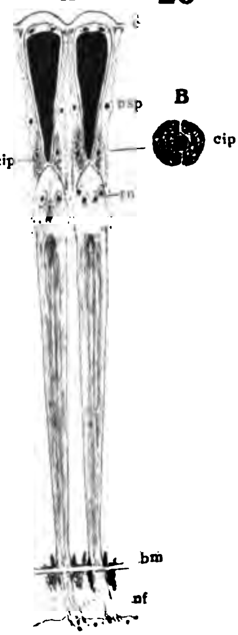

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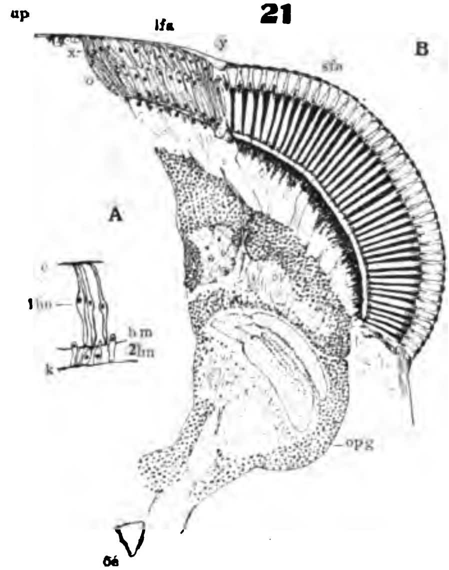

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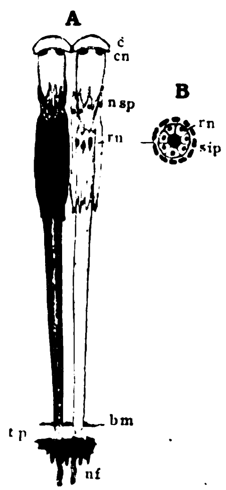

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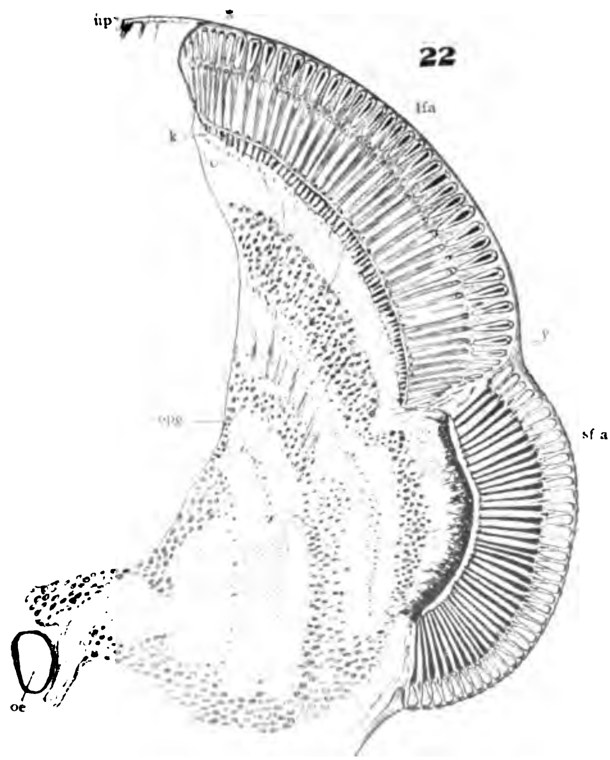

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PLATE XXVII. MICROPHOTOGRAPHS.

FIG. 23. Cross-section of head of subimago of male *C. hageni*.

FIG. 24. Cross-section of a head of adult male *C. hageni*.

FIG. 25. Cross-section of head of subimago of male *C. californica*.

FIG. 26. Cross-section of male adult of *C. californica*.

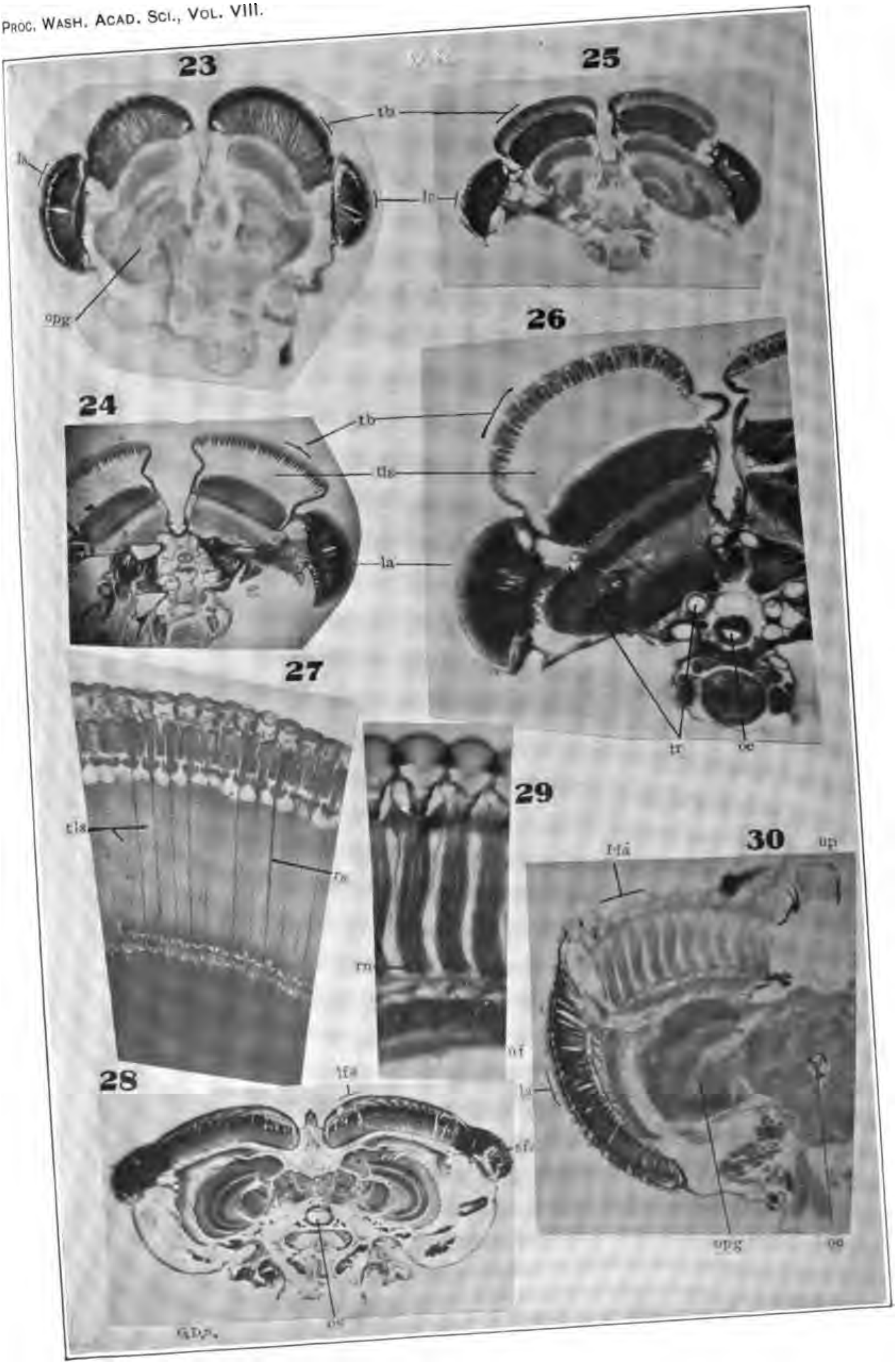
FIG. 27. Cross-section of part of large turban eye of an adult male *C. hageni*, showing the connecting strands between the proximal and distal retinulæ.

FIG. 28. Microphotograph of cross-section of head of an old nymph of *S. corrupta*, the adult of which was about to issue. The section passes through the edge, only, of the pigmented part of the eye which in its largest part was about equal to the upper large facetted area as is shown by the size of the optic ganglion.

FIG. 29. A few ommatidia from the dorsal eye of a female *B. capitata*.

FIG. 30. Left dorsal and lateral eyes of a female *B. capitata* showing optic ganglion also. Most of the cornea of the dorsal eye is torn away. See Fig. 29.

PLATE XXVII.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