On the Morphology of the Compound Eyes of Arthropods.

By

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With Plate XIX.

Prefatory Note.—The following extract and accompanying plate, from a memoir recently published in the 'Studies from the Biological Laboratory, Johns Hopkins University,' vol. iv, are here reproduced because it seems to me that they form a very important contribution to a subject which has been largely discussed in the pages of this journal, whilst they may not be readily accessible to European morphologists. In Mr. Watase's original paper a description and figures of the structure of the lateral eyes of Limulus, and of the compound eyes of other Arthropods, are given; but the diagrams in the plate now reproduced are sufficient to indicate the author's conclusions.

The distinctive feature about Mr. Watase's views is that he does not, as I did in my paper published conjointly with A. G. Bourne, on the "Eyes of Scorpio and Limulus," 'Quart. Journ. Micr. Sci.,' vol. xxiii, endeavour to derive the compound eye of Arthropods from a segregation of such diplostichous eyes as the central eyes of Arachnida; but, leaving these entirely aside, derives the commoner type of Arthropod compound eye from the monostichous lateral eyes of Limulus.

This seems to me to be a very happy suggestion. At the same time, I regret that the author has not, apparently, accepted the statements made by Bourne and myself as to the simple monostichous structure of the lateral eyes of Scorpions—nor investigated their structure for himself. Had he done so, he would have been able to assign even a clearer and simpler starting point for the "ommatidium" of the compound Arthropod eye than that afforded by the lateral eyes of Limulus, where the anomalous central ganglion-cell discovered by him, presents us with a complication. There is, I believe, no longer any doubt that a simple monostichous structure characterises the lateral eyes of Scorpions as originally shown by Bourne and myself. It is perhaps well to note that Grenacher was the first to describe the characteristic monostichous structure of the lateral eye of Limulus, on which Mr. Watase's theory is based.

Interesting matters for investigation and speculation are opened up by Mr. Watase's views. Such matters are the relation of the diplostichous monomeniscous central eyes of the Arachnida to compound or polymeniscous ommatidial eyes of Arthropoda generally. And especially interesting, it seems to me, would be the attempt to account for that incipient segregation of the retinal cells into groups united by a five-fluted rhabdom which we find in both the lateral and the central eyes of Scorpio.

March, 1890. E. RAY LANKESTER.

Balfour[1] has given a sketch of the possible evolution of a visual organ. He starts with a simple organism in which a spot on the surface of the body may become spontaneously pigmented and therefore become specially sensitive to light. The cuticular covering of the body may become thickened at this spot and act as an apparatus for condensing the light upon the pigmented spot lying beneath it. He further expresses his view elsewhere,[2] that the lens-like dioptric apparatus of the eye, formed either as a thickening of the cuticle or as a mass of cells, was at first formed simply to concentrate the light on the sensitive spot; the power to throw an image of external objects on the perceptive part of the eye was acquired gradually afterward.

The part which is played by pigment in the physiology of vision is considered a most obscure problem. I quote the following, clearly put forward by Foster,[3] as a physiological aspect of the question bearing upon the discussion at issue:

[1] F. M. Balfour, "Address to the Department of Anatomy and Physiology, British Association, 1880," 'Nature,' vol. xxii, p. 417, 1880.

[2] 'Comparative Embryology,' vol. ii, chap. xvi, "Organs of Vision," p. 470.

[3] M. Foster, 'A Text Book of Physiology,' 4th edition, book iii, chap. ii, "Sight: the Photochemistry of Retina," pp. 515, 516.

"But in order that light may produce chemical effects (upon protoplasm), it must be absorbed; it must be spent in doing the chemical work. Accordingly, the first step towards the formation of an organ of vision is the differentiation of a portion of protoplasm into a pigment at once capable of absorbing light and sensitive to light—i.e. undergoing decomposition upon exposure to light. An organism, a portion of whose protoplasm had thus become differentiated into such a pigment, would be able to react towards light. The light falling on the organism would be in part absorbed by the pigment, and the rays thus absorbed would produce a chemical action and set free chemical substances which before were not present. We have only to suppose that the chemical substances are of such a nature as to act as a stimulus to the protoplasm of other parts of the organism (and we have manifold evidence of the exquisite sensitiveness of protoplasm in general to chemical stimuli), in order to see how rays of light falling on the organism might excite movements in it or modify movements which were being carried on, or might otherwise affect the organism in whole or part. Such considerations as the foregoing may be applied to even the complex organ of vision of the higher animals. If we suppose that the actual terminations of the optic nerve are surrounded by substances sensitive to light, then it becomes easy to imagine how light, falling on these sensitive substances, should set free chemical bodies possessed of the property of acting as stimuli to the actual nerve-endings, and thus give rise to visual impulses in the optic fibres."

Lubbock[1] advances essentially the same idea as Balfour's in his recent work on the subject, illustrated with some lucid diagrams. "In the simple forms," he says, "the whole surface is more or less sensitive. Suppose, however, some solid and opaque particles of pigment deposited in certain cells of the the skin. Their opacity would arrest and absorb the light, thus increasing its effect, while their solidity would enhance

[1] 'On the Senses, Instinct, and Intelligence of Animals,' Inter. Sci. Series, vol. lxix, 1888.

the effect of external stimulus. A further step might be a depression in the skin at this point, which would serve somewhat to protect these differentiated and more sensitive cells, while the deeper this depression the greater would be the protection."

That such steps of gradual development of visual organs have actually taken place in some forms is quite probable. In Arthropods, it seems to me worthy of remark that the ommatidium of the lateral eye of Limulus makes the nearest approach to this primitive condition. It is nothing more and nothing less than a depression in the skin, with the thickened chitinous cuticle fitting in the open cavity, and acting as a lens to condense the light. The cells which form the sensory part of the structure are modified ectodermic cells, and, like the rest of the ectodermic cells lying on the surface of the body, secrete the chitinous cuticle on a part of their surface. Assuming the surface where the chitin is secreted to be the exterior, we may describe the ommatidium of the lateral eye of Limulus as a group of modified ectodermic cells aggregated around and beneath the funnel-shaped depression in the skin. A glance at the diagrams (Pl. XIX, figs. 1 and 2) will show this clearly. The sensory cells of the ommatidium come into direct contact with the conical lens, which is the thickened part of the general cuticle; or, to express this in the phraseology of Lankester and Bourne, the ommatidium in the lateral eye of Limulus is "epistatic." The cornea and crystalline cone as such have no separate existence in this stage.

Suppose such an ommatidium to become duplicated until a considerable number be formed, as we may safely imagine to have been the case, from the general tendency in the perfection of a visual organ. What will be the result? The first effect of such an increase in the number of ommatidia in a given area will be the lengthening of each unit in the direction of the ommatidial axis, and the cells (Pl. XIX, fig. 3, *V.*) which were situated directly on the outside of the retinulæ will travel over and above the sensory portion (*Rt.* and *G.*, fig. 3).

The distal ends of such (*V.*) which were thus pushed over will meet one another in the median or the "optic axis" of the ommatidium; further, they will continue to secrete chitin (fig. 3, *c.c.*) from their original chitin-secreting surfaces which are now median and axial. The chitin thus secreted will have an independent existence from the cornea, thus forming the rudiment of the crystalline cone, and the cells themselves will form the vitrellæ (figs. 3, 4, *V.*, &c.). Finally as the deepening still further goes on, the corneal lens (*C.*) and crystalline cone (*c.c.*) will be entirely separated, thus producing a condition somewhat similar to that which obtains in Serolis (figs. 5 and 6).

From this point onward, the three chitinous structures cornea, crystalline cone, and rhabdomere, undergo a different development in different Arthropods. In some the crystalline cone assumes a transparent semi-liquid state, while the whole cell becomes extremely elongated, forming the crystalline cone of certain crustacea (Pl. XIX, fig. 7); it may form a hard chitinous ball as in Serolis (Pl. XIX, fig. 6); or a cuneiform chitinous structure, as in Talochestia (Pl. XIX, fig. 9); or, finally, the whole cell may remain as a clear, transparent body, as in several insects, forming Grenacher's "aconous type" of the compound eye.

The forms assumed by the rhabdomeres in different Arthropods are equally diverse. The rhabdomere may exist as a plain cuticular covering over the non-pigmented part of the retinula, as in Limulus or in Serolis; it may become extremely elongated and narrow as in Musca or in Callinectes (Pl. XIX, fig. 8, *Rb.*); it may become transversely folded as in Cambarus (Pl. XIX, fig. 7, *Rb.*); these transverse folds may become still finer, showing the chitinous serrature along the axial edge of the retinula, as in Penæus and Homarus; or this transverse serrature may become extremely fine and regular, as in Squilla.

The cornea undergoes equally diverse modifications according as it is purely protective, or partly protective and partly dioptric in function. The range of variation is shown by the degrees of curvatures and by the varieties of its thickness. In several of the Decapod Crustacea which I have examined, as Penæus, Cambarus, Homarus, Callinectes, Gebia, &c., the curvatures of the individual cornea on both surfaces are very slight; it is biconvex in an extremely small degree. In Talorchestia both surfaces of the cornea are parallel. In Serolis, four species of which I have studied, all having well-developed compound eyes, there exists a considerable difference in different species in the nature of the cornea. In some the curvature on the proximal surface is very strong, and the whole structure is quite thick; while in others the cornea is rather thin, and a slight development of curvatures exists. This is interesting, showing that even within the group of nearly allied species there are considerable differences in this respect.

This fact is easy to understand when we remember the functional property of the cornea and the crystalline cone. As has been noticed already, the crystalline cone is always dioptric in function, while the cornea may be partly protective and partly dioptric, or wholly protective. When the cornea becomes partly dioptric, as in Serolis and in several other Arthropods, the dioptric function in an individual ommatidium comes to be performed by two structures, the crystalline cone and the corneal lens. When the two structures act together for the same end at the same time, it is easy to see how a certain trivial peculiarity of the one may induce a correlative modification of the other, and how a slight specific peculiarity may appear exaggerated in the thickness or in the degree of curvature of the corneal lenses in different species.

After so much has been said in regard to the unity of structure of the ommatidium in different Arthropods, one important point awaits our consideration, viz. the homology and fate of the central ganglion-cell found in the ommatidium of Limulus. Unless a great many forms of ommatidia in different Arthropods be compared, a discussion on this point appears to be unprofitable. The consideration which follows is therefore a purely provisional one.

There can be no question that the central ganglion-cell is an important factor in the ommatidium of Limulus, nor can we doubt the existence of a fundamental homology between the retinulæ of Limulus and those of all the other Arthropods which I have examined. With the exception of a few problematical bodies, such as the "hyaline cells" of Serolis, there are no structures in the ommatidia of most Arthropods which correspond to the central ganglion-cell of Limulus, in spite of the existence of a fundamental homology in the other elements of the ommatidium.

What has become of the central ganglionic element of the ommatidium? Was it lost in the course of the phylogenetic history of a more complex ommatidium? Or is it reasonable to suppose that some ommatidia came into existence without it from the beginning? Or, if it were lost at all, is there any evidence which makes this supposition probable?

The colourless ganglionic cell and the pigmented rod-bearing cells which surround the former I consider as the two primitive morphological factors in the unit of the sensory part of the Arthropod retina, somewhat in the same way as the circle of rods with a cone in the centre are the two essential factors in the neuro-epithelial layer of the human retina. In the absence of enough comparative data in Arthropods at present we have to dwell largely on the analogy suggested in the other groups of animals. Whatever be the views as to the fundamental homology of the ommatidium of Limulus to a structural unit of the sensory part of the human retina, a superficial resemblance of the one to the other is certainly very strong. The structural resemblance is paralleled by a physiological one. The place where the light acts in the visual end-organ of Arthropods and of man may alike be considered as consisting of a number of definite groups of cells, each group being a morphological and a physiological unit; or, in other words, the sensory part of the retinæ in both cases consists of a mosaic of several sensitive spots. The image formed on such a surface is therefore a mosaic one, whether in an Arthropod or in a Vertebrate.

Fundamental as this arrangement appears to be in the human retina, these two factors are liable to variation in their relative distribution in different Vertebrates. In fact, the variation takes place between the two extremes where the rods alone exist on one hand and where the cones alone constitute the essential part of the retina on the other. Thus, according to Schultze, "either form of percipient element (rod and cone) may be represented by the other" in the Vertebrate. This range of variability in the distribution of the cones and rods occurs even in a single group of Vertebrates, as in mammalia, showing that the variation in the distribution of the essential factors, even within a tolerably well circumscribed group of animals, is sometimes quite extensive. The group of Arthropods is a heterogeneous one, and I see no a priori objection to believing in the existence of a phenomenon analogous to what we find in Vertebrates, viz. that the two percipient elements represented by the central and the peripheral cells in the ommatidium of Limulus may be differently represented in different Arthropods.

There is no doubt whatever that the retinula cells are homologous throughout the Arthropods. In fact, in most Arthropods which I have examined no other elements but the retinulæ have any connection with the optic nerve-fibres, and they often undergo an enormous development and acquire most complicated structures, as in Homarus or in Penæus, giving rise to the much discussed "spindle."

But what has become of the central element which is so conspicuous in the ommatidium of Limulus, if the retinulæ in all Arthropods are homologous? I believe the central cell is fully functional, judging from its position and from its veritable connection with optic nerve-fibre in Limulus. What in other Arthropods strongly reminds one of this cell is the "hyaline cell" at the bottom of the ommatidial pit in Serolis and, according to Beddard, also in the Cymothoidæ. One important difference, however, exists between the "hyaline cell" of the Isopods and the central cell in the ommatidium of Limulus, viz. that, while in the latter the cell is connected with the optic nerve, the "hyaline cell" in the former has no connection with the central nervous system whatever. Hence the "hyaline cell" cannot be sensory, even if it be homologous with the central cell of Limulus, which it resembles in its general appearance and in its position. The number of "hyaline cells" in Serolis is always two, while its supposed homologue in Limulus is, as a general rule, only one. This fact does not offer any objection to my view of their homology when we bear in mind that other elements in different ommatidia, as vitrellæ and retinulæ, show a wide range of variation so far as their numbers are concerned, and yet they can be considered as perfectly homologous.

A further embryological and comparative knowledge in regard to the "hyaline cell" in Isopods is necessary for the determination of its exact homology. Meanwhile I would observe that if the central and the peripheral cells which we see in the ommatidium of Limulus may be taken as the two essential factors of the sensory element of the typical Arthropod retina, the case of Serolis may be taken as a loss of balance in the relative development of these two factors, the central cells having lost their sensory function and remaining as a sort of supporting mechanism. We can imagine this change in the function of the central cell as carried still further, and with the excessive development of the peripheral elements, the retinulæ, the central element may finally have disappeared.

All this is, however, a mere suggestion, and my interpretation of the nature of the Arthropod ommatidium in general does not lose its force even if this section of my views in regard to the fate and homology of the central cell or cells be proved untenable. It is quite possible that the ommatidia in which there is no element corresponding to the central cell of Limulus may have originated without it from the beginning. It seems, however, more natural to suppose that such an ommatidium had it originally and lost it later, observing that the simplest form of ommatidium possesses it in its fully functional, sensory form.

Finally, we have to consider the nature of the compound eye as a whole as presented in various types of Arthropods.

That a certain structure in the body of an animal may repeat itself and give rise to a secondary aggregate, or to a compound organ, is a well-known fact; the repetition of similarly constructed uriniferous tubules forms the essential part of a Vertebrate kidney, or the similar repetition of gill-filaments forms the respiratory organ of a Lamellibranch. Sundry other examples of this nature might be given, but the above two will suffice. Tracing, as I have attempted to do, the most complicated ommatidium into a simple, open, ectodermic pit, there is to my mind no difficulty in believing that the compound eye of the Arthropod is one of the most astonishing examples of the formation of an organ by the vegetative repetition of the similar structure. Thus, according to Lubbock, there are about 4000 facets in the compound eye of the house-fly (Musca), each facet corresponding to a single tubular invagination of the skin, the ommatidium. There are 4000 independent invaginations in the area in the head of the fly occupied by the compound eye; in the gad-fly (Œstrus), 7000; in the goat-moth (Cossus), 11,000; in the death's-head moth (Sphinx atropos), 12,000; in a butterfly (Papillio), 17,000; in a dragon-fly (Æschna), 20,000; in a small beetle (Mordella), as many as 25,000. On the other hand, the number of ommatidia seems to have reached its minimum in certain Copepods, as in Corycæus, where the whole visual organ seems to be represented by a single colossal ommatidium.

Certain forms of Collembola[1] seem to have a very small number of ommatidia; thus in Templetonia only one ommatidium exists on each side of the head; Orchesella has six on each side of the head; Tomocerus, Ipsoma,

[1] Lubbock, 'Monograph of the Collembola and Thysanura,' the Ray Society, 1873, p. 57, pls. lv and lvi. Lubbock uses the term "ocellus" to designate a single element of the eye, which I here called an ommatidium. If the structure of this "ocellus" differs from the ommatidium of other Arthropods, it has, of course, nothing to do with the discussion at issue.

have seven; Degeeria, Lepidocyrtus, Smynthurus, and Papirius, eight. In the ants we observe a similar gradation in the number of ommatidia.

What reasons can we assign for this enormous multiplication of similarly constructed parts? What advantage follows from this arrangement? If the view of the nature of the compound eye which is put forward in the preceding pages be a true one, Müller's celebrated theory of mosaic vision is the only one that can account for the enormous multiplication of the similarly formed pits in the skin. The subject has been so fully discussed by Lubbock that I need not enter into details here. "According to his (Johannes Müller's) view, those rays of light only which pass directly through the crystalline cones, or are reflected from their sides, reach the corresponding nerve-fibre. The others fall on and are absorbed by the pigment which separates the different facets. Hence each cone receives light only from a very small portion of the field of vision, and the rays so received are collected into one spot of light. The larger and more convex, therefore, is the eye, the wider will be its field of vision; while the smaller and more numerous are the facets, the more distinct will the vision be. In fact, the picture perceived by the insects will be mosaic, in which the number of points will correspond with the number of facets."[1] The whole explanation of the problem seems to me to be contained in the passage above cited; and no further comment will be necessary more than a statement that the increase in the number of ommatidia is a decided advantage to their possessor. An eye like that of Limulus might by a slight change be converted into one of a more protuberant nature so as to command a wider field of vision, as we see in some species of Serolis or in some Trilobites; a slight change again might produce a protuberant ocular area mounted on an ophthalamic stalk, and accompanied by the accessory apparatus of vision, such as the socket for protection or the set of muscles to move the eye-stalk in different directions so as to command a

[1] Lubbock, 'Senses, Instinct, and Intelligence,' p. 163.

still wider field of vision. In this connection I may refer to a series of diagrams (Pl. XIX, figs. 10–17). The black heavy layer represents the ectoderm, and the region in which the ectoderm is thrown into folds the area of the compound eye. The yellow-coloured layer outside represents the chitin, and the dotted line beneath the ectoderm the basement membrane.

In Limulus (fig. 10) the ectoderm is thrown into a series of shallow folds, which, when viewed from above, would be a group of shallow pits in the skin. Each pit is an ommatidium. In Serolis (fig. 11) the invagination of the skin is a little deeper than that of Limulus, and the whole ocular area is more prominent. Fig. 12 represents the condition of the ectodermal folding in Notonecta, and fig. 13 that of Agrion larva. Fig. 14 represents the eye of Branchipus, only a part of the stalk being shown in the figure. Fig. 15 represents the eye of Cambarus; fig. 16 that of Penæus; and fig. 17 that of Lucifer.

It must not be understood that the number of folds given in the diagrams have anything to do with the actual number of ommatidia that may exist in the actual specimens; no more than a morphological expression of the eye in a simplest possible form was intended. If one suppose a single invagination of the skin, say of fig. 15, to be divided into three strata and the cells in the bottom stratum to send out nerve-fibres, those in the middle to form the crystalline cone and those in the outermost to form the cornea (fig. 7), the interpretation of the diagram will be complete.

According to this view the compound eyes of Arthropods, either in the sessile or in the stalked form, are nothing more than a collection of ectoderm pits whose outer open ends face towards the sources of light, and whose inner ends are connected with the central nervous system by the optic nerve-fibres. The cells forming the walls of the pit arrange themselves into three strata, in most cases accompanied by three regional functional differentiations. Grenacher's classification of the compound eyes of insects into "acone," "pseudocone," and "eucone" types refer to the condition of the cells and their products in the middle stratum—the vitrellæ.

Morphologically, then, the compound eye of an Arthropod is strictly single-layered, although, as is evident, the present conception is entirely different from the monostichous theory maintained by some recent writers. From Limulus to Squilla we have a series of forms showing all degrees of modification in the general structure of the eye as well as the structure of its individual elements, and there is not here a single form which invalidates the view maintained in the present paper. Moreover, this view has the advantage of greatly simplifying our conception of these structures, reducing, as it does, all of them to one primitive structure, a depression in skin, in which several organs of ectodermal nature, often of a very complicated type, find their common morphological origin. And when thus the nature of the unit is reduced into a simple invagination of the skin, the formation of the compound eye appears to be but another instance of the well-known method in the formation of a morphological organ, namely, the vegetative repetition of a similar structure.

SUMMARY.

In studying the structure of the ommatidium of the compound eye of Serolis it has been found that it may be reduced to a simple ectodermic invagination of the skin. Extending my researches over several other Arthropods, of which Talorchestia, Cambarus, Homarus, and Callinectes were mentioned in the preceding pages, the same interpretation of the ommatidium may be applied without exception. This view of the ommatidium finds its strongest support in the fact that in Limulus the ommatidium is an open pit of the skin.

By supposing that the ommatidial pit of Limulus became deeper, and that this was accompanied by modifications in the structure and arrangement of the component cells, we can show the probability of our first supposition that the omma-

tidium of the compound eye of an Arthropod is an independent invagination of the skin. *If this view is correct*, the unit of the compound eye of an Arthropod is not, after all, so complex a structure as has been supposed by some; and the enormous increase in the number of ommatidia in a given area of the skin which results in the formation of the compound finds its parallel in the well-known method of the formation of the morphological organs, viz. the duplication of a simple unit.

DESCRIPTION OF PLATE XIX,

Illustrating Mr. Watase's paper on "The Morphology of the Compound Eyes of Arthropods."

Figs. 1—5.—Diagrams showing the probable evolution of the three-layered ommatidium from the single-layered surface depression in the skin by the gradual subsidence of the neuro-epithelial elements, *Rt.* and *G.*, Fig. 1. In Fig. 2 the ommatidium of Limulus is represented, which is considered a step further advanced from the condition shown in Fig. 1. The distal end of the retinula (*Rt.*) instead of being pointed toward the exterior as in Fig. 1, in Limulus points towards the median axis of the ommatidium. The chitinous substance being still secreted on the outside, a distinct body of chitin beneath the lens-cone (*C.*) is formed, the rhabdom (*Rb.*). In Fig. 3 this deepening is supposed to have gone still further, resulting in the formation of another independent chitinous body, the crystalline cone (*c. c.*). In Fig. 4 this deepening is considered to have advanced still further, the crystalline cone (*c. c.*) being entirely separated from the corneal lens (*C*) by a distinct stratum of cell, the corneagen (*cg.*). In Fig. 5 an ommatidium with three strata of cells, each secreting chitinous substance on the part of their surface, is formed. These three strata of cells are known as the corneagen (*cg.*), the vitrella (*V.*), and the retinula (*Rt.*). Three chitinous bodies secreted by each group of cells above mentioned are the cornea (*C.*), the crystalline cone (*c. c.*), and the rhabdomere (*Rb.*), respectively.

Fig. 6.—Serolis. Diagram of the ommatidium of Serolis. The general arrangement of cells in this is not very different from that shown in Fig. 5 The place of ganglion-cell in Fig. 5, *G.*, is taken by a pair (of which only one is shown in the diagram) of transparent "hyaline cells" (*H.*).

FIG. 7.—Cambarus. This is introduced in comparison with the hypothetical ommatidia.

FIG. 8.—Callinectes.

FIG. 9.—Talorchestia.

In the last three forms no element corresponding to the central ganglion cell of Limulus nor to the "hyaline cell" of Serolis can be found. The sensory element of the ommatidium is represented by the retinulæ (*Rt.*) only.

FIG. 10.—Limulus. Diagram of the compound eye of Limulus, the black, heavy line representing the ectoderm, and each depression in this layer corresponding to an ommatidium.

FIG. 11.—Serolis. In the same way as the above, the eye of Serolis may be represented by a series of folds.

FIG. 12.—Notonecta.

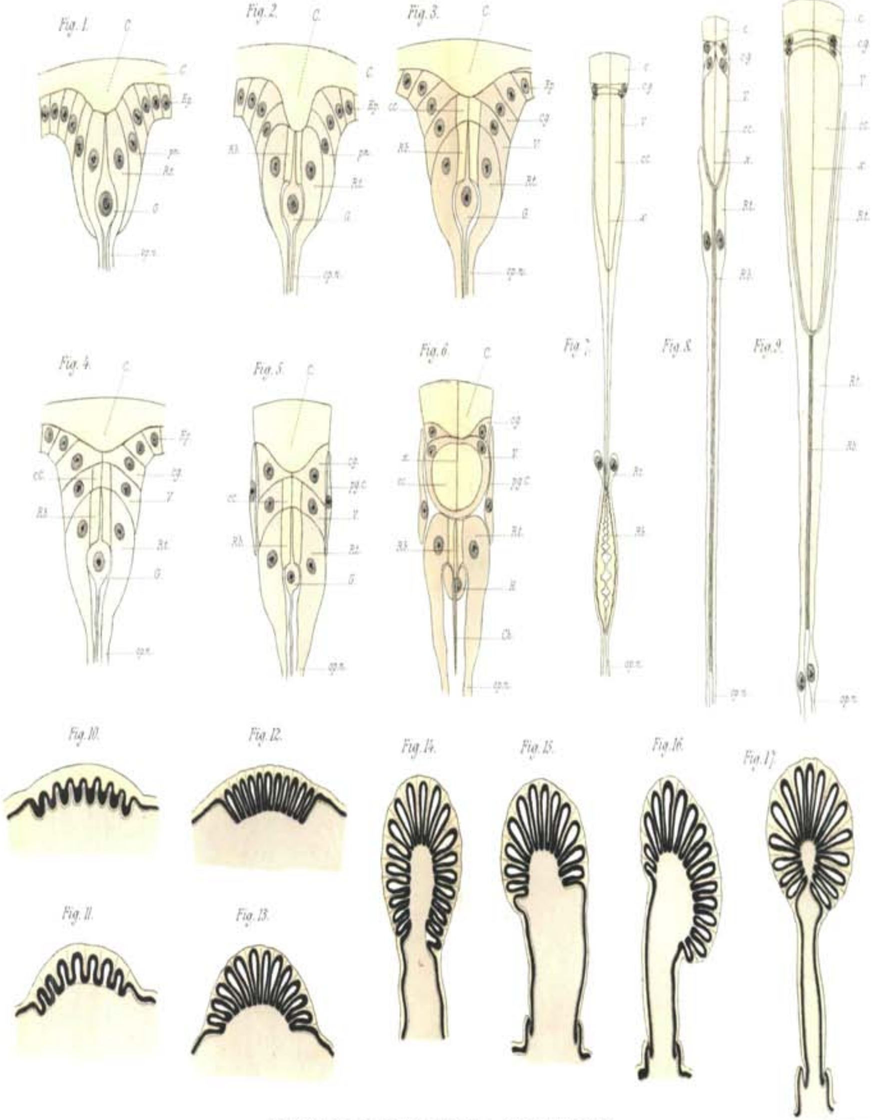
FIG. 13.—Agrion (larva).

FIG. 14.—Branchipus.

FIG. 15.—Cambarus.

FIG. 16.—Penæus.

FIG. 17.—Lucifer.



ORIGIN OF THE COMPOUND EYE OF ARTHROPODS.

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