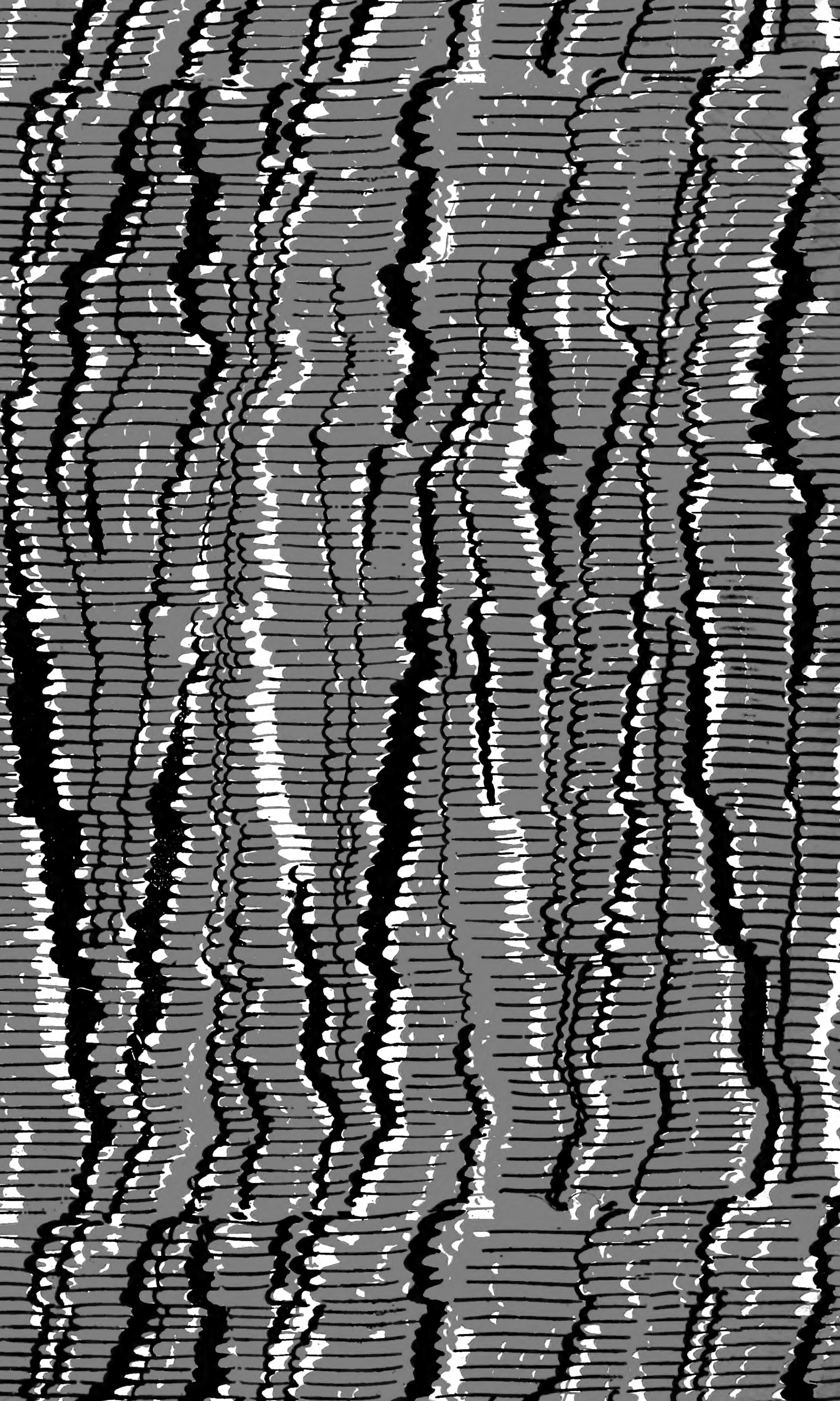

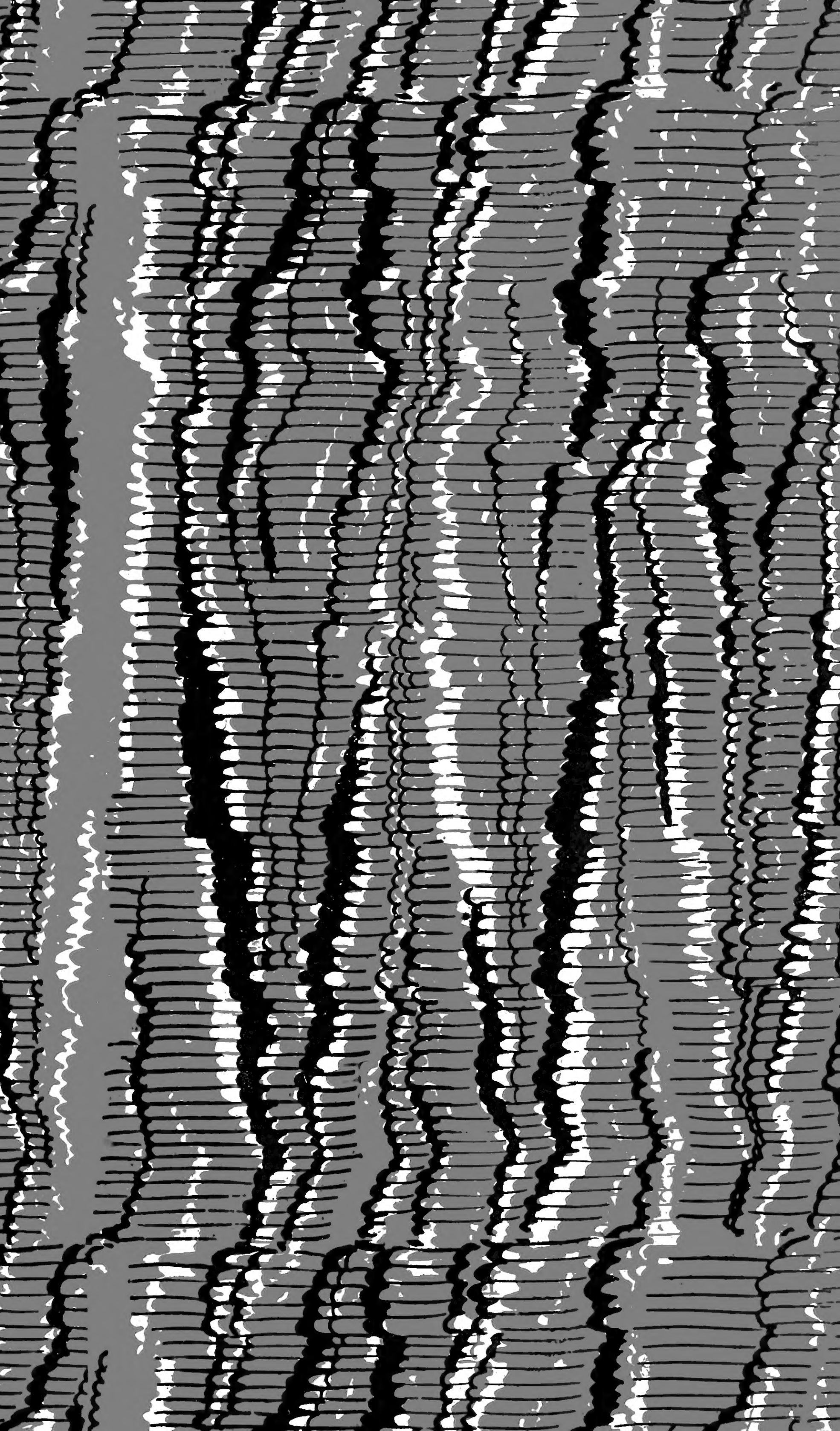

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E. L. Mark.

THE COMPOUND EYES IN CRUSTACEANS.

BY G. H. PARKER.

WITH TEN PLATES.

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No. 2.—*The Compound Eyes in Crustaceans.* By G. H. Parker.[1]

Table of Contents.

Introduction.

Some four years ago, at the suggestion of my instructor, Dr. E. L. Mark, I began the investigation of the compound eyes in Crustaceans. In order to familiarize myself with the subject, I determined to study at first in detail the structure of the eyes in a single species, and for this purpose I turned my attention to our common lobster, Homarus americanus. My results were published in a paper entitled "The Histology and Development of the Eye in the Lobster." Since the publication of that paper, I have had the opportunity of examining the eyes in a number of other Crustaceans, and my observations and conclusions concerning these eyes are contained in the following pages.

The *material* which I have used in the present study was in part supplied to me through the kindness of several friends, and in part collected by myself. Of that which I obtained myself, some was gathered in the immediate vicinity of Cambridge, but much of it came either from Wood's Holl, Mass., or from Newport, R. I. The material which I obtained at Newport was collected at the Newport Marine Laboratory during the summer of 1890, and consisted of specimens of Idotea, Evadne, and Pontella; that which I got at Wood's Holl was collected at the United States Fish Commission Station during a brief period

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXV.

which I spent there in the summer of 1889, and included much of the material which I used in studying the eyes of Decapods. For the opportunities of collecting, both at Newport and Wood's Holl, I am indebted to Dr. Alexander Agassiz. I also desire to express my thanks to Prof. M. McDonald, the United States Commissioner of Fish and Fisheries, for many courtesies shown me while at the government station at Wood's Holl.

Essentially the same *methods* as those which I used in investigating the eyes in the lobster were employed in studying the eyes in other Crustaceans. As these methods have been described at some length in my paper on the lobster's eye (Parker, '90^a, pp. 3, 4), further mention of them in this connection is unnecessary.

Before proceeding to an account of the eyes in Crustaceans, a few statements should be made concerning the use of terms. In the following anatomical descriptions, I have very generally adhered to the older and more established terms. It must be admitted that some of these, on account of their derivation, are not entirely satisfactory, but because of their general acceptance I have chosen to retain them rather than to attempt to replace them by new ones.

The term *retinula*, the use of which varies with different writers, was introduced by Grenacher ('77, p. 17), who employed it to designate the rhabdome and the group of cells by which this structure is surrounded. Subsequently, Patten ('86, p. 544) used the same term as a name for a single cell of the group to which Grenacher gave the name retinula. In my paper on the eyes of the lobster I followed Patten's usage, but in the present paper I have decided to employ the term as originally defined by Grenacher, and to designate the individual cells in the retinula as *retinular cells*, — a translation of the term already used for this purpose in many German publications.

The greater part of the present paper is taken up with descriptions of the eyes in different Crustaceans. The amount of detail thus collected is considerable, and might appear at first sight to include many unimportant particulars; but the number of observations recorded is justifiable, I believe, on the ground that the majority of them bear more or less directly upon the solution of the principal question dealt with in the paper.

The following statements will make clear the character of this question. It is now well recognized that the retina in compound eyes is composed of a number of similar units or ommatidia, and that each ommatidium consists of a cluster of cells regularly arranged around a central axis. With very few exceptions, the different ommatidia in the retina of any given Crustacean agree with one another in the number and arrangement of their cells; in other words, in a given retina any ommatidium is the structural duplicate of any other. This uniformity suggests the idea of a structural type, and already a number of such types have been described. Some of these find representatives apparently only in the ommatidia of a single species, but more frequently the type characterizes a genus, family, or even a sub-order. Types differ from one another, either in the number of their cells or in the arrangement of these cells. Of these differences, the one which involves a variation in the number of cells is the more fundamental. This difference, however, has probably arisen by the gradual modification of an ancestral type, and, granting this, it follows that the ommatidia of one type are genetically connected with those of other types. This leads directly to the statement of the principal question, namely, *What are the means by which ommatidial types are modified, and what is the significance of the changes through which these types pass?*

This question, although easily stated, is not so easily answered; the facts presented in the following pages cannot be said to settle it, and yet they seem to me to increase materially the possibilities of its solution.

A partial answer to at least the first portion of the question has already been suggested (Parker, '90^a, pp. 56–58); it can be briefly stated as follows. There is reason for believing that those ommatidia which are composed of a small number of cells more closely resemble the ancestral type than those composed of many cells. Granting this statement, one would naturally expect that the more complex ommatidia had been derived from the simpler ones by an increase in the number of their elements. Perhaps the most natural method by which this increase could be accomplished would be by the further division of the cells already forming the ommatidium. Consequently, cell division in this sense seemed to me to afford a sufficient means for the modification of ommatidial types. In the present paper it is in part my purpose to show precisely to what extent cell division can be said to have modified ommatidia, and to determine whether any other factors have been involved in this process.

THE RETINA.

The retina in those Crustaceans in which its development has been studied originates as a thickening in the superficial ectoderm. At least three types of retinal structure can be distinguished, depending upon the ultimate form which this thickening assumes.

The FIRST TYPE which will be described is in several particulars the simplest, and probably represents a primitive form from which the other two are derived. This type is characteristic of the eyes in Decapods, Schizopods, Stomatopods, Isopods, the Nebaliæ, and the Branchiopodidæ, and is represented by a simple thickening in the superficial ectoderm.

Branchiopodidæ. — In the eye of adult specimens of Branchipus the retina is a lenticular thickening occupying the inner concavity of the distal end of the optic stalk. Near its edges the retina is directly continuous with the adjoining hypodermis. Its proximal face is bounded by a basement membrane which is also continuous with the corresponding membrane of the hypodermis, and its distal face is closely applied to the inner surface of the superficial cuticula. Thus the retina in the adult has in every respect the appearance of a simple thickening in the hypodermis.

The way in which the retina originates in Branchipus confirms the opinion that this organ has the simple structure suggested in the foregoing paragraph. The development of the retina in this genus has been studied by Claus ('86, p. 309), whose account can be summarized as follows. In that part of the head from which the optic stalks eventually arise, the ectoderm becomes considerably thickened; this thickening is subsequently divided into a superficial and a deep portion; the latter sinks into the head and becomes a part of the central nervous system; the former retains its external position and is converted into the retina. In Branchipus, therefore, the retina originates as a simple ectodermic thickening which retains its superficial position throughout the life of the individual. This method of origin, and the position permanently retained by the retina, are the two principal characteristics of the first retinal type.

Isopoda. — In adult specimens of Idotea irrorata, as sections perpendicular to the external surface of the eye show (Plate V. Fig. 49), the retina bears the same relation to the hypodermis as it does in Branchipus. Similar structural relations occur also in the eyes of Idotea robusta and of young specimens of Serolis Schythei.

The development of the retina in Isopods has been observed by Dohrn and Bullar. As early as 1867, Dohrn ('67, p. 256) described the eye in Asellus as originating in connection with a thickening in the lateral wall of the head, presumably in the ectoderm of that region. The details of the development of this organ were not followed on account of the continual increase of pigment. Bullar ('79, pp. 513, 514) in a paper on parasitic Isopods described the development of the retina in Cymothoa. His account is substantially as follows. In the course of the development of the cerebral ganglion, when this structure is separated from the superficial ectoderm, the latter remains on the exterior of the embryo as a layer of considerable thickness. From this superficial layer is developed the retina, i. e. all parts of the eye which in the adult lie between the basement membrane and the corneal cuticula.

I have studied a few stages in the development of the eyes in Idotea robusta. The retina in this species originates as a simple thickening in the superficial ectoderm, in essentially the same manner as Bullar has observed in Cymothoa.

The retina in Isopods, both in respect to its method of development and its general structure in the adult, is unquestionably a representative of what I have called the first type of retinal structure.

Nebaliæ. — In Nebalia, as the figures given by Claus ('88, Taf. X. Figs. 8 and 17) show, the retina and adjoining hypodermis are directly continuous, and the former presents all the characteristics of a simple thickening in the hypodermis.

Stomatopoda. — In an adult specimen of Gonodactylus which I examined, the relation between retina and hypodermis was the same as in Nebalia.

Nothing is known, I believe, of the development of the retina in either the Nebaliæ or the Stomatopods. The structure of the eyes in the adults of both groups, however, shows very conclusively that their retinas belong to the same structural type as those of Branchipus.

Schizopoda. — In describing the development of Mysis chamelio, Nusbaum ('87, pp. 171–185) states that the retina arises from a thickening in the superficial ectoderm, and adds that its formation, so far as his observations extended, was not complicated by an involution.

In Mysis stenolepis, a Schizopod whose eyes I have studied, the retina and hypodermis in the adult are directly continuous, as in Branchipus. This relation is what would be expected from the method of development described by Nusbaum.

Decapoda. — Carrière ('85, p. 169), in his account of the eyes in Astacus, showed very clearly that in the adult the retina and hypodermis formed a continuous layer. This relation was subsequently observed by me in Homarus (Parker, '90^a, p. 5), and I have since seen the same condition in Gelasimus, Cardisoma, Cancer, Hippa, Palinurus, Pagurus, Cambarus, Crangon, and Palæmonetes. There is, therefore, considerable ground for the support of Carrière's generalization, that the relation of the retina to the hypodermis as shown in Astacus is characteristic of all Decapods.

The development of the retina has been more fully studied in Decapods, perhaps, than in any other group of Crustaceans. Nevertheless, the accounts given by various writers are by no means in agreement, but differ in several important particulars. In a former paper (Parker, '90^a, pp. 31–43), I devoted considerable space to the discussion of these accounts, and I shall therefore not reopen the subject here. Suffice it to say, that since the publication of the paper referred to nothing has transpired to alter my belief that the retina in Decapods originates as a simple thickening in the superficial ectoderm.

In a recent preliminary communication by Lebedinski ('90) on the development of a marine crab, Eriphya, a brief description of the origin of the eye is given. This description, however, is so very much condensed that it is not easily understood, and since the author himself confesses that, on account of the complexity of the subject, a description without figures must be almost unintelligible, it would be unwise to hazard a presentation of his views. I shall therefore pass over this paper without further comment.

The evidence advanced in the course of the preceding paragraphs leaves no doubt in my mind that the retinas in the Branchipodidæ, the Nebaliæ, the Isopods, Stomatopods, Schizopods, and Decapods, belong to the same structural type, and that this type is represented by a thickening in the external ectoderm (hypodermis), which retains permanently its superficial position.

The SECOND RETINAL TYPE is more complicated than the first, and differs from it in that the retina does not retain its position at the surface of the body, but becomes buried beneath a fold of integument. Our knowledge of this type is largely due to the researches of Grobben ('79). The type is represented in the eyes of the Apusidæ, the Estheridæ, and the Cladocera.

Estheridæ. — In adult specimens of Limnadia Agassizii the two lateral eyes are rather closely approximated, and occupy a position in the ventral anterior portion of the animal's body (Plate IV. Fig. 33). The relation of the eye to the surface of the body can be seen most satisfactorily in sagittal sections. In such a section (Fig. 35) the eye has the appearance of a stalked structure which projects anteriorly into a cavity, the optic pocket (*brs. oc.*); this pocket communicates with the exterior by means of a small opening (*po. brs.*), the optic pore. The free surface of the stalked portion of the eye is covered with a delicate cuticula, which, after being reflected from the base of the stalk over the inner surface of the wall of the pocket, becomes continuous at the pore of the pocket with the superficial cuticula. The retina (Fig. 35, *r.*) occupies the greater portion of the optic stalk. Its distal face is bounded by the delicate cuticula already mentioned, and its proximal face is limited by a basement membrane (*mb. ba.*). This membrane becomes indistinct as the base of the stalk is approached, but the retina itself is apparently continuous in this region with the layer of cells which rests on the cuticular wall of the optic pocket, and which finally unites at the pore of the pocket with the superficial hypodermis. Thus the retina may be said to be continuous with the hypodermis.

The structure of the eyes in Limnadia Agassizii is such that they can be described as stalked eyes which have been surrounded by a fold of the integument, so as to become enclosed within a space, the optic pocket, which communicates with the exterior only by means of the optic pore.

An eye of essentially this structure has been described by Grobben ('79, p. 255) in Limnadia Hermanni, Limnetis brachyurus, and Estheria ticinensis, and in the last genus enough of the development of the eye was observed to indicate that the optic pocket was formed by the growth of a fold of integument over the optic stalk.

Apusidæ. — In Apus, according to Grobben ('79, p. 256), the plan of the eye is essentially similar to that in the Estheridæ. The eyes project into an open pocket, the cavity of which permanently communicates with the exterior. Judging from the figure given by Claus ('86, Taf. VII. Fig. 11, compare p. 366), the right and left retinas in Apus are not so close to one another as in the Estheridæ (compare Plate IV. Fig. 34).

Cladocera. — The structure and development of the retina in the Cladocera has been carefully studied by Grobben. My own observations on this group have been limited to a single genus, Evadne, and as this genus is not very favorable for the determination of the general relations of the retina I must rely almost entirely upon Grobben's descriptions.

In the development of Moina, according to Grobben ('79, p. 253), the retinal thickening is covered by a fold of the integument in such a manner that an open optic pocket is produced, as in Limnadia. By the closure of what corresponds to the optic pore, this pocket eventually loses its connection with the exterior, and becomes reduced to a closed sac on the distal face of the retina. With the closure of the sac, the continuity of the retina with the superficial hypodermis becomes interrupted.

In other Cladocera, especially the genera Sida and Daphnia, Grobben has found evidence to believe that the eyes are of essentially the same structure as in Moina. In a majority of the Cladocera the two compound eyes coalesce even more completely than in Limnadia.

In the development of Moina, as the preceding description indicates, the eye passes through a phase which closely resembles the permanent condition in Limnadia. The eye in the latter may therefore be interpreted as representing a stage in the phylogeny of the eye in Moina.

In accordance with the facts presented in the foregoing account, the second retinal type can be described as one in which the retina does not retain its primitive external position, but sinks below the surface of the animal and becomes covered by a fold of the integument. The optic pocket thus formed may remain permanently open, as in the Apusidæ and Estheridæ, or may become closed and partially obliterated, as in the Cladocera. The right and left retinas either remain separated, as in the Apusidæ, or become closely approximated, as in the Estheridæ, or fused, as in the Cladocera.

The minor modifications which this retinal type presents are not without importance. Bearing in mind the general statement that the compound eyes in Crustaceans are separate, paired, superficial structures, it is evident that the eyes in the Apusidæ, in which the retinas are separate and the optic pocket permanently open, depart only slightly from the primitive condition. In the Estheridæ, in which the two retinas are closely approximated, the eye is farther removed from the original type; but not so far as in the Cladocera, in which not only the two retinas are fused, but the optic pocket is closed and partially obliterated, thus entirely disconnecting the retina from the hypodermis. The three groups — the Apusidæ, the Estheridæ, and the Cladocera — may consequently be taken to represent a series in the differentiation of the second retinal type. That this series is a natural one, and that it culminates in the Cladocera, is shown from the fact that in the development of Moina, and perhaps many other Cladocera, the eyes pass through stages which reproduce the essential features of the permanent condition in the Apusidæ and Estheridæ.

In the THIRD RETINAL TYPE, as in the more differentiated form of the second, the retina is completely separated from the hypodermis.

The method by which the separation is here accomplished is not by the closure of an involution, as in the second type, but by a process the nature of which will be described in the following pages. The third type is represented by the eyes in Amphipods, and possibly in Copepods.

Amphipoda. — The peculiar relation which the retina bears to the hypodermis in Amphipods can be easily seen in Gammarus. In this genus, as Carrière ('85, pp. 156–160) has clearly demonstrated, the retina lies immediately below the hypodermis, and is separated from the latter by a well defined structure, the corneo-conal membrane (Fig. 1, *mb. crn'con.*). This membrane, although visible with perfect clearness, is nevertheless extremely delicate, and has the appearance of a single lamella. I believe, however, that its structure is more complex, and that it is composed of two very intimately united membranes, one of which is produced by the retina, the other by the corneal hypodermis. This belief is based upon the fact that at the edge of the retina the apparently single membrane separates into what may be considered its two constituents. One of these becomes the basement membrane of the general hypodermis, and the other, which I have called the capsular membrane, passes over the edge and proximal face of the retina, and is finally reflected over the optic nerve (Fig. 1, *mb. n. opt.*). In addition to the capsular membrane, the eye in Gammarus possesses still another membrane (Fig. 1, *mb. ba.*). This is a delicate lamella, which is approximately parallel to the deep face of the eye at a level between the rhabdomes and retinular nuclei (compare Fig. 2), and which consequently divides the space within the capsular membrane into two chambers, a larger distal and a smaller proximal one. At its periphery this intercepting membrane unites with the capsular membrane.

The corneo-conal and capsular membranes in Gammarus show no evidence of being perforated, but together constitute a closed capsule, which separates the retina from all adjoining tissues except the optic nerve. Both membranes are composed apparently of a homogeneous substance, in which I have never been able to distinguish any trace of cells. It is therefore probable that these membranes are cuticular.

The intercepting membrane, unlike either the capsular or the corneoconal membrane, is pierced by a great number of holes, through which the proximal ends of the retinular cells project. This membrane, therefore, has the form of a meshwork. According to Carrière ('85, p. 158) it is composed of numerous connective-tissue cells, but this statement is not confirmed by my own observations. In depigmented sections of the retina the intercepting membrane had the appearance of a delicate lamella, in which I was unable to find any trace of cells. Not unfrequently the nuclei of certain accessory pigment cells (Fig. 2, *nl. h'drm.*) appear to touch the membrane, and even at times to lie with their long axes parallel to it, but in no case could these nuclei be said to be *in* the membrane. In sections of the retina from which the natural pigment had not been removed, it was often difficult to decide whether a given nucleus was *in* the membrane or only *next to* it. Possibly appearances such as these have led Carrière to believe that the membrane was cellular. My own opinion is, that the intercepting membrane, like the other two membranes, is a cuticula, and does not contain cells.

From the foregoing account, it will be seen that in an adult Gammarus the retina lies immediately under an undifferentiated corneal hypodermis, and is enclosed, excepting where the optic nerve emerges from it, by a non-perforated cuticular capsule. The space within this capsule is divided by a perforated cuticular membrane into a large distal and a small proximal chamber.

In Hyperia, judging from the figure given by Carrière ('85, p. 161, Fig. 123), the retina has essentially the same structure as in Gammarus. The intercepting membrane is in a position proximal to the rhabdomes and distal to the retinular nuclei. The layer of pigment cells, which Carrière ('85, p. 161, Fig. 124) apparently considers the intercellular membrane itself, in my opinion marks only approximately the position of that membrane. Probably in Hyperia, as in Gammarus, these cells rest on the distal face of the intercepting membrane.

In Phronima each side of the head is occupied by two eyes, instead of one, contrary to the condition in the more typical Amphipods. Of the two eyes, one is dorsal, the other lateral. This difference in position affords a convenient means of distinguishing them. The lateral eye presents all the essential structural features of the single eye in Gammarus (compare Carrière, '85, Figs. 125 and 121). The dorsal eye, although differing considerably in shape from the lateral one, is nevertheless constructed upon the same morphological plan. Its most important peculiarity is the shape of its intercepting membrane and the adjoining structures. In the dorsal eye the intercepting membrane, instead of lying in a plane nearly parallel with the external surface of the retina, as in the lateral eye, is cone-shaped. The axis of this cone corresponds to the axis of the eye; its apex is near the brain, and its base faces the external surface of the eye (compare Claus, '79, Taf. III. Fig. 20, and Taf. VII. Fig. 58). The ommatidia are arranged approximately parallel to its principal axis; distally, they terminate in the region of its base; proximally, they end either at its apex or on its lateral walls near the apex. The rhabdomes lie within the cavity of the cone, i. e. they are distal to the intercepting membrane, as in other Amphipods. The retinular nuclei cover the apical portion of the external surface of the cone, i. e. they are proximal to this membrane. These nuclei are covered externally by a second cone-shaped membrane, which separates them from the surrounding tissue. This membrane occupies the position of the capsular membrane of other Amphipods, and is unquestionably homologous with it.

The fact that both the lateral and dorsal eyes in Phronima are constructed upon the same plan as the single eye in Gammarus, supports the view that these two eyes have arisen by the division of a primitively single retina into two parts, and the subsequent independent differentiation of each part.

As the preceding account shows, in all Amphipods whose eyes have been studied carefully, the retinas conform to one structural type well exemplified by Gammarus. In this type the retina is characterized by two peculiarities: first, it is not continuous with the hypodermis, but lies immediately below that layer; and secondly, it possesses what appear to be two basement membranes, the capsular and the intercepting membranes. The significance of these peculiarities will be discussed in the following paragraphs.

The separation of the retina from the hypodermis is characteristic of only the more mature conditions of the eye in Amphipods; for as Pereyaslawzewa ('88, p. 202) has shown in Gammarus, and Rossiiskaya ('89, p. 577, and '90, p. 89) has demonstrated in Orchestia and Sunamphitoë, the retina originates as a thickening in the superficial ectoderm, in the same manner as in the majority of Crustaceans. So far as I am aware, however, no one has observed the detachment of the retina from the hypodermis, a process which must take place before the adult condition is reached. In the figure of the developing eye in Gammarus given by Pereyaslawzewa ('88, Plate VI. Fig. 120), the distal portion of the retinal thickening contains almost nothing but developing cones. In sections of my own from a corresponding region in a young specimen of Gammarus, the distal portion of the retina contains not only developing cones, but also isolated nuclei, which occasionally lie between the cones, but more frequently occur in positions distal to them. These nuclei are as numerous in the centre of the distal face of the retina as on its edges, and at this stage can always be easily distinguished from the nuclei of the cone cells. I believe they represent the nuclei of the corneal hypodermis. The retina proper is probably separated from this hypodermis by delamination; at least, the corneo-conal membrane is formed at a stage slightly older than that last mentioned, and, judging from the appearances at this stage, its formation is not accompanied by any folding of the hypodermis or retina, but is the result of a differentiation in place. Unfortunately, none of the specimens which I studied showed any steps in the formation of the corneo-conal membrane, and I am therefore uncertain as to the exact method of its growth.

Of the two membranes in the basal portion of the retina of Gammarus, presumably only one corresponds to the basement membrane of other Crustaceans. The position occupied by the two membranes, as well as their structure, serves to indicate which is the true basement membrane. At first sight one might suppose that the capsular membrane, at least in its proximal portion, corresponds to the basement membrane, but this interpretation is not probable, for the reason that the capsular membrane is not pierced by the fibres of the optic nerve, a characteristic of the true basement membrane of the eye. I therefore believe that the intercepting membrane, since it is perforated by these fibres, is the homologue of the basement membrane, and that that portion of the capsular membrane which might be regarded as a basement membrane is in reality merely the cuticular sheath of the optic nerve.

So far as I can foresee, the only objection to be urged against this interpretation of the intercepting membrane is found in its relation to the retinular nuclei. These nuclei in the eyes of almost all other Crustaceans lie on the *distal* side of the basement membrane. Granting that the intercepting membrane is the basement membrane, one must admit that in Amphipods they lie on the *proximal* side of this membrane. This admission might at first sight appear to offer an obstacle to the homology which I have suggested; but it can be made with consistency, I believe, provided one can show that the position of the retinular nuclei is not necessarily fixed. That such is the case is evident from the following facts. In Decapods the retinular nuclei usually occupy a position in their cells distal to the rhabdome. In Porcellio, as Grenacher ('79, Taf. IX. Fig. 96) has shown, they have a more proximal position, lying in the same transverse plane as the rhabdome itself. In Serolis they are midway between the rhabdome and the basement membrane. These conditions show, I believe, that the retinular nuclei may occupy very different positions in their cells, and that the step from the condition shown in Decapods to that shown in Serolis is not greater than that from Serolis to the Amphipods. It seems to me, therefore, that the objection suggested at the beginning of this paragraph is almost without weight. This conclusion, moreover, is supported by the fact that in Idotea (Plate V. Fig. 49) the retinular nuclei lie proximal to the basement membrane, whereas in the majority of other Isopods they are distal to that membrane.

From the preceding discussion, I conclude that the retina in Amphipods originates as a simple thickening in the superficial ectoderm, and that this thickening subsequently becomes separated, probably by a process of delamination, into a deeper portion, the retina proper, and a more superficial portion, the corneal hypodermis. The latter alone retains its original connection with the adjacent hypodermis. Of the two membranes present in the basal portion of the eye in Amphipods, that which I have called the intercepting membrane is homologous with the basement membrane of the retina in other Crustaceans, and that which has been designated as the capsular membrane is in large part the cuticular sheath of the optic nerve.

Copepoda. — The retinas in the Branchiura and Eucopepoda, the two divisions of the Copepods, present such different structural conditions that for purposes of description it is better to consider them separately.

Branchiura. — In adult specimens of Argulus, the retina is completely separated from all surrounding tissue, excepting the optic nerve, by an intervening blood space (Plate II. Fig. 11, *cœl.*). This peculiar condition was first clearly described by Leydig ('50, p. 331), although as early as 1806 Jurine ('06, p. 447) remarked that the eye in this genus was contained in a transparent membranous sac, which apparently contained a fluid, and Müller ('31, p. 97) some twenty-five years later described the retina as separated from the "cornea" by an intervening space filled with fluid. It remained, however, for Leydig to determine the extent of this space, and to demonstrate that the fluid which it contained was blood. The more essential features of Leydig's description have since been confirmed by Claus ('75, pp. 254–256).

The development of the eye in Argulus has not been studied with sufficient fulness to allow one to determine the relation of its retina to the hypodermis. But from the strong resemblance which the eye in the adult bears to that in Amphipods, it is probable that the course of development in the two cases is not unlike. Probably the retina in Argulus originates as a thickening in the superficial ectoderm, and subsequently not only suffers delamination, as in the Amphipods, but becomes actually withdrawn from the superficial layer (corneal hypodermis).

If this course of development really takes place, the various structures in the eye of an adult Argulus can be easily homologized with those in Amphipods. Thus the corneal hypodermis and corneal cuticula of Amphipods would probably be represented by the hypodermis and cuticula dorsal to the eye in Argulus (Fig. 11). The basement membrane of this hypodermis would correspond to the corneal component of the corneo-conal membrane of Amphipods, and the conal constituent would be represented by what is called the preconal membrane in Argulus (Fig. 11, *mb. pr'con.*). Proximally, the preconal membrane becomes continuous with the sheath of the optic nerve (Fig. 11, *mb. n. opt.*), the equivalent of the capsular membrane of Amphipods. The basement membrane of the retina in Argulus, as in Amphipods, is the membrane pierced by the fibres of the optic nerve (Fig. 11, *mb. ba.*).

Grobben ('79, p. 258) has suggested that possibly the eye in Argulus is of the same type of structure as in Phyllopods, but I do not share in this opinion for the following reasons. In Estheria, the delicate cuticula which covers the optic stalk is morphologically a portion of the outer surface of the body, and, as I hope to show subsequently, is subtended by a true corneal hypodermis. There is no corneal hypodermis beneath the preconal membrane of Argulus. Moreover, there is nothing in the eye of Argulus to correspond to the optic pocket of the Estheridæ, or to the optic sac of the Cladocera, except the circumretinal blood space, and it seems to me very improbable that this space was once a cavity in communication with the exterior, and afterwards became converted into a blood space. I therefore believe that the plan of the eye in Argulus is not similar to that in the Phyllopods, but rather that it represents a modification of the type presented by the Amphipods. The satisfactory determination of this question can be settled, however, only by embryological evidence.

Eucopepoda. — In adult specimens of those true Copepods which possess rudiments of the lateral eyes, — the Pontellidæ and Corycæidæ, — the retina is apparently separated from the hypodermis. In the Corycæidæ it usually lies at some considerable distance from the hypodermis, and in Pontella the two structures, although near one another, are nevertheless not continuous.

The development of the lateral eyes in the Corycæidæ and Pontellidæ has not been studied, and consequently it cannot be stated with certainty whether the retinas in these Crustaceans originate from the hypodermis or not. In the metanauplius larva of Cetochilus, a Copepod which as an adult has no lateral eyes, Grobben ('80, p. 262) has described a pair of thickenings, which extend from the superficial ectoderm of the antero-lateral part of the head to the brain. These thickenings are present only in the early stages of development, and represent the unsevered connection between the brain and the superficial ectoderm. They closely resemble the developing lateral eyes of Branchipus, and Grobben has therefore very justly considered them rudiments of the lateral eyes. If the rudiments of the lateral eyes in Cetochilus develop from the superficial ectoderm, it is probable that the lateral eyes in other Copepods have a similar origin.

To which of the three retinal types already described the eyes in Copepods belong is not easily decided. The absence of any indication of an optic pocket, either in the development of what Grobben considers the rudiments of the lateral eyes in Cetochilus, or in the fully formed eyes in other genera, seems to me to preclude the possibility of these eyes belonging to what I have described as the second type. The separation of the retina from the hypodermis prevents them from being classed with the first type, and, especially in the case of the Branchiura, brings them into close relation with the third type. It is my opinion, that, if the lateral eyes in Copepods are not representatives of a fourth type, essentially different from the three already described, they must be considered members of the third retinal type.

Certain species of Cumaceæ, Ostracods, and Cirripeds possess optic organs which probably represent the compound eyes of other Crustaceans ; but so far as I am aware, the relation of these structures to the hypodermis is unknown. It is therefore impossible to state whether those eyes represent other retinal types, or belong to one of the three already described.

According to the preceding account, three retinal types can be distinguished in the compound eyes of Crustaceans. In the first of these the retina is a simple thickening in the superficial ectoderm (hypodermis). This type is characteristic of the eyes in Isopods, the Branchiopodidæ, the Nebaliæ, Stomatopods, Schizopods, and Decapods. In the Isopods, the eyes are sessile ; in the other groups of the first type, they are borne on the distal ends of movable optic stalks.

In the second type, although the retina, as in the first type, originates as a thickening in the superficial ectoderm, it ultimately becomes enclosed within an optic pocket. This may remain permanently open, as in the Apusidæ and Estheridæ, or it may become closed, as in the Cladocera. In the Apusidæ, so far as I am aware, the eyes are not capable of motion, and in the Estheridæ they are, if at all, only slightly movable. In the Cladocera, where the second type probably reaches its greatest differentiation, the retina is remarkable for the freedom of its motion.

In the third type the retina originates from thickened hypodermis, which subsequently separates into two layers, the corneal hypodermis and the retina proper (a layer of cones and retinulæ). This separation is accomplished either by the formation of a corneo-conal membrane, as in Amphipods, or by what I believe to be an actual withdrawal of the retina proper from contact with the hypodermis, as in Copepods. Only in the representatives of the extreme modification of this type, the Copepods, are the eyes movable.

The course of development taken by each of the three types very clearly indicates their mutual relations. Evidently the first type is a primitive one, and since the first steps in the development of the second and third reproduce the permanent condition of the first, these two may therefore be considered derivatives from the first. It is interesting to observe that in the simpler condition of each type the retina is fixed, whereas in the more differentiated form it has become movable. The sinking of the retina into the deeper parts of the body, as represented in the second and third types, may have been induced by the protection thus obtained for the eye. After the three types were differentiated, each one seems to have been modified in a special way to give rise to a movable retina.

Arrangement of the Ommatidia.

The ommatidia in the retinas of some Crustaceans are so few in number that they can scarcely be said to be grouped according to any system. Where they are numerous, however, they are arranged upon one or the other of two plans. These may be designated the hexagonal and tetragonal plans of arrangement. In the hexagonal plan the imaginary outline of the transverse section of an ommatidium is a hexagon, and each ommatidium, excepting those on the edge of the retina, is surrounded by six others. In the tetragonal arrangement the ideal transverse section of an ommatidium is a square. Each of the four sides of this square is occupied by one of the four faces of an adjoining ommatidium.

The arrangement of the ommatidia can usually be determined by a careful inspection of the external surface of the eye; this determination is considerably facilitated by the presence of a facetted cuticula. Sometimes the form of a single facet is sufficient to indicate the plan of arrangement. Thus, hexagonal facets have never been observed except in connection with the hexagonal plan of arrangement. Circular facets are likewise known to occur only with this method of grouping. Square facets, on the other hand, may accompany either the hexagonal or tetragonal arrangement of deeper parts.

The hexagonal arrangement is apparently characteristic of the ommatidia in all Crustaceans,[1] except the Decapods. In the Decapods, as will be shown presently, the ommatidia are arranged either upon the hexagonal or the tetragonal plan. Before proceeding, however, to a description of the arrangement of the ommatidia in Decapods, it would be well perhaps to call attention to the rather peculiar grouping of these structures in Gonodactylus, a Stomatopod.

For a clear understanding of the arrangement of the ommatidia in this Crustacean, it is necessary to have some previous knowledge of the shape of its optic stalk. In Gonodactylus the stalks are elongated cylinders, the distal ends of which are rounded. In alcoholic specimens the stalks in an undisturbed position rest with their longitudinal axes approximately parallel with the chief axis of the animal, and with their distal ends directed forward. The retina occupies the free end of the stalk. Dorsally it extends over the distal half, ventrally over only the distal third of the stalk.

The ommatidia in Gonodactylus are of two kinds, large and small, which are always easily distinguishable from each other, although they differ in no essential respect except size. The large ommatidia are definitely arranged in six rows, which extend as well defined bands from the dorsal posterior edge of the retina anteriorly over its rounded distal end, and posteriorly over its ventral surface to its ventral posterior edge. This band thus occupies both dorsally and ventrally the median portion

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[1] Judging from the figures as well as the statements made by the authors quoted, the hexagonal arrangement is characteristic of the ommatidia in the following Crustaceans (exclusive of the Decapods): *Branchipus* (Burmeister, '35, p. 531, Spangenberg, '75, p. 30), *Nebalia* (Claus, '89, Taf. X. Fig. 10), *Gammarus* (Sars, '67, p. 62), *Orchestia* (Frey und Leuckart, '47, p. 204), *Phronima* (Claus, '79, Taf. VI. Fig. 48), *Cymothoa* (Müller, '29, Tab. III. Figs. 5, 6, Bullar, '79, p. 514), *Lygidium* (Lereboullet, '43, p. 107, Planche 4, Fig. 2^b), *Serolis* (Owen, '43, p. 174), *Arcturus* (Beddard, '90, Plate XXXI. Fig. 4), *Anceus* (Hesse, '58, pp. 100 and 103, Dohrn, '70, Taf. VIII. Figs. 33, 34), *Squilla* (Milne-Edwards, '34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Leydig, '55, p. 411), and *Mysis* (Sars, '67, Planche III. Fig. 7, Grenacher, '79, Taf. X. Fig. 112). I have observed the hexagonal arrangement in the following genera: *Apus*, *Branchipus*, *Estheria*, *Evadne*, *Argulus*, *Gammarus*, *Caprella*, *Talorchestia*, *Idotea*, *Serolis*, *Porcellio*, *Sphæroma*, *Mysis*, and *Gonodactylus*.

of the retina, and separates the remaining retinal surface into two parts, one on either side of the stalk. In alcoholic specimens this median band is readily visible with the aid of a hand lens, and a little closer scrutiny shows that it is composed of six lines. These lines, of course, correspond to the six rows of ommatidia previously mentioned. The smaller ommatidia, on either side of the median band, are also arranged in lines parallel to those in the band; but, on account of their smaller size, the lines formed by them are not visible with an ordinary lens.

The smaller ommatidia in Goniodactylus are arranged upon the typical hexagonal plan (see the left half of Fig. 93, Plate VIII.). The larger ones have a somewhat similar grouping, although the fact that they are in six longitudinal rows rather obscures their hexagonal arrangement. (See the right half of Figure 93, in which three rows, and a part of a fourth, of large ommatidia are shown.) The hexagonal arrangement is not disturbed, as might be expected, on the line which separates the larger from the smaller ommatidia, but both kinds form parts in a common system. That this is true can be seen from Figure 93, where it will be observed that the *centres* of any two small ommatidia lying in the same vertical line are as far apart as the *centres* of the corresponding larger ommatidia. Moreover, as I have demonstrated by actually counting the ommatidia of long parallel series, a vertical band which contains twenty-five large ommatidia has the same length as one composed of a corresponding number of small ones. The apparent difference in numbers at first sight presented by lines of the two kinds of ommatidia is principally due to the fact that the larger ommatidia are arranged in distinct rows, whereas the smaller ommatidia are so grouped that the individuals in one row are slightly interpolated between those of the two adjoining rows (compare Fig. 93).

In Decapods the ommatidia are arranged either upon the hexagonal or tetragonal plan. In the Brachyura,[1] as well as in three families of the Macrura, the Hippidæ, Paguridæ, and Thalassinidæ,[2] the arrangement

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[1] The presence of hexagonal facets has been recorded in the following genera of Brachyura: *Portunus* (Will, '40, p. 7); *Ilia* (Will, '40, p. 7, Leydig, '55, p. 411); *Cancer; Maja; Carpilius* (Frey und Leuckart, '47, p. 204); *Herbstia, Dorippe*, and *Lambrus* (Leydig, '55, pp. 407, 410, and 411, respectively). This form of facet is present only when the ommatidia are hexagonally arranged. Leydig ('55, p. 411) states that the outline of each facet in *Dromia Rumphii* is square, but, as his description clearly indicates, the facets are arranged upon the hexagonal plan. As my own observations show, the ommatidia in *Cardisoma Guanhumi*, Latr., *Cancer irroratus*, Say, and *Gelasimus pugilator*, Latr., are hexagonally grouped.

[2] The outline of the corneal facets is stated to be hexagonal in the following genera: *Pagurus* (Swammerdam, '52, p. 88, Cavolini, '92, p. 130, Milne-Edwards,

of the ommatidia is invariably hexagonal. In the remaining macrurous Decapods[1] the ommatidia are grouped on the tetragonal plan. This last statement, however, is not without exceptions, for in Typton, and at times also in Galathea,[2] the hexagonal arrangement appears to prevail. An explanation of these exceptions will be offered in a subsequent paragraph.

Before attempting this explanation, however, it will be well to gain a precise idea of the relation of the hexagonal and tetragonal methods of arrangement. At first sight, it might appear that these two methods had no definite relations, and were simply characteristic of different Decapods. Such, however, is not the case; for, as the development of the lobster shows, the ommatidia in a *single* animal can be arranged at first according to one plan, and afterward according to the other. In the lobster the hexagonal arrangement characterizes the earlier stages of development, and is replaced only subsequently by the tetragonal grouping. A similar change also occurs in the spiny lobster. Thus, in Phyllosoma, the larva of either Palinurus or Scyllarus, the hexagonal facets observed by Milne-Edwards ('34, p. 115) afford unquestionable evidence of the hexagonal arrangement at this stage. In the adult condition, however, both of Palinurus and of Scyllarus, according to my own observations, the ommatidia are tetragonally grouped. In the common lobster and the spiny lobster, then, the hexagonal arrangement of the early stages is replaced by the tetragonal one in the adult. These ob-

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'34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Chatin, '78, p. 8); *Calltanassa;* and *Gebbia* (Milne-Edwards, '34, p. 117). In *Pagurus longicarpus*, Say, and *Hippa talpoida*, Say, I have observed a hexagonal arrangement of the ommatidia.

[1] Judging from the figures given by various authors, the ommatidia of the following genera are characterized by the tetragonal arrangement: *Galathea* (Will, '40, Fig. III. c.); *Astacus* (Müller, '26, Tab. VII. Fig. 13, Leydig, '57, p. 252, Fig. 134, Reichenbach, '86, Taf. XIV. Fig. 226, Huxley, '57, p. 353); *Homarus* (Newton, '73, Plate XVI. Fig. 3, Parker, '90^a, p. 8); *Palæmon* (Grenacher, '79, Taf. XI. Fig. 118 A, Patten, '86, Plate 31, Fig. 115); *Penæus* (Patten, '86, Plate 31, Fig. 75). As my present observations have shown, the tetragonal arrangement is characteristic of the ommatidia in *Palinurus Argus*, Gray, *Cambarus Bartonii*, and *Palæmonetes vulgaris*, Say.

[2] According to Chatin ('78, p. 13) the outline of the facet in *Typton* is hexagonal. Presumably the arrangement of the ommatidia in this genus is upon the hexagonal plan. In *Galathea*, according to the figures given by Patten ('86, Plate 31, Fig. 116), the ommatidia are hexagonally arranged, although it must be borne in mind that Will's ('40, Fig. III. c.) figure of the facets in *Galathea strigosa* affords unmistakable evidence of a tetragonal arrangement.

servations appear to me to afford considerable evidence in favor of the view that the hexagonal arrangement is phylogenetically more primitive than the tetragonal.

Granting this conclusion, a number of otherwise exceptional observations can be explained. Thus, as long ago as 1840, Will ('40, p. 7) called attention to the fact that in Astacus, where the ommatidia are normally arranged upon the tetragonal plan, facets near the edge of the retina are often irregularly hexagonal. The edge of the retina is well known to be the last part produced, and therefore it is probably the part least differentiated. Admitting the hexagonal arrangement to be a primitive one, it is only natural to expect that, if it persists at all, it will persist in the less modified portion of the retina. Hexagonal facets also occur on the periphery of the retina in Homarus, and are to be explained, I believe, in the same way.

On the assumption that the hexagonal plan is primitive, the occurrence of a few genera with ommatidia hexagonally arranged, in a group in which the tetragonal arrangement is the rule, can also be explained. In Typton, for instance, the hexagonal plan obtains, although in almost all Crustaceans closely related to it the tetragonal system prevails. This condition may be explained, however, by the fact that the eyes in Typton show evident signs of degeneracy, due in all probability to the parasitic habits of the Crustacean. If the hexagonal arrangement represents an early ontogenetic phase in the development of Decapods related to Typton, it would be natural to expect that in Typton itself, where the normal development of the eyes is interrupted by parasitism, this arrangement would persist permanently.

In Galathea, as I have already mentioned in a note on page 63, the ommatidia according to Will are arranged tetragonally; according to Patten, hexagonally. At first sight these observations might appear to be irreconcilable, but such is not necessarily the case. So far as I have been able to ascertain, Patten does not mention the name of the species which he studied. Possibly he may have examined some other than G. strigosa, the one from which Will's figures were drawn. In such an event, a difference in the arrangement of the ommatidia may have been characteristic of the two species, although, if both possessed well developed eyes, this difference would be somewhat anomalous. If this is not the true explanation, it is still possible that the specimens studied by Patten were somewhat immature, in which case the hexagonal arrangement might very naturally be present. From what has been said, I think it must be evident that the apparent contradiction in Will's and

Patten's statements is not so serious as might at first be supposed, and that, admitting the relations already mentioned between the two plans of arrangement, the observations of these two writers can be explained without supposing either of them to be wrong.

The probable method of rearrangement by which the hexagonal plan is converted into the tetragonal has been suggested in a previous paper (Parker, '90^a^, p. 50). It involves two changes: the conversion of the hexagonal outline of the ommatidium, as seen in the corneal facet, into a square one, and the slipping of the rows of ommatidia one on the other, so that the lines which bound the four sides of each facet finally form parts of two series of lines which cross each other at right angles.

A condition somewhat intermediate between the hexagonal and tetragonal arrangement is shown in the retina of Crangon (Plate X. Fig. 123). In this genus the outlines of the ommatidia as seen in the facets are square, although their arrangement suggests the hexagonal type. The permanent grouping of the ommatidia in Crangon represents a stage slightly in advance of the condition seen in some young lobsters (compare Parker, '90^a^, Plate IV. Fig. 55), and the particular features in which this advance is shown are two. First, the distal retinular nuclei in Crangon (Fig. 123) are grouped in pairs, more as they are in adult lobsters, and not in circles of six, as in young ones (compare Parker, '90^a^, Figs. 5 and 55). Secondly, the arrangement of the ommatidial centres in reference to the hexagonal plan is more symmetrical in the young lobster than in Crangon, where the rows of ommatidia have apparently slipped somewhat upon one another so as to resemble more nearly the condition in the adult lobster.

I have been unable to determine with certainty what occasions the change from the hexagonal to the tetragonal arrangement. Apparently it accompanies an excessive growth on the part of the individual ommatidia. In the lobster, for instance, the ommatidia rearrange themselves between the times when the young animal is one inch and eight inches long. During this period the ommatidia increase about ten times in length and about five times in breadth. The increase is especially noticeable at their distal ends, and particularly in the cone cells. In young lobsters of one inch in length (Parker, '90^a^, Plate IV. Fig. 55), the space between the cones of adjoining ommatidia is considerable; in adults, it is proportionally very much less (compare Parker, '90^a^, Plate I. Fig. 5), and the cones are crowded against one another. Under these conditions, the hexagonal arrangement apparently gives way to the tetragonal. So far as I am aware, the tetragonal arrangement occurs only in connection with this crowding of the cones, a condition found for the most part only in macrurous Decapods.

In accounting for the rearrangement of the ommatidia, the eyes in the Stomatopod Gonodactylus afford some important evidence. As I have previously mentioned, the ommatidia in this genus are of two sizes. The larger ones have several of the peculiarities characterizing the tetragonal arrangement: their facets are generally square; they are arranged in single lines, and these lines, so far as the relations of the individual ommatidia are concerned, show evidences of having slipped upon one another. The smaller ommatidia have hexagonal facets, and are clearly arranged according to the hexagonal plan. The larger ommatidia are rather closely packed; the smaller ones are arranged with more open space between them (compare Plate VIII. Fig. 93). In this genus, then, as in the lobster, the tetragonal arrangement occurs in connection with the crowding of the ommatidia.

How an increase in size, accompanied by a crowding of the retinal elements, can induce the change in arrangement which seems to follow it, I am at a loss to explain. Nevertheless, the two phenomena appear to be in some way connected.

From the preceding discussion concerning the arrangement of the ommatidia, the following conclusions can be drawn. The ommatidia, when numerous enough, present one of two plans of arrangement, the hexagonal or the tetragonal. The hexagonal plan is phylogenetically the older, and is characteristic of the eyes of all Crustaceans except some families of the macrurous Decapods, especially the Galatheidæ, Palinuridæ, Astacidæ, and Carididæ. In these the hexagonal arrangement is usually replaced by the tetragonal; but in the adults of some species, especially those in which the eyes are partially rudimentary, the hexagonal arrangement persists. The change from the hexagonal to the tetragonal arrangement is connected apparently with an increase in size, and consequent crowding, of the ommatidia.

The Structure of the Ommatidia.

Each ommatidium, as I have previously mentioned, consists of a cluster of cells more or less regularly arranged about a central axis. The greatest number of kinds of cells which an ommatidium is known to contain is five. These are the cells of the corneal hypodermis, the cone cells, the proximal and distal retinular cells, and the accessory cells.

The cells of the corneal hypodermis are usually arranged in a very thin layer, and constitute the most superficial tissue in the retina. They either present no definite arrangement, as in Amphipods, or they are regularly grouped in pairs, one pair for each ommatidium, as in the majority of Crustaceans. On their external faces they produce the corneal cuticula. This is unfacetted in those Crustaceans in which the corneal cells are not regularly arranged and facetted when they are grouped in pairs.

The cone cells in each ommatidium are united to form the cone, a transparent body which extends from the corneal hypodermis proximally through the ommatidium at least as far as the rhabdome. The cone occupies the axis of the distal portion of the ommatidium.

The proximal retinular cells are usually limited to the proximal portion of the ommatidium. They are definitely arranged around the axial structure of that region, the rhabdome, and together with it form a single body, the retinula. The optic nerve fibres terminate in the proximal retinular cells.

The distal retinular cells are present in only the more differentiated ommatidia. They are two in number, and invest the sides of the cone distal to the plane at which this structure emerges from the retinula. When distal cells are present, the remaining cells of the retinula will be distinguished as proximal cells; when the distal cells are wanting, the other cells will be called simply retinular cells.

The accessory cells fill the space between the elements of an ommatidium, or between separate ommatidia. Their number is apparently inconstant, and they present a variety of forms. They may or may not contain pigment. Depending upon their source, two kinds can be distinguished, ectodermic and mesodermic.

In describing the ommatidia, I shall consider them according to the groups of Crustaceans in which they occur. Under each group the elements comprising the ommatidium will be described in the order in which they have just been mentioned.

My object in the following account is to determine, as far as possible, what the different kinds of ommatidial types are, and to define these types by a brief statement of the number and kinds of cells which characterize them.

Compound eyes are known to occur in some Ostracods, and in the larvæ of some Cirripeds, but their histological structure, I believe, has never been studied. I am therefore compelled to dismiss these two groups without further comment, and proceed with the description of the ommatidia in other Crustaceans. The order in which the groups will be considered is one which is intended to emphasize their relations only in so far as the structure of their ommatidia is concerned. Naturally, this order will vary somewhat from the one usually given in systematic treatises. I shall begin with the Amphipods.

Amphipoda.

Within recent years the more important types of eyes in the Amphipods have been studied with such care that the structure of their ommatidia is perhaps better known than that of any other large group of Crustaceans. My own observations do little more than confirm the accounts already published.

The species of Amphipods whose eyes I have examined are Gammarus ornatus, M. Edw., Talorchestia longicornis, Say, and an undetermined species of Caprella. Of these the specimens of Gammarus and Caprella were collected at Nahant, Mass., where I also obtained several sets of eggs representing stages in the development of the former. Examples of Talorchestia were kindly supplied me from the collections in the Museum.

The *corneal hypodermis* in Amphipods was first satisfactorily described by Claus ('79, p. 131) in his account of the eyes in Phronima. It is represented in this genus by a layer of undifferentiated cells lying between the corneal cuticula and the membrane which limits the distal ends of the cone cells. A corneal hypodermis similar to that in Phronima has likewise been described by Mayer ('82, p. 122) in Caprella and Protella, by Carrière ('85, p. 156) in Gammarus, by Claus ('87, p. 15) in the Platyscelidæ, by Della Valle ('88, p. 94) in the Ampeliscidæ, and by Watase ('90, p. 295) in Talorchestia. I have also identified this structure in Gammarus, Caprella, and Talorchestia.

In Gammarus, as Carrière ('85, p. 156, Fig. 121) has clearly shown, the corneal hypodermis at the edges of the retina is directly continuous with the general hypodermis. According to my own observations this condition is not only met with in Gammarus, but also in Caprella and Talorchestia.

In Phronima, according to Claus's figures ('79, Taf. VI. Figs. 48 and 49, *Ma Z.*), the arrangement of the cells in the corneal hypodermis bears no definite relation to the subjacent cones; the distal end of each cone presents an area which is covered by about a dozen hypodermal cells. In Gammarus I have observed (Plate I. Figs. 2 and 3) an essentially similar distribution of the hypodermal cells; as in Phronima, the number of cells which cover the area of each cone is about twelve. A corneal hypodermis of this same character also occurs in Talorchestia, although in this instance the number of cells over a cone is only about nine.

According to Watase ('90, p. 295), in the species of Talorchestia which he studied there were only two cells in the corneal hypodermis opposite each cone, or, as he expresses it, under each facet. When compared with the results recorded in the preceding paragraph, this observation appears somewhat striking, and the more so since two, the number of cells recorded, is the usual number found under each facet in other Crustaceans. If Watase's observation be correct, the relation which would thus be established between this Amphipod and other Crustaceans would be an interesting one. The desirability of confirming Watase's observation must, therefore, be evident; but unfortunately he has not given the name of the species of Talorchestia which he studied, and I have therefore not been able to verify his statement. In the only species of this genus which I have examined, viz. T. longicornis, the arrangement of the cells in the corneal hypodermis is very different from that described by Watase.

The conclusions which I draw from the preceding account are, that in the eyes of Amphipods a corneal hypodermis is present, and the cells composing it are usually not arranged with regularity.

The peculiar bodies observed by Schmidt ('78, p. 5) in the membrane between the corneal hypodermis and the retina proper in Phronima, and considered by Claus ('79, Taf. VI. Figs. 48, 49, *B. nu.*) as nuclei, are apparently not represented in other Amphipods. Their significance is still a matter of doubt.

The *corneal cuticula* in Amphipods has been described by almost all observers as unfacetted.[1] According to Della Valle ('88, p. 94), however, in some of the Ampeliscidæ this cuticula is facetted, and Watase ('90, p. 295) has also observed facets in Talorchestia. But with these two exceptions the corneal cuticula of Amphipods has been described

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[1] An unfacetted corneal cuticula has been recorded in the following genera of Amphipods: *Amphithoe* (Milne-Edwards, '34, p. 116); *Caprella* (Frey und Leuckart, '47^{a}, p. 103); *Cyamus* (Müller, '29, p. 58, Frey und Leuckart, '47, p. 205); *Gammarus* (Müller, '29, p. 57, Frey und Leuckart, '47, p. 205, Pagenstecher, '61, p. 31, Sars, '67, p. 61, Leydig, '78, p. 235, Grenacher, '79, p. 109); *Hyperia* (Gegenbaur, '58, p. 82, Grenacher, '79, p. 111, Carrière, '85, p. 160); *Phronima* (Pagenstecher, '61, p. 31, Schmidt, '78, p. 5, Claus, '79, p. 131); *Talitrus* (Grenacher, '79, p. 109); and the *Platyscelidæ* (Claus, '87, p. 15). I have observed an unfacetted corneal cuticula in *Gammarus, Caprella,* and *Talorchestia longicornis.*

as smooth. The absence of facets from Amphipods is naturally accounted for by the absence of a definite arrangement among the cells of the corneal hypodermis.

In the genus Tenais, the systematic position of which is probably somewhere between the Amphipods and Isopods, the corneal cuticula is stated by Müller ('64, p. 2) to be facetted, at least in the males. According to Blanc's ('83, p. 635) more recent observations, however, it is claimed to be unfacetted.

The *cones* in Amphipods have long been known to be segmented. The number of segments of which each cone is composed has been differently stated, however, by different observers. According to Claparède ('60, p. 211), the cones in Hyperia are each composed of four segments. This also is the number given by Sars ('67, p. 61) and by Leydig ('79, p. 235) for Gammarus. Both Hyperia and Gammarus have since been carefully studied, and these observations are now known to be inaccurate. Claparède was perhaps influenced in his statement by his belief that all cones were composed of four cells. Sars was probably misled by the supposed fact that in Gammarus the cone is surrounded by four bands of pigment, which sometimes give it the appearance of being divided into four segments.

The actual number of segments in the cone of Amphipods is two. This number was first recorded by Pagenstecher ('61, p. 31) for the cones of Phronima. Pagenstecher believed, however, that the cones in this Crustacean increased in numbers by division, and that they showed no indication of being composed of two segments except when they were undergoing this process. I need scarcely add that subsequent investigations have not confirmed Pagenstecher's belief. Cones composed of two segments have been observed in some six or seven genera of Amphipods.[1]

The *retinula* in Amphipods is stated by different observers to consist of either four or five cells. Five have been seen by Grenacher ('74, p. 653) and Carrière (85, p. 160) in Hyperia; by Grenacher ('79, p. 112), Claus ('79, Taf. VIII. Fig. 65), and Carrière ('85, p. 164) in Phronima; and by Mayer ('82, p. 122) in Caprella.

In Gammarus, Sars ('67, p. 61) observed that the cone had four

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[1] In *Caprella* (Mayer, '82, p. 122), in *Gammarus* (Grenacher, '79, p. 110, Carrière, '85, p. 156), in *Hyperia* (Grenacher, 74, p. 652), in *Oxycephalus* (Claus, '71, p. 151), in *Phronima* (Schmidt, '78, p. 5, Grenacher, '79, p. 112, Claus, '79, p. 130), in *Talorchestia* (Watase, '90, p. 296), and in the *Platyscelidæ* (Claus, '87, p. 15). In *Gammarus ornatus, Talorchestia longicornis,* and *Caprella,* each cone is composed of two cells.

longitudinal bands of pigment on it. Grenacher ('79, p. 110) took this as an indication that there were at least four retinular cells in the ommatidium of this genus, but he was unable to satisfy himself as to whether there were a greater number or not. Carrière ('85, pp. 156, 157) easily identified the four cells first seen by Sars, and in favorable cases observed what he thought might be indications of a fifth cell. In Gammarus ornatus, as the present observations show, the retinula is certainly always composed of five cells, one of which, as Carrière observed, is usually much smaller than the other four (compare *cl. rtn.'*, Figs. 4–7).

In Talorchestia, according to Watase ('90, p. 296), the retinula is composed of only four cells. I have studied T. longicornis with the purpose of determining the number of retinular cells, and I find that, although there are four large retinular cells, there is also one small one, which is even more reduced than in Gammarus. Hence I conclude that the total number of retinular cells in an ommatidium of Talorchestia is five, not four.

Claus's statement ('71, p. 151), that in Oxycephalus the retinula is usually composed of four cells, is probably inaccurate, as Grenacher ('79, p. 114) suggests; and the same is perhaps true of Della Valle's ('88, p. 94) observation, that in the Ampeliscidæ the retinulæ contain only four cells each. It is therefore probable that the retinula in all Amphipods is composed of five cells, although possibly in some exceptional cases the number may be four.

The retinular cells in Gammarus envelop the sides of the cone, as Carrière suspected, and extend distally as far as the corneal hypodermis (Plate I. Fig. 2). In Hyperia and Phronima, according to the description and figures given by Carrière ('85, p. 161, and Fig. 128, p. 165), these cells appear to be limited to the proximal part of the retina.

The *rhabdome* in Amphipods, first described by Pagenstecher ('61, p. 30) as the cylindrical element in the eye of Phronima, presents a very simple structure. In Hyperia, according to Grenacher ('77, p. 31), it is a simple rod-like body, composed of five rhabdomeres, one for each retinular cell. In Phronima, as Claus ('79, p. 128) has shown, the rhabdome is a tubular structure with five sides. Each side of the tube, as can be seen in the figure given by Carrière ('85, p. 165, Fig. 128), corresponds to a rhabdomere. In Gammarus locusta, Grenacher ('77, p. 111) has shown that, in transverse section, the distal end of the rhabdome is cross-shaped. In G. pulex, according to Carrière ('85, p. 157), the distal end of the rhabdome in section shows four rays, the proximal five. In Carrière's opinion, these rays indicate the five rhabdomeres. In Gammarus ornatus, the species which I have studied, the rhabdome (Plate I. Fig. 6, *rhb.*) is cross-shaped in transverse section throughout its length. Each rhabdomere has the form of an elongated plate, which is folded on its longest axis, so that its halves are at right angles to each other. In the rhabdome, the four rhabdomeres lie so that their folded edges occupy the axis of the ommatidium. Each of the four large retinular cells rests in the furrow produced by the folding of a rhabdomere (compare Fig. 6). The fifth retinular cell always lies at the end of one arm of the cross-shaped rhabdome. The two rhabdomeric constituents of that arm usually separate slightly, so as to allow the small retinular cell to slip in between them. Possibly this cell produces a small rhabdomere, as the corresponding cell in G. pulex does; but if such is the case, the rhabdomere must be a very small one, for I have not been able to discover it. A rhabdome of essentially this structure occurs in Talorchestia.

As the preceding account shows, the rhabdome in Amphipods always presents some indication of the number of rhabdomeres of which it is composed. This number is usually five, although it is possible that in Gammarus it may be only four.

In addition to the cells which have thus far been described as entering into the composition of the retina in Amphipods, certain other cells may be present. These may be embraced under the one head of *accessory pigment cells.*

In Gammarus, as Carrière ('85, p. 159) has shown, the space between the ommatidia is filled with rather large cells, the nuclei of which are usually visible with ease (Fig. 2, *nl. h'drm.*). These cells extend from the basement membrane very nearly, if not quite, to the corneal hypodermis. In the fresh condition they contain a whitish opaque pigment. On account of their having no definite arrangement, it is difficult to estimate their number, but there are probably two or three for each ommatidium. Cells similar in position to these have been described by Watase ('90, p. 296) in Talorchestia.

In Hyperia there are apparently three kinds of accessory pigment cells. One kind occurs in the region of the basement membrane (Carrière, '85, p. 161, Fig. 124, *m.*); another kind surrounds the proximal portion of the cones (Carrière, '85, p. 161); a third kind is applied to the retinulæ, and, according to Carrière, exactly equals in number the cells of the retinula itself. Possibly the cells which Grenacher ('79, p. 112) described as lying at the distal end of the retinula in Hyperia belong to this third kind, although, as must be remembered, Grenacher states that there are only two such cells for each ommatidium.

These three kinds of accessory pigment cells, with the possible exception of those which surround the retinula, occur in the lateral eyes of Phronima (Carrière, '85, p. 164).

Almost nothing is known about the source of the accessory pigment cells in Amphipods. Those in Gammarus have no resemblance to the loose mesodermic tissue which lies in the neighborhood of the eye, and they are probably derived from the original ectodermic thickening which gave rise to the retina. Although some of the accessory pigment cells in Hyperia and Phronima have been called connective-tissue cells (Claus, '79, p. 125, Carrière, '85, p. 160), a name which might be taken to imply that they have come from a mesodermic source, nothing is really known about them which would be inconsistent with an ectodermic origin.

From the foregoing account of the ommatidia in Amphipods the following summary can be made: cells of the corneal hypodermis not definitely arranged, from about nine to twelve, — possibly two to each ommatidium; cone cells, two; retinular cells, five, — possibly in some cases four; accessory pigment cells (ectodermic ?) present. Of these last there may be only one kind, as in Gammarus and Talorchestia, or there may be three kinds, as in Hyperia.

Phyllopoda.

The ommatidia in the eyes of Phyllopods present at least two structural types, one of which obtains in the Branchiopodidæ and Apusidæ, the other in the Estheridæ and Cladocera. On account of the greater convenience, the eyes in the Apusidæ and Branchiopodidæ will be considered first, then the eyes in the Estheridæ, and finally those in the Cladocera.

Branchiopodidæ and Apusidæ. — The ommatidia in these two families, and especially in the Branchiopodidæ, have been carefully studied by a number of competent investigators; their structure is consequently well known.

The material which I used in studying these eyes consisted of specimens of Branchipus, probably B. vernalis, Verrill, which I had collected in the neighborhood of Philadelphia, and which had been preserved for some time in strong alcohol. Through the kindness of Dr. W. A. Setchell, I was also able to examine a specimen of Apus lucasanus, Packard.

A *corneal hypodermis* has been described by Claus ('86, pp. 321, 322) in Branchipus and Apus. In Branchipus torticornis, according to Claus, the nuclei of the hypodermal cells are arranged around the distal end of each cone in circles of six; each nucleus participates in three circles, so that there are in reality only twice as many hypodermal cells as there are ommatidia. The corneal hypodermis in the eye of Branchipus vernalis (Plate IV. Fig. 30, *nl. h'drm.*) is similar to that described by Claus in B. torticornis. According to Patten ('86, p. 645), a corneal hypodermis is present in Branchipus Grubii, but the cells, instead of being regularly placed, as in either Branchipus torticornis or B. vernalis, are stated to be indefinitely arranged.

The *corneal cuticula* in Apus is described as unfacetted by Müller ('29, p. 56), Burmeister ('35, p. 533), Zaddach ('41, p. 46), and Frey und Leuckart ('47, p. 205). In Branchipus stagnalis the cuticula is smooth according to Spangenberg ('75, p. 30), marked by concavo-convex facets according to Grenacher ('79, p. 114), and smooth externally but facetted internally according to Leydig ('51, p. 295). This difference of opinion is probably due to the fact that in this species the facets are so poorly developed that their form can be determined only with difficulty. In Branchipus vernalis, although the corneal cuticula is facetted, the facet is not thickened in its centre, but has the form of a simple concavo-convex elevation, as described by Grenacher in B. stagnalis. In Branchipus paludosus according to Burmeister ('35, p. 531), in B. torticornis according to Claus ('86, p. 320), and in B. Grubii according to Patten ('86, p. 645), the corneal cuticula is unfacetted.

The *cone* in Branchipus, as Spangenberg ('75, p. 30) first demonstrated, is composed of four segments. This observation has since been confirmed by Grenacher ('79, p. 115), Claus ('86, p. 320), and Patten ('86, p. 645). In Branchipus vernalis (Fig. 31, *con.*) the cone, according to my observation, consists of four segments. The cellular nature of each segment was first clearly stated by Grenacher. Each cone in Apus, according to both Grenacher ('79, p. 115) and Claus ('86, p. 321), is composed of four cells.

The *retinula* in both Apus and Branchipus consists of five cells. This number has been seen in both genera by Grenacher ('74, p. 653) and by Claus ('86, p. 319). Spangenberg, however, ('75, p. 31) counted *four* nuclei in the retinula of Branchipus. Since these unquestionably represent the nuclei of the retinular cells, and since these cells are usually five in number, Spangenberg's enumeration is probably inaccurate. Possibly he was influenced when counting the nuclei by his belief that the number four was characteristic of many structures in the ommatidium. In Branchipus vernalis (Plate IV. Fig. 32, *cl. rtn.'*) the retinula contains five cells.

The *rhabdome* in Apus is short; in Branchipus (Fig. 30, *rhb.*) it is relatively long. In transverse section (Fig. 32, *rhb.*) it is circular, or at times squarish, but never pentagonal, as might be expected from the fact that it is surrounded by *five* retinular cells.

The retina in B. vernalis contains no other cells than the three kinds already described. According to Claus ('86, p. 319), blood corpuscles may make their way into the base of the retina of B. torticornis.

From the preceding account, the number of cells in the ommatidia of the Branchiopodidæ and Apusidæ can be stated as follows: cells of the corneal hypodermis, usually two, possibly variable in number in some species; cone cells, four; retinular cells, five. In Branchipus torticornis the interommatidial space may contain blood corpuscles.

Estheridæ. — The species which I studied as a representative of this family was Limnadia Agassizii, Packard. This species can usually be obtained in great abundance during summer in small fresh-water pools in the neighborhood of Wood's Holl, Mass., where my material was kindly collected for me by Mr. W. M. Woodworth.

The external surface of the retina in Limnadia, as I have mentioned in my account of the general structure of the eye in this genus, is covered with an extremely delicate corneal cuticula. This cuticula does not show the least trace of facets.

Immediately below the corneal cuticula are numbers of small nuclei (Plate IV. Fig. 37, *nl. crn.*). These, from their position, are probably to be regarded as the nuclei of the corneal hypodermis. They are not regularly arranged, and, although they sometimes lie between the cuticula and the distal end of a cone, they more frequently occur next to the cuticula in the spaces between the cones.

As a rule, each *cone* in Limnadia is composed of *five* cells (Plate IV. Figs. 37 and 38). In this respect it resembles the cones in Estheria californica and E. tetracera described by Lenz ('77, p. 30). In Limnadia Agassizii, however, cones composed of *four* cells are not infrequently met with (compare Figs. 37 and 38). Grube's ('65, p. 208) observation that the cone in Estheria is composed of two segments is probably erroneous, but Claus's ('72, p. 360) statement that in Limnadia the cone consists of four segments may be accurate, contrary to the opinion of Lenz.

The *retinular cells* in Limnadia cover the greater part of the sides of the cones, and completely hide the rhabdome (Plate IV. Fig. 36). Their number can be determined in transverse sections in the region of the rhabdome. In such sections each rhabdome is surrounded by five retinular cells (Fig. 39, *cl. rtn.'*). Occasionally nuclei can be distinguished in the pigment about the base of the cone. These are probably the nuclei of the retinular cells.

Besides the elements thus far enumerated, the retina in the Estheridæ is not known to contain other kinds of cells. The cells in the ommatidia of this family are, therefore, as follows: cells of the corneal hypodermis, not regularly arranged; cone cells, usually five, sometimes four; retinular cells, five.

Cladocera. — The extreme minuteness of the ommatidia in the eyes of the Cladocera renders their study especially difficult. In an undetermined species of Evadne which I have studied, the ommatidia are comparatively large, and in this respect are especially favorable for investigation. In the particular specimens which I used, however, I was entirely unsuccessful in all attempts to differentiate the nuclei. Although I tried a number of dyes and reagents, I was never able to make these structures visible. In consequence of this, there are several important questions concerning the eyes in the Cladocera which I have not been able to answer.

It is reasonable to believe that a corneal hypodermis much like that in Limnadia is present in Evadne, but, probably on account of my inability to stain the nuclei, I have seen no traces of it.

The *cones* in Evadne are very clearly composed of five segments (Plate IV. Figs. 41, 42). At their distal ends the cone cells are expanded so that their peripheral membranes (Fig. 41, *mb. pi'ph.*) are in contact with one another. At this level, however, the substance of the cone proper is collected about the axis of the ommatidium. Proximally the peripheral membranes of each cone contract, and under these circumstances the cavity of each cone cell is apparently filled completely with the differentiated material of the cone itself (Fig. 42).

A cone composed of five segments has been observed in a considerable number of Cladocera. Thus it is known to occur in Bythotrephys (Leydig, '60, p. 245, Claus, '77, p. 144), Daphnia (Spangenberg, '76, p. 522, Grenacher, '79, p. 117), Polyphemus, Evadne (Claus, '77, p. 144), Podon (Grenacher, '79, p. 117), and Leptodora (Carrière, '84, p. 678). Weismann's assertion ('74, p. 364) that the cone in Leptodora is composed of four segments is disproved by Carrière's later observations, and

Claus's statement ('76, p. 372) that the same number of segments occurs in the cone of Sida is probably erroneous. There is, therefore, reason to believe that the cones in the Cladocera are always composed of five segments.

The composition of the *retinula* in Cladocera, so far as I am aware, has never been fully worked out. In Evadne, on account of the relatively large size of the ommatidia, the number of cells in the retinula can be determined. At the proximal end of the cone, this structure is surrounded by *four* distinct masses (Fig. 43). The regularity with which these masses occur leaves no doubt as to their number. Each one probably represents a retinular cell. In transverse sections made through the rhabdome (Plate IV. Fig. 45), this structure is surrounded by *five* bodies, each one of which I take to be a retinular cell. It is therefore probable that the retinula of Evadne is composed of five cells, four of which approach nearer the surface of the eye than the fifth.

In Evadne I have seen no evidence of the existence of other cells than those belonging to the cone and retinula. According to Carrière ('84, p. 678), the interommatidial space in Leptodora contains a number of cells which envelop the cones more or less completely. These are probably to be regarded as accessory pigment cells.

From the foregoing account the following general statement can be made for the ommatidia in the Cladocera: corneal hypodermis, not observed; cone cells, five; retinular cells, five (in Evadne); accessory pigment cells present (in Leptodora).

Copepoda.

I have studied the lateral eyes in Pontella and Argulus, as representatives of the Copepods. As is well known, the eyes in these two genera differ greatly in structure, and I shall therefore describe them separately, beginning with the eyes in Pontella.

Eucopepoda. — The species of Pontella which I studied was extremely abundant at Newport in August, 1890. This animal was so transparent when living, that the general structure of its eyes could be ascertained by a simple microscopic inspection of it. In addition to its median eye, which occupies a ventral position, it possesses a pair of lateral eyes (compare Claus, '63, Taf. III. Fig. 5) situated one on either side of the sagittal plane at the antero-dorsal angle of the head.

Each lateral eye in Pontella, as Claus ('63, p. 47) has already stated, is provided with a spherical lens (Plate II. Fig. 18, *lns.*), which is usually firmly attached to the superficial cuticula. Immediately behind this lens, and in fact covering much of its proximal face, is a rather irregular mass of cells, the retina. In the living animal the cells of the retina contain a great quantity of black or reddish black pigment. This coloring matter, however, is so readily soluble in alcohol, that in specimens preserved in that fluid all traces of it disappear. The optic nerve (*n. opt.*, Fig. 18), an imperfectly defined bundle of fibres, emerges from the retina near its posterior dorsal edge, and passes directly backward to the brain.

The lenses of the two lateral eyes in Pontella are so near each other that their median faces are almost in contact (compare Plate III. Fig. 29). The retinas of the two eyes, as Claus ('63, p. 47) has observed, are united with one another on their median faces, and so intimately that they are apparently incapable of independent motion.

The two retinas together may be rotated on their lenses through an angle of about forty-five degrees. The plane of this rotation corresponds to the sagittal plane of the body, and the rotation is accomplished by two pairs of muscles, one for each retina (compare Claus, '63, Taf. III. Fig. 6). One pair of these muscles is shown in Figure 18. They occupy a plane approximately parallel to the sagittal plane of the body, and the effects of their contractions must be apparent from their positions. When both muscles are relaxed, the retina occupies a position substantially as shown in Figure 18. By the contraction of the posterior muscle, the retina may be drawn upward and backward over the surface of the lens, till its axis, instead of pointing dorsally, is directed forward and upward at an angle of about forty-five degrees with its original position. The retina is not usually held for any great length of time in this position, but is soon returned by the contraction of the anterior muscle to its normal place. The backward motion of the retina is accomplished with such rapidity that the animal has the appearance of winking. The forward motion is rather slower.

Each lens in Pontella is composed of concentric laminæ (Plate III. Fig. 29, *lns.*). A considerable portion of its distal surface is intimately connected with the superficial cuticula (Plate II. Fig. 18), although a line of demarcation between lens and cuticula can always be distinguished.

When the anterior half of the body of Pontella is boiled in a strong aqueous solution of potassic hydrate, and afterwards subjected to the action of concentrated nitric acid, all the soft parts are dissolved, and only the very resistant chitinous structures remain. In specimens treated in this way, the lenses retain their firm connection with the superficial cuticula, and differ in appearance from those in the living animals only in that their concentric lamellæ are somewhat more distinct. The fact that the lens is composed of concentric layers indicates that it is secreted, and the resistance which it offers to reagents is weighty evidence in favor of its chitinous nature. In my opinion, therefore, the lens in Pontella is a chitinous secretion.

The development of the lens in Pontella is rather peculiar. Apparently a new lens is formed with each moulting of the general cuticula; at least, in a rather large proportion of the number of individuals examined, the lenses were abnormally small, having a diameter of one third or even one fourth of that shown in Figure 18. Moreover, in all such individuals the superficial cuticula was correspondingly thin and delicate, and when the animal was subjected to boiling potash, the segments of its body and appendages separated with a readiness never observed in specimens with large lenses. There can be no doubt, I believe, that the small lenses are always accompanied by thin cuticula, a relation which is to be explained by the immature condition of both structures.

The smaller lenses differ from the larger ones in only one important particular besides that of size. They are not in contact with the superficial cuticula. This relation can be determined better in optical sections than in actual ones, for in the latter the position of the lens is usually somewhat changed by the resistance which it offers to the knife. The centre of the small lens occupies a position relatively the same as that of the large lens, the space between the surface of the small lens and the external cuticula being filled with a cellular mass. This mass, as seen in optical sections, apparently envelops the lens on all sides, and is undoubtedly composed of the cells which secrete that structure. As the lens increases in size, the cells are probably excluded from the region between it and the cuticula, and as they retreat cement the lens to the cuticula. Upon the completion of the lens, the cells which have shared in producing it probably withdraw slightly from it to form the hypodermal thickenings which occur beneath the adjoining cuticula (Plate II. Fig. 18, and Plate III. Fig. 29, *h'drm.*). These thickenings are rich in nuclei, and often have delicate strands of protoplasm stretching to the surface of the lens (Fig. 18).

I believe that these facts justify the opinion that the lenses in the lateral eyes of Pontella are composed of chitin, that they are produced unconnected with the superficial cuticula, and that they are secondarily cemented to it. Like the cuticula itself, they are products of the hypodermis, a new lens being generated in all probability with each new formation of cuticula.

Lenses similar in position to those in Pontella have been identified in the lateral eyes of several other genera of Copepods. Gegenbaur ('58, p. 71) described such lenses in Sapphirina, and Leuckart ('59, p. 250) observed similar ones in the lateral eyes of Corycæus and Copilia. In all these genera the lenses, although biconvex, are not spherical, as in Pontella. Gegenbaur ('58, p. 71), following Leydig's generalization, believed that in Sapphirina the lenses were thickenings in the cuticular covering of the body, and Claus ('59, p. 271) considered them morphologically equivalent to a single corneal facet. Leuckart ('59, p. 250), without definitely committing himself as to the nature of the lens, states that in Copilia and Corycæus the lens is implanted in the superficial cuticula, and further describes it in Corycæus as composed of two parts, an outer and an inner. According to Grenacher ('79, p. 67), both parts can be identified in the lens of Copilia; the outer part is a portion of the superficial cuticula; the inner part, both in its optical properties and its behavior toward reagents, is unlike the cuticula. The inner part, however, contains no traces of cells, but is composed of a homogeneous substance, probably secreted. This view of the duplicity of the lens contrasts with the older idea of its origin as a thickening in the superficial cuticula.

It is possible that the lenses in the Pontellidæ and Corycæidæ are not homologous structures, but on account of their similarity I am inclined to consider them as such. Since in Pontella both parts are derived from the cuticula, I believe that a similar origin will be demonstrated for these parts in the Corycæidæ. The differences which Grenacher has pointed out between the two parts of the lens in Copilia do not necessarily oppose this view. It is possible that the cuticular secretion which forms the proximal part of the lens may originate separately from the other cuticula, as in fact it does in Pontella; and it may also be true, although this is not supported by the condition in Pontella, that the two parts, although both secretions of the hypodermis, may differ enough in their substance to account for all the peculiarities observed by Grenacher.

The *retina* and lens in Pontella are not separated by an intervening space as in the Corycæidæ, but are in immediate contact. The retina is composed of a mass of cells, the number and arrangement of which can be seen in the figures on Plate III. These figures represent a series of consecutive sections cut in planes transverse to the axis of the eye, i. e. parallel to the horizontal plane of the animal (compare Fig. 18, Plate II.). The series is complete in that it represents all the sections which pass through the retina. The most ventral section is shown in Figure 20, the most dorsal in Figure 29.

Immediately below the lens the central part of the retina is occupied by a roundish granular mass (Fig. 18, *con.*), which in the living animal is the only part without pigment. In transverse sections this mass is seen to consist of two bodies (*cl. con. 1,* and *cl. con. 2*, Fig. 25), which extend as far as to the lens (compare Figs. 25–27). Each body contains a nucleus (*nl. con.*, Figs. 25 and 27) and consequently represents a cell. From the position which the mass occupies, and from the fact that it contains no pigment, it represents, I believe, a cone, and the two cells of which it is composed are its two segments.

Claus ('63, p. 47) states that in Pontella each retina is provided with six or more small crystalline cones, but my own observations do not confirm this statement. The body which, on account of its position, I have described as the cone in Pontella, is probably homologous with what Dana ('50, p. 133) first described as the inner lens in Corycæus, and with what subsequent investigators have called the crystalline cones in Sapphirina (Gegenbaur, '58, p. 71) and Copilia (Leuckart, '59, p. 252). Nothing, I believe, is known of the cellular composition of the cone in these genera.

The arrangement of the elements in that portion of the retina which surrounds the cone in Pontella is not easily made out. The most conspicuous structures in this region are rod-like bodies, which probably represent rhabdomeres. Eight of these, arranged in three groups, are present in each retina. The largest group, composed of five rods, lies directly beneath the cone. The rods of this group have been numbered from one to five in the retina to the left in Figures 21, 22, and 23. Posterior to this group, in the same retina, is the sixth rod, seen in Figures 24, 25, and 26. Anterior to it are the seventh and eighth rods, seen in Figures 26, 27, 28, and 29.

The outlines of the cells to which these rods belong cannot always be distinguished; that there is a cell for each rod is evident from the fact that near each rod there is a large nucleus. The nucleus belonging to the cell from which the eighth rod was produced is shown in Figure 28 (*nl. rtn.'*); those belonging to the cells from which the sixth and seventh rods arose are indicated in Figure 26 (*nl. rtn'.*), and those belonging to the cells from which the central group of five rods came are seen, four in Figure 24 and one in Figure 25 (*nl. rtn.'*).

In addition to these nuclei, which judging from their positions and number are unquestionably the nuclei of the cells to which the rhabdomeres belong, the retina contains a number of smaller nuclei (Fig. 21, *nl. h'drm.*). These nuclei have been drawn in the figures of the various sections in which they occur, and probably represent undifferentiated cells.

To what extent the retina of Pontella can be resolved into ommatidia may be seen from the foregoing account. Evidently the two cone cells, the subjacent groups of five retinular cells, and probably some of the undifferentiated cells, are the equivalent of one ommatidium. The sixth cell, with its rod, is probably the representative of a second ommatidium, and the seventh and eighth cells are probably representatives of one, or perhaps two, more.

If this interpretation be correct, the cells in the one complete ommatidium in Pontella would be as follows: corneal hypodermis, undifferentiated; cone cells, two; retinular cells, five; undifferentiated pigment cells (ectodermic?) present.

Each retina in Sapphirina, according to Grenacher ('79, pp. 69, 70), contains one group of three rhabdomeres. These are accompanied, as in Pontella, by an equal number of large nuclei. The body designated at *y*, and perhaps some of those marked *x*, in Grenacher's figure of Sapphirina (Fig. 43), may also represent isolated rhabdomeres. In Copilia, Grenacher believes that the number of rhabdomeres in each retina is three. Possibly in this genus, as in Sapphirina, the body marked *x* by Grenacher (Taf. VI. Fig. 40) may represent an isolated rhabdomere. Grenacher's observations, when coupled with what I have seen in Pontella, show that in Copepods the number of retinal elements is open to considerable variation, and that what would correspond to the retinula in Sapphirina, and perhaps in Copilia, consists of a cluster of only three cells, instead of five, as in Pontella.

Branchiura. — The ommatidia in Argulus are rather small, and their structure is consequently imperfectly known. The specimens of this Crustacean which I studied were obtained from an aquarium in which the common Killifish, Fundulus heteroclitus, had been kept. I have not been able to determine the species to which these specimens belong.

The *corneal hypodermis* in Argulus is separated from the retina proper by a space filled with blood (Plate II. Figs. 11, 12, *cœl.*). The cells in this layer (Fig. 12, *h'drm.*), as in the corneal hypodermis of Amphipods, are not arranged in groups, but are irregularly scattered. On their distal faces they produce the corneal cuticula (Fig. 12, *cta.*), which, as Müller ('31, p. 97) observed, is without facets. Proximally they are separated from the blood space by the delicate corneal membrane (Fig. 12, *mb. crn.*).

The distal face of the retina proper in Argulus is bounded by a delicate preconal membrane (Figs. 11–13, *mb. pr'con.*) and its proximal face is limited by the basement membrane (Figs. 11–13, *mb. ba.*).

The most conspicuous objects in the retina are the *cones* (Fig. 11, *con.*), which lie with their distal ends usually somewhat below the preconal membrane (Fig. 13). Each cone, as Claus ('75, p. 256) has observed, is composed of four segments (Fig. 14). The segments correspond to cells, and although the cone itself terminates proximally before reaching the rhabdome, the cone cells form an axis free from pigment and extending from the cone to the rhabdome (compare Fig. 12). In depigmented sections the peripheral membranes of the cone cells (Fig. 13, *mb. pi'ph.*) can be distinguished as sharply marked lines which extend from the sides of the cone to the sides of the rhabdome. The intercellular membranes of the cone cells in the region between the cone and rhabdome are apparently marked by thickenings which appear in both longitudinal and transverse sections (compare Figs. 13 and 15). At the distal end of the rhabdome the four cone cells separate, and, after passing partly around the rhabdome, become lost in the adjoining tissue (Fig. 16, *cl. con.*). I have not been able to discover the nuclei of the cone cells.

It is difficult to determine the number of cells in the *retinula* of Argulus. Slightly below the proximal end of the rhabdome, the retinula is divided into five distinct pigmented masses (Fig. 17, *cl. rtn.'*). Since the rhabdome (Fig. 16, *rhb.*) is composed of five rhabdomeres, it is highly probable that the retinula consists of five cells; but I have not been able to determine with precision the outline and extent of these cells.

The nuclei which are visible in the retina of Argulus closely resemble one another. They are limited for the most part to two regions (Fig. 13), one near the level of the cones, the other near the basement membrane. Apparently there are no nuclei immediately below the preconal membrane. Those which are near the cones (Figs. 13, 14, *nl. h'drm.*), judging from their arrangement and position, probably represent interommatidial pigment cells. Those near the basement membrane (Fig. 13, *nl. rtn.'*) may be the retinular nuclei, as their position seems to indicate. For some distance proximal to the basement membrane, nuclei (Fig. 13, *nl. h'drm.'*) occur among the nerve fibres. Possibly they represent scattered cells in this region, but the strong resemblance which they have to the nuclei on the distal side of the membrane induces me to believe that they too are retinular nuclei, which, as in the Amphipods, have migrated to a position below the basement membrane.

The cells in the ommatidium of Argulus are as follows: cells of the corneal hypodermis, not arranged in definite groups; cone cells, four; retinular cells, probably five; accessory pigment cells probably present.

Isopoda.

The material which I used in studying the eyes in Isopods came from several sources. I collected specimens of Asellus and Porcellio in the neighborhood of Cambridge, and the two species of Idotea which I studied were obtained at Newport. Specimens of Serolis Schythei, Lütken, and of an undetermined species of Sphæroma, were kindly furnished me from the collections in the Museum.

The ommatidia in Isopods present two types of structure: one of these is characteristic of the eyes in a majority of the members of this group; the other, so far as is known, is represented only in the genus Serolis. These two types will be considered separately, and the one which is common to the greater number of Isopods will be described first.

The *corneal hypodermis* in the more common of these two ommatidial types was first identified by Grenacher. In Porcellio, according to this author ('79, p. 107), the proximal surface of each facet is covered with two comparatively thin cells. These are the cells of the corneal hypodermis. Bellonci ('81ª, p. 98, Tav. II. Fig. 11 n.) figures similar cells in the ommatidium of Sphæroma, and Beddard ('90, p. 368) concludes justly, I believe, that, of the four nuclei found near the distal end of the cone in Arcturus, two represent cone cells and two cells in the corneal hypodermis. In Idotea irrorata I have identified two cells in the corneal hypodermis for each ommatidium. The nuclei of these cells lie very near the nuclei of the cone cells (compare *nl. con.* and *nl. crn.* in Figs. 50 and 51, Plate V.). In an ommatidium of Porcellio, Grenacher ('79, pp. 107, 108) observed that the plane which separates the two cone cells also separates the two cells in the corneal hpyodermis. In Idotea, also, both kinds of cells are separated by a single plane.

The facetted condition of the *corneal cuticula* of Isopods was observed as early as 1816 by G. R. Treviranus ('16, p. 64), in wood-lice, and subsequently in the same animals by Lereboullet ('43, p. 107, '53, p. 119). The shape of the facets in different Isopods has given rise to some difference of opinion. According to Müller ('29, p. 42), in Cymothoa each has the form of a biconvex lens. Leydig ('64ª, p. 40) states, however, that in Oniscus the facets are concavo-convex with their hollow faces innermost. In Asellus, according to the figure given by Sars ('67, Planche VIII. Fig. 14), they are plano-convex with their flat faces innermost. These differences, although at first sight somewhat contradictory, are not matters of great importance, for it is probable that each time an Isopod sheds its cuticula and a new one is formed, the lens assumes, at successive stages of its growth, outlines which coincide very closely with those recorded by the different observers. Thus, an early stage would be represented by the concavo-convex lens described by Leydig, an intermediate stage by the plano-convex lens figured by Sars, and the final condition by the biconvex lens mentioned by Müller. Either this is the explanation of the differences, or the observations of Leydig and Sars are probably erroneous, for the results of the more recent investigations point to the conclusion that the facets in Isopods have the form of a biconvex lens. Facets of this shape have been seen by Grenacher ('77, p. 29) in Porcellio, and by Bellonci ('81^a, p. 98) in Sphæroma. According to my own observations, they also occur in Idotea, Asellus, Porcellio, and, as I shall show subsequently, in Serolis. In the four genera mentioned the inner face of each facet is distinctly convex; this is also true of the outer face in Asellus and Porcellio. In Serolis and Idotea (Plate V. Fig. 50), however, the outer face is so slightly curved that it is difficult to decide whether its curvature is that of the general corneal cuticula or one peculiar to the facet itself.

That the *cone* in Isopods is composed of two segments was first observed by Leydig ('64^a, p. 41, and '64, Taf. VI. Fig. 8) in Oniscus. According to this author, each segment is spherical. Each ommatidium, therefore, contains two spheres, and these, as Leydig's figure shows, are placed side by side immediately below the corneal facet.

It is now well known that in many Isopods, especially in the woodlice, the cone itself is nearly spherical, and its two segments would consequently be hemispheres, not spheres as figured by Leydig. How Leydig's statement of the spherical shape of the segments can be accounted for, is not apparent. Since the two spheres described by him occupy the same relative positions as the hemispherical segments of a normal cone, there is not much question in my mind that they represent these segments. Possibly their separation and spherical form may have been due to the swelling action of some reagent which Leydig may have used to make the tissue transparent. A cone composed of two segments has been observed by Sars ('67, p. 110) in Asellus, by Leydig ('78, p. 256) in Ligidium, by Grenacher ('77, p. 29) in Porcellio, by Bellonci ('81^a, p. 98) in Sphæroma, by Sye ('87, p. 23) in Jæra, and by Beddard ('90, p. 368) in Arcturus. In the three genera which I have examined, Idotea, Asellus, and Sphæroma, each cone consists of two segments.

These observations naturally lead to the conclusion that in all Isopods each cone is composed of two segments. To this general statement, however, there are two noteworthy exceptions, one recorded by Sars, the other by Beddard. Sars ('67, p. 110) has shown that, of the four ommatidia in each eye of Asellus aquaticus, three have cones composed each of two segments; in the fourth, however, the cone is divided into three parts. This observation has been confirmed by Carrière ('85, p. 155). It is important to observe that in the figure given by Sars ('67, Planche VIII. Fig. 12) the three parts of the cone are not of equal size; one is about as large as a single segment in the cones of the other three ommatidia, whereas the remaining two are each about half as large. In the eyes of the species of Asellus found about Cambridge, the ommatidia are usually twice as numerous as in the European species, A. aquaticus, and, so far as I could observe, the cones in the American species were always composed of only two segments. In Arcturus, according to the figures given by Beddard ('90, Plate XXXI. Figs. 1 and 4), cones of three segments are occasionally met with.

The cellular composition of the *retinula* in Isopods was first made out by Grenacher ('74, p. 653), who found that in Porcellio this structure consisted of seven cells. Distally these cells surround the cone; proximally they are continuous with the optic-nerve fibres. A retinula consisting of seven cells has also been demonstrated by Buller ('79, p. 513) in Cymothoa, and by Beddard ('88, p. 443) in Æga and Ligia. As Beddard ('88, Plate XXX. Fig. 13) has shown, the seven cells in the retinula of Æga pass through the basement membrane and become continuous with the nerve fibres. In Porcellio, as I have observed, the fibrous ends of the seven retinular cells not only can be identified as nerve fibres below the basement membrane, but each cell contains a well developed fibrillar axis (Plate V. Fig. 46, *ax. n.*), and I therefore conclude that in Porcellio all seven cells are functional as nervous elements.

In Idotea robusta, transverse sections of the retinula in the region where the rhabdome is thickest present the outlines of what seem to be *seven* retinular cells (Plate V. Fig. 48). In positions either distal or proximal to this, however, only *six* cells appear. These six cells pass through the basement membrane and taper into nerve fibres, and their nuclei, unlike the corresponding nuclei in other Isopods, occur in that part of the cell which is proximal to the basement membrane (Figs. 49 and 50, *nl. rtn'.*). The seventh body (Fig. 48, *cl. rud.*), in those sections in which it occurs, has in all essential respects the same appearance as any one of the adjoining six cells. It differs from these, however, in that it is usually somewhat smaller, and I therefore conclude that it is a rudimentary cell. It does not appear to contain a nucleus; granting, however, that it is a rudimentary retinular cell, one would look for its nucleus, not in the region about the rhabdome, but in the region of the nuclei of the other retinular cells, i. e. proximal to the basement membrane. Owing to the irregularity with which the fibrous ends of the retinular cells are arranged in this region, I have not been able to identify any nucleus with this rudimentary cell. Neither have I found any fibrous projections reaching from the rudiment of the cell toward the basement membrane such as might be expected provided the nucleus and a part of the rudimentary cell persisted below the membrane. Nevertheless, I believe, for the reasons already stated, that the retinula in Idotea robusta is composed of seven cells, one of which is extremely rudimentary.

In Idotea irrorata (Plate V. Figs. 53, 55) the retinula consists of only six cells, all of which possess fibrillar axes, and are therefore probably functional as nervous structures. In one retina of the several pairs of eyes which I examined, there was a single ommatidium with *seven* functional cells (Fig. 54). With this one exception, however, I have not been able to find any trace of the seventh cell in Idotea irrorata. In Arcturus, according to Beddard ('90, p. 368), the retinula is also composed of six cells.

In Sphæroma, Bellonci ('81, p. 98, Tav. II. Fig. 12) has figured and described a retinula consisting of *five* cells. These cells alternate with five other cells, which probably represent accessory pigment cells. If Bellonci's statement is correct, it must be admitted that the number of cells in the retinulæ of Isopods may be as few as five. My own observations, however, do not confirm Bellonci's account. In the species of Sphæroma which I have studied, there are *seven* cells in the retinula, four of which are large and three small (Plate V. Fig. 58). All these cells pass through the basement membrane; all the large ones, and certainly some of the small ones, are also connected with nerve fibres.

These observations indicate that in the Isopods the retinula is composed of either six or seven cells. If Bellonci's statements prove to be correct, this structure may be composed in some cases of only five cells, but my own observations are opposed to this view.

The *rhabdome* in Isopods presents two types of structure, one of which has been well described by Grenacher ('77, p. 30) for Porcellio scaber. In this species the rhabdome is composed of seven rhabdomeres, each of which remains in connection with the retinular cell which produced it. In transverse section the rhabdome has the form of a seven-pointed star, a ray corresponding to a rhabdomere. Each ray projects into its retinular cell, not between two cells. My own observations on Porcellio confirm Grenacher's statements. A second representative of this type of rhabdome has been described by Bellonci ('81, p. 98) for Sphæroma. Here, however, the rays, although they agree in number with the retinular cells, project *between* the cells, not into them.

The second type of rhabdome is well represented in the eye of Arcturus furcatus. In this species, according to Beddard ('90, pp. 368, 369), the distal portion of the rhabdome, although surrounded by *six* retinular cells, is bounded by *four* perpendicular sides. Each of the six cells appears from its position to contribute to the formation of the rhabdome, and yet in the greater part of this structure segments corresponding to rhabdomeres are not visible. In its proximal portion, however, the rhabdome, according to Beddard, is divided into six rhabdomeres, each of which is applied to its proper retinular cell. In Idotea robusta the rhabdome (Plate V. Fig. 48, *rhb.*) is nearly square in transverse section. So far as I have been able to discover, it does not show at its proximal end any indication of rhabdomeres.

Of these two types of rhabdome, the one in which the rhabdomeres are evident is probably more primitive than the one in which their individuality is almost, if not completely lost.

The retinas of Isopods may contain, in addition to those already mentioned, two other kinds of cells. Of these the one most frequently met with fills the space between ommatidia. Cells of this kind have been identified in Porcellio by Grenacher ('79, p. 107), and it is probable that the pigment cells described by Bellonci ('81, p. 99) as intervening between the retinular cells in Sphæroma belong to this class. I have observed interommatidial cells in Idotea; here they contain few or no pigment granules, but are easily recognized by means of their nuclei (Plate V. Fig. 54, *nl. h'drm.*).

The source of these cells is not definitely known, but there appears to be no evidence in favor of their having been derived from outside the retina. Grenacher believed that those in Porcellio are undifferentiated hypodermal cells; this interpretation probably holds good for those in Sphæroma and Idotea.

The hyaline cells, the second kind of accessory cells, have been identified by Beddard ('87, p. 235, '88, Pl. XXX. Fig. 9, *h.*) in Æga and Cirolana. Since these cells are best developed in the eyes of Serolis, a full description of their structure will be deferred until the account of the eyes in that genus is given.

The cells which characterize the ommatidia in Isopods (except Serolis) are as follows: cells of the corneal hypodermis, two; cone cells, two; retinular cells, seven, six, or possibly five. Undifferentiated hypodermal cells are sometimes present, and hyaline cells occur in a few genera.

The structural peculiarities of the *ommatidia in Serolis* were first described by Beddard ('84, pp. 339–341) about seven years ago. Recently Beddard's observations have for the most part been confirmed by Watase ('90), and it must now be admitted without question that the ommatidia in Serolis differ in several important respects from those of many other Isopods.

The material which I used in studying the eyes in this Crustacean consisted of advanced embryos and matured individuals of Serolis Schythei, Lütken. This material was collected in Patagonia by the Hassler Expedition, and was preserved in strong alcohol. Fortunately, it was in good histological condition, and sections prepared from it showed very clearly the finer structure of the eyes. My observations, as the following account will show, differ in no very important respects from those of Beddard and Watase.

Although Patten's generalization, that a *corneal hypodermis* was to be found in the compound eyes of all Crustaceans, led Beddard ('88, p. 447) to look for it in Serolis, he was not able to identify it. Watase ('90, pp. 290 and 293) was more fortunate, and succeeded in finding under each facet two cells in the corneal hypodermis. I have not been as successful as Watase was in determining the exact number of hypodermal cells in an ommatidium, but I have seen enough to convince me that such cells are present. In sections approximately tangential to the external face of the adult retina, one occasionally finds nuclei (Plate VI. Fig. 60, *nl. crn.*) between the distal ends of the cone cells and the corneal cuticula. These represent unquestionably the cells of the corneal hypodermis, and are not to be confused with the nuclei of the cone cells, which lie in a deeper plane. In making sections, the corneal cuticula splintered so irregularly that the tissue immediately below it was completely disarranged. It was therefore possible to get only irregular fragments of the tissue in this region, such as Figure 60 shows, and these fragments were always too small to admit of an accurate determination of the number of hypodermal cells under a single facet. I have also been equally unsuccessful in my attempts either to isolate these cells or to study them *in situ* on the corneal cuticula.

The eyes in the adult, owing to the thickness of the cuticula, are unfavorable for the study of the corneal hypodermis; but in embryos of even an advanced stage, the cuticula is so thin that the hypodermis can be studied with comparative ease. An ommatidium from the eye of an advanced embryo is seen in Figure 65; the ommatidium is viewed from the side. Distal to the cone (*con.*) four nuclei can be seen; one (*nl. crn. 1*) is superficial in position, three are deep. The relation of these nuclei to the ommatidium can be satisfactorily studied in sections transverse to the axis of the ommatidium. A series of three such sections is seen in Figures 66, 67, and 68. Of these, the most distal is that shown in Figure 66. This includes only the most superficial layer of the retina, and contains two nuclei (compare *nl. crn. 1*, in Figs. 65 and 66). These nuclei, as their position clearly indicates, represent cells of the corneal hypodermis. In the plane of the section which includes the three deeper nuclei of Figure 65, four nuclei are in reality present (Fig. 67); two of these (*nl. con.*) are large, and lie directly below the superficial ones in the corneal hypodermis; two are small (*nl. crn. 2*) and lie between the ends of the deeper large nuclei. Of the deep nuclei, the two large ones (*nl. con.*) rest one above each segment of the cone; in fact, as a section in a slightly deeper plane shows (Fig. 68, *nl. con.*), these nuclei coincide so closely with the segments of the cone that they must be regarded as the nuclei of the cone cells.

It is difficult to state what nuclei in the adult correspond to the smaller of the four deep ones in the embryo. The number of these nuclei (two) in the embryo equals the number of pigment cells which Watase ('90, p. 294) has described as surrounding the cone; but that these nuclei do not belong to such cells is evident from the fact that in the embryo, the nuclei of the pigment cells can be identified in a position somewhat proximal to that in which the smaller of the four nuclei occur (compare *nl. dst.* in Figs. 65 and 69.) Possibly the cells represented by these small nuclei in the embryo become in the adult the small interommatidial pigment cells, or it may be that they retain their relatively superficial positions, and, while occupying the space between the corneal facets, perhaps produce the cuticula of that region. In the fragments of the adult retina, from immediately below the corneal cuticula, small nuclei are not unfrequently met with in the spaces between the ommatidia. These are possibly derived from the smaller deep nuclei of the embryo.

It will thus be seen that my conclusions concerning the corneal hypodermis agree in the main with those of Watase; namely, that for each ommatidium there are two cells in this layer. Besides these, however, it is possible that the hypodermis may contain an equal number of other cells, which occupy positions immediately under the cuticula and between the ommatidia.

The facets in the *corneal cuticula* of Serolis, when viewed from the exterior, are irregularly circular in outline, often approaching a six-sided form. As I have already observed, they are arranged on the plan of the hexagonal type. The distal face of each facet is flat, or only slightly convex; the proximal face is decidedly convex. The curvatures of the two faces and the thickness of the cuticula in the facet of S. Schythei was about the same as that figured by Watase ('90, Plate XXIX. Fig. 1) for the species which he studied.

The *cone*, as Beddard ('84, p. 340) first demonstrated, and as Watase ('90, p. 290) afterwards confirmed, is composed of two nearly hemispherical segments, which correspond to the two cone cells. The protoplasmic material of each cone cell covers the curved surface of the segment to which it belongs, and contains a nucleus in its distal portion. These relations have been well shown by Watase ('90, Plate XXIX. Fig. 1).

From the condition presented even in advanced embryos (Fig. 65) it is evident that the part of the cone earliest formed, is the one which is nearest the applied faces of the two cone cells, and that from this as a centre the cone has continued to increase outwards. Although at this stage the outline of the cone itself is sharply marked (Fig. 65), the external limits of the cone cells are only approximately indicated by the distribution of the pigment granules, which have begun to form in the surrounding pigment cells.

In Serolis, as in Porcellio and Idotea, the cone cells and the cells of the corneal hypodermis are separated by the same perpendicular plane. There are some complications in the structure of the cone cells which can be discussed subsequently with greater clearness.

The *retinula* in Serolis, as Beddard ('84, p. 340) first observed, is peculiar in that it is composed of only *four* cells. My own observations add almost nothing that is new to the previous accounts of this structure. The figure which Watase has drawn ('90, Plate XXIX. Fig. 1) of the characteristic form of the retinular cell when viewed from the side and its relation to its rhabdomere, reproduces very closely the structural conditions which I have observed in S. Schythei.

The *rhabdome* in Serolis has been carefully studied by Beddard ('88, pp. 448–450). Owing to the complexity of its structure, one meets with difficulties in attempting to interpret its parts in terms of the relatively simple rhabdome of many Crustaceans. The peculiarities of this structure can be approached most satisfactorily perhaps from the side of its adult anatomy.

In a transverse section of the distal end of the rhabdome, five structures can be observed (Fig. 61). Four of these (Fig. 61, *rhb'm.*) are squarish pieces confluent on one side with a retinular cell, and in contact with one another only at their angles The sides of these pieces which are directed towards the axis of the ommatidium are convex, and together bound a central area which contains the fifth or axial structure (*cl. con.*). Each of the squarish pieces also exhibits a line slightly concave towards the axis of the ommatidium. This line, which might be taken for the separation between the axial and peripheral structures, is in reality entirely within the latter. That these are five separate structures is indicated by the fact, that in transverse section, when for any reason the elements have been broken apart, the separation almost always occurs on the lines which I have described as the limits of the different pieces.

Evidently the squarish masses (*rhb'm.*) on the axial faces of the retinular cell correspond to the rhabdomeres of other Crustaceans, and like these structures are produced by the cells to which they are attached. It is more difficult to explain the axial element, for it shows no indication of having been produced by the surrounding retinular cells, nor are there other cells in the neighborhood to which its production could be referred.

When the longitudinal extent of these structures is considered, the difficulty of explaining the axial portion is increased. In S. Schythei the rhabdomeres extend only a short distance distally and proximally, but throughout the whole of that distance they are closely applied to the axial face of the retinular cells. This condition has been well figured by Watase ('90, Plate XXIX. Fig. 1), and supports the statement already made that these bodies correspond to the rhabdomeres in other Crustaceans. I have never observed a rhabdomere, such as that figured by Beddard ('87, p. 234), in which the proximal half of the structure is not in contact with the retinular cell. The axial part has a much more considerable extent in a longitudinal direction than the rhabdomeres. Apparently it is continued proximally into a fibrous bundle which stretches towards the basement membrane, where according to Beddard ('88, p. 449) it may terminate as a single fibre.

From what has just been stated it must be evident that the so called rhabdome of Serolis consists of two sets of structures, one of which includes the four rhabdomeres and the other the axial part with its proximal fibrous prolongation.

The development of these structures has been studied by Beddard ('88, p. 450). In the youngest embryos which he examined, the axial portion was already formed, and at that stage it was closely invested by the four retinular cells and two other cells, the hyaline cells. Judging from their positions, Beddard believes that both kinds of cells may contribute to the formation of the axial structure, although the fact that this body is squarish in transverse section leads him to conclude that the four retinular cells play the more important part in its formation. Beddard regards the axial body as the rhabdome of the immature eye. In his opinion, the rhabdome in the adult is produced by subsequent secretions from the retinular cells, and presents the form of the four rhabdomeres already described. Although these rhabdomeres form the principal part of the rhabdome in the adult eye, he believes that the rhabdome of the earlier stages persists as the axial fibrous structure in the later stages, and constitutes perhaps the greater part of its distal continuation between the rhabdomeres.

Unless some such explanation of the origin of the axial part of the rhabdome as that proposed by Beddard be accepted, it is difficult to understand how the fibrous portion could arise as a secretion; for in the adult the proximal portion of it is touched by neither retinular nor hyaline cells.

Granting for the moment the adequacy of Beddard's explanation of the origin of the axial part, we are still confronted by what appears to me to be unparalleled in the structure of the eyes in Arthropods, namely, an ommatidium which produces two distinct rhabdomes. This may not be an impossibility, but if it occurs at all, it is certainly exceptional.

I believe, however, that the so called axial part of the rhabdome in Serolis is capable of another interpretation, against which the objections already suggested cannot be urged. That the axial portion terminates proximally on the basement membrane has been fairly well established by Beddard. The distal termination of it, however, has not been so clearly made out. It is my belief that the axial structure is directly continuous distally with the cone cells; in other words, that this structure is to be regarded as a proximal extension of the cone cells, not as a part of the rhabdome. The termination at the basement membrane of this prolongation of the cone cells, as observed by Beddard, is perfectly consistent with the interpretation which I have suggested, and makes the condition in Serolis similar to that in Homarus, where the fibrous ends of the cone cells also terminate on the basement membrane. That the fibrous structure should be present in the embryo of

Serolis before the formation of the rhabdome proper is rather in favor of my interpretation than opposed to it. The direct evidence that the axial body is a proximal extension of the cone cells is not as conclusive as could be desired. The condition which most favors this view is as follows. In longitudinal and transverse sections of the ommatidia, both in adult and embryonic specimens, no line of separation has been observed between the protoplasm at the deep end of the cone and the substance which occupies the axial part of the ommatidium proximal to the cone (compare Fig. 65). In attempting to determine the true relation, it is important to keep clearly in mind the fact that the proximal end of the cone, usually bounded by a sharply marked line, is *not* the proximal end of the cone cells; but, as Watase ('90, Plate XXIX. Fig. 1) has well shown, the cone is surrounded proximally as well as laterally by the protoplasmic material of its cells. It is this material, not that of the cone proper, which forms the proximal elongation.

I had hoped that by isolating the elements of the retina I could obtain more conclusive evidence of the connection of these parts, but my efforts were of no avail. My ill success was due, I believe, not to any want of connection between the structures treated, but to the fact that the material at my disposal had been kept so long in strong alcohol that it had become unfit to serve for isolation. This conclusion seems to me to be confirmed by the fact that I was unable even to isolate satisfactorily the retinulæ, structures which are usually separable with ease in the fresh retinas of most Crustaceans.

If the view which I have set forth in the foregoing paragraphs concerning the interpretation to be put upon the axial part of the so called rhabdome of Serolis be correct, it follows that the true rhabdome of this Crustacean must be considered as composed of four rhabdomeres, each of which is applied to the axial face of its appropriate retinular cell, and that these four rhabdomes are prevented from uniting with one another by a proximal extension of the cone cells which occupies the axis of the ommatidium from the cone to the basement membrane.

Beddard ('84^a, p. 21), in his account of the eye in S. Schythei, states that the cone is "enclosed in a sheath of deep black pigment cells," and Watase ('90, p. 294) has observed that in this genus there are two such cells for each ommatidium. I believe that the number has been given correctly, for although I have not satisfactorily isolated the cells, I feel confident that I have identified their nuclei, and the number of these is twice that of the ommatidia.

The nuclei of these pigment cells are most satisfactorily seen in advanced embryos (compare *nl. dst.*, in Figs. 65 and 69). In transverse sections at this stage (Fig. 69) each cone is surrounded by a circle of six nuclei. Each nucleus, however, participates in three adjoining circles, consequently there are only twice as many nuclei as ommatidia. In the adult the nuclei of these pigment cells (Fig. 60, *nl. dst.*) occupy the same relative positions as in the embryo; in the latter, however, they are usually somewhat hidden by the pigment which surrounds them.

In the embryo the nuclei of the pigment cells surrounding the cone resemble very closely, except in point of size, the nuclei of the retinular cells (compare *nl. dst.* and *nl. px.* in Fig. 65). In the nuclei of the retinular cells there is usually one distinct nucleolus, sometimes two, but as a rule no finer particles. This condition also obtains in the nuclei of the pigment cells. Not only are the nuclei of these two kinds of cells similar in the embryo, but they are also much alike in the adult (compare *nl. dst.* in Fig. 60 with *nl. rtn.'* in Fig. 63).

Because of this resemblance, I believe that the pigment cells which surround the cone can be fairly considered to be modified retinular cells, which have lost their sensory function in precisely the same way as in the case of the distal retinular cells in Decapods (see Parker, '90^a, p. 57). If this interpretation of the pigment cells be accepted, it follows that in Serolis, as in Decapods, two kinds of retinular cells are present, proximal and distal, and that the primitive ommatidium from which that of Serolis was derived probably contained six retinular cells functional as nervous structures. It need scarcely be added, that this number is characteristic for the ommatidia of many Isopods.

The retinula in the species of Sphæroma which I studied presents an appearance which suggests the differentiation of simple retinular cells into proximal and distal cells. In Sphæroma there are seven retinular cells (Plate V. Fig. 58); three of these are considerably reduced; the remaining four are large, and recall the four retinular cells of Serolis. In transverse sections it can be shown that the four large cells in Sphæroma not only resemble in appearance the four proximal cells in Serolis, but that they occupy the same relative positions in the ommatidium. In Serolis the plane which separates the two cone cells of any given cone, when extended, separates the four proximal retinular cells into two groups of two cells each (compare Plate VI. Fig. 68 with Figs. 71 and 72). The plane of separation in the cone of Sphæroma divides the retinula by passing *through* the single small retinular cell shown in the lower part of Figure 58 (Plate V.) and *between* the two small cells on the opposite side, thus separating the four large retinular cells into two groups, as in Serolis.

The change which would convert an ommatidium like that in Sphæroma into one like that in Serolis is easily imagined. It would consist in the complete abortion of one of the three small retinular cells, and the conversion of the other two into the pigment cells surrounding the cone.

In addition to the elements which have already been described in the ommatidium of Serolis, there are certain small pigment cells which occur for the most part in the region of the retinulæ. Beddard ('84^a, p. 21) describes these as long branching "connective-tissue cells," a name which might imply that they originated from the mesoderm, and were therefore intrusive. Watase ('90, p. 293, Plate XXIX. Fig. 1) has also described and figured these cells, but distinctly states his belief that they are reduced ectodermic cells. In the adult I have observed in the region of the cones, as well as near the retinulæ, certain small nuclei which are usually surrounded with more or less black pigment. These, I believe, represent the cells described by Beddard and Watase. In the embryo certain scattered nuclei (*nl. h'drm.*, Figs. 65 and 70) occur in the spaces between the ommatidia. It is probable that these nuclei are ectodermic in origin, and I am at a loss to know what has become of them in the adult, unless they form the pigment cells already mentioned. I am therefore inclined to believe, with Watase, that the small additional pigment cells are reduced ectodermic cells.

The presence of the *hyaline* cells in the ommatidium of Serolis is, as Beddard has pointed out, almost a unique feature. These cells, usually two in each ommatidium, fill the space immediately below the rhabdome. They are bladder-like (Fig. 62, *cl. hyl.*) and contain each a large granular nucleus. Although it is stated that there are usually two of these cells in each ommatidium, I never found more than one to an ommatidium in the several eyes of S. Schythei which I examined. This circumstance, however, is not surprising; for, as Beddard ('84^a, p. 22) has remarked, the number of these cells is subject to variation, there being sometimes one, sometimes two, for each ommatidium. In S. Schythei the single hyaline cell envelops more or less completely the distal part of the fibrous portion of the cone cells, so that this part seems to pierce the hyaline cell. A closer inspection, however, will usually show two lines extending from the fibre to the periphery of the hyaline cell (compare Fig. 62), and these lines indicate, I believe, the two walls of the cell which have been infolded by the presence of the fibre during the growth of the hyaline cell.

The source of the hyaline cells is not definitely known. Their nuclei (Fig. 65, *nl. hyl.*), as Beddard ('88, p. 450) has observed, are present in the retinas of embryos; and, although the cells may possibly be intrusive, the evidence on the whole favors the view that they are ectodermic in origin.

Several functions have been attributed to the hyaline cells. Their close connection with what Beddard took to be the proximal extension of the rhabdome led him ('88, p. 450) to suspect that they might be rudimentary retinular cells, but, as he (p. 451) further remarks, the fact that no nerve fibres are connected with them opposes this view. Their transparency suggested to him ('84^a, p. 22) that they might form a part of the dioptric apparatus; but it is difficult to understand, considering their position, precisely what that function would be. I am inclined to believe, with Watase ('90, p. 293), that they are chiefly concerned with the support of the structures occupying the basal portion of the retina.

In the retina of S. Schythei many of the open spaces between the cones and the basement membrane contain free non-pigmented cells (Fig. 61, *cp. sng.*). These have a distinct nucleus, finely granular protoplasm, and a sharply marked outline. On account of the extreme variations in form which the different cells present, it is probable that when living they exhibited amœboid motion. In appearance they correspond exactly to the blood corpuscles of the body spaces, and as they occur not only in the retina, but also in the rather large openings through the basement membrane (compare Fig. 64), and in the space proximal to this membrane, I am of opinion that they are blood corpuscles.

The peculiarities which have led me to consider the ommatidium in Serolis separately from that of other Isopods, are two: the possession of one or more hyaline cells, and the presence of only four retinular cells. The latter peculiarity, as I have already shown, is not fully established; for in this genus, as in many other Isopods, the ommatidium really contains six cells, although two of these, the distal ones, are probably no longer functional as nervous structures. The other peculiarity, the possession of hyaline cells, is not a very important characteristic, for, as Beddard ('87, p. 235) has shown, these cells also occur in Æga; and it is probable, moreover, that they must be regarded as abnormally enlarged elements, specialized from among those cells which in other Isopods fill the spaces between the ommatidia. What distinguishes the ommatidium in Serolis from that of other Isopods is, therefore, not so much the possession of hyaline cells as the fact that its retinular cells are differentiated into two sets, proximal and distal.

In accordance with the facts already presented, the number of cells contained in the ommatidium of Serolis can be stated as follows: cells of the corneal hypodermis, two, with possibly two others interommatidial in position; cone cells, two; retinular cells, six, two distal and four proximal; hyaline cells, one or two; a variable number of small pigment cells of ectodermic (?) origin.

Leptostraca.

The histological structure of the ommatidia in the Nebaliæ has been investigated, so far as I am aware, only by Claus ('88, pp. 65-84). I have had no material for the study of the eyes in these Crustaceans, and I can therefore only present, in the form of a summary, the more important results of Claus's exhaustive study.

In Nebalia there is a *corneal hypodermis* (Claus, '88, pp. 68 and 69), the cells of which are grouped in pairs. As in many of the higher Crustaceans, there is one pair of these cells for each ommatidium. The *corneal cuticula* is facetted; the outlines of the facets are circular, and adjoining facets are separated from one another by a small amount of intervening cuticula (Claus, '88, Taf. X. Fig. 10). The *cones* are composed of four segments (Claus, '88, p. 69). The structure of the *retinula* is somewhat complex. The greater part of the rhabdome is surrounded by seven retinular cells. Distal to these cells, however, are seven pigment cells, which enclose the proximal prolongation of the cone cells and the distal end of the rhabdome. Such a relation between pigment cells and retinular cells is not of common occurrence among Crustaceans, and it is possible that the bodies which Claus has taken for pigment cells are really the distal ends of the retinular cells. Claus describes and figures what he believes to be the nuclei of both kinds of cells, but I think his figures fail to show that these nuclei are within the limits of the cells to which they are said to belong. It seems to me quite possible that what he has described as two circles of seven cells each may be merely one circle seen at two different levels, as the correspondence in numbers suggests. This single circle would be of course composed of retinular cells, the nuclei of which are probably the distal ones of the two sets described by Claus. The proximal nuclei, which, according to Claus, belong to the retinular cells, occupy positions not unfrequently taken by the nuclei of accessory pigment cells, and I am inclined to think that such is their real nature. This interpretation would be more in accordance with the conditions found in ommatidia which have seven retinular cells than is the one given by Claus; but as I have not had the opportunity of studying the eyes in Nebalia, I can offer it merely by way of suggestion.

Probably two kinds of accessory cells are present in Nebalia; one of these extends from the corneal cuticula to the basement membrane, the other, the presence of which is not so fully established, probably occurs near the basement membrane.

Cumaceæ.

Excepting what is contained in Burmester's ('83, pp. 35–37) account of the degenerate eyes in Diastylis (Cuma) Rathkii, nothing, I believe, is known of the finer structure of the eyes in the Cumaceæ. The specimens at my disposal for the study of these eyes proved upon examination to be blind. At least, the optic plates of all the individuals which I examined, both when studied from the exterior and when examined in sections, showed no evidence of eyes. My material consisted of specimens of Diastylis quadrispinosa, G. O. Sars, and of three other undetermined species, two of which belonged to the genus Diastylis and one to Eudorella. These were kindly sent me by Prof. S. I. Smith.

Schizopoda.

The species of Schizopod the eyes of which I have studied is Mysis stenolepis, Smith. Specimens of this Crustacean were kindly collected for me at Wood's Holl, Mass., by Mr. C. B. Davenport. I am also under obligations to Dr. H. V. Wilson, of the United States Fish Commission, who at my request sent me specimens of this species freshly preserved in Müller's fluid.

In several of the previous accounts of the eye in Mysis the nuclei of the *corneal hypodermis*, although recognized, have been described as Semper's nuclei, i. e. as nuclei of the cone cells. The differences between the hypodermal nuclei and those of the cone cells can be easily seen in Mysis stenolepis (Plate VII. Fig. 73). In this species the hypodermal nuclei (*nl. crn.*) lie in a plane somewhat nearer the external surface of the eye than the nuclei of the cone cells (*nl. con.*). In transverse sections at the proper levels, each ommatidium will be seen to contain two elongated nuclei (Fig. 75, *nl. crn.*) belonging to the corneal hypodermis, and two oval nuclei (Fig. 76, *nl. con.*) in the cone. The hypodermal nuclei occupy such positions that the plane of separation between their cells would be at right angles to that between the cone cells (compare Figs. 75 and 76). The group of four nuclei, two belonging to the corneal hypodermis, and two to the cone cells, correspond without much doubt to the so called four Semper's nuclei mentioned by Claparède ('60, p. 194) in Mysis flexuosa, and described by Sars ('67, p. 33) in M. oculata. Nusbaum ('87, p. 179) also observed four similar nuclei in the developing eye of Mysis chameleo, and Grenacher ('79, p. 118) described the same number in Mysis vulgaris. In the last named species, according to Grenacher, the four nuclei are grouped in two pairs, one of which occupies a more distal plane in the ommatidium than the other. The more superficial pair undoubtedly belongs to the corneal hypodermis, the deeper pair to the cone cells.

It must be evident, then, that the nuclei of the cone cells and corneal hypodermis have not always been carefully distinguished. In all cases where they have been separated, the corneal hypodermis has been shown to possess two nuclei for each ommatidium.

The *corneal cuticula* in Mysis, as Frey and Leuckart ('47^a, p. 113) first pointed out, is facetted, and the outline of the facet is a circle. In Mysis stenolepis the circumference of the facet is tangential to the circumferences of six adjoining facets (Fig. 74). In Mysis vulgaris, Grenacher ('79, p. 118) has shown that the facet is not lens-like, but is of uniform thickness throughout. In M. stenolepis, however, the cuticula is often slightly thicker at the middle of the facet than at its edges (Fig. 73, *cta.*). In this respect, therefore, different species probably vary.

The *cones* in Mysis vulgaris, according to Grenacher ('79, p. 118), are composed of two segments. The same number is also present in the cones of M. stenolepis (compare Figs. 76–78, *con.*). In longitudinal sections the cone (Fig. 73, *con.*) appears to consist of a uniformly and finely granular substance enveloped in a delicate but distinct membrane. Near the distal end of the cone the material which composes it becomes more coarsely granular; in this the nucleus of the cone cell is usually lodged. Cones (Fig. 92) which have been isolated in macerating fluids are plumper and apparently not so contracted as those which have been subjected to the process of cutting. The nuclei also are rounder and fuller. The cone proper (Fig. 92 *con.*) occupies a more central position in the cone cells, and is surrounded by a finely granular material, which is especially abundant at the proximal end. The difference between the cone proper and this granular material was not generally observable in *sections* of the cones. In all of the many cones which I succeeded in isolating, the proximal ends invariably had a broken appearance. Consequently, I believe that I have never completely isolated a pair of cone cells. The question of the proximal extent of the cone I shall recur to later.

The *retinular cells* in Mysis are of two kinds, proximal and distal. The proximal cells extend from the basement membrane distally to the level at which the cone rapidly contracts. The pigment which they contain is for the most part concentrated around the rhabdome, and their nuclei occupy a distal position in the cell (Fig. 73, *nl. px.*).

In Mysis the number of cells comprising the retinula is at least seven (Figs. 85–87). Possibly, as I have elsewhere suggested (Parker, '90ª, p. 55), the total number of cells in this retinula, as in that of Homarus, may be eight.

In order to determine this question, I have counted the number of nuclei in several retinulæ of Mysis. The enumeration of these can be easily followed in Figures 79 to 82. These figures represent successive transverse sections through four ommatidia, in the region occupied by the proximal retinular nuclei. The axis of each ommatidium is marked by the fibrous portion of the cone cells (*cl. con.*), and the same ommatidium is designated in different sections by the same Roman numeral. The nuclei in ommatidium II. can be counted the most readily. In Figure 79, which represents the most distal section of the series, the cone in ommatidium II. is surrounded by a circle of six nuclei, which have been numbered from 1 to 6. Each of these nuclei, however, participates in three circles (compare nucleus 5), and hence only two of the six can be referred to ommatidium II. Two similar circles occur, one in the sections shown in Figure 80, and one in that shown in Figure 81. As in the former instance, two nuclei in each circle belong to ommatidium II. In these three circles, then, there are in all six nuclei to be allotted to ommatidium II. In addition to these nuclei, it will be noticed that to the right of the cone in Figure 80 there is one more nucleus (No. 7), and still another in a similar position in Figure 82. These two nuclei, when added to the six already summed up for ommatidium II., make a total of eight nuclei for this ommatidium.

The same number of nuclei occurs in each of the other three ommatidia, but their arrangement is not quite so regular as in the one just counted. From this I conclude that the number of nuclei in a retinula of Mysis is eight.

The different nuclei in this retinula usually present a very uniform appearance. The most proximal one differs somewhat from the others in being more elongated (compare Figs. 73 and 82). The seven distal nuclei, on account of their general resemblance, belong, I believe, to the seven functional retinular cells. The single proximal nucleus probably represents an eighth rudimentary cell. The position of this nucleus, proximal to the other retinular nuclei, is similar to that occupied by the nucleus of the rudimentary retinular cell in Homarus (compare Parker, '90^a, pp. 20, 21).

The *rhabdome* in Mysis stenolepis lies in the proximal portion of the retina. It is rather stout, blunt at its distal end, but sharper proximally (Fig. 90). Its surface is marked with coarse corrugations. In transverse section, its outline is a square; this is subdivided by two lines into four smaller squares, a condition already observed by Grenacher ('79, p. 119) in M. flexuosa. The relation of the retinular cells to these divisions of the rhabdome can be clearly seen in Figure 87.

According to Grenacher's account ('79, p. 118), a rod-like structure extends, in Mysis vulgaris and M. flexuosa, through the axis of the ommatidium from the distal end of the rhabdome to the region of the proximal retinular nuclei. Whether this rod be a proximal continuation of the cone, or a distal extension of the rhabdome, Grenacher found it difficult to decide. He is inclined, however, to the former opinion.

A similar structure occurs in the ommatidia of Mysis stenolepis. Although I have made repeated attempts, I have never succeeded in isolating the rod in connection with either the rhabdome or the cone cells. In transverse sections, the distal end of it appears in a position slightly proximal to the retinular nuclei (Figs. 73 and 83). The cone cells extend proximally as a transparent axis to this region, and the most distal indications of the rod are four fibres which lie on the periphery of what I take to be the proximal end of the cone cells (Fig. 83). Somewhat deeper than this, the four fibres thicken, and finally fuse (Fig. 84), producing a body which in transverse section has the outline of a four-pointed star. In a plane slightly more proximal, the outline changes to a squarish one (Fig. 85), and this is retained almost to the proximal end of the rod. Throughout its extent, this problematic rod is closely surrounded by the seven proximal retinular cells (Fig. 85). It is separated from the rhabdome by what appears to be an open space (Fig. 90, at the level of the dotted line 86). In transverse sections (Fig. 86), however, this space is seen to be divided by delicate membranes into four compartments.

These facts, however, do not aid much in deciding the relationship of the rod. The fact that it shows indications of being composed of four parts suggests its connection with the rhabdome. The four parts of which it consists do not, however, correspond in position to the segments of the rhabdome, but fall between them. (Compare Figs. 83 and 87.) On the other hand, if it were an extension of the cone, one would expect it to be composed of two, instead of four parts. Its position, however, is one which is more frequently occupied in other Crustaceans by a slender extension of the cone cells than by a process from the rhabdome, and, notwithstanding its division into four parts, I am inclined to agree with Grenacher, and to regard it as belonging to the cone cells rather than the rhabdome.

The distal retinular cells in Mysis surround the lateral faces of the cones (Fig. 73, *cl. dst.*). Apparently they reach the cuticula; their proximal ends are attenuated and become lost in the region of the nuclei of the proximal cells. Their pigment is limited to their proximal halves, and consists of a distal layer of brownish material, proximal to which is a much more extensive deposit of blackish granules. Each cone is surrounded by six of these cells, as can be seen from their outlines (Fig. 78, *cl. dst.*), and still more satisfactorily from the arrangement of their nuclei (Fig. 75, *nl. dst.*). Each cell, however, participates in three circles; consequently, there are only twice as many of these cells as ommatidia.

The axis of each distal retinular cell is occupied by a transparent rod, which in transverse section has the appearance of a light spot (Fig. 77). In depigmented sections stained with Kleinenberg's hæmatoxylin, these rods are deeply colored (Fig. 78). I shall recur to their probable significance.

The pigment which is found in the region of the rhabdomes in Mysis is of two kinds: blackish granules, and a fine flaky material, white by reflected light, yellowish by transmitted light. The black granules are for the most part contained in the retinular cells. The lighter pigment is always associated with certain nuclei, two of which are shown in Figure 90 (*nl. ms'drm.*). These nuclei are closely invested by the pigment, and probably belong to the cells in which the pigment is contained.

The source of the yellowish pigment cells is not easily determined. Apparently they are not limited to the retina, but also occur in the spaces below it. At least these spaces contain masses of pigment and nuclei which in all essential respects are similar to those distal to the membrane (compare the two nuclei, *nl. ms'drm.*, Fig. 90). In one case the nucleus of one of these cells was found apparently caught in its passage through an opening in the basement membrane (Fig. 91). For these reasons I believe that the yellowish pigment cells on the two sides of the membrane have had the same origin. The question as to the source of the yellowish pigment cells in the retina, therefore, appears to me to involve that of the origin of the similar cells beneath the retina. If I am right in this conclusion, all these cells must either have arisen in the retina, many of them migrating in a proximal direction out of it, or they must have had some extra-retinal origin, some of them migrating into it. On account of the considerable numbers in which they exist in the spaces below the retina, it seems to me much more probable that they have had an extra-retinal origin than that they have come from the retina itself. If this is their source, it is evident that those which are in the retina are intrusive. The nucleus which has already been mentioned as caught in an opening of the basement membrane (Fig. 91) has more the appearance of a body which is making its way into the retina than of one which is moving in the reverse direction, and may therefore be regarded as confirming to some extent the view of the extra-retinal origin of these cells. Their source, however, cannot be stated with certainty. Their power of migration implies amœboid activity, and this might be taken as an indication of their mesodermic origin.

The following cells characterize the ommatidium of Mysis: cells of the corneal hypodermis, two; cone cells, two; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory pigment cells (mesodermic ?) present.

Stomatopoda.

The material which I have had for the study of the eyes in the Stomatopods consisted of two specimens of Gonodactylus chirarga, Latr. These were kindly given me by Mr. W. S. Wadsworth, who had collected them in the Bermudas. One of them had been killed in hot water and preserved in alcohol; the other was both killed and preserved in strong alcohol; both were in excellent histological condition.

In Gonodactylus, as I have previously mentioned, there are two kinds of ommatidia; these differ in no important respect except size.

Longitudinal sections of both kinds are represented on Plate VIII.; the figure of the larger kind (Fig. 94) is taken from a depigmented section, that of the smaller one (Fig. 95) from a section containing the pigment in its natural condition. In the following description I shall give an account of the structure of the larger ommatidia, alluding to the condition of the smaller ones only when it differs in some important respect from that of the others.

The *corneal hypodermis* is represented in the ommatidium of Gonodactylus by two cells, the nuclei (Figs. 94–96, *nl. crn.*) of which can be recognized easily. Directly under the corneal cuticula each pair of hypodermal cells is in contact with similar pairs belonging to adjoining ommatidia, so that the layer here forms a continuous sheet. In a more proximal plane the neighboring pairs of hypodermal cells are not in contact (compare Fig. 93, a tangential section in which the extreme right-hand edge represents the condition immediately below the cuticula, while the parts to the left represent central portions successively more proximal in position). The only indication of a separation between the two hypodermal cells of each pair is seen in the distal projection of the cone between the two hypodermal nuclei (compare Figs. 94 and 96, *con.*).

The *corneal cuticula* in Gonodactylus is facetted, but the proximal and distal faces of the facets are apparently plane. Over the smaller ommatidia the facets are hexagonal in outline, whereas over the larger ones they are rectangular, and their arrangement is often indicative of the tetragonal system. In Squilla mantis, according to Will ('40, p. 7), the facets are hexagonal.

The *cones* in Gonodactylus are composed for the most part of a uniformly granular substance. Distally, they are pointed and probably touch the corneal cuticula; proximally, they terminate at the rounded end of the rhabdome (Fig. 94). Each cone contains in its distal enlargement four nuclei (Fig. 97, *nl. con.*), two of which lie directly proximal to the nuclei of the corneal hypodermis, while the remaining two alternate with them (compare Figs. 96 and 97). The proximal part of the cone is divided longitudinally into four segments (Fig. 98). Each segment, if extended distally, would include one of the four nuclei, and corresponds to one of the four cells by which the cone was produced. In Squilla mantis, according to Steinlin ('68, p. 17), the cone is also composed of four segments.

The *retinular cells* of Gonodactylus are of two kinds, proximal and distal. The proximal cells, constituting the retinula itself, surround the rhabdome completely, and extend distally only a short distance beyond it (Fig. 95). They contain only a small amount of pigment, which is concentrated in two regions, at their distal ends and near the basement membrane. The rhabdome is surrounded throughout its length by a thin but rather dense layer of pigment. This layer is more extensive in the smaller ommatidia (Fig. 102) than in the larger ones. The nuclei of the proximal retinular cells (Figs. 94 and 95, *nl. px.*) are located near their distal ends.

The number of cells in the retinula of Squilla, as described by Grenacher ('77, p. 33) and by Hickson ('85, p. 341, Fig. 2), is seven. In

Gonodactylus (Fig. 101) the retinular cells are certainly as numerous as in Squilla; but seven obvious cells in the retinula, as I have already shown in Mysis, may suggest the presence of eight in all, one of them being rudimentary. This condition is in fact characteristic of Gonodactylus also, as can be seen in the series of ommatidia shown in Fig. 100. These six ommatidia represent consecutive individuals in one of the bands of larger ommatidia previously mentioned. The band as a whole is cut obliquely, and in such a way that the ommatidia from 1 to 6 are cut successively in deeper or more proximal planes. In ommatidium 1 the rhabdome is surrounded by seven retinular cells, four of which are upon the right side and three upon the left. In addition to these, a large nucleus (*nl. px.*) lies close to the rhabdome. Ommatidium 2 has essentially the same structure as ommatidium 1. In ommatidium 3 the nucleus corresponding to the one seen in ommatidium 1 and 2 is no longer visible, but in its stead there is a small mass of granular protoplasm. A similar mass is also seen in ommatidia 5 and 6. It is usually present directly proximal to the nucleus figured in ommatidia 1 and 2, and is, I believe, the protoplasmic body of the cell to which this nucleus belongs. In ommatidium 4, the seven nuclei of the seven large (functional) retinular cells can be seen. These nuclei appear very large in transverse section compared with the cells in which they occur. It is probable that the cell wall is distended by them, although, owing to the indistinctness of the cell boundaries, I have not obtained positive evidence of this. In ommatidium 6 the seven retinular cells are seen in section at a plane proximal to that in which their nuclei lie. As in ommatidium 1, three of them are upon one side of the rhabdome and four upon the other. In a part of the ommatidium more proximal than that shown in number 6 (Fig. 100), the transverse section of the retinula has the appearance seen in Figure 101. Here the retinular cells have the same relation to the rhabdome that they do in ommatidium 6 (Fig. 100), except in the case of the upper right-hand cell of that figure. This cell enlarges in its more proximal portion, and comes to occupy a position directly below the cell whose nucleus is shown in ommatidium 1 (Fig. 100). The gradual disappearance of this distal cell as one proceeds in a proximal direction from the plane of number 6, Figure 100, to that of Figure 101, and the gradual shifting in the position of the cell which replaces it proximally, can be followed so easily that there is not the least question as to the accuracy of the relations described. It is evident, then, that in Gonodactylus, as in Mysis, the retinula consists of eight cells, one of which is rudimentary.

The *rhabdome* (Figs. 94 and 95, *rhb.*) in Gonodactylus is an elongated rod-like structure of uniform thickness, which extends from the region of the proximal retinular nuclei to the basement membrane. It shows a distinctly toothed edge (Fig. 94), especially in specimens which have been treated with potassic hydrate. In transverse section it is squarish. Owing to its small size, the exact relation of the seven surrounding cells to its four faces cannot be easily determined. The single unpaired cell (Fig. 101) certainly lies opposite a face, not an angle. In this respect it agrees with the unpaired cell in Squilla as figured by Grenacher ('79, Taf. XI. Fig. 122). Probably in Gonodactylus the remaining six cells are related to the sides of the rhabdome as the corresponding ones are in Squilla (compare Grenacher's Fig. 122). In Gonodactylus the retinular cells and rhabdome are in close contact with one another. The separation of these elements as figured by Grenacher in Squilla is probably artificial, as Grenacher himself suggests. In Squilla, according to both Steinlin ('68, p. 17) and Grenacher ('79, p. 125), the rhabdome in transverse sections is subdivided into four equal parts, somewhat as in Mysis. I have not observed this condition in Gonodactylus.

The *distal retinular cells* in Gonodactylus occupy the usual position near the cones. They contain very little pigment, and their number can be determined only by that of their nuclei. These agree with the nuclei of the proximal cells in the possession of a single well defined nucleolus, which is most readily seen in depigmented sections (compare *nl. dst.* and *nl. px.* in Fig. 94). The distal nuclei, especially in the region of the larger ommatidia, are arranged in rows which alternate with the rows of cones (Fig. 99, *nl. dst.*). Although the nuclei are not very definitely arranged, they often show a tendency to be grouped in pairs, and these pairs are so placed that in each row there is evidently one for each adjacent ommatidium. Moreover, in equal lengths of adjoining rows of nuclei and cones, the nuclei are always double the number of cones. I am convinced by these facts that there are two distal retinular cells for each ommatidium.

Besides the cells already described, certain others occur in the proximal part of the retina in Gonodactylus. These are represented by a few small, elongated nuclei (Fig. 94, *nl. ms'drm.*), which are very similar in appearance to certain nuclei occurring in the spaces below the basement membrane. I therefore believe that in Gonodactylus, as in Mysis, the proximal portion of the retina is occupied by intrusive cells, which are probably mesodermic in origin.

The kinds of cells found in the ommatidium of Stomatopods are as follows: cells of the corneal hypodermis, two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells (mesodermic?) present.

Decapoda.

I have studied the eyes of the following species of Decapods: Gelasimus pugilator, Latr.; Cardisoma Guanhumi, Latr.; Cancer irroratus, Say; Hippa talpoida, Say; Palinurus Argus, Latr.; Pagurus longicarpus, Say; Homarus americanus, Edw.; Cambarus Bartonii, Fabr; Crangon vulgaris, Fabr.; and Palæmonetes vulgaris, Say. I collected much of this material at the Station of the United States Fish Commission at Wood's Holl, Mass. The specimens of Cambarus were obtained in the vicinity of Philadelphia. I am under obligations to Mr. Herbert M. Richards for specimens of Palæmonetes collected by him at Newport, R. I. A number of eyes of two Crustaceans, Cardisoma and Palinurus, were kindly obtained for me by Mr. Isaac Holden; they were collected on the coast of Florida by Mr. Ralph Munroe, to whom I am indebted for the careful way in which they were preserved.

The *corneal hypodermis* in Decapods was first recognized by Patten ('86, pp. 626 and 642), who observed it in Penæus, Palæmon, Pagurus, and Galathea. Since Patten's announcement of the presence of this layer in Decapods, it has been identified in a number of other genera: in Crangon by Kingsley ('86, p. 863), in Alpheus by Herrick ('86, p. 43), in Astacus by Carrière ('89, p. 225), in Cambarus and Callinectes by Watase ('90, pp. 297 and 299), and in Homarus by myself ('90^a, p. 6). More recently I have observed it also in Palæmonetes (Plate IX. Fig. 103, *cl. crn.*), Crangon, Cambarus, Palinurus, Pagurus, Hippa, Cancer, and Cardisoma.

In almost all Decapods in which the arrangement of the cells in the corneal hypodermis has been observed, these elements have been found to be grouped in pairs, and so distributed that each pair occupies the distal end of an ommatidium (compare Figs. 103 and 106, Plate IX.). This arrangement has been observed, either by others or by myself, in the genera mentioned in the preceding paragraph, except Callinectes, in which the exact arrangement of the cells has not been recorded. Reichenbach's statement ('86, p. 91), that in Astacus there are four hypodermal cells under each facet, is probably erroneous, as Carrière's observations show.

Although Patten was the first investigator who clearly demonstrated the presence of the corneal hypodermis in Decapods, Grenacher, in 1879, described, I believe, the nuclei of this layer, without however correctly interpreting them. In his account of the ommatidium in Palæmon, Grenacher ('79, p. 123) mentions two kinds of bodies in what he takes to be the distal ends of the cone cells. Of these, the more distal ones (Taf. XI. Fig. 117, *n.*) represent, in his opinion, the nuclei of the cone cells; the more proximal (Fig. 117, *Kk*^{1}.) he considers as differentiated parts of the cone itself. The positions occupied by these bodies in Palæmon, and by certain bodies which I have observed in Palæmonetes (Plate IX. Fig. 103), are so similar that I believe the structures in the two genera to be homologous. In Palæmonetes the distal bodies lie in the cells of the corneal hypodermis (Fig. 103 *cl. crn.*), and are the nuclei of these cells. They represent what Grenacher considered the nuclei of the cone cells in Palæmon. The proximal bodies in Palæmonetes (Fig. 103, *nl. con.*) are unquestionably the nuclei of the cone cells, yet they correspond to what Grenacher considered the four pieces of the distal segment of the cone. I therefore believe that what Grenacher has described as the nuclei of the cone cells are really the nuclei of the corneal hypodermis, and that what he considered distal segments of the cone are the nuclei of the cone cells.

The *corneal cuticula* in Decapods, in correspondence with the differentiated condition of the corneal hypodermis, is facetted. The outline of the facets is either hexagonal or square. The particular genera in which these different kinds of facets occur have already been mentioned in dealing with the arrangement of the ommatidia in Decapods. The faces of the facets in Decapods are usually very nearly plane, but in Palæmon according to Grenacher ('79, p. 123), and in Palæmonetes (Plate IX. Fig. 103, *crn.*) according to my own observations, the facets are slightly biconvex. In Homarus, as Newton ('73, p. 327) has observed, and in Astacus according to Carrière ('85, p. 167), the distal surface of the facet is plane, the proximal slightly convex. In even the most extreme cases, however, the convexity of the facets in Decapods is not sufficient to make them very effective as lenses.

The facets in Decapods are generally bisected by a fine straight line. This line, as Patten has suggested, probably represents the plane of separation between the two subjacent hypodermal cells. In the square facets this line either divides the facet diagonally, as in Homarus (Parker, '90^{a}, Fig. 2), or transversely, as in Palæmonetes (Plate IX. Fig. 105). In the hexagonal facets it either bisects opposite sides, as in Cancer (Plate X. Fig. 126), or unites opposite angles, as occasionally in Galathea (Patten, '86, p. 644, Plate 31, Fig. 114). Leydig's ('57, p. 252,

Fig. 134) figure of Astacus, in which each facet is subdivided by *two* diagonal lines into four areas, and Newton's ('73, p. 327) statement that the same condition occurs in Homarus, are probably incorrect.

The *cones* in Decapods are composed of four segments. This number was first observed by Will ('40, p. 13) in Palæmon, and has since been recorded in many other genera. So far as I am aware, there are no Decapods in which the number of segments is not four. As Claparède ('60, p. 194) first pointed out in Galathea and Pagurus, each segment contains a nucleus and represents a single cell. Although the significance of these nuclei was without doubt first fully appreciated by Claparède, it is probable that they were previously seen by Leydig ('55, Taf. XVII. Fig. 31) in the crayfish.

As a rule, the distal termination of the cone cells is on the proximal side of the corneal hypodermis. In the lobster, however, and in Palæmonetes (Plate IX. Fig. 104), the pointed ends of these cells pass between the two cells of the corneal hypodermis, and probably come in contact with the corneal cuticula near the middle of a facet.

It is difficult to determine with accuracy the proximal termination of the cone cells. They can be easily traced to a region immediately distal to the distal end of the rhabdome. In this region, as Schultze ('68, Taf. I. Figs. 9 and 11) has clearly demonstrated in Astacus, the fibrous ends of the four cone cells separate, and pass partially around the rhabdome. In Homarus, these fibres extend proximally, and finally terminate at the basement membrane. A similar method of termination also occurs in Palinurus. In the other genera which I have studied, the fibres, although visible near the distal end of the rhabdome, are lost in the adjacent tissue, and I do not know whether they terminate in this tissue without special attachment, or whether they make their way as excessively fine fibres to the basement membrane. The separation of the fibrous ends of the cone cells, near the distal end of the rhabdome, has been observed by Steinlin ('66, p. 93) in Palæmon, and by Schultze ('67 and '68) in several other Decapods. The statement made by many of the older investigators, and recently reaffirmed by Patten, that the cone and rhabdome are parts of one continuous structure, is without doubt incorrect.

The resolution of the *retinula* into its cellular constituents was first attempted in Decapods by Leydig ('55, p. 408), according to whom the retinula of Herbstia contains four cellular bodies, the nuclei of which can be distinguished in the distal part of the structure. A somewhat similar condition was described by Newton ('73, p. 333) for Homarus;

in this genus, as in Herbstia, it was maintained that there were only four cells. Subsequent investigators have not confirmed this conclusion. In transverse sections of the retinula of Palæmon, Grenacher ('77, p. 32) has demonstrated that the rhabdome is surrounded by *seven* retinular cells. He also ('77, p. 33, and '79, p. 125) observed the same number in the retinulæ of Astacus and Portunus. Since the publication of Grenacher's observations, a retinula containing seven cells has been seen in Astacus by Carrière ('85, p. 169), in Penæus, Palæmon, Galathea, and Pagurus by Patten ('86, pp. 630 and 643), and in Cambarus by Watase ('90, p. 299).

In Homarus, as I ('90^a, p. 21) have already shown, the retinula contains, in addition to the seven functional retinular cells, an eighth rudimentary one, which is little more than a nucleus. In order to ascertain the presence or absence of this eighth cell in other Decapods, I have been careful to record the number of retinular nuclei, as well as the number of functional retinular cells. In some genera, such as Cardisoma and Hippa, I have not been able, on account of the unfavorable condition of the tissue, to make this determination; but in Palæmonetes, Palinurus, Cambarus, Crangon, and Cancer, I have succeeded in ascertaining the number both of the functional cells and of the nuclei in the retinulæ.

In Palæmonetes each rhabdome is surrounded by at least seven retinular cells (Plate IX. Fig. 114, *cl. px.*). The nuclei of these cells usually lie slightly distal to the rhabdome (Fig. 104, *nl. px.*). Their arrangement is shown in Figures 110, 111, and 112, which represent a series of consecutive sections through the region occupied by the proximal retinular nuclei of five ommatidia. The nuclei of the different ommatidia are arranged upon the same plan, and the corresponding nuclei in the different sets have been marked by the same number. In several instances, nuclei have been cut in two, and their parts are found in consecutive sections; in such cases the separate portions have been marked with the same number. As can be seen in these figures, the number of nuclei in the distal portion of each retinula is seven. But in addition to these, there is also another one, which occupies a position near the rhabdome. This nucleus resembles the others in all respects except that it is somewhat longer and narrower. It is drawn in Figure 103 at the level marked 114, and in Figure 114 one can see the regularity with which it occurs. This nucleus is the eighth in the retinula of Palæmonetes, and since it differs somewhat in structure from the other seven, and occupies a more proximal position, I believe it represents a rudimentary retinular cell.

In the distal portion of the retinula in Cambarus there are eight nuclei. The arrangement of these, as seen in successive transverse sections, is shown in Plate X. Figs. 118 to 122. In Figure 118, which represents the most distal section of the series, there are four nuclei, and these are so arranged that there is evidently one for each ommatidium.[1] In the next section (Fig. 119) there are seven nuclei, none of which were seen in Figure 118; the place for an eighth is indicated by an open area, and the eighth nucleus itself is seen somewhat out of place in Figure 120 (x). Four of the eight nuclei belonging in Figure 119 are arranged in a manner similar to those in the preceding section, but are not to be confounded with them. The remaining four are so placed that there are two for each ommatidium. Hence in this plane there are, as a whole, three times as many nuclei as there are ommatidia. In the next section (Fig. 120), omitting the nucleus marked x, which has been recorded as belonging to the preceding section, there are four nuclei, so arranged that there is one for each ommatidium. In the following section (Fig. 121) the nuclei, omitting the one marked x, which will be considered as belonging to the next following section, are so arranged that there are two for each ommatidium. In the last section (Fig. 122), the nuclei are not so regularly grouped as in the previous section, but when taken with the nucleus marked x in Figure 121, they constitute a group of four, the arrangement in which is such that each nucleus is intermediate between *four* groups of cone cells rather than between *two*, and therefore in the plane of this section there is one nucleus for each ommatidium. From this enumeration it is evident that the total number of retinular nuclei is eight; namely, one in the first section, three in the second, one in the third, two in the fourth, and one in the fifth. The structure

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[1] The nuclei shown in Figures 118 to 122 are arranged upon either the plan shown in Figure 118 or that in Figure 121 (omitting nucleus x). Imagine the arrangement in Figure 118 extended over a large surface. The groups of four cone cells could then be regarded as forming lines in the direction of the length of the plate. These lines would alternate with lines of nuclei, and as the nuclei in any line would alternate with the groups of cone cells in an adjoining line, the number of nuclei must equal exactly the number of groups of cone cells; i. e. in this arrangement there is one nucleus for each ommatidium. In a similar way, alternating vertical lines may be constructed from the arrangement in Figure 121. One line would be composed entirely of nuclei situated one opposite each group of cone cells; the other, of alternating nuclei and groups of cone cells. In the former, as well as in the latter, there would be as many nuclei as groups of cone cells. Hence, in this arrangement the nuclei are twice as numerous as the groups of cone cells; i. e. there are two nuclei for each ommatidium.

of these nuclei affords no clue as to which one belongs to the rudimentary cell.

In Palinurus (Plate X. Fig. 125, *nl. px.*), the eighth nucleus is regularly present and easily seen. In Cancer (Fig. 129, *nl. px. 8*) it occupies a position between the adjacent retinulæ. It can also be identified in Crangon.

The retinulæ in Decapods, according to all recent observers, contain seven functional cells. In Homarus, Palinurus, Cambarus, Crangon, Palæmonetes, and Cancer, the retinulæ contain, in addition to the seven nuclei of the functional cells, an eighth nucleus, which represents, I believe, a rudimentary cell. It is probable, therefore, that in all Decapods each retinula really contains eight cells, one of which is rudimentary.

The *rhabdome* in Decapods presents a very uniform structure. It is usually an elongated body, pointed both at its distal and its proximal end, and completely covered, except at its distal tip, by the proximal retinular cells. In those Decapods in which it is large enough to be conveniently observed, its transverse section is squarish, and usually subdivided by two straight lines into four smaller squares (Plate IX. Fig. 113). As Grenacher ('77, pp. 31, 32) first demonstrated in Palæmon, the retinular cells are rather peculiarly arranged around the rhabdome. One of its four sides is flanked by *one* cell, the other three by two cells each. This arrangement can be seen in Palæmonetes (Fig. 113), and probably obtains for all Decapods.

In Palinurus Argus (Plate X. Fig. 124) there appears to be no rhabdome, unless the translucent axial portion of each retinular cell can be said to represent segments of it. The fibrous ends of the cone cells (*cl. con.*) can be easily identified between the retinular cells, but the centre of the retinula is filled with pigment, and shows not the least trace of a rhabdome. This peculiarity of Palinurus was noticed as early as 1840 by Will ('40, p. 15), who described the ommatidium in this genus as being without a transparent mass (= rhabdome).

Although the *distal retinular* cells in Decapods were collectively recognized by Müller ('26, pp. 355, 356) some sixty years ago as a definite pigment band in the distal portion of the retina in the crayfish, they were not identified as separate cells until quite recently. The first investigator to observe them was Carrière ('85, p. 169), who described them in Astacus as a pair of pigment cells flanking each cone. In Cambarus, Crangon, and Homarus, they also cover the sides of the cone, and in the last named genus they are produced proximally into long fibres, which perhaps pass through the basement membrane. In Palæmonetes (Plate IX. Fig. 108, *cl. dst.*) and in Cancer (Plate X. Fig. 127, *cl. dst.*) they are reduced to pigmented threads, which, starting from comparatively large bases, twine around the lateral surfaces of the cones.

The arrangement and number of the distal retinular cells can be most readily determined from their nuclei. In Cancer (Plate X. Fig. 128) the cells are arranged in circles of six around each group of cone cells; each cell, however, participates in three circles, and consequently there are in reality only twice as many cells as ommatidia. This arrangement of the cells also occurs in Cardisoma, Hippa, and Pagurus. In Crangon (Fig. 123), as I have previously remarked, the nuclei of the distal retinular cells are arranged in rows alternating with the rows of cones. There are twice as many nuclei as cones; hence I conclude that here also there are two distal cells for each ommatidium. In Homarus, Palinurus, Cambarus, and Palæmonetes (Plate IX. Figs. 103 and 109, *nl. dst.*) the nuclei are grouped distinctly in pairs, one pair for each ommatidium.

Each cone in Penæus, according to Patten ('86, p. 634), is surrounded by two pairs of pigment cells, and Watase ('90, p. 299) states that in Cambarus the dioptric part of the ommatidium is sheathed by *four* pigment cells. In Cambarus Bartonii I have been able to find only two such elements, the pair of distal retinular cells already described, and in the other Crustaceans which I have studied I have observed nothing which supports Patten's statement concerning the four pigment cells in Penæus. I am therefore inclined to doubt the accuracy of these two observations.

The interommatidial space in the basal part of the retina in Palæmonetes contains a light pigment similar to that described in the retina of Mysis. Like this the pigment in Palæmonetes is white by reflected light, and yellowish by transmitted light (compare Plate IX. Fig. 115). It is apparently contained within cells (Fig. 103, *cl. ms'drm.*) whose outlines are very irregular, and whose nuclei (Fig. 104, *nl. ms'drm.*) are small and somewhat variable in form. These cells occur on both sides of the basement membrane. As in Mysis, they have probably migrated into the retina, and are perhaps mesodermic in origin. They have been seen by Carrière ('85, p. 169) in Astacus, by Patten ('86, p. 636) in Penæus, and by myself ('90^a, p. 25) in Homarus. I have also recently observed them in Crangon, Cambarus, Cardisoma, Pagurus, and Palinurus, as well as in Palæmonetes.

From what has preceded it is evident that the ommatidium in Decapods contains the following elements: cells of the corneal hypodermis, two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells, mesodermic (?) in origin, often present.

Table of Ommatidial Formulæ.

I have now concluded my account of the structure of the ommatidia in Crustaceans, and for the purpose of presenting in a condensed form its more important features I have devised the following table. This consists of a series of ommatidial formulæ constructed upon the plan which I have described in the Introduction. The figures indicate the numbers of particular kinds of cells present in the ommatidium of a given group. The abbreviation *pr.* (present) marks the presence of any kind of cell when the number of that kind is not constant for different ommatidia in the same individual.

Table showing the Cellular Composition of the Ommatidian Crustaceans.

Groups of Crustaceans.	Cells of Corneal Hypodermis.	Cone Cells.	Retinular Cells.			Accessory Cells.
			Undifferentiated.	Differentiated.		
				Proximal.	Distal.	
Amphipoda,	pr.	2	5			pr. (ect. ?)
Branchiopodidæ and Apusidæ,	2	4	5			0
Estheridæ,	pr.	5 (4)	5			0
Cladocera,	?	5	5			pr. (ect. ?)
Copepoda: Pontella,	pr.	2	5			pr. (ect. ?)
Sapphirina,	?	?	3			?
Argulus,	pr.	4	5			?
Isopoda: Idotea,	2	2	6			pr. (ect. ?)
Porcellio,	2	2	7			pr. (ect. ?)
Serolis,	2 (+?)	2		4	2	pr. (ect. ?)
Nebaliæ,	2	4	7			pr. (ect. ?)
Schizopoda,	2	2		7 + 1	2	pr. (mes. ?)
Stomatopoda,	2	4		7 + 1	2	pr. (mes. ?)
Decapoda,	2	4		7 + 1	2	pr. (mes. ?)

A few features in the table require explanation. Among the number of cells recorded for the Estheridæ, the figure within the parenthesis under the head of Cone Cells indicates the occasional occurrence of cones containing only four cells, although the usual number is five. In the line for Serolis, under the head of Corneal Hypodermis, the parenthesis and included signs are intended to indicate the possibility of there being more than two cells in the corneal hypodermis for each ommatidium. In the Schizopods, Stomatopods, and Decapods, the number of proximal retinular cells is expressed in the form of 7 + 1 instead of 8, because one of the cells is rudimentary.

The Innervation of the Retina.

The innervation of the retina in the compound eyes of Crustaceans is chiefly interesting, because of its importance in relation to physiological questions. As this paper deals with a morphological topic, it would be obviously irrelevant to enter upon any extended discussion of this subject. Nevertheless, the innervation of the retina is not without some bearing on the general question which I have set for myself, and I shall therefore not pass it by, but put in as brief a form as possible what I have observed concerning it.

In my account of the retina in the lobster, I described the optic-nerve fibres as terminating in the proximal retinular cells. Near the ganglion each fibre consists of a bundle of fibrils, simply enclosed within a sheath, but as it approaches the retina it becomes coated with pigment. The pigment increases in quantity and the fibre correspondingly enlarges till it finally becomes continuous with the deeply pigmented retinular cell. The fibrillar axis can be distinguished in the pigmented portion of the fibre as a transparent axial structure, and it can also be traced distally through the pigment of each retinular cell till it breaks up into its ultimate fibrillæ, which are spread over the distal half of the rhabdome. This is the method of nerve termination in the lobster, and points very conclusively to the rhabdome as the terminal organ.

What I have seen of the termination of the nerve fibres in other Crustaceans confirms the account which I have already given for the lobster. In some species which I have studied, owing to the small size of the retinal elements, I was unable to determine the cells with which the nerve fibres connected. The termination of the fibres in the cells of the retinula was observed, however, in the following genera: Branchipus, Limnadia, Pontella, Gammarus, Talorchestia, Idotea, Porcellio, Sphæroma, Serolis, Gonodactylus, Mysis, Palæmonetes, Crangon, Cambarus, Palinurus, Pagurus, Cancer, and Cardisoma. In the majority of these, a fibrillar axis could be distinguished.[1] In Cambarus, as in Homarus, the nerve fibrillæ spread over the distal portion of the rhabdome.

In Serolis an exceptionally interesting condition is presented. At the level of the basement membrane each retinular cell contains a large fibrillar axis (Plate VI. Fig. 64, *ax. n.*). This becomes somewhat subdivided in the more distal portion of the cell, and in the region of the retinular nucleus it is represented by a cluster of several smaller axes (Fig. 63). At the level of the hyaline cell, these however cannot be distinguished (Fig. 62), but the scattered condition of the pigment granules in this plane is probably to be accounted for by the presence of many separate fibrils in the substance of the cell. In the region of the rhabdome an immense number of fine lines can be seen extending from the retinular cell into the substance of each rhabdomere (Fig. 61). These, I believe, represent the fibrils of the nervous axis. They have been previously observed in Serolis by Watase ('90, p. 291), and are so readily visible that there can be no question as to their presence. Each fibril is perpendicular to the longitudinal axis of the ommatidium, and extends through the rhabdomere to its axial surface. Before reaching this, however, the fibril passes through what seems to be a delicate membrane. When closely examined, this membrane often has the appearance of a row of dots instead of a line, and in several cases I have been unable to discover any traces of it. What its significance is, I am at a loss to say. As I have previously observed, when the elements of the retinula are separated the rhabdomere shows no tendency to break along this line. Since the structure is pierced by the fibrils, and does not appear to be a natural plane of rupture, and since sometimes it is apparently absent, I believe it may be considered, from a morphological standpoint at least, as a secondary and rather unimportant modification within the rhabdomere itself.

If I am correct in maintaining that the nerve fibrils in Serolis terminate in the rhabdomere, it is probable that they have a similar method of ending in all other Crustaceans, and in such instances as Homarus, where they have been traced only to the surface of the rhabdome, their actual termination has probably not been seen.

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[1] A definite fibrillar axis was traced from below the basement membrane to the region of the rhabdome in Gammarus (Plate I. Figs. 6–8), Porcellio (Plate V. Fig. 46), Idotea (Plate V. Figs. 53 and 55–57), Mysis (Plate VII. Figs. 87–89), Gonodactylus (Plate VIII. Figs. 101, 102), Palæmonetes (Plate IX. Figs. 116, 117), Cambarus, Pagurus, Cancer (Plate X. Figs. 130 and 131), and Cardisoma.

The termination of the fibrillæ of the optic nerve in the rhabdome supports Müller's belief that the nerve fibres terminate in a region near the proximal ends of the cones, and Grenacher's more specific view that they are connected with the retinular cells, and that the rhabdome is the terminal organ. This method of termination is not consistent with the opinion of Gottsche and Leydig, that the cone is the terminal organ, nor with Patten's rather similar belief that the ultimate nerve fibrillæ are distributed to the cone. I am therefore compelled to think that these authors are mistaken in their conclusion.

Theoretic Conclusions.

In attempting to account for the variation in the number of cells in different types of ommatidia, two courses naturally suggest themselves. Either the different kinds of ommatidia vary in the number of cells which they contain, because they have had separate origins, or they are different because in some or all of them the ancestral ommatidium has suffered modification. An examination of the table on page 115 shows conclusively, I think, that in Crustaceans even the most extreme types are so little removed from one another that it is much more probable that the different kinds of ommatidia are genetically connected, than that they have been produced independently. Granting this statement, the question naturally arises, What are the means by which the primitive ommatidium was modified? I believe that a close scrutiny of the cellular structure of the ommatidia in living Crustaceans will disclose some of the factors in this process. There are at least three of these to be distinguished: the differentiation of cells, the suppression of cells, and the increase in the number of cells by cell division.

By the differentiation of cells, I do not mean the process by which hypodermal cells have become converted into retinular or cone cells, but that by which an element already differentiated in the ommatidium is secondarily modified to subserve another function. The only instance of this kind with which I am acquainted occurs among the retinular cells. In the majority of the simpler Crustaceans, the sides of the cones are covered with pigment, which is almost always contained in the distal ends of the retinular cells. In Serolis, among the Isopods, and apparently in all the genera of Stomatopods, Schizopods, and Decapods, the cones are surrounded by special pigment cells. These are always twice as numerous as the ommatidia, and represent, I believe, retinular cells which have become differentiated for the special purpose of sheathing the cones. The way in which this differentiation may have occurred has already been suggested in my paper on the lobster ('90^a, p. 57).

Although I have expressed the opinion that these cells are to be regarded as modified retinular cells, it might be maintained that they are merely enlarged accessory pigment cells, such as occur in the interommatidial space of many Crustaceans. But I believe such an interpretation of these cells would be erroneous, for the following reason. In Serolis the nuclei of the pigment cells which surround the cone (Plate VI. Fig. 65, *nl. dst.*) possess one, and sometimes two, well marked nucleoli, but no fine chromatine granules. In this respect they closely resemble the nuclei of the proximal retinular cells (*nl. px.*), and differ considerably from those of the accessory pigment cells (*nl. h'drm.*). The nuclei of the last named cells contain only fine granules. So far, then, as their nuclei are concerned, the distal retinular cells bear a much closer resemblance to the proximal cells than to the accessory pigment cells. Each retinula in Serolis contains, moreover, only four cells, and in this respect differs considerably from other Isopods, where the number of retinular cells is either six or seven. On the supposition that the pigment cells surrounding the cone in Serolis are accessory pigment cells, one would be called upon to account for the exceptionally small number of cells in the retinula of this genus; whereas, if the cells around the cone are regarded as modified retinular cells, they may be taken to indicate for Serolis a primitive retinula composed of six cells, a number characteristic of the retinulæ in other Isopods. This interpretation of the condition of the retinula in Serolis is borne out by what is known of the retinula in Sphæroma, where, it will be remembered, a transition between the condition in Serolis and that in other Isopods was distinctly indicated.

In the Stomatopods, Schizopods, and Decapods, if my observations are correct, there are no ectodermic accessory pigment cells. Consequently, a comparison between these cells and what I have called the distal retinular cells cannot be drawn. In Mysis (Plate VII. Fig. 73), Gonodactylus (Plate VIII. Fig. 94), and Palæmonetes (Plate IX. Fig. 103), as well as in all other Decapods which I have examined, the resemblance between the nuclei of the retinular cells and those of the pigment cells which surround the cone is as striking as in Serolis, and suggests the origin of these cells from retinular cells rather than from any other source. In Homarus, the pigment cells around the cone present a condition of some interest in this connection. Each pigment cell is extended proximally as a long fibre, which certainly reaches nearly to the basement membrane, and probably passes through it in company with the fibrous ends of the retinular cells (compare Parker, '90[a], pp. 17–19). Admitting that these cells are merely modified accessory pigment cells, such a condition as this is quite unintelligible to me; but granting them to be differentiated retinular cells, their fibrous extensions can be easily explained as the rudiments of the fibrous portion of the cell with which the nerve fibre was once connected. A somewhat similar case occurs in Mysis, where the centre of each of the pigment cells which surround the cone contains a small transparent axis. This axis in every respect except that of connection with a nerve fibre corresponds to the fibrillar axes described in the functional retinular cells of this Crustacean (compare Plate VII. Figs. 77, 78, and 87). Consequently, the axis in the distal cells either represents a rudimentary nervous axis, in which case the cell containing it must be regarded as a retinular cell, or it is something for which I can suggest no explanation.

These facts lead me to conclude that the pigment cells which surround the cone in Serolis, the Stomatopods, Schizopods, and Decapods, are to be regarded as modified retinular cells, and I have therefore described them under the name of distal retinular cells, in contrast to proximal retinular cells, or those which retain their primitive position around the rhabdome. In the differentiation of a group of simple retinular cells into proximal and distal cells, the latter necessarily change their function from that of terminal nervous organs to that of screens chiefly concerned in excluding the light from the sides of the cones. Wherever the distal retinular cells occur, they afford evidence, I believe, that the structure of the ommatidium has undergone a modification from the primitive ommatidial condition.

The second method by which the structure of ommatidia may be changed, namely, the suppression of cells, is perhaps the one whose presence is most easily detected because of the frequent persistence of the partially reduced cells. These rudimentary cells can be identified most readily in the cases where they belong to groups in which the number of elements is constant for different ommatidia. I know of no evidence of suppression among the groups of cells in the corneal hypodermis or the cones. Among the retinulæ, however, it seems to be of rather common occurrence. The first indication of this process is naturally a diminution in the size of the cell to be suppressed. Such a step is perhaps shown in the retinula of Gammarus (Plate I. Fig. 6), where one of the five cells, although evidently functional, is nevertheless considerably reduced. Without much doubt, the body described in the retinula of Idotea robusta represents, for reasons already stated, the seventh cell present as a functional structure in Porcellio. In Idotea irrorata the retinulæ, with very few exceptions (Plate V. Fig. 54), contain only six cells, showing no trace of the seventh cell. This condition, I believe, is to be interpreted as one in which a cell has been completely suppressed. In Stomatopods, Schizopods, and Decapods the retinulæ have been shown to contain, in addition to the nuclei of the seven functional cells, an eighth nucleus, which may represent a rudimentary cell.

In all of the cases thus far cited, it might be maintained that what I have considered rudimentary cells are really cells newly acquired by the ommatidia, and not old cells gradually undergoing suppression. The condition in Idotea, however, where the body in question apparently contains no nucleus, would be difficult to explain on this assumption, whereas, if it be considered a cell undergoing reduction, its condition can be easily accounted for. In Stomatopods, Schizopods, and Decapods, the constancy in the number of cells and in the position of the eighth nucleus, the small amount of protoplasm which surrounds it, and the striking resemblance which it has to the other retinular nuclei, are facts difficult to explain on the assumption that it represents a newly acquired cell, but easily accounted for on the supposition that it is the remnant of a partially suppressed cell. For these reasons, I believe that the instances cited are valid cases of partial suppression, and that this must be regarded as one of the actual means employed in the modification of ommatidia.

That ommatidia have been modified by an increase in the number of their cells by cell division, is a proposition not easily established. The difficulty of obtaining conclusive evidence on this point can be made clear by an example. Let it be assumed that cones composed of two cells are converted by the division of the cells into cones composed of four cells. This step, even when first taken, would probably be accomplished during the embryonic growth of an animal, and therefore before the cones themselves had begun to be differentiated. What would actually happen would probably be this: the two cells, the homologues of which in all previous animals had given rise to two cone cells, would in this case each divide, thus producing a group of four cells, which ultimately would form a cone of four segments. If we could compare the adult animal in which such a process had occurred for the first time with its immediate ancestors, the only important difference that would be observed would be in the number of the cells in each cone, and if the genetic relations of the two individuals were not known, it could not be stated with certainty whether in one case we were dealing with an animal which had lost two cone cells or in the other, with one which had gained two; in other words, it would be impossible to determine which of the two conditions was the primitive one. The importance of embryological evidence in determining this question must therefore be apparent. But evidence from even this source might not be conclusive. Thus in the development of the lobster I have traced in detail the steps by which the ommatidia are formed, and although in this Crustacean the considerable number of cells in each ommatidium would warrant one in expecting some evidence of increase by division, the division of the cells in the retina is entirely accomplished some time before these elements show any grouping into ommatidia. Hence, the exact method of origin of the cells of the ommatidium cannot at present be given. I have observed that the same is also true in Gammarus; cell division is completed before the cells are grouped into ommatidia. Perhaps in the development of some other Crustaceans evidence of the kind which I have sought may be obtained, but in the few species which thus far have been studied the evidence has not been produced.

Although the supposition that ommatidia may increase the number of their cells by the division of those which they already possess is not supported by any direct observations with which I am acquainted, there are some facts recorded which are indirectly confirmatory of it. Thus, in Phyllopods, an increase in the number of cone cells appears to accompany a progressive differentiation of the retina itself. In this group, as I have already pointed out, the simplest condition of the retina is found in Branchipus and Apus. From the retina of Apus that of the Estheridæ can be easily derived, and the retina in the Estheridæ represents a condition from which the retina of the Cladocera may have arisen. That this series of retinas, from Apus through the Estheridæ to the Cladocera, is a natural one is abundantly proved by the course taken in the development of the eye in these groups. If we regard the condition of the cones in these Crustaceans, we shall find that in the most primitive retina, that of either Branchipus or Apus, they consist of four cells; that in the more complex retina of the Estheridæ they are usually composed of five cells, although cones of four cells are not unfrequent occurrences; and finally, that in the Cladocera they are always composed of five cells. Apparently in this series the development of the retina is paralleled by a corresponding development in the cones, whereby one composed of four cells is ultimately converted into one with five cells. Since the resemblance between any two of the cells in a cone composed of five elements is quite as close as that between the cells in cones containing only four elements, I believe that the additional cell, which has increased the number of segments from four to five, has been derived by the division of one of the original four cone cells, and not from an extra-ommatidial source.

Another instance of this kind occurs among the Isopods. The cones in this group, it will be remembered, are usually each composed of two segments. According to Beddard's figures ('90, Plate XXXI. Figs. 1 and 4) in Arcturus, however, they occasionally consist of three segments, and in Asellus aquaticus, according to Sars ('67, p. 110), although three of the four cones in each eye are composed of only two segments each, the fourth regularly contains three. The size of the segments in the fourth cone differs; two are small, and together their bulk about equals that of the third, and the last is approximately of the size of a segment in one of the other cones. If we attempt to explain the condition of the cone composed of three segments by supposing it to have been produced by adding to the normal pair of cone cells a single cell from some source external to the ommatidium, we are met with the difficulty, that what is apparently the added cell — the larger one — resembles more closely a segment in the other cones than do either of the two remaining cells, although the latter must on this assumption represent the original segments. If, however, we imagine the small segments to have arisen by the division of a single larger one similar to the large one which remains in the cone, the relation of the resulting segments both in size and number is a perfectly natural one. This explanation, therefore, seems to me to be more probable than the former. For these reasons, I believe that an increase in the number of cells in an ommatidium takes place by the division of the cells already forming a part of that ommatidium, rather than by the importation of new elements hitherto foreign to the ommatidium.

The conclusion which I would draw from the preceding discussion is, that there are at least three means of modifying the numerical formulæ of ommatidia, all of which involve only the cells primitively belonging to the ommatidium, and therefore do not necessitate the introduction of new cells from extra-ommatidial sources. They are cell differentiation, cell suppression, and cell multiplication.

Having now determined the means by which the cellular structure of the ommatidia in living Crustaceans is modified, we are prepared to approach the question of the structure of the primitive ommatidium. If it could be shown that ommatidia were modified only by increasing the number of their elements, it would naturally follow that those composed of the fewest cells would more nearly resemble the ancestral type than those which consist of many cells. On the other hand, if the suppression of cells were the only means employed in modifying structure, the ommatidia containing the greatest number of elements would most nearly approach the primitive type. Since, as I believe, both means are employed in the Crustacea, the determination of the structure of the ancestral ommatidium is evidently a difficult problem. Perhaps the most satisfactory way of attempting its solution is to consider separately the different categories of cells which enter into the formation of an ommatidium, and, after reviewing the conditions presented by each in different Crustaceans, to determine, if possible, which of these conditions is the most primitive. The conclusions thus arrived at concerning each kind of cell will afford the necessary grounds for the construction of an hypothetical formula of the ancestral ommatidium. Although it is not necessary that this ommatidium should be represented in any living Crustacean, for the ommatidia in all these may have suffered modification, yet it is possible that a representative of it may still exist.

Turning now to the consideration of the different groups of cells, we find that the corneal hypodermis presents two conditions; one in which its cells are not regularly arranged, and another in which they are grouped in pairs, each pair lying at the distal end of an ommatidium. The latter condition is characteristic of the Decapods, Schizopods, Stomatopods, Nebaliæ, Isopods, and some Branchiopods; the former, so far as is known, occurs in the Amphipods, the Branchiura, and in some Branchiopods (Limnadia and some species of Branchipus). In view of the fact that the corneal hypodermis is a part of the retina which retains the function of the general hypodermis but slightly modified, and that in the latter the cells do not present a regular arrangement, it is probable that a corneal hypodermis in which the cells are not regularly arranged is of a more primitive character than one in which they are definitely grouped.

The number of cells in the individual cones of Crustaceans varies from two to five. Cones composed of two cells occur in Eucopepoda, Amphipods, Isopods, and Schizopods; cones of three cells are present only exceptionally in Isopods; cones of four cells are found in the Decapods, Stomatopods, Nebaliæ, Branchiura, and some Branchiopods; cones of five cells characterize the Cladocera and some Branchiopods. I have already given reasons for regarding the cones composed of three cells as having been derived from those containing two, and cones composed of five cells from those possessing four. Since there is no evidence of degenerate cells in any of the cones composed of two segments, I am convinced that cones with four cells are derived from those with two cells, and not the reverse. On these grounds, I conclude that the most primitive form of cone in living Crustacea is that consisting of two cells.

The retinular cells in Crustaceans are subject to considerable variation. As I have previously shown, an ommatidium may contain one or two kinds. When there is only one kind, all the cells are grouped around the rhabdome, and are known simply as retinular cells. When there are two kinds, one occupies a position around the rhabdome, and the other around the cone; the former I have called proximal retinular cells, the latter distal retinular cells. Proximal and distal retinular cells occur in Serolis, the Stomatopods, Schizopods, and Decapods; simple retinular cells apparently characterize the ommatidia of all other Crustaceans. I have already presented reasons for considering the distal retinular cells as modified simple retinular cells, which, in the separation of the cone from the rhabdome by the elongation of the ommatidium, have lost their connection with the nervous element, but have retained their place next the dioptric one. A group of retinular cells in which this differentiation has occurred is not so primitive in its structure, therefore, as one in which all the retinular cells retain their original position around the rhabdome, as in the groups of Crustacea which possess simple retinular cells.

The number of simple retinular cells in Crustacean ommatidia varies from five to seven. In Nebalia, and some Isopods, the retinula contains seven cells; in other Isopods it is composed of six cells, and in the Branchiopods, the Cladocera, some Copepods, and Amphipods it consists of five cells. It is difficult to state which of these numbers represents the primitive condition. In the Isopods, as I have previously indicated (pp. 86 and 87), there is considerable evidence to show that a retinula composed of six cells has been produced from one containing seven by the suppression of one cell. Possibly in this way the retinula with five cells was derived from that with six, but I know of no observations which favor this supposition.

A small amount of indirect evidence on this question is to be obtained from the other structural peculiarities of the ommatidia containing retinulæ with five, six, or seven cells. These retinulæ occur in connection with two kinds of rhabdomes, — one in which the rhabdomeric segments are easily distinguishable, and the other from which they are apparently absent. Of these two kinds, the one in which the segments persist is evidently more primitive than the one in which their outlines are obliterated.

Probably in Nebalia, in which the retinula is composed of seven cells, and certainly in Idotea, where it consists of six, the rhabdome shows no indication of being composed of rhabdomeres, but in Porcellio the seven retinular cells surround a rhabdome composed of a corresponding number of rhabdomeric segments. In Branchipus, the retinula consists of five cells, but the rhabdome is apparently not composed of separable rhabdomeres, whereas in Pontella, Argulus, Gammarus, Talorchestia, Hyperia, and Phronima the five retinular cells are each represented by a rhabdomere. The more frequent occurrence of a primitive condition of rhabdome with the retinula having five cells than with that having seven, favors indirectly the idea that the retinula with the smaller number of cells is the more primitive of the two. The types of cones associated with the two kinds of retinulæ offer almost no evidence on the question in hand. Thus, a retinula of seven cells is associated with a cone of four cells in Nebalia, and with one of two cells in Porcellio, and a retinula of five cells is combined with a cone of four cells in Branchipus and Argulus, and with one of two cells in Amphipods. The relation of the two kinds of retinulæ to the corneal hypodermis affords some slight evidence in support of the opinion that the retinula of five cells represents the more primitive type; for although the differentiated type of corneal hypodermis — the one in which the cells are regularly arranged — may occur with either type of retinula, the undifferentiated hypodermis — in which the cells are not regularly grouped — is known to be associated only with retinulæ containing five cells (some Branchiopods, Argulus, and Amphipods). The evidence drawn from these various sources is obviously very slight; but such as it is, it indicates that the retinula with five cells, rather than that with a greater number, represents the more primitive condition. This conclusion receives some additional support from the fact that the retinula composed of five cells characterizes the ommatidia in a number of not otherwise very closely related Crustaceans (Pontella, Argulus, the Branchiopods, and Amphipods), whereas the type possessing seven cells occurs only among certain Isopods and in the Nebaliæ. I believe, therefore, that all the evidence at present deducible from the condition of the simpler retinulæ indicates that the one which contains five cells is more primitive than that composed of six or seven cells.

In the present argument I have purposely omitted any mention of the condition of the retinula in the Corycæidæ, those Copepods in which the lateral eyes present a highly modified condition. I have done this because I believe that the lateral eyes in many Copepods are degenerate, and that therefore the evidence to be drawn from them cannot be as trustworthy as that from other sources. That the lateral eyes in Copepods are degenerate, is shown from the fact that in many members of the group the eyes are entirely absent, and that in those in which they do occur, their structure is subject to considerable variation. Thus in Pontella the retina contains, besides one group of five retinular cells, three isolated nervous cells, whereas in Sapphirina there is a group of three retinular cells, and at least one isolated nervous cell. In Pontella, Sapphirina, Corycæus, and Copilia each retina is provided with a single lens, but in Irenæus, according to Claus ('63, Taf. II. Fig. 1), there are two lenses in each eye. These variations, including the total disappearance of the organ in some members of the group, lead me to believe that the lateral eyes in the Copepods are degenerated, and therefore are organs in which the suppression of cells may have reduced them to even a simpler condition than that presented by the ancestral ommatidium.

The conclusion which I draw from the preceding argument is, that the type from which the ommatidia in all living Crustaceans are probably derived would exhibit the following structures: a corneal hypodermis in which the cells are not regularly arranged, and consequently an unfacetted corneal cuticula; a cone composed of two cells; a retinula composed of five retinular cells and having a rhabdome which consists of five rhabdomeres. The retina of the primitive eye, a simple thickening in the superficial ectoderm, would be composed of ommatidia of this type arranged upon the hexagonal plan. None of the Crustaceans with which I am acquainted possess an eye of exactly this structure. The one in which this condition is most nearly represented is perhaps Gammarus. In this animal all the requirements of the hypothetical eye are fulfilled, except that the form of the retina as a whole is somewhat disturbed by the separation of the corneal hypodermis from the layer of the cones and retinulæ by a corneo-conal membrane, and by the partially disguised condition of the basement membrane.

If my conclusions be correct concerning the structure of the primitive ommatidium and the means by which it has been modified, it follows that the principal types of ommatidia have been produced mainly by increasing the number of cells in the primitive type, and that, of the three means of modifying the structure of ommatidia, cell division has been the most influential.

Although the hypothetical ommatidium which has been described in the preceding paragraphs has been spoken of as ancestral, it is not to be supposed that the condition which it presents must be regarded as necessarily its simplest form. I feel tolerably confident, however, that the primitive ommatidium must have been at least as simple as I have assumed it to be. Possibly its retinula may have been composed of less than five cells, as is that seen in some Copepods; although, as I have previously remarked, the condition of the lateral eyes in these Crustaceans is probably influenced by degeneration, and therefore may not represent a primitive stage. What might be regarded, however, as a more primitive form of ommatidium than that which I have described, may be seen in the eye of the Chætopod Nais (Carrière, '85, pp. 28, 29). In this worm the eye lies in the hypodermis on the side of the head, and consists of a few relatively large transparent cells, the proximal faces of which are in part covered by pigment cells. It is probable that the transparent cells are merely dioptric in function, and that the pigment cells are nervous. The transparent cells may therefore be looked upon as the forerunners of cone cells, and the pigment cells at their bases as retinular cells not yet differentiated into a retinula. It is not difficult to imagine the origin of an ommatidium from a single one of the transparent cells and its accompanying pigment cells, and, by an increase in the number of such groups, the production of a retina like that of the compound eye of Arthropods.

This view of the origin of the ommatidia in Arthropods is irreconcilable with that recently advanced by Watase ('90), according to whom each ommatidium is to be regarded as a pit formed by an involution of the hypodermis. The supposed cavity of this pit occupies nearly the whole length of the axial portion of the ommatidium, and is filled by the secretions of the cells constituting its wall. The secretion in the deeper part of the pit forms the rhabdome; that which is produced nearer its mouth, the cone. During the formation of the pit, the hypodermal cells are believed to retain such mutual relations that their morphologically distal ends lie next its cavity; hence the secretions produced by these ends, the rhabdome and cone, are to be regarded as modifications of the chitinous cuticula of the outer surface of the body.

Ingenious as this theory is, I have not been able to convince myself of its tenability. It may be urged against the assumption that the retinular cells occupy a proximal position and the cone cells a distal one on the wall of a hypodermal pocket, that in Gammarus the retinular cells extend from the distal to the proximal face of the retina, and that in Homarus the cone cells have a corresponding extent; these conditions show that it is possible to interpret the cells in an ommatidium as elements in a thickened epithelium, all of which originally extended from one face of the layer to the other, and the grouping of which is not even now interfered with by any process of involution. But granting that the retinal cells are thus arranged, it must be admitted that the surface on which the rhabdomeres are produced corresponds to the *sides* of the cells rather than to their *distal ends*. This interpretation of the position of the rhabdome is not, so far as I am aware, contrary to any well established facts, and indeed it is rather more in accordance with the condition seen in the eyes of some Arthropods than that implied in Watase's theory. Thus, in the lateral eyes of scorpions the retinal cells are arranged as in an ordinary epithelium, and the lateral wall of each cell is in part occupied by a rhabdomere. In this instance, then, it must be admitted either that the rhabdomeres are produced on the *sides* of the retinal cells, or that each cell has independently rotated upon itself, so as to bring its morphologically distal end into a position corresponding to the side of an ordinary epithelial cell. But there is neither direct evidence to show that this rotation of single cells has occurred, nor, in this case, can there be any motive assumed which might have induced the rotation of single elements. I therefore believe that in the lateral eyes of scorpions the rhabdomes are on the sides of the retinal cells in the strictest morphological sense; and if they can occur in this position in the eyes of scorpions, I can see no reason why they might not occur in similar positions on the retinal cells of compound eyes. Hence it seems to me as reasonable to interpret the retina in compound eyes as a layer of modified epithelium unaffected by involutions, as it is to consider it a layer in which each ommatidium represents an infolding.

When, moreover, an attempt is made to show how a particular ommatidium has arisen by involution, some difficulties are encountered. Thus in Gammarus, in which the ommatidium is of a primitive type, each ommatidial pocket would involve seven cells, two of which, the cone cells, must be imagined as forming the neck of the involution, while the remaining five, the retinular cells, would constitute the deeper portion of the pocket. The mechanical difficulty which would accompany the formation of an involution involving so small a number of cells must be obvious, and offers, I believe, an obstacle to the successful operation of the process assumed in Watase's theory.

The one instance in which Watase has described an actual involution to form the eyes in Arthropods is the lateral eye of Limulus. These eyes consist of a cluster of hypodermal pits, over each of which there is a cuticular lens. Although there cannot be the least doubt that in this case each pit is a hypodermal involution, the belief that each one is homologous with an ommatidium is by no means so well founded. In structure the wall of the pit differs considerably from that of an ommatidium; it contains no cells which can be definitely denominated, either as cone cells or as cells of the corneal hypodermis, and it does contain a large ganglionic cell, which is only questionably homologous with any element in an ommatidium. In most respects in which these pits differ from ommatidia, they resemble simple eyes, and I therefore regard them as such, rather than as representatives of an early condition in the formation of an ommatidium.

When to the objections raised in the preceding paragraphs the statement is added, that in both Homarus and Gammarus — representatives of the extremes of organization — the ommatidia are developed without showing any trace of infolding, Watase's theory of the formation of ommatidia by means of involutions appears in a still less favorable light. I therefore regard ommatidia, not as the result of involutions, but as differentiated clusters of cells in a continuous unfolded epithelium.

I have not observed anything that would lead to the conclusion recently expressed by Patten ('90), that an ommatidium is a hair-bearing sense bud. I believe, on the contrary, that they have had a very different origin.

In conclusion, I may add, that if my idea of the origin of ommatidia be correct, it supports Grenacher's opinion, that compound eyes are not derived directly from aggregations of simple eyes, but from groups of optic organs which were even more primitive in their structure than simple eyes. Possibly such primitive organs were the antecedents of both the compound and simple eyes of Arthropods, as Grenacher suggests; but possibly the two kinds of eyes may have had totally different origins.

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EXPLANATION OF FIGURES.

All the drawings were made with the aid of an Abbé camera. Unless otherwise stated, the specimens from which the drawings were made were stained in Czokor's alum-cochineal and mounted in benzol-balsam. The reagent used in depigmenting sections was an aqueous solution of potassic hydrate $\frac{1}{4}\%$.

ABBREVIATIONS.

a.	Anterior.
ax. n.	Axis of nerve fibrillæ.
brs. oc.	Optic pocket.
cl. con.	Cone cell.
cl. crn.	Cell of corneal hypodermis.
cl. dst.	Distal retinular cell.
cl. hyl.	Hyaline cell.
cl. ms'drm.	Mesodermic cell.
cl. px.	Proximal retinular cell.
cl. rtn.'	Retinular cell.
cl. rud.	Rudimentary retinular cell.
cnch.	Shell.
cœl.	Body cavity.
con.	Cone.
cp. sng.	Blood corpuscle.
crn.	Corneal cuticula.
cta.	Cuticula.
d.	Dorsal.
dsc.	Sucking disk.
dx.	Right.
gn. opt.	Optic ganglion.
h'drm.	Hypodermis.
hp.	Liver.
in.	Intestine.
lns.	Lens.
mb. ba.	Basement membrane.
mb. crn.	Corneal membrane.
mb. crn'con.	Corneo-conal membrane.
mb. i'cl.	Intercellular membrane.
mb. n. opt.	Membrane of optic nerve.
mb. pi'ph.	Peripheral membrane.
mb. pr'con.	Preconal membrane.
mu.	Muscle.
n. fbr.	Nerve fibre.
nl. con.	Nucleus of cone cell.
nl. crn.	Nucleus of cell in corneal hypodermis.
nl. dst.	Nucleus of distal retinular cell.
nl. h'drm.	Nucleus of hypodermal cell.
nl. hyl.	Nucleus of hyaline cell.
nl. ms'drm.	Nucleus of mesodermic cell.
nl. px.	Nucleus of proximal retinular cell.
nl. rtn.'	Nucleus of retinular cell.
n. opt.	Optic nerve.
oc.	Eye.
omm.'	Ommateum.
p.	Posterior.
po. brs.	Pore of optic pocket.
r.	Retina.
rhb.	Rhabdome.
rhb'm.	Rhabdomere.
rtn.'	Retinula.
s.	Left.
v.	Ventral.
va. sng.	Blood-vessel.

Such other abbreviations as have been used are explained in the description of the figures with which they occur.

PLATE I.

Gammarus.

Fig. 1. A section of the right eye in a plane transverse to the chief axis of the body and through the central part of the retina. × 115.

" 2. A section lengthwise of an ommatidium. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and mark the levels at which the latter were taken. × 475.

" 3. A transverse section in the plane of the corneal hypodermis. × 475.

" 4. A transverse section through the distal ends of the retinular cells and cone. × 475.

" 5. A transverse section through the proximal portion of the cone and through the adjoining retinular cells. × 475.

" 6. A transverse section through the retinula in the region of the rhabdome. × 475.

" 7. A transverse section through the retinular cells somewhat proximal to the basement membrane. × 475.

" 8. A transverse section through a single retinular cell in the region of its nucleus. × 475.

" 9. The proximal portion of a retinular cell viewed from the side. (Compare Fig. 2.) Isolated in Müller's fluid. Not stained. × 475.

" 10. A cone isolated in Müller's fluid and viewed from the side. Not stained. × 475.

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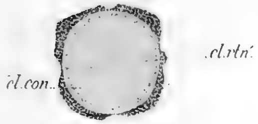

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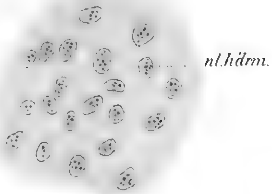

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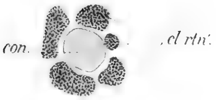

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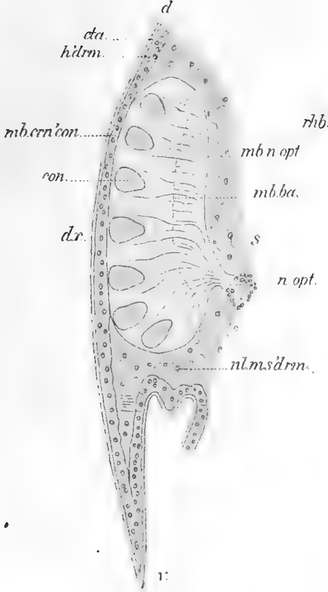

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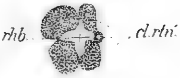

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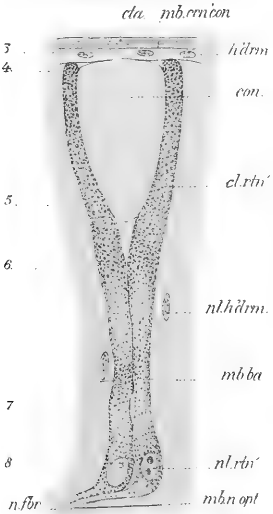

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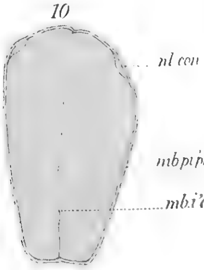

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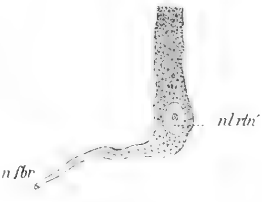


G.H.P. del.

GAMMARUS.

B. Meisel, lith. Boston.

PLATE II.

Argulus.

(Figs. 11–17.)

Fig. 11. A section in a plane transverse to the chief axis of the body and through the right eye. Depigmented. × 140.

" 12. A longitudinal section of an ommatidium. × 475.

" 13. A longitudinal section of an ommatidium which had been depigmented. The numbers at the left of the figure correspond to the numbers of the four following figures of transverse sections, and mark the levels at which the latter were made. × 475.

" 14. A transverse section through the distal end of a cone and the surrounding pigment cells. × 475.

" 15. A transverse section through the proximal portion of a group of four cone cells. The intercellular membranes of the cells present four thickened regions. × 475.

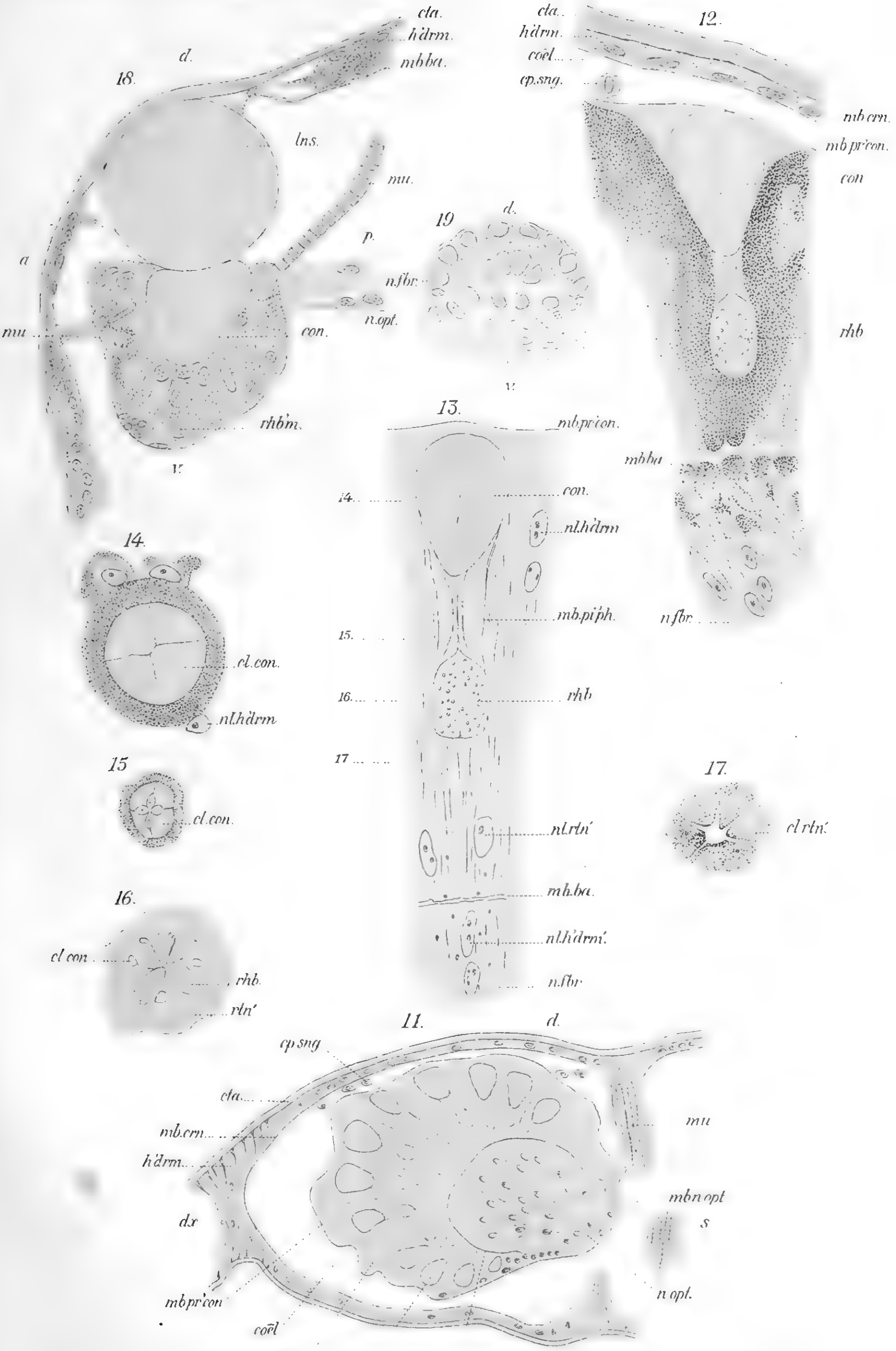
" 16. A transverse section through the rhabdome. Depigmented. × 475.

" 17. A transverse section through the retinula somewhat proximal to the rhabdome. × 475.

Pontella.

Fig. 18. The left lateral eye seen from the left side. The section is an optical one; its plane is very nearly parallel to the sagittal plane of the body. Depigmented in alcohol (see p. 78). × 275.

" 19. A transverse section of the optic nerve from a region immediately posterior to the retina. The sagittal plane divides the nerve into symmetrical halves; the fibres in each half belong exclusively to the lateral eye of the corresponding side. × 400.



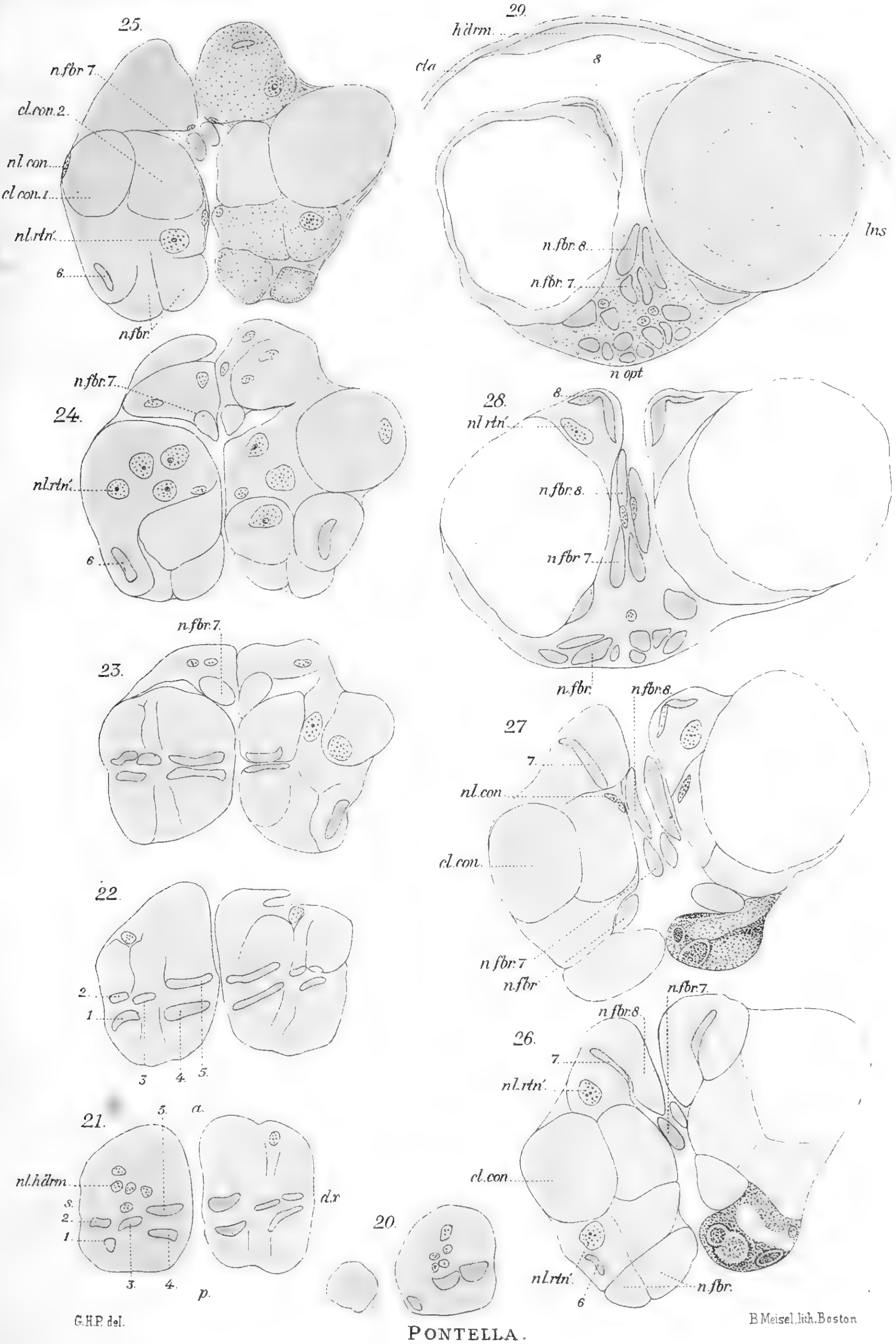
G.H.P. del. B. Meisel, lith. Boston

COPEPODA.

PLATE III.

Pontella.

Figs. 20–29. A complete series of ten consecutive sections through the right and left retinas in planes parallel to the horizontal plane of the animal. The sections are viewed from their dorsal faces. Figure 20 represents the most ventral section; Figure 29, the most dorsal. The plane of Figure 25 is approximately indicated by the incomplete dotted line *mu. con.* in Figure 18 (Plate II.). In the sections on the present plate the different bodies in the left retina have been designated by appropriate letters and figures. The eight rhabdomeres have been indicated simply by numbers; the same number always refers to the same rhabdomere. For the sake of distinction, the two cone cells have been marked *cl. con. 1* and *cl. con. 2*. Some of the nerve fibres (*n. fbr. 7* and *n. fbr. 8*) have been numbered in reference to the particular rhabdomeres with which they are associated. × 400.



G.H.P. del.   B. Meisel, lith. Boston

PONTELLA.

PLATE IV.

Branchipus.

(Figs. 30–32.)

Fig. 30. A longitudinal section of an ommatidium. × 400
" 31. A transverse section through the distal end of four cones. × 400.
" 32. A transverse section through the middle portion of a retinula. × 400.

Limnadia.

(Figs. 33–39.)

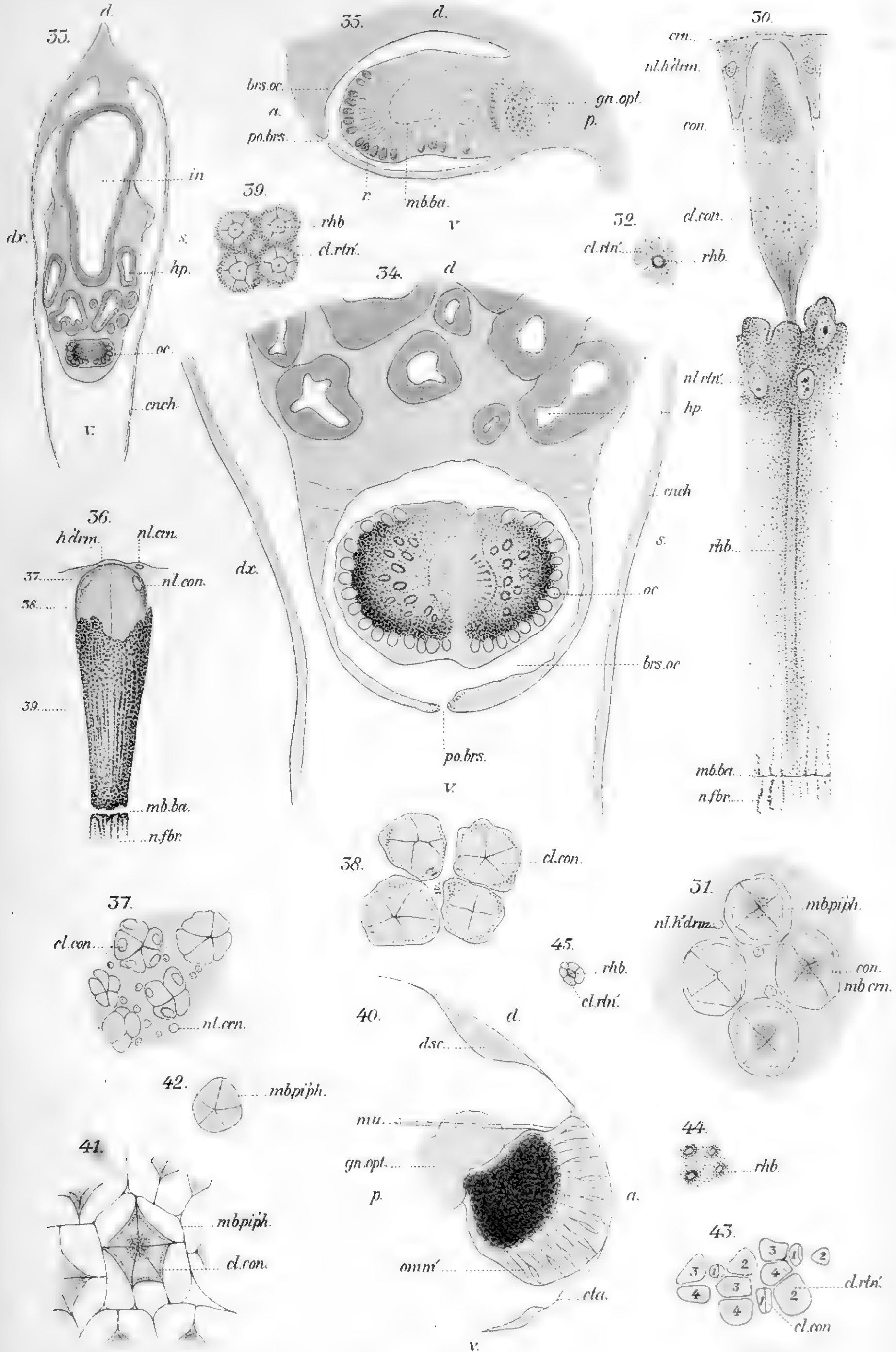
Fig. 33. A section through the anterior part of the body, including the eye, in a plane transverse to the chief axis. × 25.
" 34. An enlarged portion of a section from the same series as that from which Figure 33 was drawn, but in a position slightly anterior to the latter. × 115.
" 35. A section through the eye cut in the sagittal plane of the animal. Depigmented. × 90.
" 36. A lateral view of an ommatidium. The numbers at the left of the figure correspond to the numbers of the three following figures of transverse sections, and mark the levels at which the latter were taken. × 475.
" 37. A transverse section through the corneal hypodermis and distal ends of the cones. × 475.
" 38. A transverse section through four cones at the level where they are thickest. × 475.
" 39. A transverse section through the central portion of four retinulæ. × 475.

Evadne.

(Figs. 40–45.)

Fig. 40. An optical section through the eye and adjoining structures in a plane approximately parallel to the sagittal plane of the body, but lying somewhat to the right of it. × 140.
" 41. A transverse section through the distal ends of the cones. × 475.
" 42. A transverse section through the proximal end of a cone. × 475.
" 43. A transverse section through the distal ends of three groups of retinular cells. In each group the corresponding cells have been designated by the same number. × 475.
" 44. A transverse section through the central part of four rhabdomes. × 475.
" 45. A transverse section through a retinula. Depigmented. Kleinenberg's alum-hæmatoxylin. × 475.

PARKER – CRUSTACEAN EYE. PL. IV.



G.H.P. del.

B Meisel, lith. Boston.

PHYLLOPODA.

PLATE V.

Porcellio.

Fig. 46. A transverse section through a retinula in a plane slightly distal to the basement membrane. The single, light, central spot represents the proximal end of the rhabdome. × 475.

Idotea robusta, Kroyer.

(Figs. 47, 48.)

Fig. 47. A transverse section through the distal end of a retinula. The bodies, one of which is marked *x*, are spheres of coagulated material which occur in the interommatidial spaces, and which have been brought into prominence by the action of the hardening reagent. × 475.

" 48. A transverse section through three ommatidia in the region of their rhabdomes. × 475.

Idotea irrorata, M. Edws.

(Figs. 49–57.)

Fig. 49. The anterior face of a section transverse to the chief axis of the body, and passing through the eye on the right side of the head. × 140.

" 50. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of the following six figures of transverse sections and mark the levels at which the latter were taken. × 475.

" 51. A transverse section through the distal ends of the cones. × 475.

" 52. A transverse section through the middle region of a cone. × 475.

" 53. A transverse section through the middle of a retinula. Near the centre of each cell can be seen a small axis of nerve fibrillæ. × 475.

" 54. A transverse section through a retinula composed of seven cells instead of six. This section was cut approximately at the same level as that shown in the preceding figure. × 475.

" 55. A transverse section through a retinula near its proximal end. Each fibrillar axis is much larger at this plane than in that shown in Figure 53. × 475.

" 56. A transverse section of several groups of retinular cells immediately proximal to the basement membrane. × 475.

" 57. A transverse section of four retinular cells at the level in which their nuclei occur. The axis of nerve fibrillæ in the plane of this section and in that of the preceding one (Fig. 56) are smaller than they are at the base of the retina (compare Fig. 55).

Sphæroma.

(Figs. 58, 59.)

Fig. 58. A transverse section of a retinula at a level slightly distal to the basement membrane. × 475.

" 59. A transverse section of the fibrous ends of the cells from a single retinula. The plane of section is slightly proximal to the basement membrane. The only indication of an axis of nerve fibrillæ is the more transparent condition of the central part of the cells, due to the partial absence of pigment granules. × 475.

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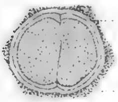

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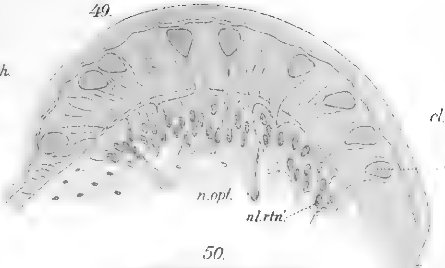

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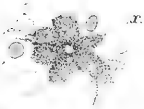

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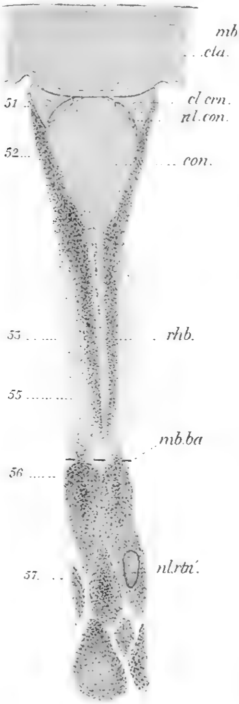

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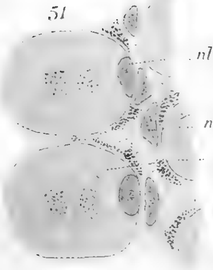

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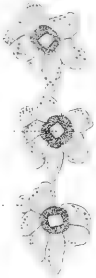

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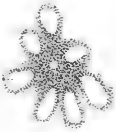

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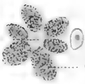

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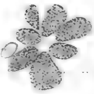

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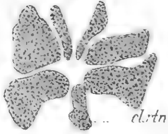

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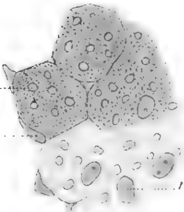

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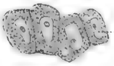

59.

G.H.P. del.

ISOPODA.

F. Meisel, lith. Boston

PLATE VI.

Serolis.

Figures 60 to 64 inclusive represent the structure of the ommatidium in the adult. Figures 65 to 72 are drawn from sections of ommatidia in well advanced embryos. All figures are magnified 475 diameters.

Fig. 60. A tangential section through the most distal portion of the retina. This section includes a portion of a cone and the tissue lying between it and two adjoining cones.

" 61. A transverse section of a retinula in the region of its rhabdome. The arrangement of the pigment granules and nerve fibrillæ is indicated in only one of the four cells. Of the two lines which appear to separate the cone cells (*cl. con.*) from the rhabdomere (*rhb'm.*), the one nearer the axis of the ommatidium is the real line of separation; the other lies within the substance of the rhabdomere itself (compare p. 92).

" 62. A transverse section through a retinula proximal to the rhabdome and in the region of the hyaline cell. As in Figure 61, the pigment granules are drawn in only one of the retinular cells.

" 63. A transverse section through a single retinular cell in the region of its nucleus. The axis of nerve fibrillæ is represented by several small axes in the substance of the cell at one side of the nucleus.

" 64. A transverse section of the fibrous ends of the cells of one retinula in their passage through the aperture in the basement membrane. Each cell shows a well marked fibrillar axis, the centre of which is often occupied by a core of pigment. The basement membrane is viewed from its distal face. The irregularly oval body in the upper left-hand corner of the figure is probably a nucleus. It lies on the proximal face of the membrane through which it is seen.

" 65. A longitudinal section through the ommatidium of an advanced embryo. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and indicate the levels at which the latter were taken. Figure 68 represents a section so nearly in the same plane as that shown in Figure 67 that its number has been omitted.

" 66. A transverse section at the level of the corneal hypodermis.

" 67. A transverse section through the distal end of a cone.

" 68. A transverse section made in a plane only slightly proximal to that shown in Figure 67.

" 69. A transverse section through the region of the distal retinular nuclei.

" 70. A transverse section through the proximal ends of the cones.

" 71. A transverse section through the retinula in the region of the rhabdome.

" 72. A transverse section at the level of the proximal retinular nuclei.

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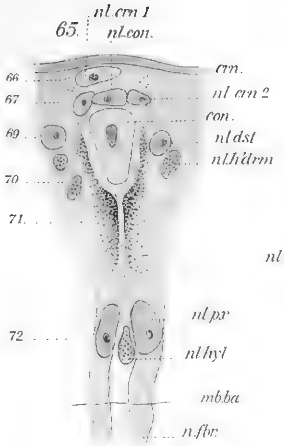

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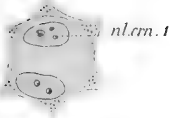

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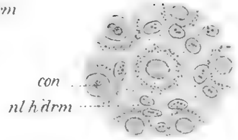

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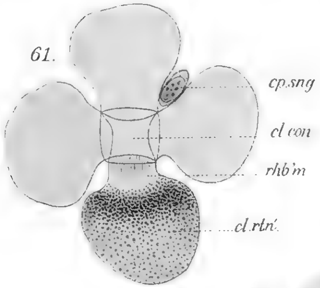

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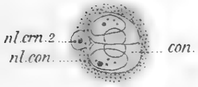

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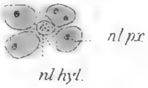

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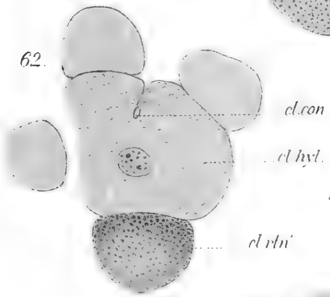

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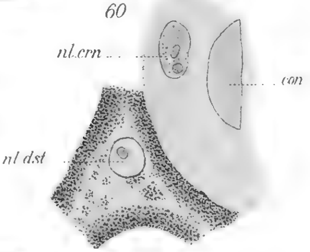

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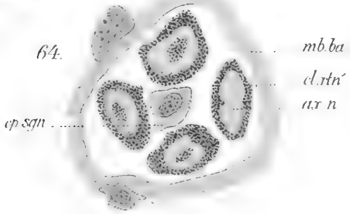

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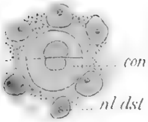

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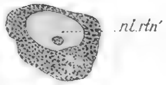


G.H.P. del

SEROLIS.

B.Meisel, lith. Boston.

PLATE VII.

Mysis.

Fig. 73. A longitudinal section of an ommatidium. The numbers at the left of the figure indicate the levels at which the sections for Figures 75–89 were taken. × 475.

" 74. The distal face of a corneal facet, cleaned in potash and examined in water. × 475.

" 75. A transverse section of three ommatidia in the plane of the corneal hypodermis. × 475.

" 76. A transverse section through the distal end of a cone. × 475.

" 77. A transverse section through the proximal end of a cone and the adjoining distal retinular cells. × 475.

" 78. A transverse section similar to that shown in the preceding figure, except that it is depigmented and stained in Kleinenberg's alum-hæmatoxylin. × 475.

Figures 79 to 82 inclusive represent consecutive transverse sections through the region of the proximal retinular nuclei of four adjacent ommatidia. The centre of each ommatidium is indicated by the group of cone cells (*cl. con.*), and the corresponding ommatidia in different sections are designated by the same Roman numeral. The nuclei around ommatidium II. have been numbered in Figures 79–81. Figure 79 represents the most distal section, and Figure 82 the most proximal one of the series.

Fig. 79. The bodies marked *x* and *y* are portions of nuclei the rest of which are correspondingly marked in Figure 80. × 475.

" 83. A transverse section of the four fibres at the distal end of the rod (compare p. 102). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 84. A transverse section of the rod at a slightly more proximal level than that shown in Figure 83. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 85. A transverse section of the retinula somewhat distal to the distal end of the rhabdome (compare Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 86. A transverse section from the region between the distal end of the rhabdome and the proximal end of the rod (compare 86 in Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 87. A transverse section through the rhabdome and surrounding retinular cells. × 615.

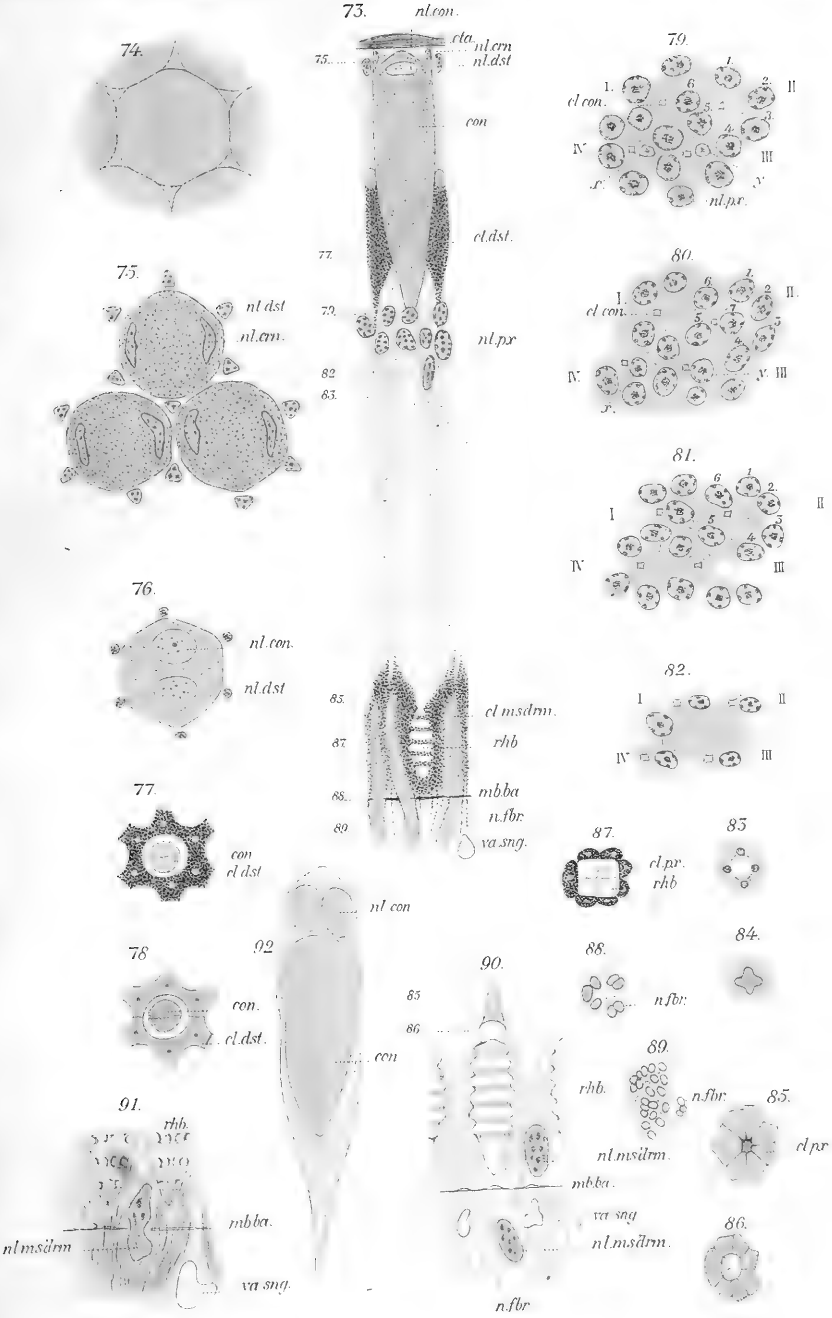
" 88. A transverse section, at the level of the basement membrane, through the nerve fibres from a single retinula. Depigmented, and stained in Weigert's hæmatoxylin. × 615.

" 89. A transverse section through the fibres of the optic nerve at a level midway between retina and optic ganglion. Preparation as in Figure 88. × 615.

" 90. A longitudinal section through the basal portion of one and parts of two adjoining ommatidia. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 91. A section cut in the same plane as that shown in the previous figure, but including only the proximal ends of two rhabdomes. Preparation as in Figure 90. × 615.

" 92. A cone viewed from the side. Isolated in Müller's fluid and studied in water. × 475.



G.H.P. del.

MYSIS.

B. Meisel, lith. Boston

PLATE VIII.

Gonodactylus.

Fig. 93. Part of a tangential section through a superficial portion of the retina. The extreme edges of the section both right and left are immediately beneath the corneal cuticula; the central portion is farthest from the cuticula. At the right of the middle line are seen the ends of the larger ommatidia; at the left, those of the smaller. × 275.

" 94. A longitudinal section of a large ommatidium. The numbers at the left of the figure correspond to the numbers of six figures of transverse sections (Figs. 96–101), and mark the levels at which the latter were made. Depigmented. × 275.

" 95. A longitudinal section of a small ommatidium containing its natural pigment. × 275.

" 96. A transverse section through the cells of the corneal hypodermis and the distal end of the cone in a large ommatidium. × 275.

" 97. A transverse section through the distal part of a cone in a large ommatidium. × 275.

" 98. A transverse section through the middle of a cone from a large ommatidium. × 275.

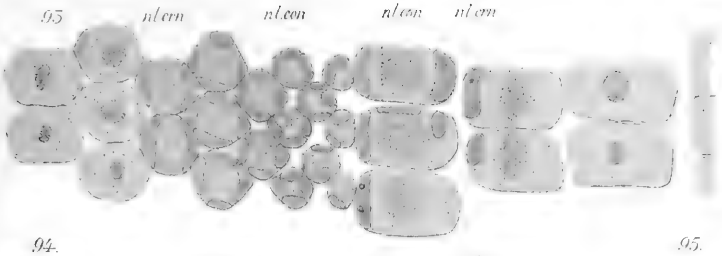
" 99. A tranverse section through a number of cones at the level of the distal retinular nuclei in the large ommatidia. × 275.

" 100. A transverse section through six retinulæ of the large ommatidia in the region of the proximal nuclei. Each retinula is numbered. The plane of this section is slightly oblique, so that retinula 1 is cut at a relatively higher level than any of the others, and retinula 6 at the lowest level. × 475.

" 101. A transverse section of a retinula from one of the larger ommatidia, in a plane not far from the basement membrane. Depigmented. × 475.

" 102. A transverse section of a retinula from one of the smaller ommatidia cut in a plane nearly corresponding to that of Figure 101. × 475.

93.



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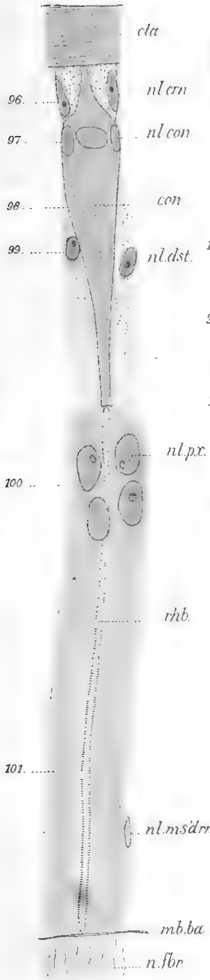

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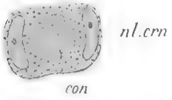

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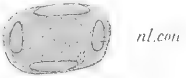
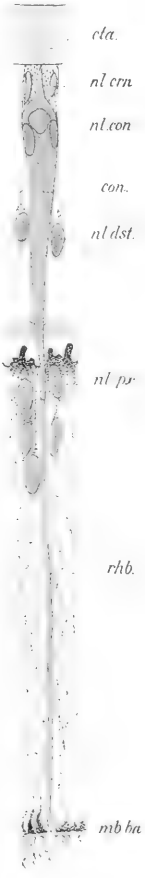


95.



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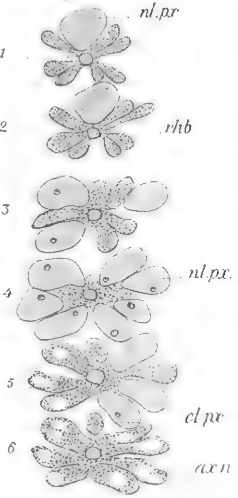

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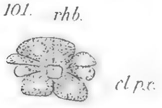

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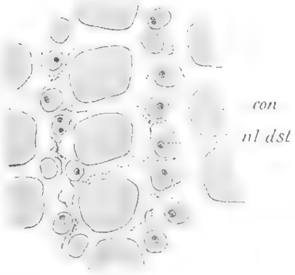


G.H.P. del.

B. Meisel, lith. Boston.

GONODACTYLUS.

PLATE IX.

Palæmonetes.

In all Figures on this plate the magnification is 475 diameters.

Fig. 103. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of nine of the following figures of transverse sections, and mark the levels at which the latter were taken.

" 104. A longitudinal section of an ommatidium which has been depigmented. The bodies marked x resulted from the action of the depigmenting reagent.

" 105. A facet from the corneal cuticula; cleaned in strong potassic hydrate, and examined from its distal side in water.

" 106. A transverse section through the region of the corneal hypodermis.

" 107. A transverse section through the distal end of a cone in the region of the nuclei of the cone cells.

" 108. A transverse section through the middle of a cone.

" 109. A transverse section through parts of four ommatidia in the region of the distal retinular nuclei.

Figures 110–112 represent three successive transverse sections, each through five ommatidia, in the region of their proximal retinular nuclei. Only the outlines of the nuclei and the five groups of cone cells (*cl. con.*) are drawn. The nuclei in each ommatidium are numbered from 1 to 7, and as their plan of arrangement is the same in the different ommatidia, corresponding nuclei have been designated by the same number. In some cases the nuclei were cut in two, and consequently appear in two adjoining sections. In such cases the two parts have been marked with the same number. Figure 110 is the most distal of the series; Figure 112, the most proximal.

Fig. 113. A transverse section of the retinula near the distal end of the rhabdome. Depigmented.

" 114. A transverse section of four retinulæ at the level of the eighth retinular nucleus.

" 115. A transverse section through four retinulæ in the region of the accessory pigment cells; viewed by *reflected* light. The retinulæ appear as dark masses embedded in a whitish field composed for the most part of the substance of the accessory pigment cells.

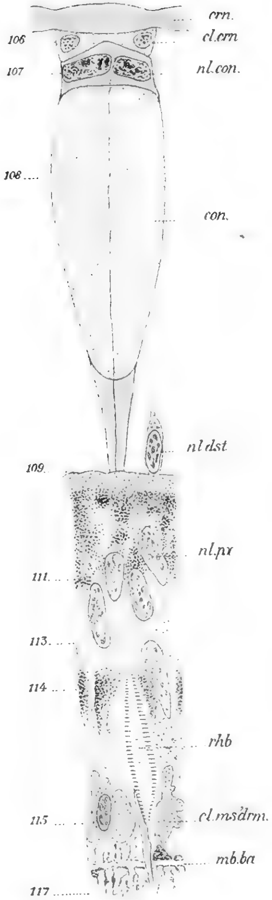
" 116. A transverse section through a retinula at about the same level as that shown in Figure 115. Depigmented.

" 117. A transverse section through the optic nerve fibres at a level slightly proximal to the basement membrane.. Depigmented.

PARKER – CRUSTACEAN EYE.

PL. IX.

103



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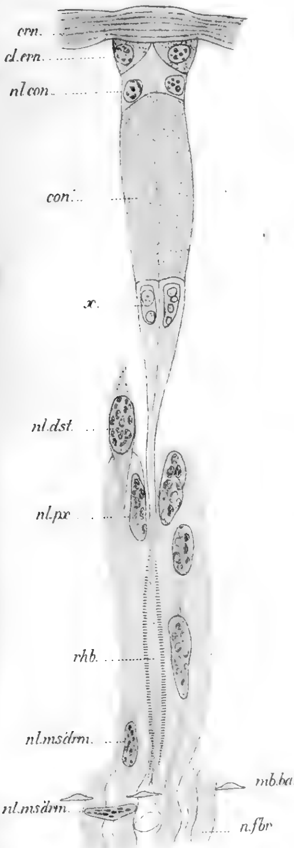

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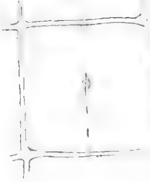

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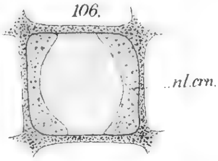

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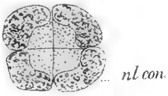

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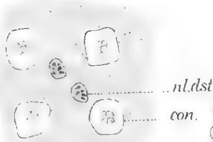

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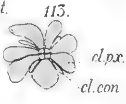

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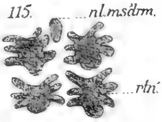

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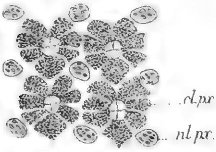

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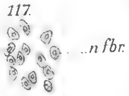

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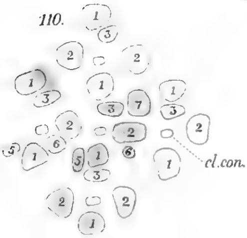


111.

112.

G.H.P. del.

B. Meisel. lith. Boston.

PALÆMONETES.

PLATE X.

In all Figures on this plate the magnification is 475 diameters.

Cambarus.

Figures 118–122 represent a series of five successive transverse sections through one and parts of four adjoining ommatidia in the region of their proximal retinular nuclei. Figure 118 represents the most distal section in the series; Figure 122, the most proximal. In these figures, only the outlines of the nuclei and the groups of cone cells are drawn.

Crangon.

Fig. 123. A transverse section through a number of ommatidia in the region of their distal retinular nuclei.

Palinurus.

Fig. 124. A transverse section through a retinula in its middle region. The outlines of the retinular cells cannot be distinguished; the position of each cell is marked by an irregular light mass in its centre.

" 125. A transverse section through a retinula in the plane of its eighth nucleus. Depigmented.

Cancer.

(Figs. 126–131.)

Fig. 126. A corneal facet viewed from its distal surface. The cuticula from which this facet was drawn was cleaned by being boiled in a strong aqueous solution of potassic hydrate. It was examined in water.

" 127. A transverse section of the distal end of a cone.

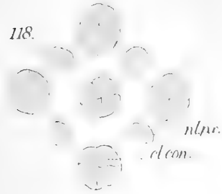
" 128. A transverse section through three ommatidia at the level of the distal retinular nuclei. The pigment granules have been indicated in only the lower circle of cells.

" 129. A transverse section through the distal region of four retinulæ. In the two on the right, the pigment granules have not been drawn

" 130. A transverse section through a retinula near the base of the retina.

" 131. A slightly oblique section through the basement membrane. The upper part of the figure represents the retinulæ as seen in transverse section distal to the basement membrane; the part marked *mb. ba.* represents the region in which the membrane itself appears in section, and the lower half of the figure shows the cut fibres of the optic nerve. The pigment granules are omitted from the right side of the figure. The transition from the retinular cells to the nerve fibres is evident in passing over the section from top to bottom.

118.



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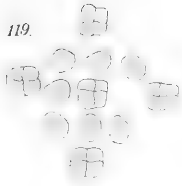
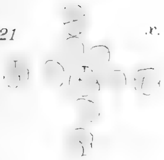


120.

121



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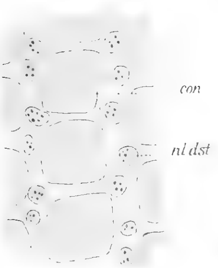

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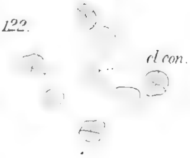

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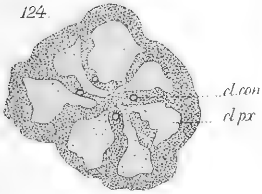

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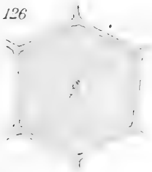
126



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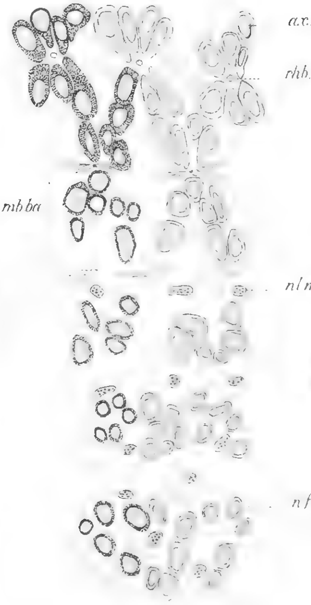

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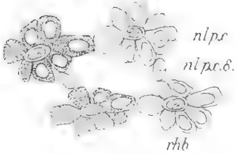

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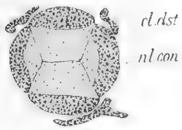

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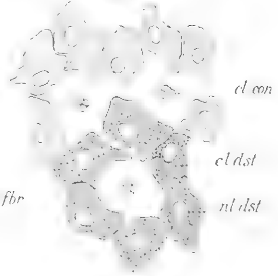

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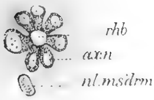

G.H.P. del.

DECAPODA.

B. Meisel, lith. Boston.

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OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT HARVARD COLLEGE.

There have been published of the Bulletins Vols. I. to XX.; of the Memoirs, Vols. I. to XVI.

Vols. XVI. and XXI. of the Bulletin, and Vols. XI., XIV., and XVII. of the Memoirs, are now in course of publication.

A price list of the publications of the Museum will be sent on application to the Secretary of the Museum of Comparative Zoölogy, Cambridge, Mass.

ALEXANDER AGASSIZ, *Director.*