A Study of
The Comparative Anatomy of the Lateral Compound Eyes of Arthropods

VOLUME I

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Introduction.

In this thesis the interest has centered mainly on the comparative anatomy of the lateral eyes of Arthropods, especially the compound eyes, with some particular reference to those of Chilopods. The comparative anatomy of the eyes of Chilopods seemed to be of interest, since they possess in most cases simple lateral eyes, which are not characteristic of the adults of any other group of Arthropods, except Arachnids, to which the Chilopods are only remotely related. In a few cases - in the Scutigeridae - "compound" eyes are present, which are very unusual in their internal anatomy.

The following possibilities with regard to the relationships of the Chilopod eyes present themselves. The simple eyes may be the products of degeneration. of a compound eye. Alternatively they may be ocelli of a very primitive pre-compound eye type, persisting, where in some cases a compound eye has failed to develop. As a third possibility they may have been separately evolved in forms, in which the compound eye was lost or failed to develop. In the last case they would appear to be unrelated to those of any other Arthropods, except possibly those of Diplopods, to which they are very similar in structure.

The "compound" eyes may be of the same type as the compound eyes in the remaining Arthropods, with the differences due to degeneration, or to specialisation. Alternatively they may be of a separate type and formed secondarily, either as a single new structure, or by coalescence of ocelli.

The enquiry into the inter-relationships of these eyes and their relations to the eyes of other Arthropods raises several points for investigation.

For the compound eyes it is necessary to decide whether they were primitively present in the ancestors of some or all of the classes of Arthropods, and whether they have a common or more or less diverse origin with some evolutionary convergence.

For the lateral simple eyes it is necessary to decide whether there are any indiciations in phylogeny, ontogeny or anatomy of the primitive or secondary formation of a compound eye by the aggregation of numerous ocelli or the elaboration of one of these. Such information might be expected to throw light on the origin of the Scutigerid eye. Alternatively any indications of the formation of simple from compound eyes might show whether the Chilopod simple eyes could have evolved in this way from a Scutigerid or some other compound eye.

Median eyes are present in some Trilobites, Eurypterida, Crustacea, Hexapods and Arachnids. Although they exhibit considerable variations in structure, they are all

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clearly simple eyes. As they are absent in Chilopods and in the remaining Arthropods are entirely separate in origin from the lateral eyes , with a separate seat of innervation, their comparative anatomy is of little interest in this case.

The main portion of the thesis deals with the comparative anatomy , origins and relationships of the different types of compound lateral eyes . The second part comprises a short appendix dealing with similar aspects of the lateral ocelli.

Detailed descriptions and figures have been given for the eyes of eight species. Some mention is also made of points observed in the internal or external anatomy of species which were studied in less detail. The theoretical conclusions are based on material from the available literature and from these descriptions.

Preliminary note I.

The basic structure of the ommatidium or compound eye unit.

All Arthropod sense organs consist of the following parts :-

a) An external receptor, usually a hypodermal secretion, which limits reception to, and enhances the effect of, a particular stimulus.

b) Sense cells, which are either primary nerve end cells or secondarily innervated epidermal cells, through which the stimulus passes into the sense cell and thence via the nerve to the brain.

c) Modified, hypodermal, accessory cells, which may either augment the intensity of a stimulus falling on the sense cells by concentration, or protect these cells from the entry of an excessive stimulus by absorbtion.

In the eye unit the receptor consists of the dioptric or light refracting and condensing structures - namely the corneal lens or facet and the cone or vitreous body. These are transparent, colourless, homogeneous structures admitting and concentrating the light without undue distortion, and protecting the underlying sense cells from mechanical damage. The corneal lens and the hypodermal cells secreting it are continuous with the corresponding structures in the general body wall. The underlying cone, secreted by the hypodermal vitreous cells, is an additional dioptric structure.

/Below

Below the cone are the retinal sense cells, which are numerous, deeply sunken for protection, not externally exposed as in cases in which the stimulus is a coarse mechanical one. (Compare Berlese's diagrams of the units of the other senses in Arthropods - 1909, Figs. 762-801). In each ommatidium several sense cells form a retinular group arranged about a single longitudinal axis. These are primary sense cells, each the generating cyton of an optic nerve fibre, bearing along its inner longitudinal axis a rhabdomere. The rhabdomeres of a retinular group are more or less approximated to form a rhabdom. According to some authors these are cuticular in origin - (Berlese, 1909, p. 605). According to others, however, the rhabdom is sensory in function and contains the thickened ends of the optic neurofibrillae. A fuller account of these different views is given in the following pages.

The hypodermal, accessory cells may be modified to increase or concentrate the stimulus, as in the case of the dioptric cone cells and the tapetal or reflecting cells. The latter reflect light back from the base of the eye on a second journey through the sense cells. Alternatively these cells may be modified as pigmented structures absorbing any excess light harmful to the sense cells. In addition to the accessory, interommatidial, pigment cells,

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the retinal cells as a rule contain pigment. The arrangement of pigment depends on the conditions of illumination. The optical isolation of the sense cells ensures that each ommatidium receives light from a small area only. Thus the image, projected through a multiple lens system into a discontinuous retina, with the units optically isolated, consists of a mosaic of many point "images" of fields of intensity, each corresponding to a small part of the field of vision. When the optical isolation is complete the field of each ommatidium is sharply defined and the vision is described as of the "apposition" type. In dim light the pigment may be withdrawn so that light entering one ommatidium obliquely is not absorbed but passes into the adjacent ommatidia. The image is presumably somewhat blurred and is known as of the "superposition" type.

Some other views on the structure of the ommatidium.

Of the earlier views the most important are those of Grenacher (1879) and Patten (1886).

Grenacher (1879) considered that the eye was composed of two layers, the upper consisting of four cone cells, secreting both the cornea and the crystalline cone, the lower made up of groups of nerve end cells, bearing cuticular rhabdomeres - which are united into a rhabdom.

/Each

Each optic nerve fibre corresponded to the retinal cells of one ommatidium. There were two basement membranes, one at the base of the eye and one separating the cone from the retinal cells. The interommatidial spaces were filled with scattered pigment cells. This view was based on a study of numerous different Arthropod eyes.

The structure of the cornea, cone, retinal cells, rhabdomeres, pigment cells, nerve fibres and basement membrane has remained in the modern view much as in Grenacher's. Grenacher's view differs from that at present generally accepted in the absence of a corneal hypoderm, the separation of the eye into two clearly defined layers and the presence of an upper membrane below the cones. The corneal hypoderm, which is now known in a very large number of forms, was presumably missed by the earlier authors on account of the ease with which it is damaged or overlooked. Later authors have persistently failed to find a membrane separating the cone and retinal cells. It was possibly included by Grenacher merely on theoretical grounds, as he considered that the eye was made up of two superimposed, hypodermal cell layers.

Patten's views (1886, p. 666 et. seq.) were based on the idea that a homologous basic structure should be traceable in the eyes of all the Invertebrates. His

/attempts

attempts to force homologies between the eyes of Arthropods and those of Molluscs seem to have resulted in a rather far fetched theory of the structure of the ommatidium. Although he hoped "to reduce the essential parts of all visual organs to one structural plan, which can be followed up through the whole animal kingdom from the lowest to the highest", as Beddard (1887, p.446) pointed out, "his views would have had additional merit if they rendered clear the modification of the eye within the Crustacea alone".

Although his views now appear aberrant, they had some considerable currency in his time. Consequently there are many traces of his somewhat confusing nomenclature in the literature of the late nineteenth century, when a large part of the work on eyes was done. A short account of his views is given to define his nomenclature and to indicate what widely different interpretations have been placed upon the eye structure.

He considered that the eye consisted of two layers. The upper was a corneal hypoderm responsible for the secretion of the cuticle. (Grenacher had attributed this function to the cone cells.) Although he was not the first to describe this layer (see p.108), as he claimed was the case, he was the first to insist on its universal presence - (Patten, 1886, p. 666)-and to point out that it is reduced in the adults, as compared with the young.

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The lower layer consisted of ommatidia each made up of concentric groups of cells, the innermost ring comprising four colourless retinophorae surrounded by circles of pigmented cells or retinulae. Each cell secreted a rod or retinidium in the primitive condition but the rods of the retinulae disappeared in the more complex forms, including Arthropods, leaving the retinophoral rods. These constituted a crystalline cone, continuous through a short stalk, or style, with the striated pedicel- Grenacher's rhabdom. The cone was enclosed in a calyx- an enlargement of the retinphoral cells at their upper ends. For the rest the retinophorae were reduced to thin hyaline bacilli, continuous from the hypoderm to the basement membrane. The pedicel and cone were regarded as continuous and as secreted by the same cells. The pedicel was regarded as dioptric and the cone as sensitive. Pigment cells - the retinulae - were arranged in circles about the retinophorae, each circle with an expansion of its cells at one level, containing pigment and nuclei. Otherwise the cells were reduced to slender, colourless bacilli, reaching from the hypoderm to the basement membrane. There were two sets of nuclei about the cone (corresponding to Grenacher's accessory pigment cells) and one about the pedicel (corresponding to Grenacher's retinulae). Irregular cells containing reflector material were described at

/the

the base of the eye. No generating cytons appear to have been described for the optic nerve fibres, which pass through the basement membrane and run up as an axial strand between the retinophorae to form a branching net on the cone. Each ommatidium received four branches from each of four different nerve fibres and all of the cells were innervated at their bases.

Patten's views differed from Grenacher's in the following respects : in the presence of a corneal hypoderm ; in the continuity of the remaining cells from the hypoderm to the basement membrane; in the continuity of the cone and pedicel (or rhabdom); in the secretion of the pedicel (or rhabdom) by the colourless retinophoral cells and not by the pigmented retinulae; in the cone as the seat of innervation and not the retinal cells; in the regular arrangement of the pigment cells and in their homogeneous nature - (he did not distinguish accessory from retinal, pigment cells); in the absence of correspondence between the nerve fibres and the ommatidia; in the innervation of all of the cells and not only the retinulae. Patten's view therefore differs from the modern view in all of these respects except in the presence of the hypoderm cell layer.

Patten's views were developed in connection with the Branchiopods and Decapods, in which the cones and rhabdoms were contiguous and the number of segments in each the same. His views are, however, totally incompatible with the condition in Isopods, in which the cone and rhabdom are not so closely in contact and in which there is a disparity between the number of cone cells and the number of pedicel or rhabdom segments. In Isopods the cone and rhabdom are most clearly the products of different types of cells present in different numbers - see <u>Ligia</u> (p.38) and <u>Philoscia</u> (p.57).

Most of the remaining earlier authors were concerned with the optical properties of the eye rather than with the details of its anatomy. A summary of these earlier views on the compound eye as an optical system has been made by Eltringham (1919, pp.8-22).

The first morphological problem to attract interest was the location of the ending of the fibrillae of the optic nerve and the question of the nature of the rhabdom. Many located the nerve endings in the cone. Among these Müller (1824, p.1 et. seq.), Wagner (1835, p. 372), Leydig (1855, p. 376), Schultze (1868, p.1 et.seq.) and Patten (1886, p. 666) claimed to have traced the nerve fibrils up onto the cone.

Claparede (1860, p.191), Dor (1861, p.22), Chatin (1877, p.1 et.seq.), Kingsley (1886, p.600), and Johnas (1911,p.218) appear to have accepted this view, on theoretical grounds, although they could not follow the course of the nerve

/fibrils

fibrils in any detail.

Many of the earlier authors attempted to find homologies between the eyes of Arthropods and those of Vertebrates but these were far fetched and without sound morphological basis. The chief of these were Newton (1873, p. 325 et. seq), Kingsley (1886, p. 597 et seq) and Locy (1886, p.103). No later attention appears to have been paid to this matter, which is now of little but historical interest.

Lowne held the remarkable view (1875, p. 577, 1890, p. 406) that the eye should be divided into two parts (without nervous connection). The upper was the "Dioptron" and the lower the "Neuron" - the optic ganglion of later authors. The upper was exclusively dioptric in function, and the lower exclusively nervous. This has been disproved by practically all later observation but at the time was a subject of heated controversy in a correspondence in "Nature" (1885, pp.341, 342, 433, 504, 508)

Practically all of the authors subsequent to Grenacher except Kingsley (1886), Patten (1886) and Johnas (1914) as well as two earlier - Muller (1826) and Schultze (1868) - have regarded the retinal cells as nerve end cells containing the ultimate ends of the optic nerve fibrillae. This appears to have been conclusively demonstrated by Sanchez (1916) [illegible], with the use of

/silver

silver impregnation techniques. His results were confirmed by Eltringham (1919, p. 8). The views on the exact location of the endings of the optic nerve fibrillae and their relation to the rhabdom have been diverse. To complete this account an outline of these views is given below.

Some authors have regarded the rhabdom as containing the ultimate ends of the optic neuro-fibrillae. Although Schultze (1868, p.1 et. seq.) and Johnas (1911, p. 218) regarded the rhabdom as composed of nerve fibrils, they thought that these ran straight up onto the cone. Hesse (1901, p. 347 et seq.) and Constanineanu (1930,p.253 et seq.) have described the nerve fibrillae as running up through the cytoplasm of the retinal cells, round the nucleus to end on the rhabdom plates or "*Stiftchen*". Hesse described a clear unpigmented "*Schaltzone*" below the striated "*Stiftchensaum*". The passage of the neuro-fibrils through the "*Schaltzone*" up to their endings on the rhabdom plates lent the clear zone a striated appearance. In some cases there were said to be minute thickenings at the base of each of the neuro-fibrils. According to Constantineanu the structure was sometimes obscured by a cementing together of the plates. This view of the rhabdom had a very wide currency in text-books, for example in those of Berlese (1909, pp. 649-650)

650), Comstock (1933, p.137), Imms (1938, p. 82) and Snodgrass (1935, pp. 532-533, Fig. 278).

Other authors have considered the rhabdom as a purely cuticular structure. This was the view of Grenacher (1879, p.1 et seq.), Watase (1890, p. 287), Exner (1891, p.1 et seq.), Jorschke (1914, p.153), Eltringham (1919, p.8, 1933, p.10), Altenberg (1927, p.38), Nowikoff (1931, p. 29), Machatschke (1936, p.109) and Wigglesworth (1939, p.113). Although these authors have described the rhabdom plates in some at least of the forms which they have investigated, and have traced the neuro-fibrillae for some distance into the retinal cells, they have found no connection between the two. Eltringham (1933, p.10) considered that the rhabdom was probably primitively a skeletal rod, which later achieved symmetry and a dioptric function. Nowikoff (1931, p. 19) and Machatschke (1936, p. 109) regarded the rhabdom as a cuticular, skeletal, refracting structure dispersing the light concentrated by the cones onto the photosensitive, pigmented protoplasm of the retinal cells, in which the nerve fibrils ended. In support of their view these authors compare the structures described by Hesse with those observed in ordinary developing chitin, pointing out that developing chitin frequently has a striated appearance similar to that of Hesse's "*Stiftchen*". Below this is a clear zone of protoplasm striated in the direction of its secretion and interpreted by Hesse as a "Schaltzone" containing neurofibrillae. Diagrams illustrating this comparison are given by Nowikoff (1931, p.23 Figs. 3, 4). This is the view which has been supported by most of the recent workers.

Wigglesworth (1939, p.113) considers that the rhabdom "is composed of highly refractile material, so that light entering it will be totally reflected from its walls" and it thus forms "an ideal structure to receive and conduct light without loss". (This is in contrast to the view of Nowikoff (1931, pp. 325-329), who considers that the rhabdom scatters and refracts the light and does not retain it by total reflection). He considers moreover that the light "brings about a photochemical change in the structure of the rhabdom, the products of which stimulate the surrounding sense cells."

Whatever the exact mode of action of the rhabdom and method of transmission of the stimulus from this structure to the nerve fibrillae of the retinal cells, it is clear that in the modern view of the morphology of the rhabdom there is a general tendency to regard this as cuticular in origin and dioptric in function.

Although the exact nature of the rhabdom and its method of functioning remain undecided at the present time, these are not issues which are likely to prejudice the

/questions

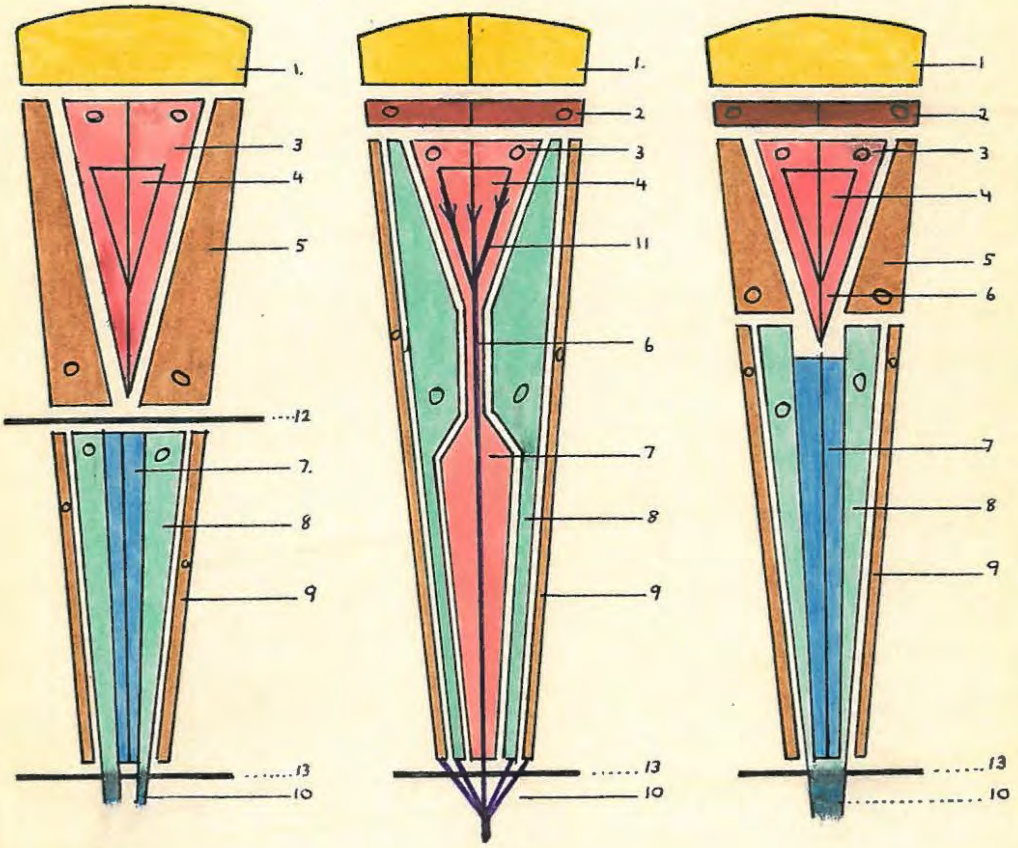
questions of comparative anatomy, and the investigation of the matter is beyond the scope of this thesis.

The views mentioned here are illustrated in the accompanying coloured plates.

PLATE I.

VARIOUS VIEWS ON THE BASIC STRUCTURE OF THE OMMATIDIUM OF THE ARTHROPOD COMPOUND EYE.

LONGITUDINAL SECTIONS.



Grenacher's View :-
Cone and retinal cells in two layers separated by a basement membrane;
Rhabdom produced by pigmented retinular cells not in contact with cone.

Patten's View :-
Corneagen and remaining cells form two layers;
"Rhabdom" produced by retinophoral colourless cells and continuous with cone.
(Rhabdom = Pedicel)

Modern View :-
Corneagen, cone and retinal cells form three layers with the last two not sharply separated;
Rhabdom produced by pigmented retinal cells and contiguous, not continuous with cone.

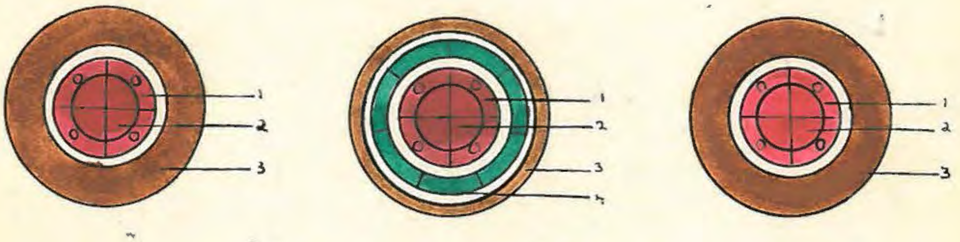
KEY.

1. Corneal lens
2. Corneagenous cells
3. Cone cells
4. Cone secretion
5. "Iris" pigment cells
6. Continuation of cone betw. retinal cells _ Patten's "style"
7. Rhabdom _ Patten's "pedicel"
8. Retinal cells _ pigmented
9. Interommatidial pigment cells
10. Optic nerve fibres
11. Continuation of optic nerve ramifying on cone.
12. Upper basement membrane.
13. Lower basement membrane.

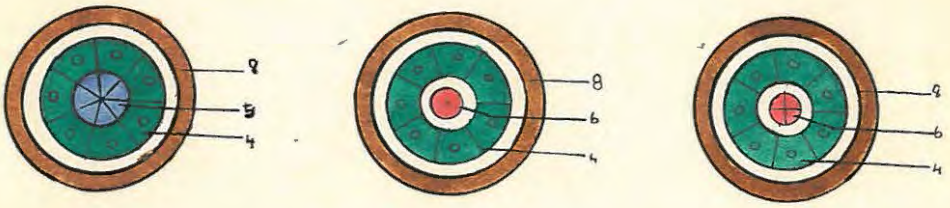
Various Views on the Basic Structure of the Ommatidium of the Arthropod Compound Eye

Contd:-

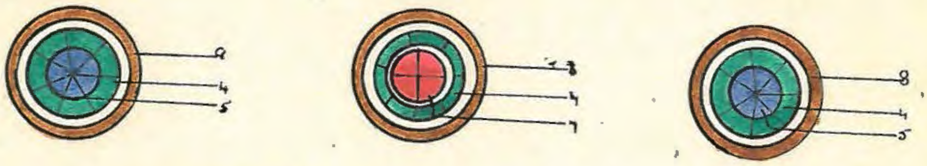
Transverse Sections



Through the upper regions of the cones.



Through the upper regions of the retinular cells.



Through the lower regions of the retinular cells

Grenacher's View.

Patten's View

Modern View.

Key.
1. Cone cells - Patten's retinophorae
2. Cone secretion.
3. "Iris" pigment cells
4. Retinal cells
5. Rhabdom produced by the retinal cells.
6. Cone extension between the upper ends of the retinal cells - Patten's style.
7. Patten's pedicel corresponding to Grenacher's rhabdom but produced by retinophorae not retinulae.
8. Variable numbers of pigment cells - not shown individually

Preliminary note 11.

The nomenclature of visual units and the separation and definition of compound eyes, simple eyes, ocelli and some intermediate types.

Some confusion appears to exist as to the precise meaning of the terms compound eye, complex eye, simple eye and ocellus. Compound eyes are made up of aggregations of units known as ommatidia whose structure has been described in detail above. Ommatidia conforming to this ideal structure are found only in the compound eyes of Insects and Crustacea, which are sometimes termed "true compound" eyes.

Lateral eyes made up of aggregations of units approximating to the ommatidial condition are found in Xiphosura and in Scutigeromorpha and are customarily and conveniently termed compound eyes (or sometimes "pseudo-compound" eyes, where it is desired to emphasise their structural departure from the plan of the "true compound" eyes).

On account of their corneal structure the lateral eyes of Trilobites and Eurypterida are usually termed compound, although no trace of the internal structure is preserved to confirm this. (The majority of the eyes of Trilobites appear to resemble those of Crustacea, while those of some at least of the Eurypterida approach the condition in Xiphosura).

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The lateral aggregations of ocelli (not ommatidia) found in some Diplopods as well as in the eyes of Strepsiptera among the Insects, are often termed compound eyes. They are more correctly denoted as "complex" or "ocellar compound" eyes.

The term "simple" eye is a somewhat indefinite one, loosely used and conveniently retained, to denote in general any unorganised, visual, pigment spot, ocellus or single ommatidium.

An ocellus is a particular type of simple eye having a structural grade more highly organised than that of a pigment spot and less highly differentiated than that of a compound eye. Confusion in the employment of these terms is common but the customarily sanctioned usage is as follows.

Lateral simple eyes, which may be properly termed ocelli, are those of Chilopods (excluding Scutigeromorpha), the separate, simple eye of Diplopods and the units of their complex eyes (possibly with some doubtful fossil exceptions), the simple eyes of Arachnida (other than Xiphosura), the units of the complex eye of Strepsiptera, the single, lateral, simple eye in Aphaniptera, and the great majority of the lateral eyes of Insect larvae. The median eyes of all Arthropods, in which these are present, are ocelli, although some are of a very highly organised type.

/The

The so-called lateral ocelli of Crustacea and adult insects (other than those mentioned immediately above), as well as the simple lateral eyes of Trilobites are really the ommatidial remnants of a reduced compound eye.

Intermediate types, neither truly compound (or ommatidial) nor truly ocellar in form, occur in some cases. Excluding the instances of complex and pseudo-compound eyes enumerated above, these intermediate forms are common only in Insect larvae. These larval eyes are traditionally termed ocelli, although in some cases they approach a condition not substantially divorced from that of the eye units of some Apterygota - here termed ommatidia. Such larval eyes are perhaps best termed "simple" eyes.

Thus the term simple eye is used where no definite implication of either ommatidial or ocellar grade of organisation is presently intended. The table on the following pages is a rough guide to the separation of ocelli from compound eyes or their component ommatidia. This applies only to the separation of the more extreme cases of both types.

(It is not possible to list concisely all the intermediate variations found in pseudocompound eyes, complex eyes and ommatidia-like ocelli).

A comparison of the structure of an ocellus with that of a compound eye or of its ommatidial units.

Ocelli	Compound eyes and their component ommatidia.
The corneal lenses.	
Each ocellus has a single lens.	Each compound eye has numerous contiguous lenses.
Ocelli may form an aggregation as in "complex" or "ocellar compound" eyes.	Sometimes reduced in number, even to a single ommatidium, and separated.
Circular in outline except where closely approximated	Hexagonal or tetragonal, except where separated, when they are circular.
Biconvex in sections.	Highly biconvex only when degenerate. Otherwise weakly biconvex, concavo-convex or plano convex. Flattened where there is a coalescence of adjacent lenses.
The corneal hypoderm cells.	
Variable in number. Numerous.	Typically a small fixed number for each ommatidium.
Somewhat irregularly arranged.	Regularly arranged, except where the facets are lost.
Forming a continuous layer below the lens or laterally disposed about its sides. Always in fairly close contact with part of the lens.	Form a continuous layer below the lens. Laterally displaced in some cases and may lose practically all contact with the lens in the adult.
May form an iris layer of pigmented cells surrounding the upper part of the lens.	May form an iris layer of pigmented cells surrounding the accessory lens (the cone).
Sometimes elongated with the cytoplasm highly refractive. Serves then as an additional lenticular structure known as the "vitreous body".	Never forms a "vitreous body".

Ocelli	Compound eyes and their component ommatidia.
Accessory dioptric structures.	
Nothing morphologically comparable with the crystalline cone cells is present, (except in the ommatidia-like simple eyes of some Insect larvae). This is functionally replaced by the "vitreous body" in which there are usually a large number of irregularly arranged cells.	The crystalline cone cells, together with their secretion, when present, form an additional lens, absent only in *Limulus* and exocone Insect eyes, when the corneal lens is very well developed. The cone cells are few in number and regular in arrangement, with one group corresponding to each lens.
The retinal cells.	
A varying number of cells, usually large.	A small and definite number of cells.
Disposed in a single continuous layer below the lens or in the form of a cup. Cells not grouped (except to a small extent in the lateral ocelli of some Arachnida and the median eyes of some other Arthropods).	Grouped into units (retinulae) one corresponding to each lens and cone. Usually in a single layer but sometimes in two more or less distinct superimposed layers.
Cells may be perpendicular or parallel to the axis of the eye and the entrant light rays.	Cells parallel to the axis of the unit and to the entrant light rays.
The rhabdom	
Each retinal cell bears a morphologically apical rhabdom structure. This may sometimes be transferred to the axial face of the cells, apparently when they are elongated and compressed.	Each retinal cell bears a morphologically axial rhabdom structure.
Even where axial, the rhabdom structures never extend along the entire length of the axial faces of the cells.	The rhabdom structure extends along the entire longitudinal axis of the cells.

/Rhabdom

Rhabdom structures are not shared between adjacent cells except a few exceptional cases, where the retinal cells are grouped.	Rhabdom structures of adjacent cells in a retinula group show all degrees of fusion.

The pigment cells.

Interneural pigment cells are scattered among the pigmented retinal cells, in some cases, and like the retinal cells are not arranged on any definite pattern in relation to the dioptric apparatus.	Interommatidial pigment cells (accessory and distal retinal pigment cells) supplement the pigment of the retinal cells, and in some cases of the hypoderm cells, in the isolation of the ommatidia. Like the retinal cells and the dioptric system, these are arranged on a definite pattern except where they degenerate.

Preliminary note 111.

The changes involved in converting compound eyes into ocelli, and ocelli into compound eyes.

In considering the comparative anatomy of eyes, it is desirable to know what changes might be expected to take place in the transformation of ocelli to compound eyes and compound eyes to ocelli. These changes are readily enough obtained from the above table of comparison, but it seems convenient at this point to state them separately for future reference.

The changes necessary to convert a well-developed compound eye into a group of ocelli (with the ocelli corresponding to the ommatidia) are the following :-

1. A decrease in the number of units, their separation and a consequent decrease in the convexity of the ocular area as a whole.
2. The assumption by each of the units of a cup-like rather than a conical form, accompanied by a shortening and widening of the individual cells.
3. An increase in the size and convexity of each corneal lens, accompanied by the assumption of a biconvex curvature and circular outline.
4. An increase in the number of hypodermal cells in each unit, accompanied by a tendency to irregularity in

/their

their arrangement.

5. A loss of the cone apparatus, with or without the compensatory formation of a "vitreous body" by the corneal hypoderm cells.

6. An increase in the number of retinal cells related to each lens, accompanied by their arrangement in a single, continuous layer (and not in the form of an organised retinula group) with the cells either parallel or perpendicular to the entrant light rays and to the longitudinal axis of the eye.

7. Decrease in the size of the rhabdom structures and their transference to the apical face of the cell (or to a small part of the axial face), accompanied by the loss of the complex shared rhabdom and a transference of its parts, one to each of the retinal cells.

8. Reduction in number and simplification in arrangement of the pigment cells.

The changes necessary to convert a group of ocelli into a compound eye are the direct reversal of those listed above, namely :

1. An increase in the number of units, their aggregation, and a consequent increase in the convexity of the eye as a whole.

2. A flattening and elongation of the units and their individual cells with a decrease in size of the cells at the base of the eye (since the optic nerve ending does not copy the expansion of the outer part of the eye).

3. A decrease in the size and convexity of each of the lenses and their assumption of an hexagonal or tetragonal form.

4. A decrease in the number of the retinal cells and a greater regularity in their arrangement.

5. A loss of the vitreous body and a development of the cone apparatus from special hypoderm cells other than those secreting the lens.

6. A decrease in the number of retinal cells, accompanied by their arrangement under each lens in a retinula group, with the cells parallel to the longitudinal axis of the unit.

7. An increase in the size of the rhabdom structures, their extension throughout the length of the retinal cells, and transference to the axial faces of these to form in each retinula a complex shared rhabdom.

8. An increase in number and elaboration in arrangement of the pigment cells.

The changes necessary to convert a single ocellus into a compound eye are as follows :-

1. Segmentation of the eye into a number of closely approximated units, accompanied by an increase in size and convexity of the whole.

2. The differentiation of the cells into elongated groups and a general increase in the number of cells.

3. Decrease in the convexity and increase in the area of the lens and its differentiation into small, less convex,

/hexagonal

hexagonal (or tetragonal) facets.

4. Restriction of the hypoderm cells to regularly arranged groups, corresponding to the ommatidia and a loss of any vitreous body formed in the ocellus by these cells.

5. The development of a cone apparatus to correspond to each lens.

6. An increase in the total number of retinal cells and their arrangement in retinula groups, one corresponding to each lens, with the cells parallel to the axis of the eye.

7. The elongation of the rhabdom structures, their transference to the axial faces of the cells and their arrangement in groups with the component units tending to fuse in each retinula.

8. An increase in the number and complexity of arrangement of the pigment cells isolating the ommatidia.

The changes necessary to convert a group of ommatidia into a single ocellus are the reverse of these, and seem so obvious as to need no enumeration.

THE COMPARATIVE ANATOMY OF THE LATERAL COMPOUND EYES OF ARTHROPODS.

Chapter 1.

CRUSTACEA

Introduction to the eyes of Crustacea.

A study of the lateral compound eyes of Crustacea has been undertaken in order to compare their anatomy with that of the other Arthropod, lateral, compound eyes. In the first part of this chapter, original descriptions of three species are given with Figures, and a study is made of the changes related to a degeneration of the compound eye as indicated by a comparison of two of the types described.

In the second part an attempt has been made to adduce from the available literature and from original observations the range of variation in structure and the primitive and typical conditions (as far as these can be decided upon) of each part of the eye. A summary is appended to each section. The third part comprises the conclusions drawn from this work, on the comparative anatomy origins and relationships of the lateral compound eyes of Crustacea.

I. The lateral eyes of *Ligia natalensis*, Collinge (1920, p. 474)

Hewitt (1907, p.25, pl, IV, Fig. 1) has given a short description of the eye in *Ligia Oceanica*, and has illustrated this in a diagrammatic figure. In the available literature on Crustacean eyes, no other work on the eye of this genus has been found.

The eyes in the adult *Ligia natalensis* are a pair of large, compound, laterally placed organs, which are sessile and immovable. They are well developed and deeply pigmented in accordance with the active habits of the species, which lives in the light, on the surfaces of rocks along the water line of rivers. The outer cuticular layer is transparent, so that through it the pigmented cellular part of the eye is visible. The head is flattened dorso-ventrally and the eyes are borne on either side of the vertex, a wide, flat area on top of the head, between the frontal line and the occipital groove. Their position with reference to the morphology of the rest of the head is as described by Jackson (1926, pp.885-889, Figs.1 - 3) for *Ligia oceanica*, but they differ slightly in shape from the eye of this species. The main part of the eye is on the dorsal surface. Laterally it is curved slightly down to extend for a short distance over the ventro-lateral surface, along almost the entire length of the side of the head. Seen from above, the eyes appear as two blackish-brown areas, more or less triangular in outline, though the margins are slightly

/convex

with reference to the centre of the triangle. The longest side is lateral, with the apices pointing to the dorsal mid-line of the head. The posterior of the two lines enclosing the apex of the triangle is slightly longer than the anterior. The eye as a whole is uniformly convex with the curvature considerably greater than that of the surrounding body surface.

External cuticle.

The eye is covered by a thin layer of transparent cuticle, continuous with that of the general surface of the body and of roughly the same average thickness- about 9 μ - see Fig. 3 for comparison of the corneal facets and the body cuticle. On removal of the rest of the eye with caustic potash, the eye cuticle as a whole is seen as a smoothly convex layer, bulging sharply away from the body cuticle. Surrounding the eye and separating it from the general cuticle of the head, there is a clear ring of smooth, unthickened, transparent chitin, marked off clearly from the rest of the cuticle. The eye-cuticle consists of regular rows of hexagonal facets, which are completely transparent and colourless and without external decoration. The facets are uniform throughout the eye with no noticeable thickening, diminution in surface area, or change in shape or curvature at the eye margins. This is seen in Fig. 3, where the underlying parts of the different ommatidia are cut at corresponding levels throughout the eye. Externally the

/facets

are regular equilateral hexagons, symmetrically arranged and contiguous with one another. There are about 700 to 800 of these facets, all of which are concavo-convex with the convexity external. Each is slightly thicker centrally than peripherally, the thicknesses being respectively 9µ and 5µ. There is no sign of any division to correspond to the formation of each facet from two separate hypoderm cells. Though such a division has been shown in other Crustacea, it does not seem to have been demonstrated in Isopoda. Its absence is presumably due to an early and close approximation of the products of secretion of the two separate cells.

The cuticle over the eye, as over the rest of the body, consists of two layers. The thin outer layer, which does not exceed 1µ in thickness, takes up haematoxylon and other nuclear stains more deeply than the rest of the cuticle. The outer layer is uniform, while the thicker, inner layer is deposited in a series of even lamellae, presumably laid down successively in growth. In these particulars the eye cuticle does not differ from that of the body. It differs, however, in being completely transparent and colourless. According to Yonge's work on the cuticle in Crustacea (1932, p.300) the outer layer is not chitinous, while the inner part is composed of lamellated chitin. As far as is known, the outer part consists of lipin material, and the deep stain obtained here with haematoxylon is not due to the presence of calcium [illegible]. Yonge points out (l.c.) that

/the presence

presence of calcium in the cuticle is restricted to the inner layer of the cuticle. This corresponds closely to the condition in Insects - see below.

Since the corneal lenses are much harder than the remaining parts of the eye, they tend to become detached in sectioning, and are therefore omitted from some of the drawings, as in Figs. 1 and 2, but they are shown in their normal relations in Fig. 3.

Corneal hypoderm cells. The internal face of each facet abuts on the ommatidium or eye-unit underlying it. The uppermost cells are those of the corneal hypoderm, which give rise to the cuticle. Two such cells are found below each facet. They are situated above the cones and are found in Figs. 1, 2, 4 and 5. (c. hyp) but not in Fig. 3, since the staining and thickness of this section make it unsuitable for the demonstration of such delicate structures. These cells are clearly corneagenuous in function but in the adult they lie under a small area only of each corneal facet, to the whole of which they must have given rise. The evenly laminated deposition of the facet-cuticle indicates that the corneagenous cells must originally have formed a complete layer. The protoplasm of the cells is thin and weakly stained, compared with that of the neighbouring cone cells, and it seems probable that they have been reduced in size and displaced, as their function decreased and as the underlying cones simultaneously increased in size.

/The nuclei

The nuclei give similar indications of reduction. They are smaller than those of the cone cells and on a level slightly above the latter, as is shown in Figs. 2 and 4 on comparison of c.hyp.n. (corneal hypoderm nucleus) with c.c.n. (cone cell nucleus). The outer membrane of the nucleus stains fairly deeply. Its contents appear fairly uniform and coarsely granular. A single nucleolus is generally visible - see Fig. 4 c.hyp. n.n.

The boundaries of the cells are not clear. The external, lateral walls, between the hypoderm cells of adjacent ommatidia, appear at first to be distinct, as shown in Figs.1 and 2 - the division between them being in a line with that between the underlying adjacent cone cells. This impression is, however, simplified by the low magnification. Fig. 4, a slightly oblique transverse section of the outermost layers, under oil immersion, shows the relations more clearly. The sides of the hypoderm cells of adjacent ommatidia are here seen not to be contiguous. (To understand the figure, it has to be remembered that the section is oblique with the angle of obliquity indicated by the elongation of the cones, as compared with those of Fig. 2).

In Fig. 4, at least in the case of the ommatidia C and D, the corneal cells, which are cut through, are those of the ommatidia in the next row in series in front of that in which the cones are shown. The corneal cells are here

/rounded off

rounded off and withdrawn towards the centre of the facet, to which they give rise, so that the lateral walls of successive units are not in contact with one another. This condition therefore differs from that of Ligia oceanica, as given by Hewitt (1907, Pl, IV, Fig. 1), where the cells are figured as having laterally distinct but contiguous, inter-ommatidial walls, and where they are displaced laterally and outwards from the centre of the ommatidium, so that they do not meet over its surface. Boundaries and cell contents are not described in detail, so that it is not possible to tell whether this is a specific difference, or whether Hewitt has taken the positions of the nuclei and delimited the cells diagrammatically about these, placing the latter in a position which they assume in many other Crustaceans. Figure 4 shows that the cells, in becoming reduced, are in this case not laterally, but centrally, displaced, so that the two cells of a single ommatidium are coalesced and enclosed in the upwardly projecting arms of the surrounding pigment cells.

The inner walls, dividing the hypoderm from the cone cells are not clear, as is shown in Fig. 4 in ommatidia A and B, where the section passes through a single ommatidium in each case. (In ommatidia C and D of this Figure the apparent differences are due to the cone and corneal cells belonging to different ommatidia). Hewitt (1907, Pl. IV Fig. 1) shows this division clearly for Ligia oceanica,

/Whether the

Whether the dissimilarity is due to fixation methods, which he does not give, or to diagrammatisation, or to a real specific difference, is again uncertain. The cytoplasm of these cells differs from that of the adjacent cone cells, being coarser and sparser, as is apparent in Fig. 4, though not in the lower magnification of Fig. 1 or Fig. 2. Possibly the fact that the boundaries of these cells are so indistinct is indicative of a general decrease in the organisation of the cell, which seems to have occurred in both cytoplasm and nucleus.

Cone secreting cells.

The dioptric, or light collecting and refracting part of the eye, consists of a corneal facet which has been described above, and a so-called "crystalline cone". The "cone" in each ommatidium, which in this species is spherical, is secreted by two cells which lie under, and are not always readily distinguishable from the hypoderm cells. These are shown in Figs. 1, 4 and 5

The cone cell nuclei are smaller, have a thinner wall, and stain less deeply than those of the hypoderm cells. The contents are coarsely granular and not uniform, without a nucleolus. The nuclei are situate below those of the corneal hypoderm, as is seen in Fig. 2D and in Fig. 4. They always lie above the cones and are placed in the two cells, one on each side of the cone, on its upper surface. Their

/arrangement

is most obvious in Fig. 4. In Figs. 1 and 2 the outer cells have not been as well preserved as in Fig. 4, and the magnification is not as great. The evidence which they afford is, however, in accordance with this description.

The boundaries of the cone cells are distinguishable from those of the hypoderm cells and the surrounding pigment cells with difficulty. The two cone cells of each ommatidium meet above the cone, where their cytoplasm runs together so that no boundary can be distinguished between them. This is the condition in Figs. 1 and 4. In Fig. 2A there appears to be such a boundary but it is seen, on examination, to be due to an overlapping of the two cells, caused by the shrinkage of that on the left.

As has been described, the upper boundary of the cone cells is not entirely distinct. The hypoderm cells along their lower surfaces are continuous with the upper part of the underlying cone cells, as is shown in Figs. 4A and 4B. (The condition in Figs. 4C and 4D has been explained above.) In Fig. 4 the cone cells appear to extend up beyond the level of the cone in each ommatidium, on either side of the corneal hypoderm cells of that ommatidium, to the facet. In this figure no lateral limits are distinguishable between the cone cells of adjacent ommatidia. Due to complete de-pigmentation of the section from which Fig. 4 was drawn, the evidence which this oblique section offers, as to the lateral limits of

/the upper parts of

parts of the cone cells of adjacent ommatidia, is misleading. The undepigmented longitudinal sections in Figs. 1 and 3 give a clearer idea of the cell relations. Here the lateral limits between the upper parts of the cone cells of adjacent ommatidia are distinct. The figures show the pigment cells, which lie between successive ommatidia, and which extend dorsally to the level of the cornea, and thus form a thin layer of cytoplasm, isolating the cone cells of each ommatidium. It is this upward continuation of the pigment cells, which is seen in Fig. 4 and might there be mistaken for a continuation of the cone cells. In the case of Fig. 4 these upward continuations of the pigment cells are not clearly marked off from the cone cells, since their cytoplasm is very similar, when completely depigmented. The lateral limits of the upper parts of the cone cells are therefore distinct and the cells of successive ommatidia are separated by thin upward arms of the inter-ommatidial pigment cells, which show up more clearly in longitudinal and only partially depigmented sections, as in Fig. 1, than in those such as Fig. 4. The dorsal limits of the cone cells are therefore as shown in Fig. 4, except that the apparent upward extensions are due to confluence of the cone cells with the pigment cells. The dorsal and lateral limits of the cells have been described, and it remains to delimit their ventral extent.

The cone cells lie mainly over the central part of the ommatidium but their cytoplasm extends laterally downwards to

/a varying extent.

extent. Where the cone is cut through its largest area in longitudinal section, that is through its centre, the cytoplasm ends at a level perpendicular to the longitudinal axis of the ommatidium and only slightly below that tangential to the upper extremity of the cone: see Figs. 3A and 3C. This continuation of the cone cell cytoplasm down the sides of the cone is more marked in those sections passing more superficially, that is through a smaller area of the cone. The maximum length along which this extension is carried is a little greater than that of the radius of the cone sphere. The cytoplasm of the cone cells therefore forms a complete mantle round the upper end of the true cone. This varies in length but does not exceed fifteen to eighteen μ. In section it has the form of a wedge and tapers strongly at its lower extremity, where it comes in contact with the upper edges of the accessory cone, to which it gives rise. This is clearly seen in Figs. 2A and 2D on the left hand side of the ommatidia.

On top of the cones, the cap formed by the cone cells is closely applied to the secretion of these cells - Laterally, however, the cells shrink away from the cones in most preparations, as is seen in Fig. 3B. This is probably a consequence of fixation and embedding. The cones and their cells are presumably normally in entire contact in the living eye.

/The cytoplasm

The cytoplasm of the cone cells is slightly less dense than that of the hypoderm cells and more dense than that of the pigment cells, as is seen in Fig. 2.

The Cones.

The cone cells secrete a spherical, transparent structure generally known as a "crystalline cone". In this case, however, the staining properties of the cone seem to be identical with those of the outer layer of the cuticle. These refractive bodies are the most conspicuous parts in the outer regions of the eye. They are perfectly uniform, solid, secretions, arranged in a regular layer under the cone cells, which, before staining, appear as clear, pale yellow and highly refractive. They take up most of the nuclear stains readily and in particular haematoxylon and carmine. Iron alum haematoxylon, which can readily be selectively discharged from the various cell components, is retained by the cones slightly longer than by the rhabdoms, i.e. is differentiated in the cones less rapidly than in the rhabdomes on treatment with the alum differentiation solution. According to the degree of differentiation employed in connection with the nuclear stain, the cones can be clearly demonstrated, by either a nuclear or a cytoplasmic stain, in a double staining method.

The chemical nature of the cone is uncertain. It is insoluble in alcohol, chloroform and warm 5% acetic acid. Although generally described as "crystalline", it is of

/extreme hardness

extreme hardness and is apparently chitinised.

Since there are two cone cells, the cone is presumably originally secreted in two parts. Though one might think that such a condition would be likely to interfere with the light refracting properties of the cone, it seems to have been very generally figured in Crustacean eyes. Hewitt (1907, Pl 1V, Fig. 1, p.25) indicates a longitudinal division of the cone in _L. oceanica_, where this is made up of two hemispherical masses with their flat surfaces opposed. In _L. natalensis_ a crack is occasionally visible down the centre of the cone. This is not, however, a straight line as is indicated for _L. oceanica_, but is regularly curved. It is sometimes accompanied by smaller cracks, which, from their irregularity, are obviously artefacts. The main line may possibly represent a line of weakness between two originally distinct segments. The cone proper has a major axis of about 25μ

The accessory cone.

The accessory cone is a peculiar structure apparently restricted among the Crustacea, the only Arthropods in which it occurs, to a few Isopods. The accessory cone is represented in Figs. 1, 2 and 5. It occurs immediately below the crystalline cone and is apparently very nearly homogeneous with it in its material. It is of the same refractive index as the true cone (as nearly as can be judged without the use of special instruments), but differs from the latter in staining reaction, since it takes up all the stains employed rather

/less deeply

less deeply than the true cone.

The accessory cone in L. natalensis is "chalice" shaped, with a thin walled cup surrounding the greater part of the true cone, and a stem, which is in contact with the upper end of the rhabdom. The cup has a greatly thickened base while the walls of the "chalice" decrease in thickness towards the outer edge of the eye. At their upper ends the accessory cones make contact with the lower ends of the cone cells, which form a lid to the "chalice" over the tops of the cones. The cone cells, as pointed out above on p37, pass down the sides of the cones for a small distance and at the tips come into contact with the upper ends of the accessory cones, to which they give rise by secretion. The inner surface of the base of the accessory cone surrounds but is not completely in contact with, the adjoining part of the true cone. This contact is probably complete in the living eyes. The thickened base of the cup of the accessory cone passes gradually into the stem. This stem is, in width, about half the radius of the cone sphere, about 12 μ in length, a little longer than the diametre of the sphere (about 25-30 μ). The lower end of the stem rests on the rhabdom of the corresponding ommatidium. The surface of contact between the two is not plane but roughly dovetailed - see Fig. 2B.

The accessory cone, like the true cone, probably consisted, originally, of two segments. In this species no division of the accessory cone into two parts is ever seen. In L. oceanica such a cleavage is found, in both the true and

/the accessory cone

accessory cones. In the figure of the eye of this species in Hewitt's paper (1907, pl. IV, Fig. 1), the shape of the accessory cones is very different from that given here for *L. natalensis*. The position with regard to the true cone is approximately the same as in *L. natalensis*, though the contact with the rhabdom is obscured by pigment. As far as the shape and relative size of the accessory cone of *L. oceanica* are concerned, it is as if the stem of the accessory cone in *L. natalensis* had been cut off and the base thickened and then cut up perpendicularly, the split having a small round notch at about one third of the way up from its proximal end.

Retinular cells.

The structures so far described are the dioptric parts of the eye, concerned with the collection, refraction and condensation of the light. After passing through these structures the light enters the sensitive parts of the eye below the corneal lenses and cones. These sensitive parts are the retinal cells which, in each ommatidium, form a retinular group. The retinular rods or rhabdomes in each ommatidium are, to some extent, united to form a rhabdom. The retinal (or retinular) cells are, throughout the eye, uniform in size and arrangement, at corresponding levels in different ommatidia, so that in longitudinal section they form an obvious layer, separate from that of the cones. Since the external surface is considerably curved and since the ommatidia are arranged radially, so that their distal

/ends converge

converge to the point of exit of the optic nerve, the inner ends of the ommatidia have to be considerably narrower than the outer.

In each ommatidium there are six retinal cells. In each retinular group these six cells decrease in diametre towards the base of the ommatidium, but are symmetrical in arrangement about the longitudinal axis of the group throughout their length. Their outlines are fairly definite and each cell is approximately cylindrical with an average diametre of about 7μ (taken half way down the cell) and an average length of about 55μ. At the base of the ommatidium the diametre of each cell decreases to that of a nerve fibre - about 4μ. The cells, as seen in transverse section, are arranged in a rosette, where they are in contact with one another laterally, so that their lateral walls are partially obliterated. There is usually a tendency for three of the cells to be grouped together, that is, for the cells of a single ommatidium to fall into two groups each composed of three cells.

The cytoplasm of these cells takes up plasma stains more deeply than any other part of the eye. It does not stain uniformly, since round the outside of the cell, throughout its length, the cytoplasm is more coarsely granular than it is internally. This is due to the presence of pigment granules, which are clearly visible in these parts of the ommatidium, as is seen in Fig. 2. Occasionally very large granules are found, embedded in the cytoplasm, throughout the length of the cells.

/The nuclei are spherical

The nuclei are spherical to slightly ellipsoidal in shape. Each has a very definite and darkly staining boundary and contains a small nucleolus together with very numerous granules of several sizes. The position of the nuclei varies. They may occur almost anywhere along the retinal cells. Hewitt (1907, pl. IV, Fig. 1, p.25) in dealing with *L. oceanica*, figures only one ommatidium and does not further describe these nuclei, but states that they lie at the proximal ends of the cells. Their arrangement in this species would therefore appear to be more regular than in L. *natalensis.*

The retinal groups of neighbouring ommatidia are separated from one another by a small space. Possibly they may be more nearly contiguous in the living form. Fig. 75. shows that the number of retinal cells is constant throughout the length of the ommatidium and that there is no tendency for one of the cells to be reduced in size or pushed to one side as occurs in many other Crustacea - see p. 151.

Rhabdom.

Each of the retinal cells secretes, throughout its entire length, a rod or rhabdomere. Each rhabdomere remains distinguishable, applied to the cell by which it was produced and in which it lies, along the inner longitudinal axis. The rhabdomeres are not closely associated to form a single rod, as is sometimes the case - that is their number and relation to the separate cells remains clear, though they are laterally confluent. Thus, there remains, in the centre of the retinular group, a cavity, whose more or less circular outline

/is bounded by

by the distinct rhabdomeres, which are only loosely associated into the rhabdom, which has the structure of a hollow tube.

In longitudinal section the rhabdomeres appear to be striated perpendicularly to their length. These striations are not all strictly perpendicular. Some are thicker than others and all thicken and run together at their edges. This appearance of the rhabdom is particularly well marked after fixation in sublimate acetic in sea water (for 29 hours) as in Fig. 2. The striations may be stained with either a nuclear or a plasma stain (where these two stains are used in combination) according to the degree of differentiation of the nuclear stain. The haematoxylon staining is not as deep as that in the cones, retinal cell nuclei, or outer corneal layer.

These rhabdomeres or fibrillar axes of the retinal cells reach to their extreme lower ends, where they touch the basement membrane. The theoretical aspects of the nature of the rhabdom are discussed on pp. 13-15 Most of the authors dealing, especially) a, with the eyes of Crustacea have inclined to the view that the rhabdom striations represent nerve fibrillae, arranged perpendicularly to the incident light stimulus, and continuous with the fine nerve fibrils of the optic nerve, below the basement membrane, that is, rhabdomes are often regarded in Crustacea as the terminations of the nerve fibres, or receptive areas of the retinal or nerve-

/end cells.

nerve-end cells. In this case the rhabdomes are certainly clearly striated but continuity of these striations with nerve fibrillae in the cell, could not be demonstrated. It is possible that the use of metallic impregnation techniques such as used by Sanchez (1916-[illegible]) in demonstrating the nervous nature of the retinal cells might decide this point. With ordinary staining methods, such as those used, the eye of L. natalensis leaves the question of the nervous or refractive function of the rhabdom one still open to speculation. It would admit of either interpretation, though the evidence for the nervous nature is incomplete.

The structure and arrangement of the rhabdomeres is seen in longitudinal section in Fig. 2, and in transverse section at various levels in Fig. 7. In the latter case, the staining was too deep to show the internal striations, and the sections themselves too thick for this purpose.

The relation of the position of the pigment in the retinal cells to the light was not studied, as most of the available sections were depigmented to show structural details. The rhabdomeres are usually, however, closely enveloped throughout their entire length, by masses of pigment granules, which lie in the retinal cells, round the rhabdom and round the margins of the cell, and whose position is indicated in Fig. 6 in the case of an eye exposed to daylight before death.

Pigment cells.

The upper part of each ommatidium is surrounded by

/pigment cells.

pigment cells. Their pigment is not as dense as that of the retinular cells, and the granules are, for the most part, smaller. The cytoplasm is uniform over the greater part of the cells, being slightly more coarsely granular in the region immediately surrounding the accessory cone and true cone. There is a concentration of the pigment in a cup surrounding the cone and accessory cone, which is shown in Figs. 2 and 5. The condition is probably incidentally related to the light conditions obtaining before death. (The specimens were killed in the light).

The cells form a complete mantle round the upper half of the ommatidium. At their upper end they abut on the cornea for a short space, between the ommatidia. The ommatidia are roughly triangular in outline, so that the pigment cells fill the spaces between them by becoming distally expanded.

The lower extremities of the pigment cells are obscure. They seem to end at, or just below, the upper ends of the retinular cells, but the cell boundary is not defined in this region.

The edges of the pigment cells are laterally contiguous with the chalice of the accessory cone but are separated from its stem by a considerable space, as is shown in Figs. 3 and 5.

The nuclei of these cells are of about the same size as, or slightly larger than, those of the retinal cells. They contain a nucleolus and coarsely granular material, and are surrounded by a distinct sheath. In some cases there is a

/clear space/in the

in the cytoplasm surrounding the nucleus - see Fig. 2. p.c.n.c. The nuclei lie at different levels but are always between the lower ends of the cone cells and the upper ends of the retinular cells. In longitudinal section they are seen to lie on two main levels, one near the cone and one near the apex of the retinulae. Also, as is seen in Fig. 1, the pigment cells would appear to form two fairly regularly arranged rows, disposed about the ommatidia with their nuclei at two different levels. The cell limits of the two layers cannot be distinguished, as is frequently the case in the pigment cells of the eyes of Crustacea. (See Peabody, 1939, p.532). It is therefore difficult to assess how many cells are attached to each ommatidium, and what the arrangement of the separate cells is. The maximum number of nuclei ever seen lying in one level, in a transverse section of this region, is six, as is shown in Fig. 5A.

The cells surrounding a single ommatidium are not defined in their lateral limits, as is seen in Fig. 5A. This confluence of the cytoplasm of numerous cells, together with the separation of their nuclei into two levels, renders it virtually impossible to delimit a cell, or to assign it to a particular ommatidium.

Fig. 5 gives the impression of there being six cells surrounding the cone at the level of the stem of the accessory cone. These cells, however, also surround the neighbouring/cones, and cones, and are therefore not all to be assigned to one ommatidium.

Hewitt's suggestion (1907, p.25) that these pigment cells send out processes which come to lie between the retinal cells and the rhabdomeres - the products of their secretion - does not seem to be applicable in this case. The pigment granules round the rhabdomeres - here described as part of the retinal cells - do not resemble any contained in the pigment cells. This condition would seem to preclude the possibility of the intrusion which he suggests, even apart from its unlikelihood in other respects. From his sketch (pl.IV Fig.1), his conclusion would appear to have been drawn from a somewhat thick and undepigmented section, where it is possible that the crowding of the pigment granules may have given the illusion of continuity between the two sets of pigment granules. It is most unlikely that such a considerable difference in morphology would exist between eyes of such closely related species. There is moreover no suggestion of such an intrusion of the accessory pigment cells into the retinal cells in other Crustacean eyes.

<u>The Basement membrane and nerve fibres.</u>

The basement membrane is distinct throughout the eye. It represents the membrane usually found at the base of a layer of hypoderm cells, and is continuous with the basement membrane of the body hypoderm. It is in the form of a fenestrated membrane, through which the underlying nerve fibres are continuous with the retinal cells. This

/continuity

is particularly clear between Figs. 2 C and 2D. The nuclei of interneural cells are visible between the nerve fibres below the basement membrane, see Fig. 2.i.n.c. The nerve fibres from a single ommatidium unite below the basement membrane to form a single nerve fibre which, after a short course, about equal in length to the retinal cells, enters the optic ganglion.

Figure 6 is a diagrammatic representation of one ommatidium in longitudinal section and shows the general relations and relative sizes of the cells.

Figure I.

N.B. The cornea has become detached and is not included in the drawing.

c.hyp.n.	Corneal hypoderm cell nucleus.
c.c.n.	Cone cell nucleus.
c.c.	Crystalline cone.
c.c.f.	Fissure in cone.
a.c.	Accessory cone.
p.c.n.	Pigment cell nucleus.
p.c.o.e.	Pigment cell outer end.
p.g.	Large pigment granules.
p.c.i.	Interommatidial pigment cell.
r.c.	Retinal cell.
r.c.n.	Retinal cell nucleus.
rhb.	Rhabdomere attached to one retinal cell.
r.c.i.e.	Inner end of retinal cell continuous with nerve fibre.
n.f.	Closely packed nerve fibres.

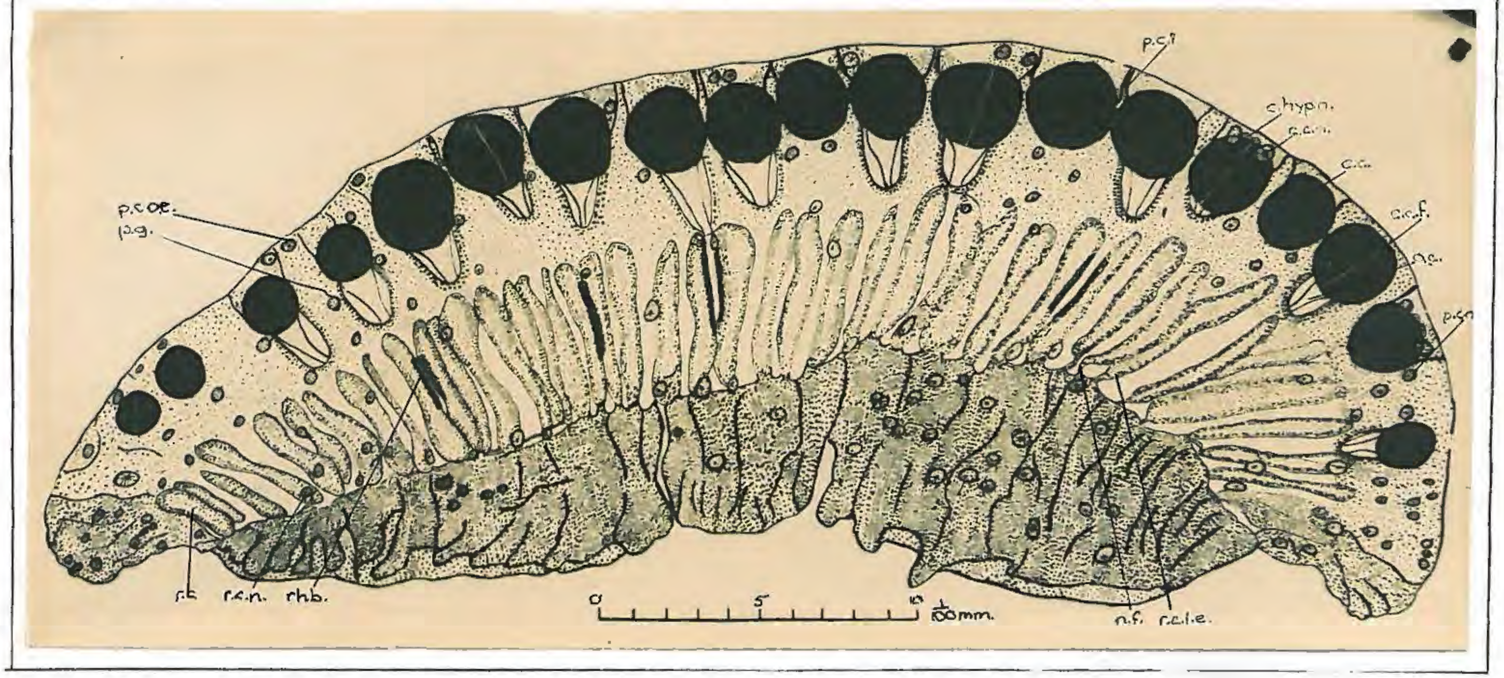


Figure I.
Longitudinal section through the entire eye of Ligia natalensis Collinge, passing through the centre of the eye and being transverse to the longitudinal axis of the body. (Particulars of preparation on following page).

Figure I .

Particulars of preparation etc.

Microscopy

4mm Apochromatic objective,
X I4 Holoscopic eyepiece.
Camera Lucida drawing.
3 μ section.

Preparation

Fixation : Saturated soln. of corrosive sublimate in sea water with acetic acid - 29 Hours.
Embedding : Double embedding in Ether :Alcohol (75:25) soln. of Celloidin and through $CHCl_3$ in 50 degrees melting point wax.
Staining : Heidenhain's Iron Alum Haemotoxylon. Alcoholic light green.
Mounted : Through toluol in toluol-clarite.

Figure B.

c.f.	Part of the corneal facet.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.c.c.	Crystalline cone cell.
c.c.	Crystalline cone.
c.c.n.	Crystalline cone cell nucleus.
c.c.f.	Cone fissure.
a.c.	Accessory cone.
x.	Contact between cone and rhabdom.
p.g.	Large pigment granules.
p.c.	Pigment cells.
p.c.n.	Pigment cell nucleus.
p.c.n.n.	Nucleolus in pigment cell nucleus.
p.c.n.c.	Clear space round pigment cell nucleus
p.c.b.	Indefinite lower border .
r.c.	Retinal cell.
r.c.n.	Retinal cell nucleus.
r.c.p.g.	Retinal cell pigment granules.
rhb.	Rhabdomere.
r.c.i.e.	Inner end of retinal cell continued into nerve fibre.
n.f.	Nerve fibre.
i.n.c.	Interneural cell.

Figure 2.

Longitudinal section of the eye of Ligia natalensis showing four complete ommatidia.

Microscopy .

4mm Apochromatic objective.
X 20 holoscopic eyepiece.
Camera lucida drawing.
2 µ section.

Preparation.

Fixation : Saturated solution of corrosive sublimate
in sea-water with acetic acid - 28 hours.
Embedding: Double embedding in Ether-Alcohol (75:25)
solution of celloidin, through chloroform
in 56 degrees melting point wax.
Staining : Depigmented in Rowland's fluid.
Heidenhain's Iron Alum haematoxylon.
Alcoholic Light green.
Mounted : Through toluol in toluol-clarite.

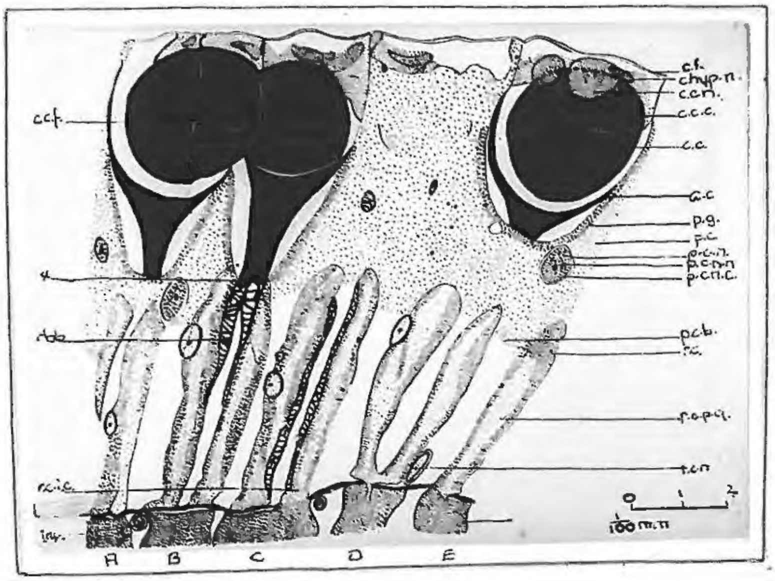
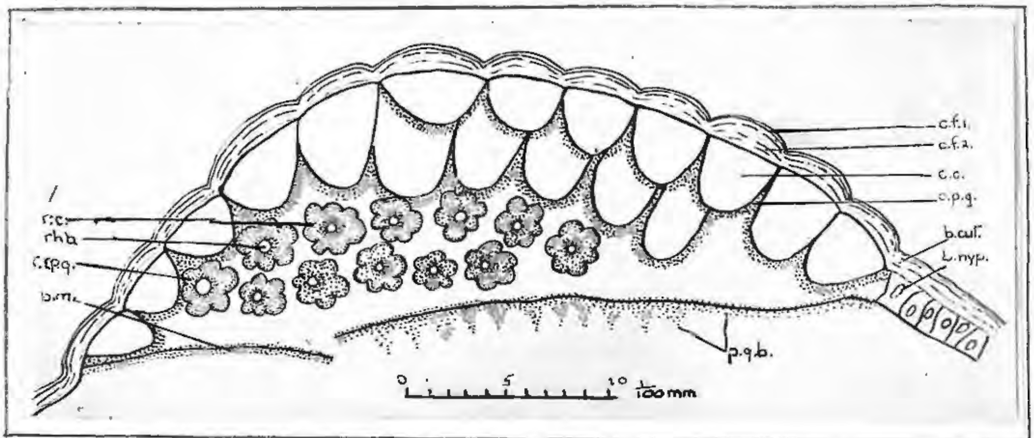


Figure 3.

c.f.I.	Hard outer part of corneal facet.
c.f.2.	Thick,laminated inner part of corneal facet.
b.cut.	Cuticle over body surface.
c.c.	Crystalline cones . (Two rows are seen since the section is both thick and oblique).
o.p.g.	Outer pigment granules in the pigment cells round the cone.
r.c.	Retinal cells.
rhb.	Refractive rhabdom.
r.o.p.g.	Pigment granules in retinal cells especially concentrated round rhabdom and periphery.
b.m.	Basement membrane.
p.g.b.	Pigment granules round basement membrane and nerves.
b.hyp.	Body hypoderm.

Figure 3.

Oblique section of the entire eye of Ligia natalensis to show the arrangement of the facets and of the pigment within the eye. This section is cut roughly transversely to the longitudinal axis of the body and obliquely to the longitudinal axis of the ommatidia.



Microscopy.

4 mm Apochromatic objective.
X20 holoscopic eyepiece.
Camera lucida drawing.
6 µ section.

Preparation.

Fixation : Picro-Chloro-Acetic acid I9 hours.
Embedding: Single embedding in 60 degrees melting point wax through Xylol.
Staining : Not depigmented.
Aqueous eosin.
Mounting : Through Xylol in Xylol Balsam.

Figure 4.

c.hyp.	Corneal hypoderm cells.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.hy.n.n.	Nucleolus in hypoderm nucleus.
p.c.u.e.	Upward extension of pigment cells.
c.c.n.	Cone cell nucleus.
c.c.	Crystalline cone.
c.c.c. and p.c.c.	Cone and pigment cell cytoplasm indistinguishable from one another.

Figure 4.

Oblique section of the outer layers of the eye of *Ligia natalensis*, showing the relation of the cone cells to the corneal hypoderm cells and to the cone.

Microscopy.

2mm objective with oil immersion.
X I4 holoscopic eyepiece.
Camera lucida drawing.
4 μ section.

Preparation.

Fixation	: Saturated solution of corrossive sublimate in sea-water with acetic acid-29 hours.
Embedding	: Double embedding in Ether Alcohol (75:25) solution of celloidin through $CHCl_3$ in wax of 50 degrees' melting point.
Staining	: As given above for Figure I
Mounting	: As given above for Figure I.

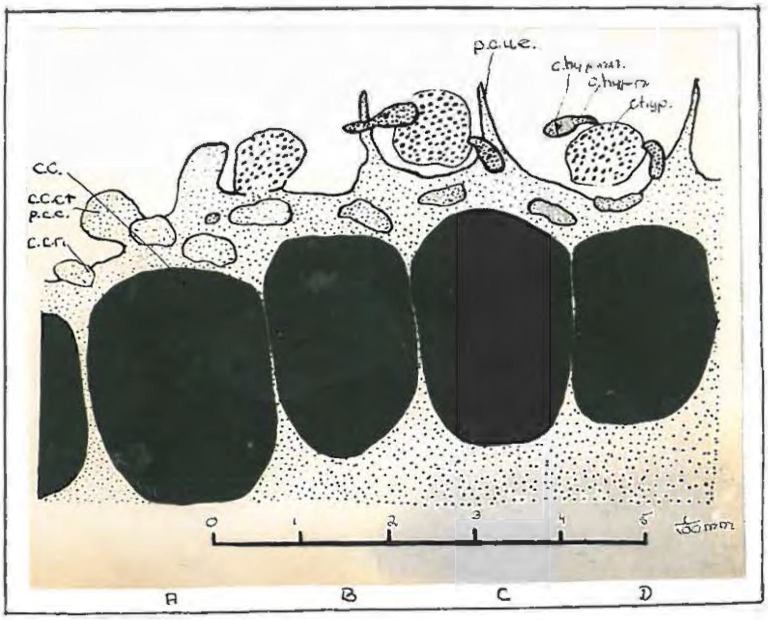
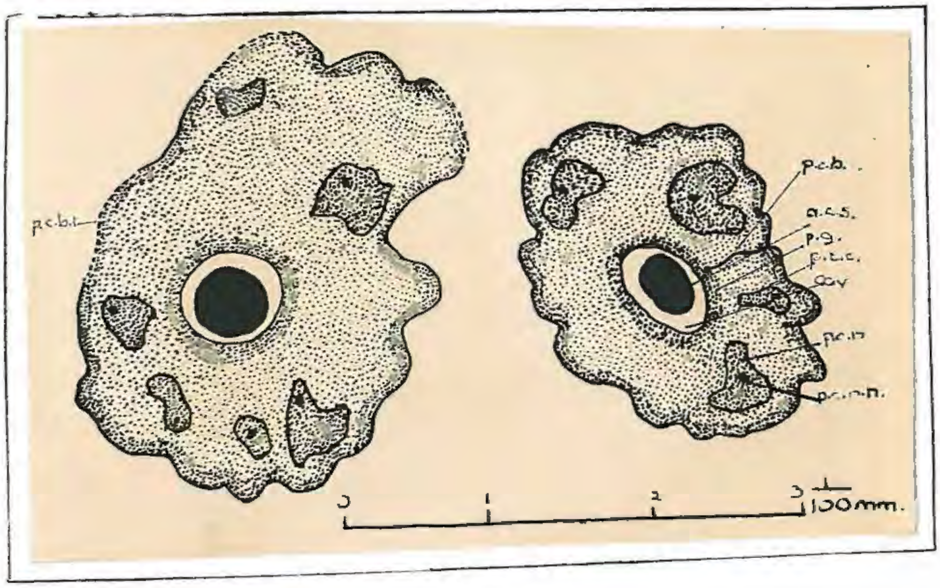


Figure 5.

a.c.s.	Stem of the accessory cone.
p.g.	Large pigment granules concentrated particularly round the cone stem.
p.c.c.	Pigment cell cytoplasm.
cav.	Cavity surrounding the cone stem.
p.c.n.	Pigment cell nucleus.
p.c.n.n.	Nucleolus in pigment cell nucleus.
p.c.b.	Pigment cell walls.
p.c.b.i.	Indistinct pigment cell boundaries.

Figure 5.

Transverse section of the eye of Ligia natalensis through the accessory cone stem and the surrounding pigment cells.



Microscope.

2mm objective with oil immersion.
X I4 holoscopic eyepiece.
Camera lucida drawing.
2-4 μ section.

Preparation.

Fixation : Saturated solution of Corrossive sublimate in sea-water with acetic acid - 29 hours.
Embedding : Double embedding with Ether-Alcohol (75-25) solution of celloidin , through chloroform in wax of 50 degrees melting point.
Staining : Depigmented in Rowland's fluid. Heidenhain's iron alum Haematoxylon. Alcoholic light green.
Mounting : Through Toluol in Toluol-clarite.

Figure 6.

c.f.I.	Thin outer layer of facet.
c,f.2.	Thick , inner, laminated part of facet.
c.hyp.c	Corneal hypoderm cells.
c.hyp.n.	Corneal hypoderm cell nuclei.
c.c.b.	Indistinct cone cell bounds marked out by dotted lines.
c.c.	Crystalline cone.
a.c.c.	"Chalice" of the accessory cone.
a.c.s.	Stem of the accessory cone.
p.c.i.	Interommatidial pigment cell.
p.c.n.I.	Pigment cell nuclei of the upper row.
p.c.n.2.	Pigment cell nuclei of the lower row.
x.	Contact between the cone and rhabdom.
r.c.	Retinal cell.
r.c.n.	Retinal cell nuclei varying in position.
p.g.r.c.	Pigment granules of the retinal cell.
b.m.	Basement membrane.
n.f.	Single nerve fibre formed from the union of strands from the retinal cells of one ommatidium.
c.c.n.	Cone cell nuclei.

Figure 6.

Diagrammatic representation of a single ommatidium of the eye of Ligia natalensis in longitudinal section constructed from figures I-5.

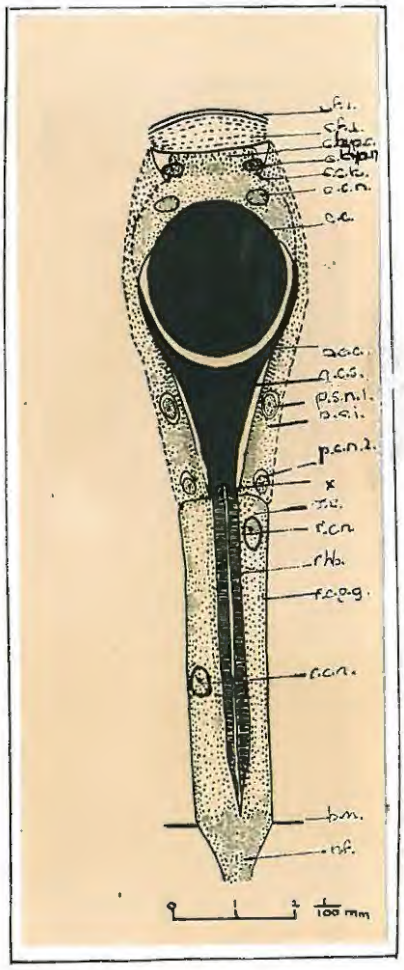


Figure 7.

r.c.	Retinal cell.
r.c.b.	Boundary between the separate retinal cells.
rhb.	Rhabdom made up of six rhabdomeres
c.cav.r.	Central cavity
r.c.p.g.	Retinal cell pigment granules.
l.p.g.	Occasional large pigment granules.
r.c.n.n.	Retinal cell nucleus with nucleolus.

Figure 7.
Transverse sections through the eye of Ligia natalensis through the rhabdomeres and the retinal cells at a series of levels from above downwards.

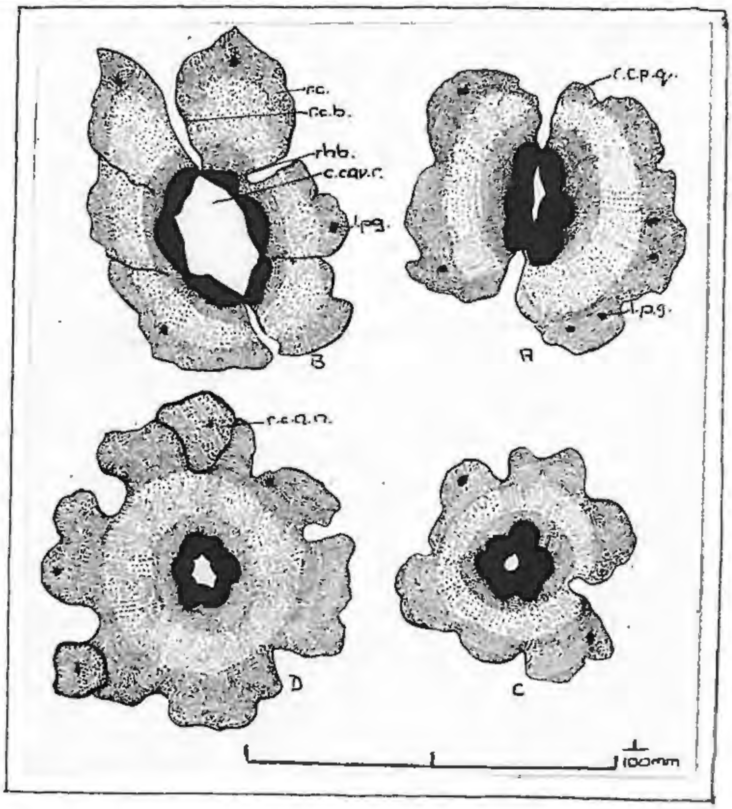
A. Transverse section through the upper end of the retinal group.

B. Oblique central section through the retinal group.

C. Transverse section through the base of the retinal group.

D. Transverse section through the centre of the retinal group and passing through some of the nuclei.

These sections show the size and arrangements of the cells and rhabdomeres at different levels.



Microscopy.
2mm objective with oil immersion.
X I4 Holoscopic eyepiece.
Camera lucida drawing.
4 μ section.

Preparation.
Fixation : Saturated solution of corrossive sublimate in sea-water with acetic acid - 29 hours.
Embedding : Double embedding in ether-alcohol (75:25) solution of celloidin, through chloroform in wax of 50 degrees melting point.
Staining : As for Figure I.
Mounting : As for Figure I.

2. The anatomy of the lateral compound eyes of Philoscia muscorum (Scopoli, 1763).

The eye in this genus does not appear to have been described previously.

External characters.

Lateral compound eyes are present as paired,sessile, immovable structures, occupying positions corresponding to those of Ligia. They are, however, much smaller and instead of consisting of several hundreds of units, are made up of ten ommatidia. Externally the eye is very nearly oval in outline, although the margins are not very smoothly defined. The major axis of the outline of the eye does not exceed 150μ , as compared with the corresponding measurement of 500μ in Ligia, The reduction of the eye is related to the habits of the species, which lives a rather inactive life in semi-darkness under stones.

The eye surface as a whole shows a more or less uniform convexity with reference to the body surface. This is much smaller than the convexity of the eye in Ligia. As in the latter, the eye externally appears facetted, with the dark pigment of the underlying cells showing through the transparent lenses.

Corneal cuticula.

The eye is covered with a series of cuticular lenses. These are shown in section in Fig. 8. Extern-

/ally

-ally they are rather loosely grouped together on the sides of the head. The lenses are, as in Ligia, continuous with the general cuticle of the body but differ from those of the latter species in being considerably thicker than the ordinary body cuticle. From the outside each lens can be seen as a separate, refractive convexity. The ordinary cuticle has an average thickness of about 5μ , while the lenses vary in thickness from about 10μ to 20μ , being thicker centrally than peripherally - see Fig. 8, which shows the lenses of the ommatidia across the eye. In this case the underlying ommatidia are not all cut at precisely the same level. The ommatidial sections under the central lenses pass through the centres of the cones, while those through the outer lenses pass through the ommatidia more superficially. From these observations, it appears that, above the cones, the lenses have their maximum depth of about 20μ , while each is peripherally reduced to about 10μ or less. The facets are not quite uniform in size and shape. Those at the edge of the eye are slightly smaller and thinner than those in the centre. Throughout the eye the lenses are biconvex and globular, in contrast with the uniformly concavo-convex lenses in Ligia. They are arranged on a pattern of more or less regular, alternating rows of roughly circular facets, each separated from its neighbour by a small area of

/cuticle.

cuticle. The lenses consist of a thin darkly staining outer layer about 1μ in depth and of uniform thickness throughout the eye, and a thick, uniform, inner layer, which does not show the laminations apparent in *Ligia.* The proportions of the two layers are shown in Fig. 8. The lenses are as in *Ligia* completely transparent and colourless without any external decoration. There is no evidence of the fusion of two halves to form the facet, although there are two cells below it.

Externally, therefore, the eye differs from that of *Ligia* in its smaller size and convexity, in the greater size and convexity of the separate lenses, in their smaller number and circular, rather than hexagonal, outline.

The corneal hypoderm cells.

These, as in *Ligia*, lie below the facet and above the cone, and are two in number. Their position is shown in Figs. 9, 10 and 11. They are situated on approximately the same level as the cone cells and not above them, as in *Ligia*. The cells are placed immediately above the upper ends of the retinular cells of the corresponding ommatidium, on whose upper surfaces their lower ends abut - see Figs. 9A and 9B.

The cytoplasm of the corneal cells of adjacent ommatidia frequently appears to run together laterally,

/the

the limits between the cells disappearing. This is the condition obtaining in Figs. 9A and 9B on the left-hand side of these ommatidia and in Fig. 11A on the right hand side.

Sometimes, however, the hypoderm cells are sharply separated from those of the neighbouring ommatidia, as in Figs. 9B and 11C on the right hand side and in Figs. 10A, 10B and 11D on both sides. The latter is probably the usual condition, with the coalescence of the cells as a secondary consequence of the general tendency shown in this eye to simplification of the cellular structure, arising from the decrease in the number of ommatidia. Since they presumably give rise to an entire hypoderm facet, each pair of hypoderm cells must, as in Ligia, originally have had a dorsal extension equal to that of the corresponding corneal lens. The development of the cone cells below them and their own decrease in size, as their function becomes less important with increasing age, are presumably factors which, as in Ligia, have contributed to the reduction of these cells and to their displacement. Unlike the cells in Ligia, which are centrally displaced, these are separated and moved to the side of the ommatidia. The two cells of a single ommatidium often appear to be discontinuous, but it is to be presumed that there was originally a bridge joining

/the

the corneal cells together and itself giving rise to the central or overlying parts of the cornea. It may be that this bridge persists, but, like the rest of the cytoplasm, has tended to fuse with that of the adjacent underlying cone cells. This might well be the case from Figs. 11A, B, C and D and 9A and 10A. Figs. 9B and 10B, however, suggest that the cells are completely separated laterally from the cone cells, in the adult condition. This seems to indicate the absence of such a bridge, in the adult eye, at least in the case of some of the ommatidia.

The corneal cells are slightly deeper centrally then peripherally. The peripheral depth on each side is about 4-6μ, the central dimension varying from 10-15μ.

Their nuclei resemble those of the cone cells and are of approximately the same size and on the same level. They are spherical and densely granular, with a nucleolus and a distinct boundary. Their cytoplasm is finely granular.

The cone secreting cells.

The cells, which give rise to the cone or chief refractive part of the eye, are two in number. They are shown in Figs. 9, 10, 11 (c.c.c.)

The position of these in relation to the adjacent corneal cells and the lateral demarkation of the cone

/cells

cells from these has been described above. The following figures in the succession given illustrate the structure of these cells by a series of sections taken at regular intervals : 9A, 9B, 10A, 10B, 11B, 11C, 11D. The condition of the cells in these sections will be described and the description of the cone cells as a whole based on this.

Figs. 9A and 9B pass immediately through the centre of the eye and through two of the rhabdomeres. The cone cells here form a layer immediately overlying the cone and filling up the entire space between it and the cornea, with the possible exception of the space occupied by the bridge of corneal cells mentioned above, if this is present at this level.

In this and the succeeding sections the nuclei can be seen. They are very similar to those of the hypoderm cells, which are at the same level above the cone. Fig. 10A shows the downward extension of the cone cells which surrounds the cone laterally. Its lateral walls are contiguous with, but distinct from, those of the surrounding retinal cells - see Fig. 11B. Its ventral extent corresponds to that of the cone. At its base this is in contact with two of the rhabdomeres of the ommatidium. The length of each cone cell is about 55μ. The contents differ from those of the hypoderm cells in being slightly

/vacuolated

vacuolated - see Fig. 9B. Fig. 10B passes more superficially than Fig. 10A, for the most part outside the downward extension or mantle of the cone cells, round the cone. A very slight indication of this mantle is present in Fig. 10B.

Fig. 11B shows a still more superficial section of the cone cells. The condition of the retinal cells, with the rhabdom not visible, indicates that the section as a whole passes through the ommatidium near its surface.

The cytoplasm of the cone cells, above the cone, is not always distinguishable from that of the hypoderm cells. In this part of the ommatidium it forms a flat layer, seen in Figs. 11B, 11C and 11D.

Figs. 11C and 11D are slightly less superficial than 11B, since they pass through the cone nuclei and the rhabdomeres.

Thus from the sections it appears that the corneal cells, seen from above, would form a complete ring round the cone cells and would presumably cap them over at least in the younger stages. Both the dorsal and lateral demarkations of the cone from the hypoderm cells are incomplete. As described above, the dorsal surface is in contact with the corresponding eye-facet, or with the lower surface of the hypoderm cell bridge, if this is present. The cells have a maximum proximal extent equal to that of the cone.

/The cones

The cones

The cones, which are secreted by, and enclosed in, the cone cells, form the main refractive part of the eye. They themselves exhibit no trace of their presumably double origin but appear as uniform solid secretions. They are roughly ellipsoidal in shape, with a rounded upper end and a slightly tapering lower end - see Fig. 9A, - a true longitudinal section of the cone. The upper rounded surface is in contact with the lower surface of the cap, formed by the cone cells above the cone. Laterally the cones are surrounded, first, by the thin mantle flaps of the cone cells, as described above and figured in 10A, 10B and 12B, and then secondly by the continuations of the retinal cells round them - see Figs. 10B and 11B.

The cones stain with nuclear stains more darkly than the corneal facets and less darkly than the rhabdomeres, as is also the case in Ligia. They vary slightly in size, but this variation does not bear any marked relation to the position of the ommatidium within the eye. Their maximum length does not exceed 55μ and their maximum width, near the upper surface, 45μ. No indication of the division of the cone into two parts, to correspond with its secretion by two cells, is visible in the adults.

/The

The accessory cones, present in Ligia, are not represented here, Their development in Ligia is not one fundamental to the compound eye in Crustacea but merely an adaptation to more perfect refraction, in connection with the obviously higher grade of optic development found in the latter species.

The retinulae.

The retinulae, or sense cells, lie below the cones, and each has its own striated border or rhabdomere, as in Ligia. These cells are seven in number and extend throughout the entire length of the ommatidium, below the cone. Apart from their greater number, they differ in disposition from those of Ligia. Unlike the corresponding cells in the eye of Ligia, they do not end at the level of the cone but extend up round it on all sides, to abut on the lower surfaces of the corneal cells. Their total length is very nearly equal to that of the ommatidium. They vary in length from about 60μ to about 90μ.

These measurements are taken to include the upward extension of the retinular cells which form a mantle round the cone and cone cells, to separate each ommatidium from its neighbours. The cells are longest in the peripheral ommatidia. They take the place of the interommatidial pigment cells in Ligia, which have

/here

here no morphological representative. The extent of the retinular cells at their upper ends corresponds with that of the lower extremity of the corneal cells, on which the particular retinal group abuts.

The nuclei of the retinal cells are larger than those of the corneal and cone cells. They lie in the upper ends of the retinal cells in the mantle round the cone. Their outline is generally darkly stained and round the edges there is a dense collection of large, darkly staining granules. The inner material is more finely granular and stains less darkly with all the stains used. One or two nucleoli are usually visible and chromatin material is scattered throughout the nucleus, which is elongated and approximately twice the size of that of the cone cells.

As is seen in Fig. 12, a section passing through the upper ends of the retinular cells, surrounding the cone cells, the divisions between the individual retinular cells are not clear here, as they are below the cones, and the cytoplasm of adjacent retinular cells runs together. Five retinular nuclei round each cone define the number of the cells.

The cytoplasm of the retinal cells is not homogeneous. For the greater part the cells are filled with coarse pigment granules. These are uniform in size,except for a few irregularly distributed, larger granules, which

/stain

stain very darkly with most plasma stains. The rest of the cytoplasm is uniform and less dense than that of the cone or corneal cells. The distribution of the pigment granules through the cytoplasm varies. They are frequently concentrated round the rhabdom and towards the centre of the cell and are less common in the upper extensions than in the parts below the cones. They also occur round the nervous continuations of the cells below the basement membrane.

The upper surfaces of the cells surround the cones fairly closely, being separated from them by a small space. They are probably adherent in life.

There are seven retinular cells to each ommatidium. The number is constant throughout the length of the ommatidium. Each cell is about 15µ in average diametre - see Figs. 13, 14 and 15. On comparison of Figs. 15A and 15C it is seen that, not only do the ommatidia of <u>Philoscia</u> differ from those of <u>Ligia</u> in the presence of an additional cell, but that in them there is a very considerable enlargement of the individual cells. In <u>Philoscia</u>, the part of the retinal cell below the cone is slightly shorter on the average than the retinal cell below the cone in <u>Ligia</u> (about 45µ as compared with about 55µ in the central ommatidia in both cases). The individual cells and their rhabdoms are of approximately twice the diametre of those in <u>Ligia.</u> This is the most

/noticeable

noticeable change in the histology of the eye, which accompanies the decrease in the number of ommatidia from several hundreds in Ligia to ten in Philoscia.

Fig. 15 illustrates the following additional points in the anatomy of the retinal cells. A is a section at the top of the ommatidium, B at the base. In B two of the cells show a distinct tendency to coalesce. This is incipient, though less noticeable, in A. B indicates that the rhabdomeres do not persist to the extreme ends of the cells, but stop a short distance above the basement membrane.

The rhabdom

For much the greater part of their length, the retinal cells are separated from one another centrally, so that the rhabdomeres along their inner edges are arranged about an axial space - see Fig. 15A. At their bases, the cells are contiguous and the space between them obliterated. This coalescence is below the rhabdomeres but above the basement membrane, as is shown in Fig. 15 B. The rhabdomeres as in Ligia are striated, and in longitudinal section the striations appear to be rather irregularly transverse. The outer longitudinal edges of the rhabdomeres are slightly thickened and the striations are perpendicular to these - see Figs. 9, 10 and 11. In transverse section the appearance differs strikingly from that of Ligia. In the latter the rhabdomeres of neighbouring cells are approximated to form a continuous lining to the axial canal of the rhabdom. In *Philoscia* the rhabdomeres are completely separate, each forming the top of one retinular cell and projecting, separately from its neighbours, into the axial canal of the retinal cell bundle. The individual rhabdomeres differ further from those of *Ligia* in being almond shaped rather than bi-convex and lenticular in appearance, in transverse section. The staining properties of these structures are very similar to those of the rhabdomeres of *Ligia* and they are presumably chitinised in both cases. In *Ligia*, in view of the small diametre of the cells, and of the rhabdomeres, it is not possible to see much of the internal structure in transverse section. The larger size of these in *Philoscia* renders their structure visible with the use of a 2mm oil immersion lens. Round each rhabdomere there is a continuous, darkly staining, more or less uniform, border. Homogeneous with this is a central, axial bar - see in Figs. 13 and 14. Fig. 14 is an oblique section, which indicates the continuity of the central axial bar throughout the length of the rhabdomere. From this there radiate out on each side a series of cross bars which are superimposed at various levels. These are roughly perpendicular to the central bar, or inclined to it at an angle of about 80 degress. The transverse bar is

/continuous

continuous with the axial bar on one side and the marginal thickening on the other. The bars on either side do not correspond exactly in number, size, or position. They are not uniform in thickness along their own length and, in particular, are thicker at either end, where they merge with the axial bar or the peripheral ring. Sometimes these structures are incomplete as in the upper right hand cells in Fig. 13. Although it seemed possible that this appearance of the rhabdom might be due to a vacuolation caused by the fixative, the regularity with which it occurs in different cells, treated with different fixatives and varieusly stained, makes it unlikely that the structure observed in the rhabdomeres is an artefact. Moreover as the rhabdomeres appear to be chitinous in nature, they are not likely to be distorted by fixation.

Thus each rhabdomere consists of a series of bars radiating out at various levels from a central, axial bar to a peripheral ring. Though not minutely symmetrical at least in the sections, the rhabdomeres as a whole have a fairly well ordered appearance, as is seen in Figures 13 and 14.

As in the case of Ligia, it is not possible with the technique employed to trace the nerve fibrils into the rhabdom. In Figure 13 however, fine radiating lines can be seen running through the cytoplasm of the sense cells (r.c.r.l.). These have the appearance of fine nerve fibrillae passing through the cells towards the rhabdomeres, though they cannot be traced into these. They appear instead to end in the pigmented cytoplasm of the retinal cells.

The arrangement of the plates in the rhabdom does not correspond to that of any other eye, of which a description has been seen. That such a unique structure should be found in an Isopod eye is not perhaps as surprising as might at first appear to be the case. The eye in Isopoda as a whole is extremely variable, particularly in the rhabdom structure, where many intergrades are found, as is described on pages II5-II6 It is not possible to account for the structure of the rhabdomeres as due to degeneration, although the eye as a whole is degenerate. Degenerate rhabdomeres are by all precedent amorphous rather than highly differentiated - see Eggert (1927, pp. 38-39) and Verrier (1943, pp.148 -150). It seems more likely that the rhabdomeres and retinal cells have been enlarged and elaborated to compensate for the degeneration of the eye as a whole by an increase in the efficiency of the units.

There are some difficulties attaching to regarding the rhabdomere plates as neurofibrillar in origin in this case. No direct communication between these and the optic neurofibrillae of the retinal cells can be seen. Moreover it is difficult to reconcile the development of such an elaborate receptive surface with the fact that the eye is, on the whole, of a low grade of development. The structure in this case is perhaps more readily accounted for by assuming that this has been evolved as an elaborate apparatus for the support of the enlarged retinal cells and that it has a dioptric function rather than a perceptive one. In dim light the condensation of the available light by the cones and its refraction by the rhabdomeres into the pigmented, photosensitive protoplasm of the enlarged retinal cells would presumably be more advantageous than an elaborate arrangement for the perception of detail.

Basement membrane.

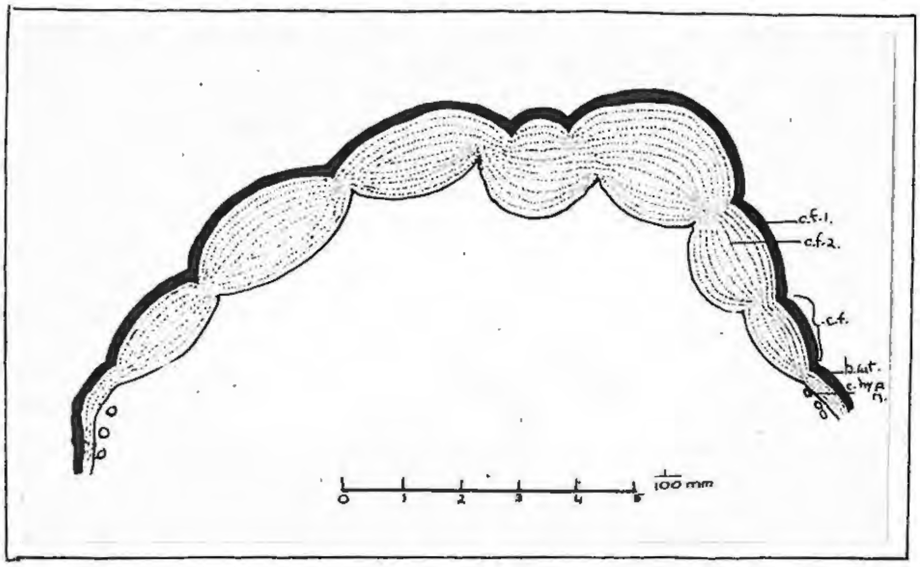
At the lower ends of the eye the retinal cells pass through the basement membrane and become continuous with the nerve fibres passing to the optic ganglion. As they pass through the basement membrane the cells are constricted and below it the retinal cells of each ommatidium unite to form a single nerve fibre - as is seen in Fig. 9B.

Figure 8.

b.cut.	Cuticle of the general body surface.
c.hyp.n.	Nuclei of the corneal hypoderm cells.
c.f.I.	Darkly staining outer layer of cuticle.
c.f.2.	Uniform inner layer of cuticle.
c.f.	Corneal facet.

Figure 8.

Transverse section through the corneal facets across the eye of Philoscia muscorum to show the thickness of the lenses and of the surrounding body cuticle.



Microscopy.

4mm apochromatic objective.
X I4 holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation.

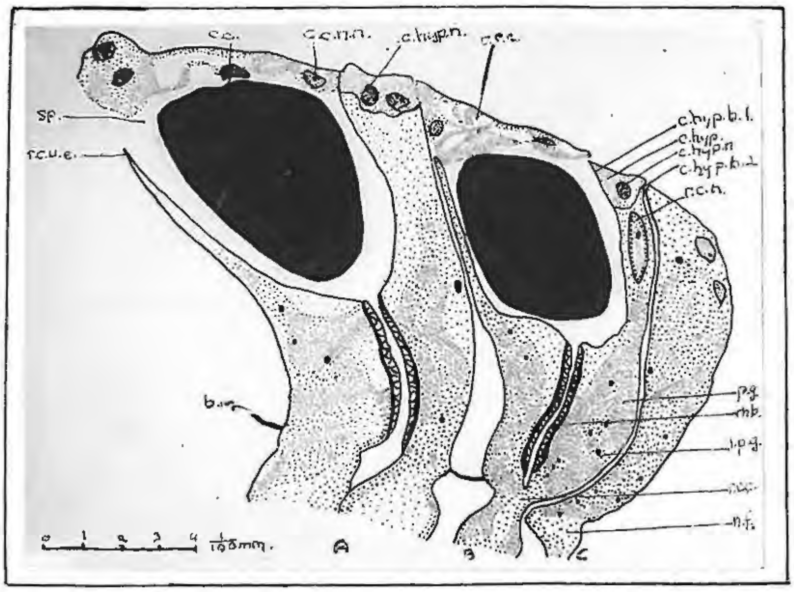
Fixation : Corr-osive sublimate in 96 % alcohol-39 hours.
Embedding : Double embedding in ether -alcohol (75.25) solution of celloidin, through chloroform in 50 degrees' melting point wax.
Staining. : Iron alum haematoxylon.
Mounting : Through toluol in toluol-clarite.

Figure 9.

c.hyp.	Corneal hypoderm cells.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.hyp.b.I.	Boundary between the corneal hypoderm and cone cell.
c.hyp.b.2.	Boundary between the corneal hypoderm and retinal cells.
c.c.c.	Vacuolated cone cell cytoplasm.
c.c.n.n.	Cone cell nucleus with nucleolus.
c.c.	Crystalline cone.
sp.	Space separating cone from retinal cells.
r.c.u.e.	Upper end of retinal cell.
r.c.n.	Elongated retinal cell nucleus.
rhb.	Rhabdomere along the inner border of the retinal cell.
p.g.	Large pigment granules in the retinal cell.
p.g.l.	Occas~~s~~ional, exceptionally large pigment granules.
r.c.c.	Continuation of the retinal cells through the basement membrane.
b.m.	Basement membrane.
n.f.	Nerve fibres,continuous with the retinal cells of one ommatidium, merge together.

Figure 9.

Longitudinal section through three ommatidia of the eye of Philoscia muscorum. Sections A and B pass through the centres of the cones. Section C passes very superficially through a third ommatidium at the edge of the eye.



Microscopy.

4mm Apochromatic objective.
X I4 Holoscopic eyepiece.
Camera lucida drawing .
3 μ section.

Preparation.

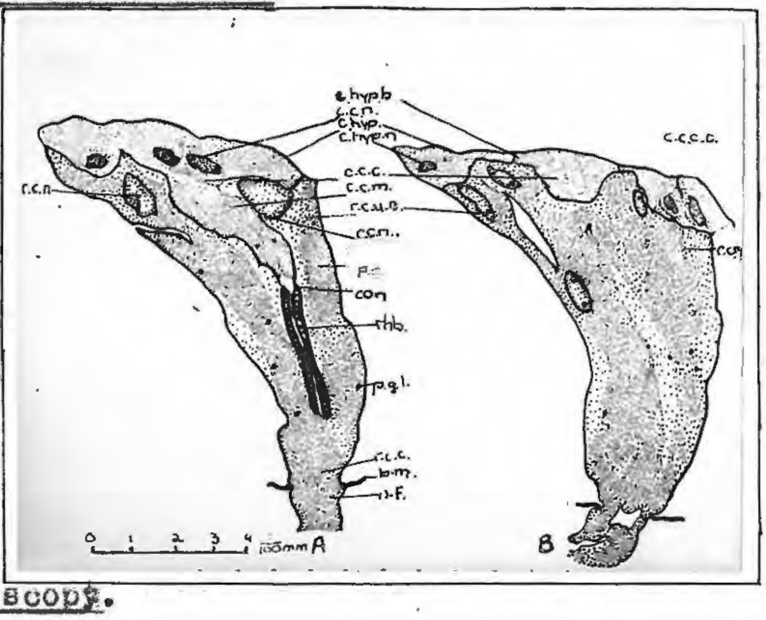
Fixation. : Corrossive sublimate in 96% alcohol - 29 hours.
Embedding : Double embedding in an ether-alcohol (75:25) solution of celloidin, through chloroform in 50 degrees' melting point wax.
Staining : Partially depigmented in Grenacher's fluid - 2hours. Delafield's haematoxylon. Aqueous Eosin.
Mounting : Through toluol in toluol-clarite.

Figure IO.

c.hyp.	Corneal hypoderm cell.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.hyp.b.	Boundary between the corneal hypoderm and cone cells in one ommatidium.
c.c.c.	Cone cell.
c.c.m.	Extension of the cone cell laterally round the cone in the form of a mantle.
c.c.n.	Cone cell nucleus.
c.c.c.c.	Vacuolated cytoplasm of the cone cell.
r.c.u.e.	Retinal cell -upper end.
r.c.n.	Retinal cell nucleus.
rhb.	Striated rhabdomeres.
p.g.	Lage pigment granules within therstinal cells.
Con.	Contact between the upper end og the rhabdomeres and the cone cell mantle.
p.g.l.	Exceptionally large pigment granules.
r.c.c.	Continuation of the retinal cells through the basement membrane.
b.m.	Basement membrane.
N.f.	Nerve fibres - those from one ommatidium merging in B.
r.c.m.	Mantle formed outside the cone mantle up the retinal cells.

Figure IO.

Longitudinal sections of two ommatidia from the eye of Philoscia muscorum, immediately outside those shown in Figure 9A. Figure IO A passes immediately outside the cone and through the cone cell mantle. Figure IO B passes through the ommatidium more supefficially and thus through only a small part of the cone mantle.



Microscopy.

4mm Apochromatic objective.
X I4 holoscopic eyepiece.
Camera lucida drawing.
3/μ section.

Preparation.

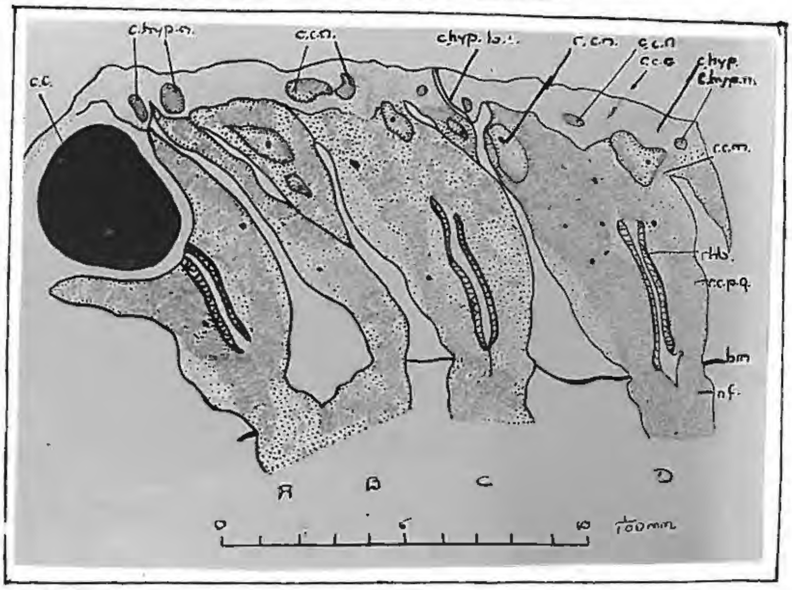
Fixation :	Corrossive sublimate in 96% alochol -29 hours.
Embedding :	Double embedding in ether-alcohol (75:25) solution of celloidin , through chloroform in 50 degrees ' melting point wax.
Staining :	Partly depigmented in Grenacher's fluid-2 hours. Delafield's haematoxylon. Aqueous Eosin.
Mounting.	:Through toluol in toluol -clarite.

Figure II.

c.hyp.	Corneal hypoderm cell.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.hyp.b.	Boundary between the corneal cells of adjacent ommatidia.
c.c.c.	Cone cell.
c,c.n.	Cone cell nucleus.
c.c.	Crystalline cone.
r.c.m.	Retinal cells forming a mantle round the outside of the cone cells and the cone.
r.c.n.	Retinal cell nucleus.
rhb.	Rhabdomere below the level of the cone.
r.c.p.g.	Retinal cell pigment granules.
b.m.	Basement membrane.
n.f.	Nerve fibres continuous with the retinal cells.

Figure II.

Longitudinal section of four ommatidia of the eye of Philoscia muscorum, of which D is nearest the edge of the eye. A passes through the cone , while the remaining sections pass outside it ,with B even more superficial than C or D.



Microscopy.

4mm Apochromatic objective
X I4 holoscopic eyepiece.
Camera lucida drawing.
3/μ section.

Preparation.

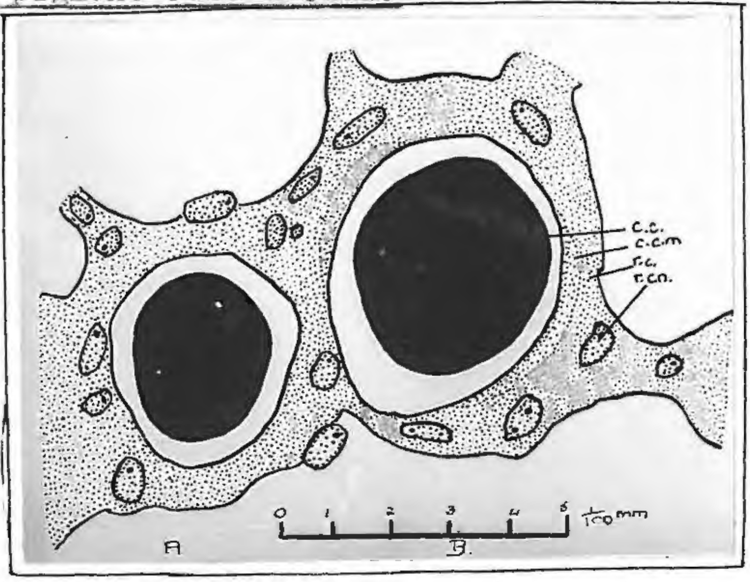
Fixation : Corrossive sublimate in 96 % alcohol 29 hours.
Embedding : Double embedding in an ether-alcohol (75:25) solution of celloidin through chloroform in 50 degrees' melting point wax.
Staining : Depigmented in Grenacher's fluid. Delafield's haematoxylon. Aqueous Eosin.
Mounting : Through toluol in toluol-clarite.

Figure I2.

c.c.	Crystalline cone.
c.c.m.	Extension of the cone cell as a mantle round the cone.
r.c.	Retinal cells in one ommatidium have run together to form a continuous pigmented sheath round the cone.
r.c.n.	Retinal cell nucleus. The number of nuclei to one ommatidium in this section cannot be assigned with certainty, since the cytoplasm of the cells in adjacent ommatidia runs together.. From lower sections it appears that the numer is definitely seven.

Figure I2.

Transverse section through the upper ends of the retinal pigment cells and through the cones in the eye of Philoscia muscorum at the level of the retinal pigment cell nuclei.



Microscopy.

4mm apochromatic objective.
X I4 Holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation.

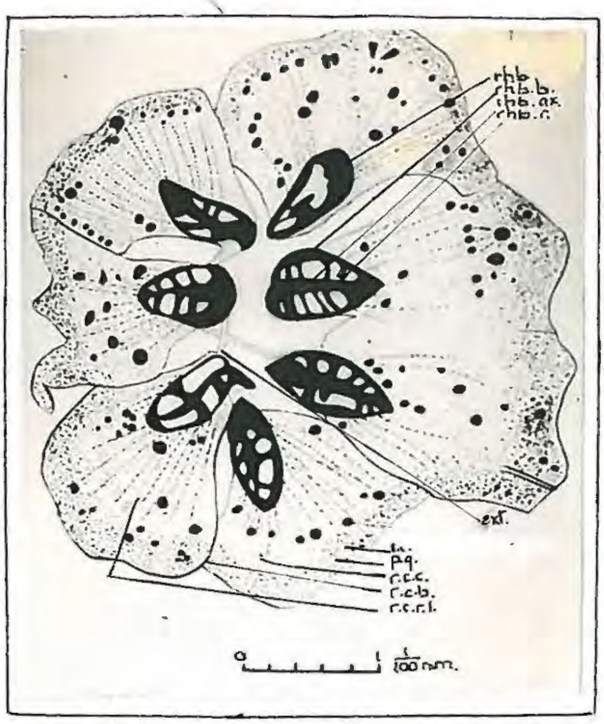
Fixation : Corrossive sublimate in 96%alcohol-29 hours.
Embedding : Double embedding in ether-alcohol (75:25) solution of celloidin through chloroform in wax of 50 degrees melting point.
Staining : Depigmented in Grenacher's fluid.
Mounting ↘ : Heidenhain's iron alum haematoxylon.
Through toluol in toluol-clarite.

Figure I3.

r.c.	Retinal cell.
p.g.	Coarse pigment granules concentrated towards the outside of the cell.
r.c.c.	Finely granular cytoplasm of the retinal cells.
r.c.b.	Boundary between adjacent retinal cells.
r.c.r.l.	Radiating lines in the retinal cell cytoplasm.
rhb.	Rhabdomeres.
rhb.b.	Thickened outer border of the rhabdomere.
rhb.ax.	Axial strand within the rhabdomere.
rhb.r.	Radiating bars within the rhabdomere.
ext.	Extraneous tissue.

Figure I3.

Transverse section through the retinal cells of one ommatididium of the eye of *Philoscia muscorum* through the rhabdomeres below the cone.



Microscopy.

3mm oil immersion objective.
X 20 Holoscopic eyepiece.
Free hand drawing with a scale from a camera lucida outline.
2 μ section.

Preparation.

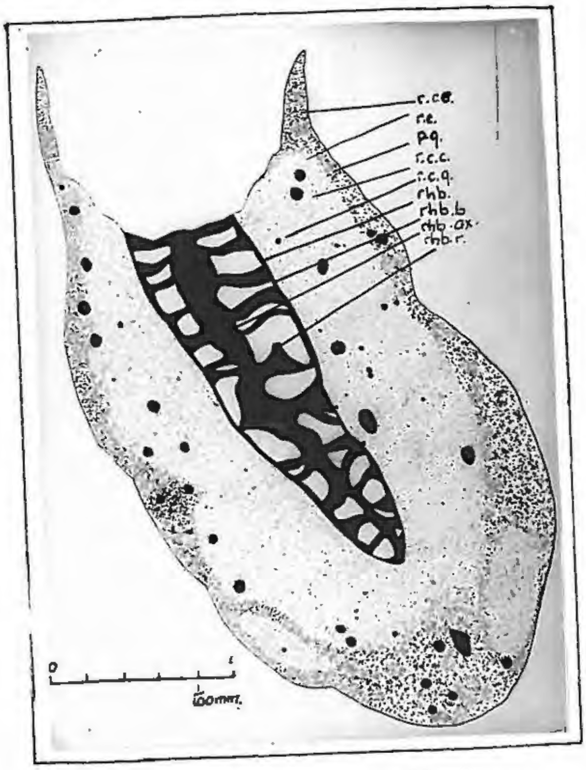
Fixation : Corrossive sublimate in 96% alcohol 29 hours.
Embedding : Double embedding in an ether-alcohol (75:25) solution of celloidin, through chloroform , in wax of 50 dggrees melting point.
Staining : Depigmented in Grenacher's fluid Heidenhain's iron alum haematoxylon.
Mounting : Through toluol in toluol-clarite.

Figure I4.

r.c.	Retinal cell.
p.g.	Coarse pigment granules.
r.c.c.	Cytoplasm of the retinal cell.
r.c.g.	Large irregular granules.
rhb.	Rhabdomere.
rhb.b.	Thickened outer border of the rhabdomere.
rhb.ax.	Axial strand of the rhabdomere.
rhb.r.	Rows of radiating bars coming off at different levels from the axial bar.
r.c.e.	Pigmented extensions of the retinal cells surrounding the cone.

Figure I4.

Oblique section through one of the retinal cells in the eye of Philoscia muscorum.



Microscopy.

2mm oil immersion objective.
X 20 holoscopic eyepiece.
Free hand drawing with the scle constructed from a camera lucida outline.
2 μ sectiom.

Preparation.

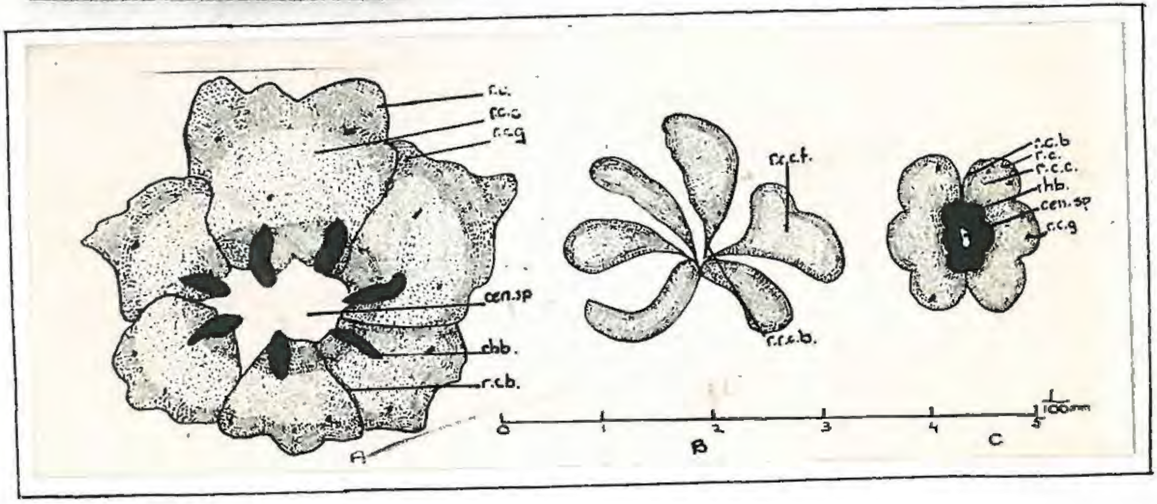
Fixation : Corrossive sublimate in 96 % alcohol 29 hours.
Embedding : Double embedding in ether-alcohol (75:25) solution of celloidin and through chloroform in wax of 50 degrees melting point.
Staining : Depigmented in Grenacher's fluid. Heidenhain's iron alum haematoxylon.
Mounting : Through toluol in toluol-clarite.

Figure 15.

r.c.	Retinal cell.
r.c.g.	Large pigment granules within the retinal cell.
r.c.c.	Retinal cell cytoplasm.
r.c.b.	Boundary between the retinal cells.
cen.sp.	Central space.
rhb.	Rhabdomere.
r.c.cf.	Two retinal cells confluent at their base, as they are incipiently in Fig.A.
r.c.c.b.	Retinal cells contiguous at their bases where they pass into the nerve fibres below the rhabdomeres.

Figure I5.

A and B are transverse sections through the retinal cells of Philoscia , A at the top of the rhabdomeres below the cones, B at the base of the cells where they pass into the nerve fibres.
C. Transverse section through the retinal cells of one ommatidium in the eye of Ligia drawn on the same scale for comparison with the size of the cells in Philoscia.



Microscopy.

4mm apochromatic objective.
X J4 holoscopic eyepiece.
Camera lucida drawing.
3-4μ sections.

Preparation.

Fixation : A and B , corrossive sublimate in 96% alcohol
C Sublimate in sea -water with CH_3COOH-29 hours.
Embedding : Double embedding in ether-alcohol (75:25) celloidin, through chlcroform in 50 degrees' melting point wax.
Staining : A and B Depigmented in Grenacher's fluid.
Heidenhain's iron alum haematoxylon.
C Depigmented in Rowland's fluid.
Heidenhain's iron alum haematoxylon
Light green.
Mounting : Toluol-clarite through toluol.

3. The anatomy of the Lateral compound eyes of Streptocephalus.

This form was found as an active swimmer in the fairly shallow waters of a fresh-water well. It was not specifically identified.

The eye does not appear to have been previously described for Streptocephalus but has been studied in the related genus Branchipus, where it has been described in several species as follows :-
B. palludosus (Burmeister, 1835, p. 531), B. stagnalis (Spangenberg, 1875, pp. 30-32), (Grenacher, 1879, pp.114-115), Branchipus sp. (Claus, 1886, pp. 78-80), B. torticornis (Claus, 1886, pp. 319-332), B. grubei (Patten, 1886, p.615), B. formiciformis and B. vernalis (Parker, 1893, p.73, Figs. 30-32), B. stagnalis (Nowikoff, 1905, pp. 432-464) and B. gelidus (Howland, 1911, pp.145-149). All of these descriptions are rather short or available to me only in abstract but the more detailed description of Streptocephalus given here agrees with these in outline.

External features.

The eyes are large, compound, laterally placed structures, differing externally from those of the other two species described, in being stalked. Each eye forms the terminal cap of an unjointed, ocular stalk, projecting from the side of the head with a forward aspect. The eye surface itself is even in curvature, and forms the major portion of the surface of a sphere. The approximate diametre of the eye is about 600μ, while that of the stalk is about 500μ.

As in the previous cases, the corneal lenses show a tendency to become detached from the inner, softer parts of the eye. Fig. 16 indicates their approximate number across the eye, their disposition, and the extent of their curvature in relation to the curvature of the eye as a whole. Fig. 17 shows that each is transparent, very little thicker in the middle than at the sides - (about 5μ in each case) - and is concavo-convex with the convexity external. The lens cuticle is very little thicker than that covering the rest of the body and resembles it in being colourless and transparent, without external decoration. The eye and body cuticula are continuous.

A slight rim of cuticle at the edge of the lens stains with basic stains more deeply than the rest. The remainder of the cuticle is uniform without perceptible laminations. The number of ommatidia is large - about fifteen hundred - about twice as many as in Ligia.

The lenses are arranged in regular, compact rows. There appears to be no change in the shape, size, curvature, thickness or arrangement in the facets

/belonging

belonging to the ommatidia at the edge of the eye. No division is visible in the facet to correspond to its secretion from two hypoderm cells.

The corneal hypoderm or corneagenous cells.

The hypoderm cells, which give rise to the cornea, are two in number and lie immediately below the cuticle, to which they bear the same relation as do the ordinary hypoderm cells to the body cuticula. In the adult they remain visible, though their cytoplasm is reduced in density, as compared with that of the cone cells, with which they are in contact. Probably they were more conspicuous in early life, when they were actively secreting the cuticular lens, as in other Crustacea - see Patten (1886, p. 645). They are shown in Figs. 16, 17, and 18.

Although they are not separated by distinct cell membranes, the number of the cells is defined by their nuclei. These are placed in the downward extensions of the cells, which pass below the level of the cone cell nuclei. Their position renders them readily distinguishable from the cone cell nuclei. The nuclei are small, spherical and densely granular, without a nucleolus. They are slightly larger than the cone cell nuclei, as is seen from Figs. 17, 18 and 19.

The cytoplasm is not as dense as in the cone cells

/and

and is more or less uniform. Fixation was generally poor in these cells although various fixatives were tried, namely Sea-water Bouin, Picro-Chloro-Acetic acid and 1% Picric acid in 96% Alcohol, which were used both hot and cold, and most of which gave satisfactory results in other cases.

The upper surfaces of the cells are contiguous with the lower surfaces of the corneal facets and are, therefore, in extent, about 40 μ. Laterally they extend down to a distance of about 20 μ The lower surface is strongly concave to fit over the upper surface of the cone cells to which, in this region, they are applied.

In some cases they appear to have been laterally displaced so that the two cells of a single ommatidium are not continuous over the cone cells but are separated by the cone cells, which then come in contact with the under surface of the corneal facet. This is the condition in Fig. 18B, while Figs. 17 B and C show the persistence of a bridge over the cone cells, joining the hypoderm cells on either side of the ommatidium, as appears to be the case in Philoscia. Laterally the hypoderm cells of successive ommatidia are clearly separated from one another, as in Fig. 17.

The cone cells.

Below the hypoderm and the cuticle, which it

/secretes

secretes, there is, in each ommatidium, a further refractive or dioptric apparatus - the crystalline cone, which is secreted by four cone, or "vitrella" cells. The cells form a cap over the top of the cone and surround it laterally throughout its length.

The cytoplasm of the cells is densely granular and with distribution of granules more or less uniform, except that the part above the cone appears to be slightly less dense than that below - [illegible] Fig. [illegible]. The cytoplasm throughout the cone cells is denser and coarser and stains more deeply, than that of the retinal or corneal cells.

The nuclei are small, spherical bodies, lying above those of the corneal cells. Like the latter, they are densely granular, stain darkly, are without a nucleolus and have a darkly staining, distinct boundary. They are situated centrally within the cells and are placed one on each side, symmetrically, in the band of cone cell cytoplasm above the cone. Fig. 18 A shows a longitudinal section through the upper part of the cone cells and indicates the disposition of the nuclei.

The cone cells form an entire mantle round the cone, separating one ommatidium off from the rest - see Fig.17A. Laterally, at the sides of the cone, they are reduced to a very thin band, as in Fig. 18 and Fig. 20 A. Above the cone the cells form the cap described above as

/containing

containing the nuclei.

In longitudinal sections the cells seem to separate from the cone around its entire surface. In transverse sections, however, they are seen, in some cases at least, to surround the upper end very closely as in Fig. 19 B, while they are separated from it by a small space lower down, as in Fig. 20 A, and again surround it closely below this, as in Figs. 20 B and 20 C. In the region above the cone, the boundaries between the four cone-secreting cells are complete, as in Fig. 19B. In the part of the cells surrounding the cone, these are absent or indistinct, as in Figs. 19B, 20 A, 20 B, 20 C. Below the cone the cells are contiguous but their boundaries remain, as in Fig. 21. The cone cells, after forming a mantle above and around the cones, meet below them and at their own bases are in contact with the rhabdoms. The cone itself is therefore not in contact with the rhabdom, as it is in Ligia and Philoscia. At their lower ends the cells penetrate between the upper ends of the rhabdom-forming cells as in Fig. 17. In transverse sections through the retinular nuclei the four cone cells can be seen with their boundaries still distinct, passing centrally between the five retinular cells, as in Fig. 21.

The cytoplasm of the cone cells takes us plasma stains, such as Erythrosin and Light Green, more deeply

/than

than any other part of the eye. Occasionally two diagonally opposite cells take up the stain less deeply than the remaining two cells, as in Fig. 20 C. This is, however, not a constant feature, and is never observed below the level of the cones. It is possibly connected with the state of the secretory activity of the cells. No accessory cones are present as in *Ligia*.

As the outside of the eye is as the surface of a sphere, and as the ommatidia converge radially toward the centre of this, there is a general tendency for the cells to be reduced in size as they pass inwards. In accordance with this, the cone cells taper towards their lower ends. Round the cones they attain a maximum depth of about 30μ and taper to their bases to about 4μ, at the point at which they are in contact with their rhabdomes. The total length is about 90μ.

The cone.

The cone cells secrete a solid, transparent, cone throughout their length. This is clearly divided into four segments, each of which arises from one of the cells. The material of the cone is a uniform secretion, and when unstained is highly refractive. It takes up stains more readily than the cornea. With cytoplasmic stains, such as Light Green, Erythrosin and Eosin, it stains about as deeply as the rhabdom, and with nuclear stains, such as

/Haematoxylon

Haematoxylon and Bismark Brown, only slightly less deeply.

The cone is approximately ellipsoidal, the major axis being about 50µ, the minor about 25µ. The symmetry of the ellipsoidal shape is not perfect. The upper end is rounded and the lower tapers considerably. The change in size of the transverse section along the length of the cone can be seen in Figs. 19B, 20 B and C, with the sections taken at approximately equal distances apart and in order from above down. The diametre of the cross section varies from about 6µ to about 25µ. Below it tapers to a blunt point. The division into four segments is regular and symmetrical. The planes of division are at right angles to one another, and are parallel to the long axis of the eye with a constant orientation in the eye as a whole.

The cone differs from those previously described in that it is not in direct continuity with the upper end of the rhabdom, while the cone cells do not shrink up round the upper end of the cone, as they do in Ligia, but form an extensive sheath round their secretion.

The retinulae.

Below the corneal and cone cells, which, with their respective secretions, form the dioptric parts of the eye, are the sense or retinal cells, with a rhabdom along their

/inner

inner edges. These cells are five in number. They are all of equal size and, in accordance with the usual arrangement, taper towards their lower ends - see Fig. 21. Their total length is about 120μ. The width of each cell varies from about 10μ at the top, to about 3μ. at the base - see Figs. 16 and 17. The upper ends of these cells, as has been pointed out, surround the lower ends of the cone cells. At its upper end, the slender stem of each retinal cell is enlarged to form one of the five calyx-like elements, which surround the cone cells. The cytoplasm of this upper, enlarged part of the retinal cell is somewhat vacuolated - see Fig. 17. The pigment granules, which are scattered throughout the retinal cells, vary in distribution, but, in animals killed in light, they generally appear to be particularly concentrated along the outer margins of the cells, at their bases, and along the edge of the rhabdom. The rest of the cytoplasm of the cells is less coarse and more or less uniform except for the vacuolation already described, at the upper end. It is notable that even the pigment granules of the retinulae do not take up plasma stains as deeply as the granular cytoplasm of the cone cells.

The nuclei are small, dark, spherical, densely granular structures, sometimes without a nucleolus.

/Each

Each is surrounded by a vacuole - see Figs. 17 and 21. They occur at the upper ends of the cells above the level of the rhabdoms - see Figs. 17 and 21.

The group of retinal cells in each ommatidium remains at an approximately constant distance from the centres of the surrounding groups. The convergence is effected mainly by a reduction in the size of the cells themselves towards their lower ends - see Figs. 22 A, B and C.

The rhabdom.

The retinular cells bear along their inner borders the sense rod of rhabdom, which is solid and uniform throughout their length. Although the rhabdom is surrounded by five equal retinular cells, there is no indication of its origin from five separate rhabdomeres. If separate rhabdomeres were originally present, they have fused and no longer maintain any relation to the separate cells, as they do in *Ligia* and *Philoscia*. The rhabdoms are square or trapezoidal, occasionally pentagonal, but the latter condition is not as regular as one would suppose, assuming that the rhabdom was originally made up of five parts. A similar anomaly has been observed in other species - see p.162. The rhabdoms extend from the base of the cone cells, below the level of the retinular nuclei, to the extreme ends of the retinal cells, just above the basement membrane. The structure of the rhabdom is very different to that of *Ligia* and *Philoscia*. Although the same fixatives were

/used

used, and embedding and staining methods were the same, no striations could be seen in this case, the rod appearing as a solid structureless secretion.

The closely coalesced condition of the rhabdom is a somewhat surprising one to be found in an eye otherwise primitive in many respects, such as in the absence of accessory pigment cells. The condition of the rhabdom is that found in many of the higher Crustacea - see p. 165 - where the rest of the eye is of a higher grade of development than that of *Streptocephalus*. It is most unlikely that the rhabdom in *Streptocephalus* is a degenerate one. It appears that the eye in this case is peculiarly advanced both in the nature of the rhabdom and in the presence of a stalk. Since the rhabdom exhibits no trace of nervous structure, it would appear in this case to be merely a skeletal and refractive rod. This would be in accordance with Nowikoff's view of the rhabdom in Arthropods generally (Nowikoff, 1931 p,23).

Accessory pigment cells.

The accessory pigment cells, present in *Ligia*, are here absent, while the retinal cells do not protrude up round the greater part of the cones as in *Philoscia*. The eye is primitive in that the cones are not surrounded by pigment. The eye is capable, therefore, of forming only a superposition image. It is possible perhaps

/that

that the very dense cytoplasm of the cone cells to some extent shields the eye from excessive illumination.

The basement membrane and nerve fibres.

The retinal groups abut at the base of the eye on the basement membrane. As in the previous cases, this is thin,non-nucleolated and structureless and is pierced by the nerve fibres from the retinal cells, with one of which each retinal cell is continuous as is seen in Figs. 16, 17. The nerve fibres from the retinal cells of one ommatidium run together below the basement membrane, before entering the optic ganglion in the eye stalk.

Figure I6.

s.s.	Spherical outer surface of the eye.
c.f.	Corneal facets not lenticular, but of more or less uniform thickness.
c.hyp.	Corneal hypoderm cells.
c.c.	Crystalline cone.
r.c.n.	Retinal cell nucleus.
r.c.	Retinal cell.
rhb.	Rhabdom.
b.m.	Basement membrane.
n.f.	Nerve fibres continuous with the retinal cells and running to the optic ganglion.

Figure I6.

Longitudinal section through the entire eye of Streptocephalus, transversely to the longitudinal axis of the body. (The eye stalk is not drawn).

Microscopy.

I6 mm objective.
X I6 holoscopic eyepiece.
Camera lucida drawing.
4 μ section.

Preparation.

Fixation : Alcoholic picro-chloro-acetid acid -23 hours.
Embedding : Through Xylol in 58 degrees melting point wax.
Staining : Depigmented in Grenacher's fluid. Heidenhain's iron alum haematoxylon. Alcoholic light green.
Mounting : Through Xylol in Xylol-Balsam.

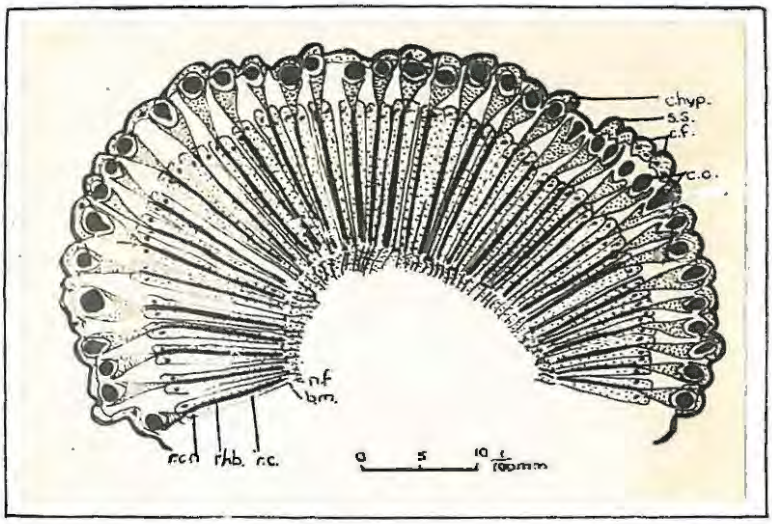
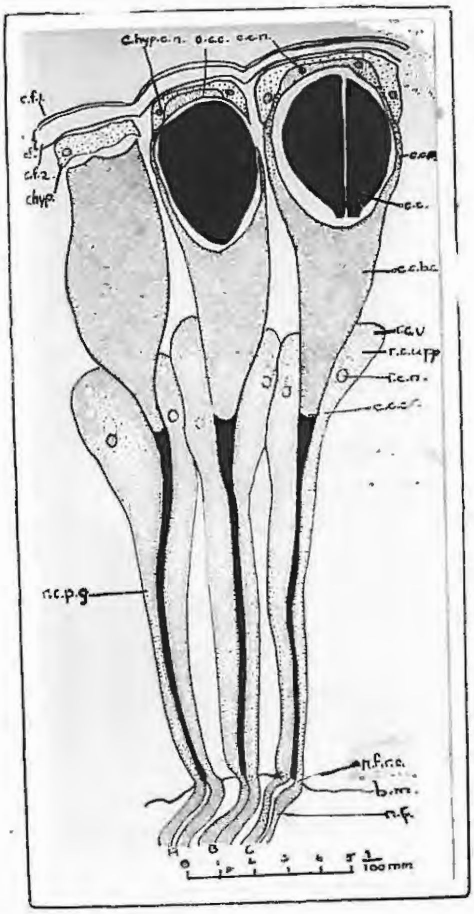


Figure I7.

c.f.	Corneal facet.
c.f.I.	Outer layer of the cornea.
c.f.2.	Inner layer of the cornea.
c.hyp.	Corneal hypoderm cell.
c.hyp.c.n.	Corneal hypoderm cell nucleus.
c.c.c.	Crystalline cone cell cap over the upper surface of the cone.
c.c.n.	Cone cell nucleus.
c.c.m.	Slender parts of the cone cells surrounding the cone.
c.c.	Crystalline cone.
c.c.b.c.	Cone~~s~~ cells below the cones.
c.c.c.r.	Cone cells in contact with the upper surface of the rhabdom.
r.c.u.pp.	Upper part of the retinal cells surrounding the lower parts of the cone cells.
r.c.v.	Vaguolated upper ends of the retinal cells.
r.c.n.	Retinal cell nucleus surrounded by a vacuole .
r.c.p.g.	Retinal cell pigment granules.
	Rhabdom.
b.m.	Basment membrane.
n.f. r.c.	Continuation of the retinal cells into nerve fibres.
n.f.	Nerve fibre.

Figure I7.

A longitudinal section of three of the ommatidia in the eye of Streptocephalus.



Microscopy.

4mm apochromatic objective.
X I4 holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation.

Fixation : I% Picric acid in 96 % alcohol- 23 hours.
Embedding : Through Xylol in 58 degrees' melting point wax.
Staining : Depigmented in Grenacher's fluid. Heidenhain's iron alum haematoxylon Bordeaux Red.
Mounting : Through Xylol in Xylol-Balsam.

Fihure I8.

c.c.	Crystalline cone.
c.c.c.I.	Upper part of the cone cells above the cone with the cytoplasm slightly less dense than below the cone.
c.c.n.	Cone cell nucleus in the cap of the cytoplasm above the cone.
c.f.	Corneal facet.
c.c.c.2,	Slender part of cone cell round the cone.
c.c.c.3.	Deeply staining coarsely granular cytoplasm below the cone.
c.hyp.	Corneal hypoderm cell separated from that on the other side of the ommatidium.
c.hyp.n.	Corneal hypoderm cell nucleus, larger than the cone cell nucleus.
c.hyp.b.	Corneal hypoderm cell boundary dividing it from the cone cell.
sp.	Space apparent in longitudinal sections separating the cone from the cone cells.

Figure 18.

Longitudinal section of the outer parts of the ommatidium in Streptocephalus. A shows the cone and cone cells. B includes with these the corneal hypoderm cells and cornea.

Microscopy.

2mm oil immersion lens.
X 14 holoscopic eyepiece.
Camera lucida drawing.
2 µ section.

Preparation.

Fixation : Alcoholic picro-Chloro-acetic acid.-23 hours.
Embedding : Through Xylol in 58 degrees ' melting point wax.
Staining : Depigmented in Grenacher's fluid. Heidenhain's iron alum haematoxylon, Light green.
Mounting : Through Xylol in Xylol-Balsam.

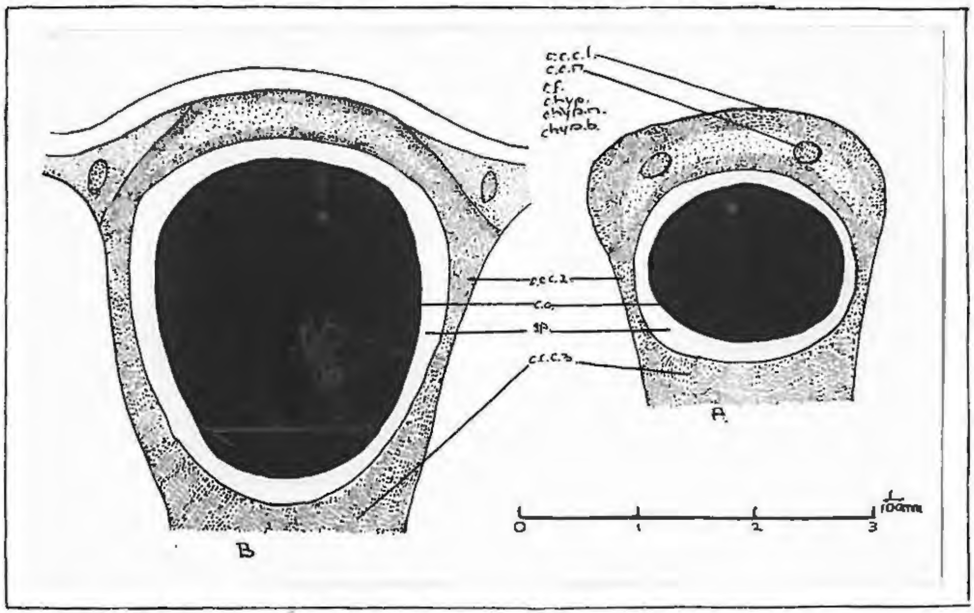
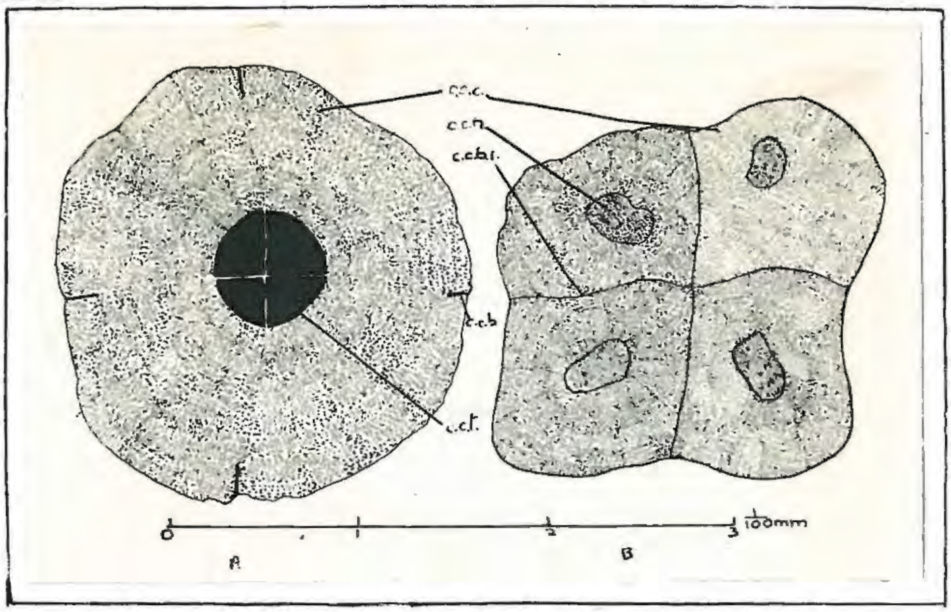


Figure I9.

c.c.c.	Cone cell cytoplasm.
c.c.n.	Cone cell nucleus.
c.c.b.I.	Boundaries between the 4 cone secreting cells above the cone.
c.c.t.	Section of the top ends of the cone segments surrounded by the cone cells.
c.c.b.	Indications of the cone cell boundaries which seem to disappear to a large extent in this region.

Figure I9.

Transverse sections through the outer regions of the eye of Streptocephalus. A. Through the cone cells at the extreme upper end of the cone. B. Through the cone cells in the region of their nuclei above the cone.



Microscopy.

2mm oil immersion objective.
X I4 Holoscopic eyepiece.
Camera lucida drawing.
3μ section.

Preparation

Fixation	: Bouin's fixative- 24 hours.
Embedding	: Through Xylol in 58 degrees' melting point wax.
Staining	: Depigmented in Grenacher's fluid. Haemalum. Acid fuschin and Orange G.
Mounting	: Through Xylol in Xylol-Balsam.

Figure 20.

c.c.	Four crystalline cone segments.
c.c.c.	Cytoplasm of the cone cells. In A this forms a thick continuous ring separated from the cone by a small space. In B this forms a thicker uniform ring immediately round the cone with no cell boundaries apparent. In C the cytoplasm of diagonally opposite cells is differentiated.

Figure 20.

Three transverse sections through the eye of Streptocephalus through the cone cells. A,B, and C are taken in order inwards.

Microscopy.

2mm oil immersion objective.
X I4 Holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation.

Fixation : Sea-water Bouin fixative - 23 hours.
Embedding : Through Xylol in 58 degrees' meltihg point wax.
Staining : Depigmented in Grenacher's solution. Heidenhain's iron alum haematoxylon. Light green.
Mounting : Through Xylol in Xylol-Balsam.

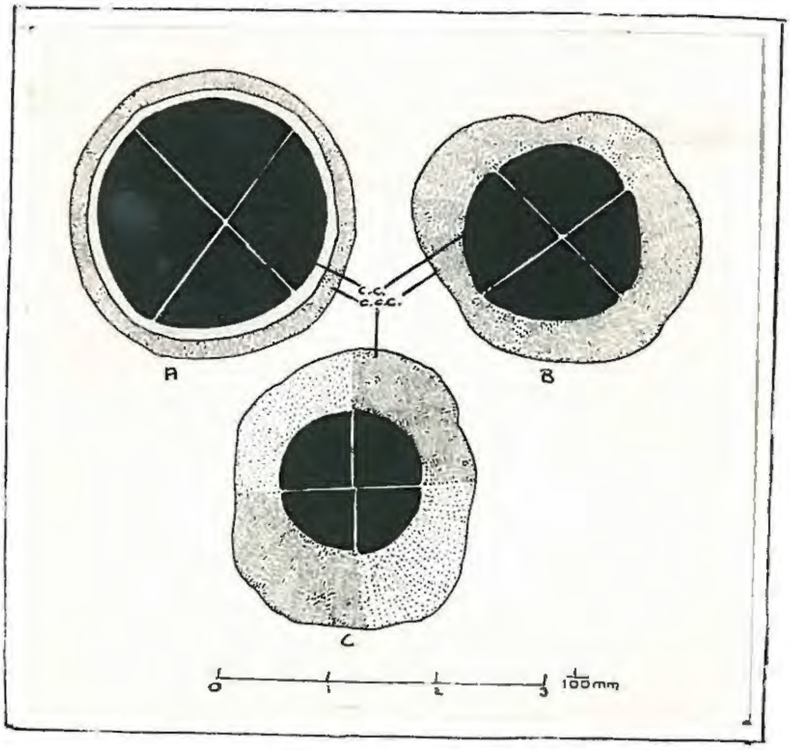
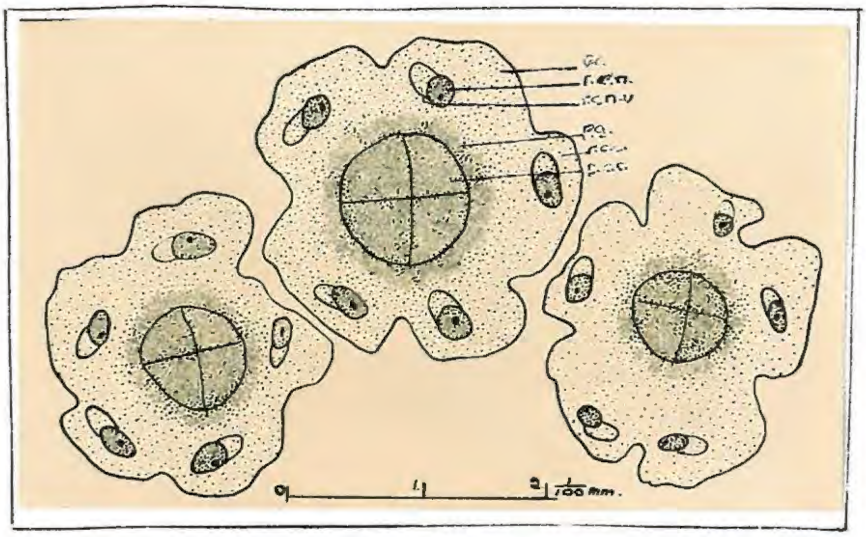


Figure 2I

r.c.	Retinal cell with boundaries indistinct.
r.c.n.	Retinal cell nucleus.
r.c.n.v.	Vacuole surrounding the retinal cell nucleus.
p.g.	Large pigment granules of the retinal cell.
r.c.c.	Finely granular and slightly vacuolated retinal cell cytoplasm.
c.c.c.	Coarsely granular and deeply staining cytoplasm of the cone cells , penetrating at their lower end between the continuations of the retinal cells above the rhabdom.

Figure 2I.

Transverse section through the eye of Streptocephalus through the retinular cells at the level of their nuclei, where they surround the lower end of the cone cells.



Microscopy.

2mm oil immersion objective.
X I4 holoscopic eyepiece.
Camera lucida drawing.
3μ section.

Preparation.

Fixation : I% Picric acid in 96% alcohol - 23 hours.
Embedding : Through Xylol in 58 degrees' melting point wax.
Staining : Depigmented in Grenacher's fluid.
Heidenhain's iron alum haematoxylon.
Bordeaux Red.
Mounting : Through Xylol in Xylol-Balsam.

Figure 22.

r.c.	One of the five retinular cells of each ommatidium.
r.c.b.	Distinct boundaries between the retinular cells.
rhb.	Diamond or square-shaped solid rhabdom.
r.c.p.g.	Large pigment granules in the retinal cells.
r.c.c.	Retinal cell cytoplasm.
sp.	Space between the retinal cell groups of the different ommatidia which decrease towards the base of the eye where the ommatidia converge. (As can be seen the retinal cells decrease in size towards the base of the eye to facilitate this convergence).

Figure 22.

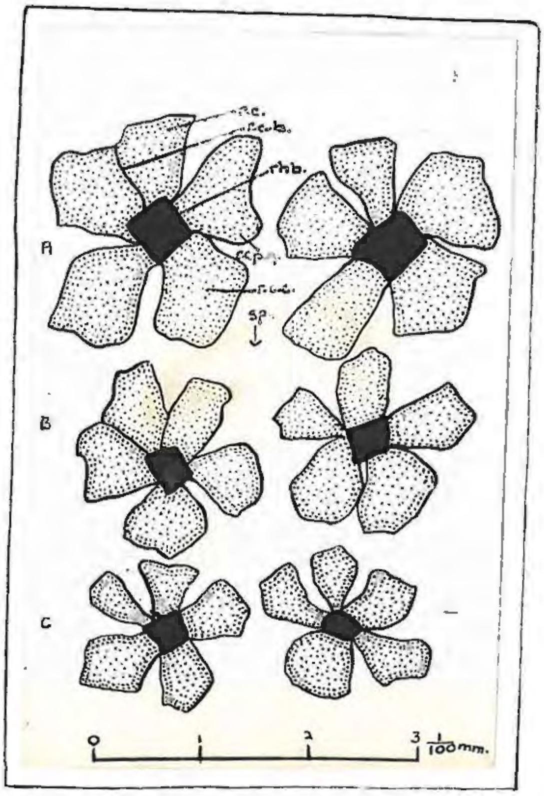
Transverse sections through the eye of Streptocephalus in the region of the retinular cells to show the arrangement of these cells and the degree of approximation of the ommatidia. A, B, and C are at successively deeper levels within a single eye.

Micoscopy.

2mm oil immersion objective.
X 14 holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation.

Fixation : Alcoholic Picro-chloro-acetic acid - 23 hours.
Embedding : Through Xylol in 58 degrees' melting point wax.
Staining : Depigmented in Grenacher's fluid.
Heidenhain's iron alum haematoxylon.
Alcoholic light green.
Mounting : Through Xylol in Xylol-Balsam.



Changes found in the degeneration of the eye.

A comparison of the eyes of Ligia and Philoscia.

Ligia and *Philoscia* were chosen as types in which the comparison of the eyes should give some indication of the changes which should occur, when a primitively, complex, compound condition degenerates into a group of separate units. It was thought that the changes involved in such a degeneration would give some indication of the changes which one would expect to find in other Arthropods on comparing the structure of the lateral groups of eyes with the compound eyes, if the former were derived from the latter by degeneration. Thus if the group of ocelli in Chilopods arose from a compound *Scutigera*-like eye, they might, on comparison with the compound eye, be expected to show the same sort of changes, which occur in the degeneration of other compound eyes into separate eye units.

The eyes of *Philoscia* represent a degeneration of a compound eye into separate units or ommatidia and not into ocelli - sensu stricto. If ocelli were produced by degeneration of a compound eye, the changes would presumably be in the same direction but carried to greater lengths.

These two types seem to lend themselves to such a comparison. Both are Isopods in which the eye must obviously, primitively have been compound. There is therefore no doubt that the *Philoscia* eye is the product of degeneration and does not represent the persistence of a primitive condition.

/Both eyes.

Both eyes are sessile and immoveable, and differences are likely to be due to degeneration in *Philoscia*, and not to environmental adaptations. Further, comparison of either of these eyes, with the typical and primitive forms, as outlined below, indicates that neither possesses any highly aberrant features which would be likely to introduce misleading complications. (The accessory cone in *Ligia*, results clearly from a secondary division, and though it does not represent the normal eye structure, it is clearly not a fundamental modification of the eye.) Although the eyes are widely enough separated to indicate the type of changes which accompany degeneration of the compound eye, neither is an extreme type - *Ligia* is not highly elaborated, nor is *Philoscia* so far degenerate, that its structure cannot be readily compared with that of a typical compound eye.

Externally a difference in size and number of the units is apparent. In *Ligia* there are 500 - 600 units : in *Philoscia* 10. The tendency to separation of the lenses and increasing size and complexity of each single lens, as the eye units become smaller in number and more "ocellar" in type, is clearly shown. Thus in *Ligia* the eye surface is fairly convex with reference to the general surface of the body, while the crowded ommatidial facets form a smooth surface of the same thickness as the body cuticle (about 9μ with each lens concavo-convex with the convexity external and little difference between central and peripheral depth.) In *Philoscia* the

/total convexity

of the eye is less marked as the ommatidia separate and the eye flattens out, while the individual lenses are more clearly separated and more highly convex, being thicker than the body cuticle (10μ to 20μ as compared with 5μ) and larger centrally than peripherally. In *Ligia* the lenses are uniform in size throughout the eye and are contiguous, symmetrical, equilateral hexagons, while in *Philoscia* the arrangement is much looser, without the regular hexagonal pattern arising from the crowding of the units. The units, too, are less regular than in *Ligia*, being smaller towards the edges of the eye, which presumably indicates that the loss of units like their growth (see Peabody,1939, pp.530-531) is peripheral. Thus the larger number of ommatidia and greater size and convexity of the eye in *Ligia* gives rise, on degeneration, to a condition in which the number of units is smaller and the size and convexity of each lens greater.

Corneal hypoderm.

There seems to be nothing of particular significance in either the similarities or the small differences in these cells. Although the lenses of *Philoscia* are rather "ocellar" in type and are very enlarged, the hypoderm secreting them retains the character of the compound eye layer. The cells in the two types are very similar, being two in number, in the same position, below the facet and above the cone, with a decrease in size in the adult, consequent upon a decrease in their own function and an increase in the size of the cone below. They are centrally displaced in *Ligia natalensis*,

/see p.33 ,laterally

see p. 33 , laterally in *L. oceanica* (Hewitt, 1907, p.26) and in *Philoscia* - see pp. 55-56. The cytoplasm is not dissimilar, being slightly coarser in *Ligia*. In both the boundaries are somewhat indistinct and the nuclei are very similar. The only difference seems to lie in the greater reduction of the cytoplasm and the lower level of the nuclei relative to the cone cells in *Philoscia*, which is a consequence of the greater development of the lens.

Cone cells.

In each case the cone cells are two in number, lying between the cone and the corneal hypoderm, with the upper surface fused with the hypoderm, with the two cells fused above, with their lateral walls distinct. The cytoplasm and nuclei are not dissimilar. The main difference lies in the downward extension of the cells. In *Ligia* they form a thin cap and a mantle round the cone, which extends down the cone proper for about one half of its depth - about 15μ, to the level where it is in contact with the lower part of the cone - the accessory cone. In *Philoscia* the shrinkage is less marked, the cells extending to the base of the cone, at the upper level of the rhabdom - a depth of about 55μ. The difference is quite probably not a consequence of degeneration in *Philoscia* but due rather to the fact that the cone cells have undergone a specialised reduction in *Ligia*, which is a reciprocal consequence of the elaboration of the cone structure.

/The cones

The cones.

The cones differ considerably in shape and size. They are much more elaborate and are presumably adapted to a more perfect vision in *Ligia*. In each case they are solid, refractive, transparent secretions, chitinised rather than "crystalline" and not divided into two parts, as one might be led to expect from the fact that they are secreted by two cells. In each case the cones are in contact with the rhabdomes. In *Ligia* the cones are transversely divided into an upper sphere and a lower, chalice-shaped accessory cone, while in *Philoscia* they are simply ovoid. Comparison of the condition in *Ligia* with that in other Crustacea - see p.127 – indicates that the formation of an accessory cone is secondary and that its absence in *Philoscia* is therefore not to be attributed to degeneration. In *Ligia* the cone has a maximum width of about 25μ and the cone apparatus a total depth of about 45μ-50μ. In *Philoscia* the corresponding dimensions are 45μ and 55μ. Thus the cone, though simpler, is much larger on degeneration of the eye - a condition common to most of the eye elements.

Retinal cells.

In each case the retinal cells are arranged in a single row with their longitudinal axes parallel to that of the ommatidium. They are uniform in size and arrangement throughout the eye and in number throughout the length of the ommatidium. All the cells are reduced slightly towards the base of the eye, but there is not any tendency to crowding out

/of one cell

of one cell, such as is found in many Crustacea. (It is possible, however, that the condition in *Ligia* may be the result of a complete suppression of one cell - see pp. I49.). The lesser reduction in the size of the cells towards the base of the eye in *Philoscia* is a consequence of the lesser crowding of the ommatidia in this region, as a result of the smaller external convexity of the eye.

The most obvious and significant differences between the eyes are those in the retinal cells. *Philoscia* has seven cells, *Ligia* six. It is more probable that this difference is due to the complete suppression of one cell in *Ligia* than the development of an additional cell in *Philoscia*, on degeneration. The condition in *Philoscia* is a consequence of the removal of those factors which are responsible for the overcrowding and reduction of the number of cells in *Ligia*. On the degeneration of the eye, the retinal cells increase in width and decrease in length below the cone. Thus in *Ligia* the diametre of one cell is about 7μ and length about 50μ In *Philoscia* the measurements are about 15μ and 40μ (below the cone).

In *Ligia* a fairly elaborate arrangement of accessory pigment cells separates the ommatidia and surrounds the cone and cone cells. In *Philoscia* these cells have disappeared and the light isolation of the adjacent cones is accomplished by an upward extension of the retinal cells.

The retinal cells are similar in the two species in their

/nuclear and

nuclear and cytoplasmic structure. The nuclei have numerous granules of varying size, a darkly staining wall and one or two nucleoli. Their position varies but is apparently not significant, being variable in Ligia natalensis, proximal in Ligia oceanica, and distal in Philoscia.

Rhabdomeres.

The rhabdomeres in each case are separate. In Ligia although the rhabdomeres are distinct and arranged around a roughly circular axial cavity, they are approximated and contiguous laterally. Each is somewhat flatly lenticular in shape, so that they form the more or less uniform walls of a hollow cylinder. In Philoscia, however, they are more completely separated, each one forming an almond shaped structure considerably larger than in Ligia, projecting on one side into the cell and on the other into an irregular central cavity. On degeneration the rhabdomeres are relatively shortened, so that they do not reach quite to the basement membrane in Philoscia as they do in Ligia. The structure becomes more elaborate. In Ligia the plates are simply perpendicular to the edge of the cell, while in Philoscia there are a series of radiating plates at various levels, perpendicular to a central axial bar. This degree of this elaboration is probably a misleading guide to the general course of degeneration in the eye. It is unlikely that the rhabdom would be so elaborate in all cases. As a consequence of the shortening of the rhabdomeres in Philoscia, the cells run together above the basement

/membrane,

membrane , while in *Ligia* they meet only below the membrane, where their nerve fibres run together. Thus degeneration has increased the width and complexity and decreased the length of the rhabdomeres, removing them from the lower part of their cells and preventing any tendency towards their coalescence.

Pigment cells .

The ommatidia in *Ligia* are isolated , in the cone region , by accessory pigment cells of uncertain number . In *Philoscia* these cells have disappeared and have been functionally replaced by upward extensions of the retinal cells.

Basement membrane .

The structure of the membrane does not change . It remains as a distinct , thin , structureless boundary, through which the retinal cells are continuous with their nerve fibres.

Summary .

As the eye degenerates and the number of its units decreases, the eye becomes flatter and the units less crowded, so that their upper and lower ends become of more nearly the same size than in compound eyes, where the great convexity of the outer surface and the large dioptric area, imposes a crowding and a reduction in size on the inner eye elements. Each corneal lens increases in size and convexity and assumes a biconvex "ocellar " form . The loss of ommatidia appears to be peripheral, the outer ommatidia showing signs of being smaller than the inner, while the eye group as a whole is not as regularly formed as in more complex types. No significant change occurrs in the hypoderm cells. There is no tendency to reduction in the size of the cone cells, so that both cone and cone cells remain in contact with the upper ends of the rhabdomeres. The cones lose any tendency to complexity but increase in size along both axes. Each of the retinal cells remains perfect, none being crowded out and the number being the maximum for the order (except for a few very exceptional cases). The retinal cells increase in width and decrease in length below the cone. With the disappearance of all additional pigment cells, the retinal cells are prolonged up round the cone. The rhabdomerés in the degenerate eye are completely separate, larger in size and more elaborate in structure, while they are slightly pushed up towards the upper end of the cell so that the retinal cells coalesce above the membrane.

Part II. Comparative anatomy of Crustacean compound eyes.

External features.

Paired, lateral, compound eyes are found in the majority of adult Crustacea. They are generally unmistakably compound in contrast to the simple, median, dorsal, nauplius eye. An exception to this is found in some Copepods, where the nauplius eye has undertaken a lateral migration, so that it might appear as a very reduced compound eye. In the typical and primitive conditions, the eye consists of several hundreds of units, and occurs in this form in practically all classes of Crustacea, living under a variety of conditions, as well as in Trilobites and the primitive Crustacean fossils of the cambrian beds (Hutchinson, 1930,p.3). A reduced number of ommatidia is secondary and associated with cavernicolous, burrowing, parasitic or deep sea habits. A large literature has been built up on this subject. The conditions in deep sea forms have been dealt with by Hickson (1894, pp. 67-73). In general a degeneration of the dioptric and visual structures is correlated with a decrease in the number of ommatidia. Thus the rhabdom is lost in the degenerate eyes of many Acanthephyridae (Welsh and Chase, 1937 pp. 57-74), while the pigment is lost in these eyes, as well as in those of Sergestidae (Welsh and Chase, 1938, pp. 364-375). Similar reductions have been recorded for other Decapods by Dobkiewicz (1912, pp. 588-617) and Verrier (1940, pp.148-150) and are

/common

in Amphipods (Grimm, 1880, p. 85), especially in Gammaridae (Vejdovsky, 1905, pp.1-40, 1909, pp. 227-245), (Sexton 1933, pp. 355-358), (Wolsky, 1934, pp. 645,670). Similar reductions have been described in Isopods by Eggert (1927, pp. 33-41), Mehely (1927,pp.81-83) and Lattin (1939, pp. 417-468).

Typically and primitively the eyes are paired. This may be complicated by the coalescence of two eyes in the midline as in Conchostraca and Cladocera, as well as in Cumacea. In the latter case, however, the eyes are distinct in the embryo and in the adults of the genus Nannastacus (Calman, 1909, p.184). A similar condition is found in Amphipods (Oedicerotidae), where the coalesced eyes are borne on a median lobe.

Another elaboration is an occasional division of the eye into two parts. The ommatidia are differently formed in respect of their refractive media or in the distribution of the pigment, and are adapted to vision under different conditions of illumination. Such divisions of the eye have been described in many Euphausiacea of the family Nematoscelinae by Chun (1896, pp. 191-262), and by Harmer and Shipley (1909, pp.150-151); in the Bathypelagic Mysidacea by Tatersall (1929, pp.185-199); among the Amphipods in some Hyperiidae and Ampeliscidae (Svenson, 1933, p.1) as well as in Tiron and Synopia among the Gammaridae, (Lang, 1891, p.351), (Calman, 1909,pp.236-/237).

-237), Double eyes similar to these also occur in Insects - [illegible] Both the coalescence and the division of the eyes are clearly secondary.

The curvature of the eye with reference to that of the surrounding body surface varies considerably in accordance with the mode of life. In the higher Crustacea - Malacostraca - the eye is typically and primitively borne on a movable stalk, of which the eye surface itself forms the convex termination. This condition prevails in Leptostraca; in most Anaspidacea (for example in <u>Anaspides</u>, although not in <u>Koonunga</u>, where the eyes are small and sessile); in Euphausiacea, in Decapods and Stomatopods - that is, in practically all members of the divisions Phyllocarida, Syncarida and Hoplocarida of the sub-class Malacostraca. In the fourth division, or Peracarida, although the eye is frequently sessile, it was probably derived from a stalked form. This is indicated by the presence of pedunculate eyes in some Mysidacea, as well as by the persistence of a stalk in Tanaidacea, which, though unjointed and immovable, is clearly marked off from the surface of the head by a groove. The eyes of most of the remaining members of the division are sessile and vary from a practically flat to a highly convex form, with the degree of convexity depending on the usefulness of the eye and on the number of the ommatidia. The oculiferous lobes, which occur in Cumacea and in Oedicerotidae among the Amphipods, where

/the eyes

are coalesced, are unjointed and immovable and are clearly secondarily formed head lobes. The same appears to be the case for the eye stalks in *Asellota* among the Isopods, where the lobes are simple projections of the head surface. In Ingelfiellidae among the Amphipods eye lobes are present (although the eyes are deficient) and are defined by suture lines from the head region. Calman points out that it is possible that these may represent the eye lobes of Tanaidacea and the ocular peduncles of the more primitive Malacostraca, though the great specialisation of the Ingolfiellidae in other respects is against this view (Calman, 1909, p.236).

Thus in the Malacostraca the presence of a movable jointed stalk is both primitive and typical. In Peracarida the stalk may disappear completely, persist as a rudiment, or be replaced by a secondary, unjointed, immovable, oculiferous lobe.

Among the lower Crustacea the position with regard to the stalked or sessile nature of the eyes is not nearly so clear. It is only in the Anostraca among the Branchiopods that a stalk is present, and this is unjointed, both in the modern forms and in the earliest fossil remains of the order - that is, in *Opabanina*, as described by Hutchinson from the middle Cambrian (1930, p.3). The eyes of the remaining Branchiopods are sessile - that is of Lipostraca (if eyes occur in this case) Conchostraca, Cladocera and

Notostraca (both in the modern forms and in the fossil Protocaris described by Hutchinson from the lower Cambrian beds (1930, p.3).

The condition of the eye in Conchostraca, Notostraca (Parker, 1891, p. 5I) and Cladocera (Blanc 1879, pp. 79-80) throws little light on its primitive nature. In these there is a gradual growth of the hypoderm over the eye, so that the eye sinks in and is protected, within an optic pocket. That this is secondary, and not a profound modification of the eye, is clear from the series in Notostraca, Conchostraca and Cladocera, where, with the gradual elaboration of the fold, the eye becomes movable within the perfect, closed socket in Cladocera. Thus, although the eye is stalked only in Anostraca, the condition in the remaining Branchiopod groups suggests that the eye was probably primitively movable and in Notostraca, Cladocera, Conchostraca and Branchiura (Herter, 1928, p.169 et.seq.) has sunk in secondarily for protection. The power of movement, found in some members of these orders, suggests that the eyes may have been derived from a primitively stalked type, with the power of movement retained or regained in some of the descendants. If this is so, the most primitive Crustacean eye was stalked. It remains possible, however, that the most primitive Crustacean eye resembled that of the Trilobites and Protocaris in the absence of a stalk, while the stalk

/in Anostraca

in Anostraca was developed later.

Among the remaining sub-classes of the lower Crustacea, there is little to indicate the primitive condition of the eye. In Cirripedes and Eucopepods the lateral compound eyes are absent, although clearly observed in the larva of the Cirripedes, where they are sessile. Grobben (1891, p.243) considered that they could be seen as sessile vestiges in the development of the Eucopepod *Calanus*. In lower Crustacea the primitive form cannot be decided on the distribution alone. The eye in these forms is typically sessile, though frequently movable. Its condition may be complicated on the one hand by the development of an unjointed stalk, and on the other by a sinking in of the eye to become enclosed in an optic pocket.

In the past there has been considerable controversy as to whether the stalk is an appendage or a modified lobe of the head, or whether it is an appendage in some Crustacea and a modified head-lobe in others. That the stalk represents an appendage was first suggested by Milne-Edwards (1864, p. 310) in the case of *Palinurus pencillatus*, since a specimen was found, in which the eye stalk was absent but its place taken by an antenna-like appendage. Howes (1887, p.468) figured the same specimen. Herbst (1895, pp. 546-547) showed that the same heteromorphic regeneration could be obtained experimentally in

/some

some Decapods, where the optic nerve, after loss of its end-organ, regenerated and innervated the sensory hairs of the new antenna-like structure. Herbst found (1891, p.551) that in *Astacus* the regenerated structure varied in complexity. The type most frequently found resembled a first antenna, rather than a second. Subsequently similar regenerations have been described by Ariola (1904, pp.248-252); in *Palinurus vulgaris*; by Zeleny (1906 p.527) in *Pelucidus testii*, a blind form; by Steel (1907, pp.240-243); in *Cambarus virilis* and *C. gracilus*; by Giesbrecht (1910 p.33) in a Stomatopod; by Wolsky, (1931, pp.18-22); in *Astacus leptodactylus* and by Yossi (1931, pp.445-447) in *Palinurus japonicus*. It will be noticed that, as far as is known, such regenerations occur only in Decapods and Stomatopods. The authors mentioned have made very varied attempts to homologise the individual segments of the regenerated structure with the joints of the Crustacean limb. The products of regeneration appear to vary greatly, both in their structure and in the interpretations which they have received.

From this evidence it was at first generally accepted that the regeneration was due to an atavistic tendency and that the ancestors of these forms must have had a third pair of antennae, similar to the first, in the place occupied by the eye stalks, as an appendage of the first head segment.

/The

The question of whether the eye stalk is appendicular or not is of considerable interest, not only from the point of view of the anatomy of the eye in Crustacea and of its primitive or adaptive significance within this class, but also from the point of view of the homology of Crustacean with other Arthropod eyes. In this connection it has frequently been stressed, for example by Sedgwick (1909, pp.349-350), that, if the Crustacean eye represents "a modified appendage of the first segment of the head", the homology between this and other Arthropod eyes is upset. In other Arthropods there is some indication of the occurrence of a jointed stalk in teratological regenerations in Insects (similar to those in Crustacea). (See Cockayne, 1924, pp. 207-216 and Cavillee, 1942, p. 497). There is nothing to suggest that the eyes of other Arthropods represent modified limbs. Moreover the preantennal segment, to which the eye stalk of Crustacea, if appendicular, must be assigned, sometimes bears a vestigeal appendage, to which the eye is unrelated. The appendage is said to be present in the embryo of the stick insect, in some Hymenopterous embryos and in the larva of Cirripedes (although these structures are not well defined appendages), while similar lobes are present in the embryo of Scolopendra cingulata (Heymons, 1901), where they seem to be generally accepted as preantennal appendages. Thus, if the Crustacean eye-stalk is to be regarded as an appendage the eye cannot be homologised with that of other Arthropods,

/unless

unless one assumes that in Crustacea the eye has been secondarily transferred to an appendage, which in other Arthropods is either completely lost or persists only as an evanescent, embryonic rudiment.

It remains to be decided, whether the evidences of anatomy and embryology, or theoretical considerations of the homology of regenerated structures, can fix the condition of the eye in the most primitive lower Crustacea or decide the nature of the stalk, as an appendage or a head lobe, both in the lower Crustacea and in the Malacostraca.

From distribution of the eye-stalk types it appears that the [illegible] stalk is primitive in the Malacostraca. In this sub-class the anatomy of the stalk itself presents considerable variations. Thus it may persist where the eye is lost or reduced to a very small apical or lateral vestige, as in some Leptostraca, or it may be variously elaborated, even in some cases where the eye is absent, to form a cup, finger-like, leaf-like, or spiniform structure or may even assume the form of transverse plates. Numerous examples of such modifications are given by Calman (1909, pp.115, 172-173). These variations do not, however indicate, whether the stalks are appendicular, or a head lobe. Though the jointed nature of the stalk lends it an appendicular appearance, this might equally well be attributed to the secondary segmentation of a head lobe.

Among the lower Crustacea, where the stalk is

/represented

represented only in the unjointed form of Anostraca, there is no anatomical justification for regarding this as an appendage. If the eye stalks were primitively appendicular it is difficult to see why they should be most fully developed and most distinctly articulated, not in the most primitive Crustacea, but in the most highly developed of the Decapods. Among the primitive forms, moreover, a stalk is lacking, not only in the Trilobites, which must have been related to the earliest of the modern Crustacean forms, but also in the lowest Crustacean fossils (Hutchinson, 1930, p.3) as well as in many of the modern lower Crustacea, while the stalk in Anostraca is probably not an appendage but a head lobe, similar to that in some spiders and in Diopsidae among Insects. On the grounds of anatomy and distribution, it seems just possible that an oculiferous lobe in Anostraca may have been replaced by a revived appendage in the Malacostraca.

The embryological evidence points to a relatively late origin of the stalk in phylogeny, but does not conclusively indicate the type of the primitive eye. Thus in Branchupus the eyes, as well as the appendages, are well differentiated before the eye-stalk appears. This is also the case in some Decapod larvae, as in Eupagurus - see Çalman (1909, p. 302, Fig. 179). The late origin of the stalk in ontogeny may indicate either that it is a late revival of a primitive appendage, on to which the eye is

/secondarily

secondarily transferred, or that it is the result of a gradual elaboration of an abstricted, lateral region of the head, which has no appendicular significance.

For the higher Crustacea, the evidence afforded by the regeneration of an antenna in place of an eye-stalk may possibly indicate its appendicular nature. No such case has been found in the lower Crustacea. This evidence does not, however, rest on very reliable theoretical grounds.

It is quite possible that this is not a truly "homoetic" regeneration "due to the assumption by one member of a meristic series of the form and characters proper to another" - (see Bateson's definition of Homoesis - 1894, p. 85). Numerous examples of similar regenerations, in which the regenerated member assumed the character of a part not strictly homologous with it, are given by Bateson. Thus the eye stalk might well be merely a lobe of the head, not originally a limb, which has assumed the character of a limb in regeneration. This view is further supported by the fact that on general theoretical grounds it has been very generally supposed, and particularly pointed out by Morgan (1901, p.215) and Morgulis (1910, pp. 101, 106), that it is not justifiable to attribute the structure of a sporadic regeneration to atavistic tendencies, or to regard it as of value in deciding homologies and interpreting relationships.

Further doubt has been cast on the validity of the regeneration evidence for the appendicular nature of the

/eye-stalk

eye-stalk by Steel (1907, p.230) who points out that the type of regeneration which occurs is dependent on the presence of part or whole of the optic ganglion. With most of the ganglion intact an eye is regenerated; with little remaining an appendage is formed; when the ganglion is removed, there is no regeneration. There is presumably a tendency on the part of the nervous tissues to form new end-organs, once the original organs have been removed. On removal of the major part of the optic nervous tissue of the stalk the remaining nervous tissue might well be expected to behave like that of any other segment of the body, so that an appendage might well be formed, in place of what was originally merely a head lobe. It is suggested that the appendage resembles an antenna, since this is the simplest appendage innervated from a region of the brain supplying the special sense organs.

Summary. Thus the only evidence for the appendicular nature of the stalk is that relating to its anatomy and regeneration in the Malacostraca. There are no such indications for the lower Crustacea. Their eyes, therefore, may have been either primitively sessile or borne on an oculiferous lobe. That the primitive eye might well have been sessile, is indicated by the absence of a stalk in Trilobites, and in the most ancient Crustacean fossils. This is also in accordance with the late ontogenetic origin of the stalk in Branchipus and this condition might

have

have given rise on the one hand to the stalked movable eye, and on the other to the sunken eyes - movable and immovable. It is possible, however, that the stalked condition of the Anostraca represents the ancestral form, and that its absence in the remaining Branchiopoda is secondary. The scanty, available fossil evidence does not settle this point finally.

There certainly seems to be in Crustacea a general tendency for the eye to become movable and to be elevated on a stalk. It is possible that in Malacostaca, this may have been accomplished, not by the abstriction of a head lobe, but by the revival of a primitive appendage, on to which the eye was secondarily transferred. The only direct indication of this is in the evidence of regeneration, which is not above question on theoretical grounds. It is, moreover, unlikely that the stalk in Crustacea would have been evolved from two distinct structures in different forms. Moreover, in no other Arthropod is the appendage concerned present in the adult, nor, where present in the embryo, is it related to the eye. It is possible, therefore, that the most primitive Crustacean eye was either sessile or, more probably, had already an incipient tendency to elevation on a head lobe, which acquired the power of movement. The lower Crustacea present a confusing variety of modification, including sessile, stalked and sunken forms, both movable and immovable. In the higher Crustacea, or Malcostraca,

/the possession

possession of a jointed movable stalk is both typical and primitive. The balance of the evidence weighs against the probability of its appendicular nature.

The cuticle

The corneal cuticle forms the outer surface of the eye and bears the same relation to it, as does the body cuticle to the hypoderm, that is, the cuticle is secreted by, and acts as an external protection for, the cell layer. The continuity of the eye with the body cuticle is always apparent and the structure of the former clearly a modification of that of the latter, in connection with its dioptric function. Since light must penetrate without distortion, the cuticle is generally colourless and transparent, and often thickens to form a condensing lens. Small amounts of pigment have been described as deposited in the inner part of the cornea in Cancer (Pearson, 1908, p.160), but this is exceptional.

The cuticle consists of two main layers. The outer is thin and takes up most stains more deeply than the rest. This contains no chitin or calcium. The inner part is made up of successively deposited laminae of varying thickness, which may be secondarily lost. (see p.). It is chitinised and may contain calcium. (See Younge, 1932, p. 300).

The cuticle may be unfacetted and merely a continuation of the general body cuticle, or it may be specialised as a separate lens over each ommatidium. The distribution of these two types of cuticle and the

/primitive

primitive and typical form will be considered in connection with the hypoderm cells -

Where facets are present, their convexity varies. All the variations are represented in Isopods, from which order the following examples are drawn. For the rest, the types are scattered among the Crustacean orders without relation to phylogeny. The facets may be practically flat to very slightly concavo-convex, with the convexity external, as in Oniscus (Leydig, 1864, p.40) and Ligia natalensis (see p. 30); or plano-convex with the convexity external, as in Ligia oceanica (Hewitt,1907,p.26); or plano-convex with the convexity internal, as in some Serolis species (Parker, 1891, p. 82); or may vary from biconvex to practically spherical as in Cymothoa (Muller, 1829, p.42); in Porcellio (Grenacher, 1879, p.29); in Sphaeroma (Bellonci, 1881, p.98), in Idotea and Asellus (Parker, 1891, p.83) and Philoscia muscorum (see p.51).

It seems probable that the concavo-convex or plano-convex type was the first and that the bi-convex was derived from this, /Since a large compound eye is clearly of very ancient origin in Crustacea, it is obvious that the facets, when they first appeared, would have been closely crowded and flattened, and not biconvex and ocellar in type. Their dioptric elaboration must, at a very early stage, have been subordinated to the need for an economic spatial arrangement. The primitive and typical form of

/the facet

facet is concavo- or plano-convex with the bi-convex type as a late specialisation, due as a rule to degeneration.

The facets may be hexagonal, square, rectangular, or circular. The hexagonal is the commonest type. It is found in the following genera, which are members of the orders Anostraca, Notostraca, Conchostraca, Cladocera, Branchiurous Copopoda, Leptostraca, Decapoda, Mysidacea, Isopoda, Amphipoda, and Stomatopoda;-Branchipus (Burmeister, 1835, p.531); ~~Streptocephalus~~ (Spangenberg, 1875, p.30), Streptocephalus (see p.67); Apus, Estheria, Evadne, Argulus, (Parker, 1891, p. 61); Nebalia (Claus, 1888, Taf.X, Fig. 10); numerous Decapoda (Parker, 1891, p. 62); Mysis (Sars, 1867, p. 67), (Grenacher, 1879, p. 112); Cymothoa (Müller 1929, Taf.111, Fig. 3, 5, 6), (Bullar, 1879, p. 514); Arctutus (Beddard, 1890, Taf.XXX1, Fig. 4); Idotea, Serolis, Sphaeroma (Parker, 1891, p. 61); Orchestia (Frey and Lauckart 1847, p. 264); Gammarus (Sara, 1867,p.62); Phronima (Claus, 1879, Taf.V1, Fig. 48); Caprella, Talorchestia (Parker, 1891, p. 71); Squilla (Milne-Edwards, 1834, p. 117).(Will, 1840, p. 7).

The tetragonal form is restricted in occurrence to the eye of some Decapods and to part of that of Gonodactylus - a Stomatopod. Among Decapods this has been noted in Galathea sturgeon (Will, 1840, Fig. 111), in Dromia, Homarus, Palinurus and Paleomonetes (Parker, 1891, p. 62).

/In Gonodactylus

Gonodactylus there are six distinct rows of large ommatidia in the median part of the eye. These have a tetrggonal outline, while around them in parallel rows are smaller hexagonal facets (Parker, 1891, p. 62).

Round facets are found, in Leptostraca in *Nebalia* (Claus, 1888, pp.68-69), and in Mysidacea in *Mysis sp.* (Frey and Leuckart, 1847, p.113), *M. vulgaris* (Grenacher, 1879, p.118) and *M. stenolepis* (Parker, 1891, p.99). They are common in Isopods and Amphipods, in which the eyes have degenerated until they are composed of a few separated units.

Thus the primitive nature of the hexagonal form is indicated by its wide-spread occurrence and also in development, where the hexagonal arrangement may precede a tetragonal. Thus in the development of *Palinurus*, the phyllosoma larva has hexagonal facets, and the adult tetragonal (Parker, 1891, p. 62). The tetragonal is clearly a lately evolved form, since it is found only in a few Decapoda and Stomatopods. Parker suggests that the tetragonal form arose from the hexagonal, as a consequence of excessive crowding in the higher forms. Thus in *Gonodactylus* the median facets are tetragonal, and the external hexagonal, in accordance with the relatively greater crowding at the eye centre (see Parker, 1891, p. 61). Thus it seems that the primitive and typical conditions are hexagonal. This type gives rise to

/tetragonal

tetragonal forms, on crowding, and circular, on separation, of the units.

The facets are sometimes divided according to the disposition of the cells by which they are secreted. Square facets, where they are marked in any way, are sometimes divided diagonally as in *Homarus* (Parker, 1890, Fig. 26); sometimes transversely as in *Paleomonetes* (Parker, 1891, Pl 1X Fig. 105). Hexagonal facets may be divided by a line bisecting opposite sides, as described for *Cancer* (Parker, 1891, Pl.1X, Fig. 120) or by a line bisecting opposite angles, as described for *Galathea*, *Palaemon* and *Pagurus* (Leydig, 1857, p.327 and Patten, 1886, p. 644, Pl.11). According to Newton (1873, p. 327) the facet of *Astacus* is divided into four parts. Parker, however, 1891, p.109) points out that there is a single diagonal division for the facet in this case. Probably there is primitively a division of the facet corresponding to its secretion from two cells. The orientation of the cells, in relation to the shape of the facet is such, that the division, where present, is diagonal or transverse both for square and hexagonal facets. Typically the division is absent and the halves firmly cemented together, at least in the adult.

The facets are generally arranged in regular, alternating, parallel rows, with the facets of adjacent rows contiguous, except where the lenses separate in

/degeneration.

degeneration. The regularity is, however, apparent rather than perfect. The surface of the eye approximates to the surface of the sphere in many cases, and in this connection it has been pointed out by Kalmus and Mayer (1941, pp. 15-16) that it is not mathematically possible for a perfectly regular series of curved, hexagonal polyhedrons to be drawn, to cover the surface of a sphere, with the units contiguous. Thus in the eye, one or more regions of disturbance must exist. Close observation generally reveals such irregularities, particularly in the shape and arrangement of the facets in the outer regions of many eyes. Such irregularities are exaggerated in many mutant types (see Bassingdale, 1933, [illegible] for Gammarus zaddachi and Sexton 1932, pp. 359-360 for G. chevreuxi). For practical purposes, the eyes may be described as typically and primitively regular in their facet arrangements.

The number of facets is not fixed in the case of fairly large eyes. The eye is added to peripherally throughout life (while the area of the individual facets also increases) - (Bělehrádek and Huxley, 1930, p. 38 - on Gammarus).

Summary of section on the cuticle

The cuticle is thickened for refraction, colourless, transparent, continuous with, but deeper than, the

/general

general body cuticle. The outer part is thin and deeply staining. The inner is thick , laminated and chitinised. The primitive condition is discussed in the section of the thesis on the hypoderm cells. Facets are typical of the eyes of higher Crustacea. The primitive and typical form is concavo- or plano-convex, though alltypes from flat to spherical occur. A bi-convex form is usually degenerate. The facets are primitively and typically hexagonal , with tetragonal and circular forms arising as modifications of this due to overcrowding and separation of the units respectively . The primitive division corresponding to that between the hypoderm cells, is typically lost and the parts are well cemented together. The arrangement approximated to that of a regular, geometrical form with the facets alternating in contiguous parallel rows . The eye may grow throughout life , adding to the size and number of the ommatidia.

Corneal hypoderm

This is the layer of cells, which on its outer face gives rise to the cuticle. It was frequently overlooked by the earliest authors, since it was delicate and apt to tear away from the rest of the eye in wax sections. The cells are, moreover, difficult to stain, and being small and thin, are readily overlooked in thickish sections. Although the nuclei were occasionally observed, they were generally ascribed to the cone cells, while the secretion of both the cornea and the cone was attributed to the upper and lower surfaces respectively of this single set of cells. Thus Grenacher (1879, p. 123) apparently saw the cells in Decapods and in Palaemon described two kinds of bodies, which he regarded as distal parts of the cone cells. According to Parker (1891, p.109), the more distal of these were the nuclei of the hypoderm cells, while the others were the nuclei of the cone cells.

The hypoderm layer of the eye was probably at one time more conspicuous than in modern forms, since, according to Patten (1886, p. 645), embryonic lobsters show the cells as a broad, distal layer, with the individual cells larger than in the adult and more deeply staining. He pointed out that they were thin and reduced in the adult, except at the moulting time, when they are actively secreting new lenses.

The cells are presumably homologous with the

/hypoderm

hypoderm layer in the ocelli of Spiders and Myriapods which, after giving rise to the cornea, generally form a thick refractive layer, and are not reduced, as in the compound eye, where the refractive function is taken over by the cone cells, which are differentiated from the hypoderm.

Patten (1886, p.729-730) was the first to insist on the universal presence of the layer in Crustacean compound eyes. His description of the layer was not new, although he considered it to be so. Beddard (1887, p.447) potnted out that the layer had previously been described for Phronima sedentaria and Gammarus pulex. Patten (1886, pp.626, 642, 645) described the layer in Branchipus, Orchestia, Penaeus, Galathea, Pagurus and Palaemon. It has been noted in practically all subsequent descriptions.

That this layer gives rise to the cuticle is obvious from ontogeny and anatomy. The hypodermal layer is clearly continuous with that of the general body surface, differing merely in the product of its secretion and the reduction of the cells in the adult.

A facetted cuticula generally corresponds to a hypoderm, in which a definite number of cells - namely two - overlies each ommatidium and is responsible for the secretion of one facet. An unfacetted cuticula is the product of an irregular arrangement of the hypoderm, in which an indefinite number of cells, generally larger than

/two

two, and ranging up to twelve - overlies each ommatidium.

Among the Malacostraca the hypoderm is regular and the cuticle facetted in all but a few forms. Thus in Leptostraca a regular arrangement of two cells occurs in the hypoderm of *Nebalia* (Claus, 1888, p. 64 et. seq.) while examination of the cuticle of *N. bipes* showed obvious facets. Among the Anaspidacea the eyes are clearly facetted in *Anaspides Tasmaniae*, but the condition of the hypoderm is not known to me. The hypoderm is regular and the cuticle facetted in Euphausiacea - for example in *Stylocheiron* (Chun, 1896 - see figure given in Sedgwick, 1909, p.466, Fig. 290) and in many other forms (see Hånstrom 1933 p. 387 et. seq.) In Decapods a facetted cuticle appears to be almost universal. It was examined, for example, in *Astacus fluviatilis*, *Hippolyte varians*, *Palaemon squilla*, *Porcellana platycheles*, *Scyllarus arctus*, *Carcinus moenas*, *Maia squamata*, *Dromia vulgaris*, etc. etc. There are a few rare cases, in which the cuticle has been described as unfacetted, as in *Polycheles sulptus* (Smith, 1880, pp. 269-273) and in *Cambarus setosus* and *C. pellucidus* (Spurgeon, 1915, p. 388). These are, however, exceptional and degenerate. A regular two-celled hypoderm has been described in *Penaeus*, *Palaemon*, *Pagurus*, *Galathea*, (Patten, 1886, pp. 626, 642); *Crangon* (Kingsley, 1886, p. 599); *Cambarus*, *Callinectes* (Watase,

/1890

1890, pp. 297-299); *Homarus* (Parker, 1890, p.6); *Palinurus*, *Hippa*, *Cancer*, *Cardiosoma* (Parker, 1891, p.108); *Paleomonetes* (Parker, 1896, p.281); *Eupagurus* (Jackson, 1913, p.40); An *Astacus* sp. has been described by Reichenbach (1886, p.91) as having four hypoderm cells. This is very exceptional and Parker (1891, p.108) discarded the observation as being incorrect. In Mysidacea the cuticular facets have been described in *Mysis sp.* (Frey and Leuckart, 1847, p. 113); *M. vulgaris* (Grenacher, 1879, p.118); *M. stenolepis* (Parker, 1891, p.101), and were observed in *Schistomysis spiritus*.

A regular hypoderm is described in the following : *M. flexuosa* (Claparede, 1860, p.194); *M. oculata* (Sars, 1867, p. 73); *M. vulgaris* (Granacher, 1879, p.118); *M. chameleon* (Nusbaum, 1887,p.79) and *M. stenolepis* (Parker, 1891, p.98). In all these cases except the last the hypoderm cell nuclei were originally described, in error, as part of the cone cells, since the existence of the hypoderm cells had not been established.

In Cumacea the facets are present, but the condition of the hypoderm is not known to me. In Tanaidacea the eye was considered as facetted, at least in the female, by Muller (1864, p.2), while according to Blanc it is unfacetted (1883, p. 635). In *Tanais tormentuosus* the eye was examined and facets found. The condition of the hypoderm cells does not appear to have

/been

been described. In the Isopoda as a whole the eye is facetted. Patten (1886, p.677) and other early authors described the eye as unfacetted, so that Beddard in describing the facetted cuticula in *Cymothoa* (1887, p.447) says "It had not occurred to me even before referring to the literature on the subject (Bullar, 1879, pl. 42, Fig. 12) that, in finding the corneal facets in *Cymothoa*, I was adding a new fact to our knowledge of Isopod anatomy". The cornea of Isopods had, however, previously been described as facetted by Muller for *Cymothoa* (1829, p. 42), Leydig for *Oniscus* (1864, p.40), Sars for *Asellus* (1867, Pl Vlll, Fig. 14) and Bellonci for *Sphaeroma* (1881, p.98). The facets were obvious in all the cases which were examined, e.g. *Janiropsis parva*, *Anilocra mediterranea*, *Idotea*, *Aega*, *Oniscus*, *Sphaeroma* etc. A regular hypoderm with two cells to the ommatidium is found in *Porcellio* (Grenacher, 1879, p.107); *Sphaeroma* (Bellonci, 1881, p.98); *Arcturus* (Beddard, 1890, p.368); *Idotea irrorata* (Parker, 1891, p. 84); *I. metallica* and *I. baltica* (Peabody, 1939, pp. 527, 532); *Ligia oceanica* (Hewitt, 1907, pp. 24, 25); *L. natalensis* - see p. 31 ; *Cymothoa* (Eggert, 1927, p.39); *Philoscia muscorum* - see p. 52 A peculiar condition of the hypoderm was described by Parker for *Serolis*. He considered (1891, p.215) that there were probably more than two cells present in the hypoderm of each facet. In contrast to

/this

observation Beddard had been unable to find this layer of cells in Serolis (1887, p. 447), while Watase described the usual two cells (1890, p.290). The Stomatopods have a regular two-celled hypoderm in Gonodactylus (Parker, 1891, p.104 - 105). The cuticle in this form is facetted as is also the case in Squilla mantis (Will, 1840, p.7). Facets were observed in S. desmarestii and S. eusebia.

Thus in the Malacostraca, except the Amphipoda, a facetted cuticle is found in all the orders, while a regular two-celled condition of the hypoderm accompanies this in all cases, in which the condition of the hypoderm cells has been described. In Amphipods the cuticle is as a rule unfacetted. This has been described as the condition in Cyanus (Müller, 1829, p.58); Caprella (Frey and Leuckart, 1847, p.103), (Parker, 1891, p. 69); Phronima (Claus, 1879, p.131); Talitrus (Grenacher, 1879, p.109); Hyperia (Grenacher 1879, pl.11), (Carriere, 1885, p.160); Gammarus, Talorchestia longicornis (Parker, 1891, p.69); Gammarus chevreuxi (Huxley and Wolsky, 1933-34, p.366), (Sexton and Clarke, 1936, p.69). No facets could be seen in an examination of the following : - Gammarus pulex, Talitrus locusta, Chelura tenebres, Callisoma hopei, Caprella aequilibra, Caprella nudifrons. In some cases, particularly in those in which the units are separated, the cones shine through the transparent cuticle, so that the eyes have a falsely facetted appearance,

/although

although the cornea itself is actually smooth. A facetted cornea has, however, been described in a few cases in Ampeliscidae (Delle Valle, 1888, p. 94) and in *Talorchestia* (Watase, 1890, p.289). In practically all cases the hypoderm is undifferentiated, and the approximate number of cells over each ommatidium varies from nine to twelve. In *Phronima* for example (Claus 1879, Taf. V1, Figs. 48, 49) and in *Gammarus* (Parker,1891, Pl.1, Figs. 1, 2, 3,) there are about twelve cells, while in *Talorchestia longicornia* there are about nine according to Parker, (1891, p.70). Watase, however, described two cells (with a facetted cornea) in *Talorchestia*, (the species was not stated,). while Della Valle, who described a facetted cuticle in Ampeliscidae, found that this was accompanied by an irregular hypoderm (1888, p.93). This appears to be a unique combination. Thus in most Amphipods the cuticle appears to be unfacetted, and the hypoderm irregular with approximately nine to twelve cells over each ommatidium. In Ampeliscidae the eye is facetted, and possibly in some species of the genus *Talorchestia*. The loss of the facets, like that of the stalk, is presumably of secondary origin in the Amphipods, so that the two celled hypoderm and the facetted cuticula are typical and primitive in the Malacostraca as a whole.

Among the lower Crustacea the eye hypoderm is usually irregular and the cuticle unfacetted. In Cladocera

/the

hypoderm is irregular in *Leptodora kindtii* (Tshuganoff, 1913, p. 356). The following species on examination shewed no facets: *Daphnia pulex*, *Alona gracilis*, *Polyphemus pediculus* and *Leptodora hyalina*. In Conchostraca the hypoderm is irregular in *Limnadia agassizii* (Parker, 1891, p.75) and the cuticle is unfacetted. No facets were found in *Estheria* sp. The cones, which shine through the thin lenses of many of these eyes, give the appearance of facets although the cornea itself, when dissected off, is flat. The eye is unfacetted but the condition of the hypoderm is unknown in Ostracods. An unfacetted cornea and irregular hypoderm prevail in Branchiura in *Argulus* sp. (Parker 1891, p.82), and *A. foliaceus* (Herter, 1928, pp.159-176). In the Anostraca an unfacetted cuticle is described in *Branchipus paludosus* (Burmeister, 1835, p.53); *B. stagnalis* (Spangenberg, 1875, p.30); *Branchipus* sp. (Claus, 1886, p.320); *B. grubei* (Patten, 1886, 715). A facetted cuticle has been described in *Branchipus stagnalis* (Leydig, 1851, p. 295), Grenacher, 1879, p.114); *B. vernalis* (Parker, 1891, p.73); *B. gelidus* (Howland, 1911, p.145). The following were examined and facets observed; *Streptocephalus* sp., *Chirocephalus* sp., *Parartemia zeitsiana* and *Artemia gracilis*. In the following the hypodermal arrangement has been described as irregular : *Branchipus* sp.(Claus, 1886, p.80); *B. grubei* (Patten 1886, p.715). Parker describes an unusual condition of the hypoderm in *B. torticornis* and *B. vernalis* (1891,p.73)

/as follows :

as follows : "The hypoderm nuclei are arranged about the cones in circles of six, each nucleus participating in three circles so that there are therefore really two to each ommatidium". A somewhat similar arrangement of six cells is described by Howland (1911, pp.145-146) in B. gelidus. The condition is unusual and possibly transitional between the nine to twelve cells associated with an unfacetted cuticle and the two cells associated with a facetted cuticle. The hypoderm of Streptocephalus sp. is regular with two cells to each ommatidium (see p.68). Thus in Anostraca the cuticle may be either facetted or unfacetted with the hypoderm regular in the former case and irregular in the latter.

Among the Notostraca the eyes of Apus and Lepidurus were examined. They are unfacetted, being covered by a smooth overgrowth of the body cuticle. This structure has been described in Apus by Muller (1929, p. 56), Burmeister (1835, p. 533), Zaddach (1841, p.46), Frey and Leuckart (1847, p.206) and Wenke (1909, p. 236 et. seq.). No regular arrangement of the hypoderm cells appears to have been described.

Thus among the higher Crustacea a facetted cuticle and a regular arrangement of paired hypoderm cells are the rule. This is practically without exception other than in Amphipods, where the cuticle is unfacetted and the hypoderm irregular in the majority of cases, while facets

/appear

appear to coexist with an irregular hypoderm in Ampeliscidae. The condition in Amphipods is clearly secondary as is the loss of the stalk in this group, while the form in Ampeliscidae is highly aberrant.

The facetted cuticle and regular hypoderm are restricted in the main to higher types and among the lower Crustacea an irregular hypoderm with nine to twelve cells and an unfacetted cuticle are the rule. The Anostraca constitute the only exception. In this case the facets may be present and the hypoderm is then regular, either with the usual arrangement of two cells to the ommatidium, or with the exceptional type found in some Branchipus sp.

From its distribution the facetted form would seem unlikely to be primitive. The presence of facets in Anostraca, however, makes this uncertain, so that it is necessary to decide the primitive presence or absence of the facets on other grounds. That the eye was primitively unfacetted, was the view held on theoretical grounds by Patten and Parker, while Watase considered it as primitively facetted. Parker hoped to derive the compound eye from a simple Spider-like ocellus, with a single continuous lens. In accordance with this, he held that the eye in primitive Crustacea - Anostraca in his view - was unfacetted (Patten, 1886, p. 545). It is clear, however, from the observations given on p. 115 that here, as in the case of Isopods, he was mistaken in his description of the eye, in

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the order as a whole, as unfacetted. His argument for the derivation of the eye from a single ocellus has had little support. No real evidence is found for such an origin in the adult form or the development of the eyes in Crustacea or of the Trilobites.

Watase on the other hand regarded the cuticle as primitively facetted, since he held that the compound eye was formed by a recent coalescence of ocelli or simple, open, ectodermal pits, such as are found in the development of Limulus (1890 b, p.123). The evidence from the development of the eyes in Crustacea, however, precludes this view. According to Herrick's investigation of the development of the eye in Alpheus (1886, pp. 42-4), Claus' of the development in Branchipus (1886, pp.78-80), and Kingsley's of the development in Crangon (1886, p. 597-598), it is formed from a continuous strip of ectoderm, in which the differentiation of the ommatidia succeeds the initial separation of the entire eye area. The eye is continuous, and there is no formation from separate pits. Although this evidence does not support Watase's reason for regarding the eye as primitively facetted, it does not exclude the possibility of its formation by a coalescence of units in a distant ancestor. If this is so, the separate pre-compound condition must have been very ancient, since all trace of it is omitted in the lower Crustacea, in Trilobites, and in Crustacean embryology.

/Parker

Parker regarded the eye as primitively unfacetted, since he held that it was formed by a thickening of the hypoderm, in which the upper part retains the primitive, continuous character of the ordinary body hypoderm, while the lower layers, after cell multiplication, are differentiated into ommatidial columns. Although he did not regard the compound eye as derived from one ocellus, he considered it as a single unit, in which the differentiation of the lenses succeeded the grouped arrangement of the cone and retinal cells. The evidence from development points to Parker's view as the most reasonable of these three.

The absence of the facets in most of the lower Crustacea points to the possibility that the facets were not developed in the primitive form. The presence of facets in Anostraca as well as in Trilobites constitutes an objection. It is possible that the facetted eye in Anostraca is peculiarly advanced in the structure of the cuticle, as it is in the form of the rhabdom - see p.143. and the presence of a stalk, and that the condition in the earliest Crustacea did not correspond to that in the Trilobites, but was less advanced in the structure of the cornea. Such a primitively unfacetted form would account for the late differentiation of the lenses in the development of higher types and possibly for the fact that in regeneration the facets are formed long after the rest

/of

the eye (and not before at least two moults have occurred) - see Steele, (1907, p.195). On the other hand, it is possible that the unfacetted form in the lower Crustacea is degenerate in Ostracods and secondary in Notostraca, Conchostraca and Cladocera and Branchiura (see p.91), where the cuticle has formed a pocket over the eye and fails to develop facets in this part. It is possible that the late origin of the facets in development and regeneration may be dictated by a need for spatial economy in the developing eye, which also accounts for the early development of the convex form. It is probable that the eye was primitively facetted although many of the lower Crustacea must have arisen from a very early offshoot, or several such offshoots, in which the facets were lost.

The form of the hypoderm cells.

Typically in the adult the cells and nuclei are reduced in size, and the cytoplasm in density. In the primitive eye they probably formed a fairly dense, thick layer, as in the embryos of later forms - see Patten (1886, p.645). That is, in both phylogeny and ontogeny, the cells are reduced and their function decreased, as that of the cone increases.

In most lower Crustacea they lie as a continuous layer between the cornea and the cone cells, with up to twelve cells over each ommatidium, irregularly arranged, as are the cells of the body hypoderm, with which they are

/continuous.

continuous. Typically in higher Crustacea they are broken up into sets of two cells, one pair lying under each facet. Where the layer is broken up into such discontinuous units, the cells of each ommatidium may either be displaced centrally and enclosed in upward extensions of the cone cells, as in *Ligia natalensis* - see p. 31 - or displaced laterally by the growth of the cone cells between them, as in *Gonodactylus* (Parker, 1891, p.105), in *Ligia oceanica* (Hewitt, 1907, p.26), in *Philoscia* (p. 52) and *Streptocephalus* (p. 69). In the latter case they are generally produced downwards for a short distance round the cone.

Presumably the boundaries were primitively distinct. This condition persists in Stomatopods (Parker, 1891, p.105). Typically, however, as the cells shrink, their boundaries become indistinct, although, where they are grouped into twos, the lateral interommatidial walls of the cells may remain, as in *Peneaus* (Patten, 1886, p. 626), *Ligia natalensis* (p. 32), and *Philoscia* (p. 53). The boundary between the hypoderm and the cone cells is as a rule lost, although in *Argulus* it is marked off by a membrane at the base of the hypoderm cells (Parker, 1891, p. 83). This is not normally present. Lateral displacement of the cells does not always effect their complete separation, and there is a tendency for the cells to be linked by a bridge of cytoplasm.

Typically the cells are orientated so that the

/division

division between them is in the same direction as one of the divisions between the four cone cells. Where two cone cells only are present, the division between the hypoderm cells is in the same direction as or perpendicular to that between the cone cells, with the former the condition in Porcellio (Grenacher, 1879, pp. 107, 108), and Idotea (Parker, 1891, p. 84), the latter in Mysidacea, (Parker, 1891, p. 99).

The nuclei of the primitive form probably resembled those of the ordinary hypoderm cells. Typically they are reduced in size and spherical or slightly elongated. Primitively they probably lie centrally within the cells and above the cone. Where the cells are laterally displaced and extend round the cone, the nuclei often lie below those of the cone cells. The contents are coarsely granular. The nucleus is surrounded by a distinct membrane and may be with or without a nucleolus.

Normally the function of the hypoderm is merely that of secreting the cornea. In Galathea, however, (Patten, 1886, p. 642) the cells are modified to form an Iris-diaphragm. The thickened cytoplasm contains a layer of opaque fat globules, which excludes the light and is provided with contractile cytoplasmic fibres, so that the opaque material can be moved to regulate the amount of light entering the eye. This is clearly a secondary modification.

Summary

The corneageneous hypoderm cells were at first overlooked, on account of their poor staining properties, small size and liability to damage in sectioning. Althoggh sometimes observed, they were misinterpreted as cone cells, the secretion of both cone and cornea being attributed to one set of cells. Their universal presence and tendency to decrease in size was first pointed out by Patten. A facetted cuticle usually accompanies a regular hypoderm,with two cells under each facet, while an unfacetted cuticle goes with an irregular arrangement of the hypoderm, with nine to twelve cells over each ommatidium. (Exceptions are constituted by the abberrant and somewhat doubtful condition in Ampeliscidae and the intermediate form of the hypoderm in some species of Branchipus.) A facetted cuticle and regular hypoderm occur in all Malacostraca except Amphipoda, where the arrangement is secondary - like the loss of the stalk. An unfacetted cuticle and irregular hypoderm are usual in Lower Crustacea, but the distribution does not decide the primitive form, since facets are present in some Anostraca (as in Trilobites) although absent in the remaining "Entomostraca". Patten's view of the eye as primitively unfacetted is regarded as untenable, being based on an unjustifiable derivation of the compound eye from a single ocellus and on incomplete

/evidence

of the distribution of the facet types. Watase's view of the eye as formed by a relatively recent coalescence of ocelli and therefore primitively facetted, is belied in development.

(If such a coalescence occurred, it was clearly pre-Crustacean). The late origin of the facets in ontogeny, in relation to the rest of the eye, is in accordance with Parker's view of the eye as a single unit, in which the lenses are the last part to be differentiated, so that the eye is primitively unfacetted, and the condition in Anostraca (like that of Trilobites), represents a peculiar advance on that of the remaining lower Crustacea, in this as in other aspects (namely the form of the rhabdom and development of the stalk). It is possible, however, that the late origin in ontogeny is merely adaptive, and related to the need for spatial economy in development - the factor responsible for the early convexity of the eye. If so, the condition in the remaining lower Crustacea could be explained as due to degeneration or to the secondary formation of the corneal pocket. From this evidence, and in view of the condition in Trilobites and other Arthropods, it seems probable that the facetted condition was primitive and the unfacetted an early offshoot persisting in most of the modern lower Crustacea.

Typically the hypoderm is irregular with nine to twelve cells in the lower Crustacea, and with regular paired cells in the higher Crustacea. Though primitively and embryonically thick, they are typically reduced and displaced in the regular types, either centrally or laterally, although the lateral displacement is never as pronounced as in Insects ([illegible]). Where the cells are regular they are symmetrically arranged in the eye as a whole and are constantly orientated in relation to the cone cells. Typically their boundaries tend to degenerate. The nuclei are regular in form and granular with or without nucleoli in the adult. The cytoplasm is typically reduced with the modification as an opaque iris in Galathea exceptional.

The cones and cone secreting cells.

In the compound eye unit the cone cells have been interposed between the hypoderm cells and the sense cells. Normally the secretion of the hypoderm cells is the seat of the reception and selection of the stimuli in an Arthropod sense organ. In the case of the eyes, the cone cells and their secretions supplement the hypodermal structures in the refraction of the incident rays and the direction of the light on/to the delicate and deeply sunken sense cells.

The cone is a highly refractive body, partly or completely enclosed by the cone cells, and is a very conspicuous part of the eye unit. It has been suggested by Peabody (1939, p.534) that the cone material may be formed directly in the cytoplasm of the cells but the observations of Huxley and Wolsky (1933-5, p. 380) indicate the origin of the cone substance as droplets within the nucleus. Whatever the exact mode of origin, the cone segments are clearly secretions of the cells, to which they correspond in number and arrangement, although this may be obscured by partial coalescence of the segments as in *Ligia* - see p. 39 - and *Philoscia* - see p. 57 .

The cone is termed "crystalline", presumably on account of its high refractive index. It is insoluble in Ether, Alcohol and Chloroform, and is solid and probably chitinised in all cases. It is uniform and more highly refractive than the corneal lens, through which the shining cone is clearly visible in most cases.

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The cone segments are typically flattened in the adult along their planes of contact, so that they form a single optic unit in each ommatidium. This is also the condition in the primitive forms. It is only in some mutants, where the cones are very imperfectly formed,(for example in the albino mutant of Gammarus chevreuxi described by Huxley and Wolsky (1933-1[illegible] p.374)) that the cone segments are unequal and separate and remain spherical and unflattened, as in the normal embryonic condition. Occasionally in the adults one or two irregular cones have been noticed, as described by Schmidt (1848, pp.1-12), in Phronima, Palaemon, Astacus and Homarus, but these are comparatively rare malformations of single ommatidia.

The size of the cones varies within the eye, as has been pointed out in connection with the eye of Philoscia - see p.57 It is apparent from Huxley and Wolsky's account (1933-1[illegible], pp. 366-367) of the development of Gammarus, that the smaller size of the peripheral cones is to be accounted for by indefinite relative growth. Bélehrádek and Huxley (1930, p. 38) and Peabody (1939, p. 531) have pointed out that the eye is added to throughout life, so that the smaller sise of the peripheral units is due to their late origin in development.

Typically the cone segments form a conical unit. This may however assume a pyramidal form as in Peneaus

/(Patten

(Patten, 1886, pp. 627-628), where the corners are bevelled, or it may be ellipsoidal as in Philoscia - see Fig. 11. The segments are symmetrical and equal and the planes of division therefore perpendicular to one another and constant in orientation throughout the eye, so that a section at this level forms a very strikingly regular pattern.

Secondary transverse divisions of the cone may occur as in Palaemon squilla (Grenacher, 1879) His figure is reproduced in Sedg~~e~~wick, (1907, p.330, Fig. 332), where the upper part of each segment is separated from the lower by a portion of the cone cell. Accessory cones, which are found only in Isopods and described above for two species of Ligia on pp.39,40, owe their formation to transverse division. The elaborate development of the cone in this case is related to the small mass and simple form of the cone cells. (This is dealt with further in connection with the cells).

A highly aberrant subdivision of the cone apparatus has been described by Tchuganoff in Leptodora kindtii (1913, pp. 356-357). In this Cladoceran the five segments of the upper part of the cone are surrounded by five normal or "end cone cells", while the lower part, in which no segmentation is described, is surrounded by two "supporting cells" of very uncertain origin. The lower part differs in its material from the upper. It appears

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from the description, that the supporting cells are not pigmented but are parts of the cone cells, some of which, like their secretions, have undergone a secondary division.

The number of the cells and therefore of the cone segments varies from two to five. Among the Malacostraca, excluding members of the division Peracarida, the number of cells is four. This is found in Leptostraca (Claus, 1888, p. 69); in Euphausiacea in general (Chun, 1896, p.191 et. seq.) and, for example, in *Meganictyphanes* (Hanström, 1927, p.243); in Decapods, for example in *Palaemon* (Will, 1840, p.13), *Galathea* (Claparede, 1860, p.194), *Peneaus*, *Pagurus* (Patten, 1886, pp.626, 643) etc., etc.; in Stomatopods in *Squilla mantis* (Steinlin, 1868, p.17) and *Gonodactylus* (Parker, 1891, p.105). For the remaining order Anaspidacea, Hanstrom's description of the eye in *Anaspides tasmaniae* (1934, Part 4), is available to me only in an abstract in which the number of cone cells is not given.

In the Peracarida, the number is generally two. Thus two cells occur in Mysidacea in *Mysis stenolepis* and *M. vulgaris* (Grenacher, 1879, p. 118). In Amphipods two cone cells have been described in *Hyperia* (Grenacher, 1874, p.652), *Phronima* (Grenacher, 1879, p.112), *Gammarus* (Grenacher, 1879, p.110), (Carriere, 1885, p.156), *Caprella*, *Talorchestia longicornis* (Parker, 1891, p.70), *Ligia* (see p. 39) and *Philoscia* (see p. 57). Four cone cells have been described in the following :- *Hyperia* (Claparede,

/1860

1860, p.211) and *Gammarus* (Sars,1867, p.61), (Leydig, 1879, p.70). According to Parker (1891, p.70) these observations are probably inaccurate, since Claparede held the general view that the cone cells were four in number in all Crustacea, while Sars and Leydig probably confused the pigment cells with the reduced cone cells in *Gammarus*. If Parker's criticism is justified, two cells are of universal occurrence in Amphipods. In the Isopoda Beddard gave the number two, as typical for the order (Beddard, 1887, p.443). The following particular cases have been described in confirmation of this :- *Oniscus* (Leydig,1864,p.41); *As~~c~~ellus* (Sars, 1867, p.110); *Serolis* (Beddard, 1884,p.20), (Watase, 1890, p.290), *Arcturus* (Beddard, 1890, p.369), *Sphaeroma*, *Idotea* (Parker, 1891, p.85); *Idotea baltica*, *Idotea metallica* (Peabody, 1939, p.524); *Ligia* (see p. 39) and *Philoscia* (see p.57). Three cone cells have been described in the following :- *Asellus aquaticus* (Sars,1867, p.110, Pl. Vlll, Fig. 12), (Carriere, 1885, p.155); *Asellus sp*. (Lattin, 1939, p. 417 et.seq.); *Arcturus* (Beddard, 1890, Pl.XXXl, Figs. 1, 4) and in *Trichoniscus* (Mehely, 1927, p.82). *Asellus* (Lattin, 1939, p.417 et.seq.) occasionally has four cells. In the case of *Asellus aquaticus* the eye contains four ommatidia, three of which have normal two segmented cones, while the third has one normally sized cone segment and two segments of half the usual size (Parker, 1891, p.122). The size and number of

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the segments of the cone are best accounted for by assuming a division of one of the original segments and not the entrance of an additional cell from outside. For the eye in Cumacea the only available description is that of Burmeister (1883, pp. 35-37) relating to *Cuma rathkii*, in which the eye was degenerate and revealed no cone structure. No description of the condition in Tanaidacea is available to me.

Thus four cells are typical of the Malacostraca except Peracarida, where there are typically two cells, with three and four cells as occasional numbers, probably arising by division from the two celled forms.

Among the lower Crustacea four cells are of regular occurrence in Anostraca, Notostraca and Branchiura. Among the Notostraca four cells have been described in *Branchipus* (Spangenberg, 1875, p.30), (Grenacher, 1879, p.115), *B. grubei* (Patten, 1886, p.645), *B. vernalis* (Parker, 1891,p.73), *B. gelidus* (Howland, 1911, p.145), *Artemia* (Moroff, 1911, p.150) and *Streptocephalus* (p.7/). Five cells are occasionally found in *Artemia* (Moroff,1911, p.150). Among the Notostraca four cells have been described in *Apus* (Grenacher, 1879, p.115),(Claus, 1886, p.321) and among the Branchiura in *Argulus* (Claus, 1875, p.256, Fig.14),(Herter, 1928, p.159 et.seq.). In Conchostraca and Cladocera the number is more variable and may be either four or five.

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In Conchostraca five cells have been described in *Estheria californica* and E.*tetracera* (Lenz, 1877, p.30) and *Limnadia* (Parker, 1891, p.75). Parker pointed out that four cells were occasionally present in *Limnadia*. Grüber had previously described (1865, p.208) two cells in *Estheria* but Parker (1891, p.75) considered that he was mistaken. In Cladocera four cells occur in the primitive genus *Sida* (Claus, 1876, p.372) and this number is also given by Weissman (1874 p.364) for *Leptodora*. Five cells have been described in *Polyphemia* and *Evadne* (Claus, 1877, p.145), *Podon* (Grenacher, 1879, p.117) and *Leptodora kindtii* (Tschuganoff, 1913, p. 360). In Ostracoda two cells are the rule (Calman, 1909, p. 66).

Thus among the lower Crustacea four cells are found in Anostraca, Notostraca and Branchiura as well as in some cases in primitive Cladocera and in Conchostraca. In the last two orders, as well as in Anostraca, five cells may occur, while two cells are usual in Ostracods and may possibly occur as an aberration in Cladocera.

Thus the numbers three and five appear to be restricted to isolated groups, in which they are of variable occurrence. Three segments appear to be formed by a secondary division of a two celled cone, while the number five appears, at least in Cladocera, to be derived from a four celled type.

/Thus

Thus either the two or the four celled condition must be the primitive one from which the other types have arisen by degeneration or multiplication of the cells.

Both Patten (1886, p.678) and Parker (1891, p.25) considered that the primitive number was two. Their views were based largely on the histological evidence, that is, that there is little or no indication of degenerate cone cells or segments remaining as vestiges in any Crustacean eyes, while there is some reason for believing, that two or four cells may increase their number by division. Patten (1886, pp.643-644) considered that there was in addition direct histological evidence of such a division having occurred in the eyes of some Decapods. Thus in Galathea and Palaemon he described one division between the cone segments as more distinct than the other and pointed out that the inner ends of the cells showed a corresponding paired arrangement, which he took to indicate a secondary division of a primitively two celled cone.

There is, however, little other positive evidence to support their views and they rest mainly on the absence of rudimentary cells as an indication of degeneration. This condition is not surprising from a physiological point of view. A degenerate and misformed cone segment might not be merely useless but possibly harmful, in impairing the perfection and symmetry of the optical system. In those

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mutant forms, moreover, where the cone segments are lost, they are lost in their entirety (Huxley and Wolsky, 1933-34, p. 374) and in normal eyes cone segments might well have been lost in the same way, without leaving histological traces of degeneration.

On general phylogenetic grounds it appears more probable that the primitive type was four celled. This is the number typical of many lower Crustacea as well as of the Malacostraca other than Peracarida, while the comparative anatomy of the eye in Peracarida indicates that in general they have diverged along a line of development separate from that of the remaining Malacostraca. Thus, while the Malacostraca have jointed eye-stalks these have been lost in Isopods and Amphipods, though they are present in the Mysidacea. Mysidacea like Decapods have eight retinal cells, while Isopods have seven or six, Amphipods five or four.

It is probable then that the primitive number was four, that the five celled types in Lower Crustacea were derived from this, and that the two celled form in Peracarida represents a secondary offshoot. The two celled form in Ostracods appears to be an isolated one. Clearly no one number can be regarded as typical of the Crustacea as a whole but four is the commonest.

In each Ommatidium the cone cells form a single

/group

group extending from the inner side of the corneal cells to the level of the upper ends of the retinulae. Typically the expanded base of the cone is outwards.

The cell boundaries are usually obscure, since the cells tend to coalesce with the adjacent hypoderm and pigment cells. At their upper ends the cells are in contact with those of the hypoderm and must primitively have been placed directly below them. As the hypoderm cells are reduced and the cone cells increase in size, they are displaced to occupy a position nearer the cornea. Thus in *Philoscia* the cap formed by the hypoderm cells over the cone may or may not be complete (see p. 56) while in *Paleomonetes* the upper ends of the cone cells pass between the corneal cells to come into contact with the cornea near the middle of each facet - (see Patten, 1886, p. Pl.1X, Fig. 66). A similar condition prevails in *Gonodactylus* (Parker, 1891, p.10) and in *Palaemon* (Jackson, 1913, p. 73). In *Ligia natalensis* (see p. 33) the displacement of the hypoderm cells is in the opposite direction, so that the cone cells are in contact with the cornea laterally. Thus the upper surfaces of the cells are in contact with the lower surfaces of the hypoderm,cells, and on account of the displacement of the hypoderm cells in the adult, approach the cornea and may come into contact with it either centrally or laterally.

/Laterally

Laterally the cone cells surround their secretion to a varying depth. From the conditions in *Ligia*, *Philoscia* and *Streptocephalus* -(described above, pp.33.56.70 it seems that either the cones or their cells must be in contact with the rhabdom and that the size of the cells is inversely related to the size and complexity of the cone. Thus, where the cone is well developed as in *Ligia*, the cells are reciprocally reduced to a small tapering mantle covering only the upper parts of the cone, while the accessory cone and rhabdom are in contact. In *Philoscia*, where the cones are moderately developed, both the cones and their cells are in contact with the rhabdom, while in *Streptocephalus*, where the cones are relatively poorly developed, the cells continue below the cone and themselves make contact with the rhabdom. According to Parker, (1891, p. 66), the cone cells always reach as far as the rhabdom. Presumably by this was intended either the cells or the cones.

The relation between the lower end of the cone cells and segments and the upper end of the rhabdom and retinal cells varies. Primitively the cone cells and their secretions - the cone segments - were either of equal extent, with both the cone secretions and cone cells in contact with the upper end of the rhabdom, or the cone secretions may not have attained this length, so that the cone cells alone would have been in contact with the

/rhabdom

rhabdom, as in Streptocephalus - see p.70 At this level of contact the retinal cells and rhabdom ended, as did the cone structures. Typically the cone cells are reduced in reciprocal relation to the degree of development of their secretions, so that the cells are no longer in contact with the rhabdom. The cone secretions, retinal cells and rhabdom end at the level of contact of the cone secretion with the rhabdom. There are several exceptions to this. The retinal cells may extend up round the cone structures for a short distance. This is the case in Streptocephalus (see p. 59) and more markedly so in Philoscia (see p.74). The cone cells may pass irregularly round the upper end of the rhabdom and gradually become lost in the retinal cells. This is the condition described by Schultze (1868, Figs. 9, 10), in Astacus and by Parker (1891, pp. 85, 110) in Argulus and Palinurus. In Mysis stenolepis (Parker, 1891, p. 83) it is the rhabdomeres, which are extended up so that they lie upon the walls of the cone cells for a small distance.

Patten (1886, p. 525) considered that the cone was directly continuous with the rhabdom and that it extended therefore right down to the basement membrane.

In this connection he considered that the cone cells were likewise continued down to the basement membrane. Although Parker considered (1891, p. 107) that such an extension of the cells might exist in Homarus, other authors

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have made no mention of the matter. The condition seems a most unlikely one, since it would jeopardise the generally accepted view of the rhabdom as a product of the retinal cells by interposing between the retinal cells and the rhabdom the extensions of the cone cells.

Laterally the cells are in contact with the pigment cells, where these are present. Frequently the limits between the two types of cells become indistinct as in *Ligia* (see p.36). The intercellular boundaries do not appear to have attracted much notice and are typically indistinct. Above the cones the cells coalesce in some cases as in *Ligia* (see p.57) but remain clear in others as in *Streptocephalus* (see p.71). Where a part of the cell intervenes between the cone secretion and the rhabdom, the cell boundaries may persist below the cone as in *Streptocephalus* (see p.71).

The nuclei are generally clearly visible and invariably distal in position as for example in *Serolis* (Watase, 1900, Fig. XX1X); *Gonodactylus* (Parker, 1891,105); *Ligia* (Hewitt, 1907, p.25); *Branchipus stagnalis* (Nowikoff, 1905, pp.194-5); *Eupagurus* (Jackson, 1913, p.31); *Idotea* (Peabody, 1939, p.533) as well as in *Ligia*, *Philoscia* and *Streptocephalus* (see pp. 36.55,71) and many other forms.

The nuclei vary in position in reference to those of the corneal hypoderm. In *Ligia* they are below, in *Philoscia*

/on

on the same level, and in *Streptocephalus* above those of the hypoderm cells. Typically the nuclei lie above the cones with their position in relation to the hypoderm nuclei depending on the extent to which the hypoderm cells have been displaced by the cone cells. Primitively the cone cells and their nuclei were below those of the hypoderm.

The nuclei are oval or spherical, regular in shape, densely granular, with a darkly staining boundary, with or without a nucleolus. They usually stain less deeply than the hypoderm nuclei and are generally larger than these.

The distal position of the nuclei, together with the solid nature of the cone secretion, defines the cone in Crustacea as of Grenacher's "eucone" type (Grenacher, 1879). The eye in *Ocypoda ceratopthalma* was originally described as an exception to this and of the "pseudoconic" type but this was subsequently corrected by Dembowski (1913, p.513 et. seq.).

The cytoplasm varies in texture. It is usually so finely granular as to appear practically uniform. *Streptocephalus* and *Mysis*, however, show exceptional conditions. In the former case it is as a whole coarse, and stains very deeply with an occasional unequal staining of the cells in some of the ommatidia, so that one pair of diagonally opposite cells is more deeply stained than the /others.

others.

In Mysis stenolepis (Grenacher, 1879, p.118) the cytoplasm is coarse at the upper ends of the cells, fine below. The cytoplasm therefore shows no constant or characteristic structure and presumably varies in the individual, according to the state of its secretory activity.

There are sometimes peculiar thickenings in the cell walls, with their material resembling that of which the cone are formed. These occur in Peneaus (Patten, 1886, p.28), where the cell boundaries develop sickle shaped thickenings occupying the small space between the cell boundary and the cone. In Argulus thickenings occur on the intercellular membranes below the cones (see Parker, 1891, p. 85). These have not been recorded for other species, and are specialisations. Their function is presumably supplementary to that of the cone, since the two are of similar material.

Summary.

The conspicuous, refractive "crystalline" cones are typically and primitively chitinous and solid and

/made

made up of a number of segments, each corresponding to a cone cell, along whose inner axis it has been secreted. This arrangement may be partly obscured by coalescence of the cells or their secretions. The segments are equal, symmetrical and of constant orientation. Although separate in the embryo and in some malformations, the segments are typically approximated and flattened to form a single unit in each ommatidium. This is conical or more rarely ellipsoidal or pyramidal. The peripheral cones are smaller than the central owing to their late formation. Secondary transverse division of the cone may occur. This may be restricted to the secretion, in which case the two parts of the segments may be separated by a portion of the cone cells or contiguous, or both cones and cells may undergo division in an irregular manner, as in the aberrant <u>Leptodora</u>. The primitive number of cells appears to be four. This is the number typical of Malacostraca, other than Peracarida as well as of Anostraca, Notostraca, Branchiura, some Conchostraca and Cladocera. The Perdcarida as well as the Ostracods have developed two cells, while the numbers three and five are restricted to isolated groups in which they are of variable occurrence and appear to be derived from two and four celled forms respectively.

Although the histological evidence has been regarded as indicating a primitively two celled condition

/of

of the cone and a tendency to multiplication rather than division, it seems probable that this is misleading and that the cones on degenerating might well leave no physiologically disadvantageous rudiments. The general phylogenetic position of the two celled types, together with the comparative anatomy of the rest of their eyes, points to the secondary nature of their cone segmentation. Thus the two celled condition of Peracarida appears to be derived from the four celled type of the remaining Malacostraca, while the two celled forms in Lower Crustacea are of rare occurrence, except in Ostracoda, and are less likely to be primitive than the four celled variety.

The upper surfaces of the cells abut on the lower edges of the hypoderm cells and show a general tendency to partial fusion with and displacement of the latter, so that the cone cells obtain a more or less complete secondary contact with the cornea either centrally or laterally. Typically the remaining boundaries are obscure both between the cells themselves and laterally between these and the pigment cells, when present.

Primitively both the cone cells and their secretions, or the cone cells alone, were in contact with the upper end of the rhabdom. Typically the cells are reduced to a depth in inverse relation to the size and complexity of the cone secretions - that is, the cone secretion alone is in contact with the rhabdom. Primitively and typically the cone structures concerned and the retinal cells and their rhabdoms end at the level of contact of the rhabdom with the cone cells and /or their secretions. More complicated arrangements occur. The retinal cells may extend round the cone or the cone cells between the retinal cells to a varying degree, while in Mysis the rhabdomeres extend upwards round the cone for some distance. Cone and rhabdom are not continuous but merely in contact. The nuclei are distal and the cones of the eucone type. Primitively the nuclei were proximal to those of the hypoderm but typically the relative position is changed and depends on the extent to which the cone cells have penetrated the hypoderm layer. The nuclei are typically larger than those of the hypoderm cells, regular in form, ovoid or spherical, densely granular, with a firm boundary, with or without a nucleolus. The condition of the cytoplasm is very variable.

The retinal cells.

The retinal cells are of two types. The true or proximal retinal cells are unipolar, pigmented nerve-end cells, each the generating cyton of an optic nerve fibre and each bearing an axial rhabdomere or rod. They are grouped in retinulae, one such group lying below the cone in each ommatidium. The second type - the distal retinal cells - are derived from these, but have lost their sensory function and with it their rhabdomeres and nervous connections. They are displaced to form pigment cells, lying around the cones and sheathing and separating the ommatidia. These latter cells will be described in connection with the accessory pigment cells - [illegible].

The proximal retinal sense cells.

The number of proximal retinal sense cells varies from four to eight and lies outside these limits only in very exceptional cases.

Among the lower Crustacea the number five is typical, while four cells are frequently found as a result of the degeneration of one of these.
Among the Anostraca five cells have been described in Branchipus in the following cases : Branchipus sp. (Grenacher, 1874, p. 653); B. vernalis (Patten, 1886, Pl. 1V, Fig. 32); B. stagnalis (Nowikoff, 1905,p.432 et seq); B. gelidus (Howland, 1911, p.147). Five cells

/are

present in *Streptocephalus*. *Branchipus* was described by Sprangenberg (1875, p.31) as having four cells. This is possibly an error.

Among the Notostraca *Apus* is described as having five cells by Grenacher (1874, p.653) and Parker (1891, p. 75). Wenke (1908, p.236 et seq) considered that there were seven cells in *Apus productus*.

Five was described by Parker (1891, p.175) as the number of retinal cells in the Conchostraca. Nowikoff (1905, p.432) described five cells in *Limnadia* and pointed out that these were occasionally reduced to four. Among the Cladocera five cells were described by Parker (1891, p. 76) in *Evadne* He pointed out that one of these had a tendency to reduction. Tschuganoff (1913, p.356) described five equal cells in *Leptodora kindtii*. The number of retinal cells in the Branchiura was described by Parker as being five - in *Argulus* (Parker, 1891, p.83)-while Herter (1928, p.159 et seq) described five cells with a tendency to form four. No description of the retinal cells in Ostracods is available to me. Thus with the exception of the seven celled form described in *Apus productus*, all the available descriptions of the eyes of the lower Crustacea, indicate the condition of the retinula group as five-celled, except in those forms in which there is a tendency to reduction of one cell.

Among the Malacostraca the retinula group is seven- or

/eight-

eight-celled except among some of the Peracarida. Among the division Phyllocarida, seven cells are typical, as in Nebalia (Claus, 1888, p.1 et seq). For the Syncarida Hanstrom's description of the eye of Anaspides tasmaniae (1934, pp.1 et seq.) is not available. Among the Eucarida seven cells are typical of Euphausiacea (Korscheldt and Heider, 1899, p.167), while among the Decapods the number of cells varies. Among these eight-celled forms are common but show a tendency to reduction of one of the cells, as in the following : Homarus (Parker, 1890, p.21); Cardiosoma, Hippa, Paleomonetes, Palinurus, Cambarus, Crangon, Cancer (Parker, 1891, pp.110, 111); Palaemon (Steele, 1907, p.170); Eupagurus (Jackson, 1913, p.41) A seven celled condition is presumably formed by the complete reduction of one of the cells of the eight celled type Seven cells occur in the following Palaemon (Grenacher, 1877, p.32); Astacus (Carriere, 1885, p.169);Peneaus, Galathea, Pagurus, (Patten,1886,pp.571,640,643); Cambarus (Watase, 1890, p. 298). Four cells have been reported in Herbstia (Leydig, 1855, p.468) and Homarus (Newton, 1873, p.333). Parker (1890, p.21) considered that his observations on Homarus discounted those of Newton, and pointed out that the four celled retinula in Decapods, as described above, had not been substantiated by any later work. If a four celled retinula

/occurs

in any Decapods it is clearly highly aberrant. It is possible that the four sided nature of the rhabdom - see p.168 - was responsible for the belief that the retin retinula was composed of four retinal cells. Among the Hoplocarida there are seven cells in *Squilla* (Grenacher, 1877, p. 33), (Hickson, 1885, p.341, Fig.2), while Parker (1891, p.101) described eight cells, one of which was rudimentary, in *Gonodactylus*. Among the Peracarida, the Mysidacea retained the eight celled form, as in *Mysis stenolepis*, in which Parker described eight cells, one of which is reduced (Parker, 1891, p.101). Lang (1891, p.355) and Sedgewick (1927, p.330) in their textbooks describe four cells in *Mysis*. Here as in the Decapods it is probable that the number of cells had been wrongly assumed to correspond to the apparent number of rhabdom divisions, since, for example in *Mysis stenolepis*, the rhabdom is square and divided into four smaller squares - (Grenacher, 1879, 1879, p.117), (Parker, 1891, p.102). No description of the condition in Cumacea and Tanaidacea is available to me. Among the two remaining orders - Isopoda and Amphipoda - the number of cells is very variable. The Isopoda show a more considerable variation in the number of cells than any other order. The number varies from four to seven and, in one exceptional case, reaches fourteen. Four cells have been described in *Serolis* (Beddard, 1887, p.451, 1888, p.27). The eye in this genus is

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clearly exceptional both in this and in other respects, see p. 190 . It seems probable that the small number of retinal cells in this case is due to a forward migration of two of the retinal cells, to form distal retinal pigment cells - see p.190 . Five cells have been reported in *Sphaeroma* (Bellonci, 1881, p. 98, Taf. 71, Fig. 2). Parker, however, gives the number in this genus as seven (Parker, 1891, p. 95. Pl.V, Fig.58). Six cells have been described in the following : *Arcturus* (Beddard, 1890, p.368), *Idotea irrorata* (Parker, 1891, p. 87), *Ligia oceanica* (Hewitt, 1907, p.24), *L. natalensis* (p.42). Seven cells, with one cell rudimentary and clearly degenerate, without a nucleus or nerve fibre, are described in *Idotea robusta* (Parker, 1891, p. 86), (Peabody 1939, p.528). Seven cells occur in the following : *Porcellio* (Grenacher 1874, p. 653), (Parker, 1891, p. 86), (Beddard, 1884, p.21); *Cymothoa* (Bullar, 1879, p.513), (Lattin, 1939, p. 417 et seq); *Aega* (Beddard, 1880, p.443), (Parker, 1891, p. 95); *Sphaeroma* (Parker, 1891 p. 87, Pl. V, Fig. 58). Seven cells also occur in *Philoscia* (p.60). Fourteen cells were described in *Trichoniscus austriacus* by Mehely (1927, p. 82). This number is clearly aberrant and found in eyes which are degenerate. The primitive number of cells in Isopods is seven, with the five and six celled types derived from this by degeneration, while the four cells form is derived from

/the

the six celled by upward migration of two of the cells.

The Amphipods have either four or five cells. Five equal cells have been recorded in the following : *Hyperia* (Grenacher, 1874, p. 653),(Carriere,1885, p.160); *Phronima* (Grenacher, 1879, p.112), (Claus, 1879, Taf 65, Fig. 77), (Carriere, 1885, p.114); *Gammarus* (Cussans, 1904, p.31); *G. chevreuxi* (Huxley & Wolsky, 1933-1934, p. 387). Five cells, of which one is reduced or rudimentary, have been recorded in *G. ornatus* and *Talorchestia longicornis* (Parker, 1891, p.71). Four cells have been described in *Oxycephalus* (Claus, 1871, p.151), in Ampeliscidae (Della Valle, 1888, p. 94) and in *Talorchestia* sp. (Watase, 1890, p.296). Sara stated that there were four cells in *Gammarus* sp. but later investigators have given the number, possibly for other species, as five (Sars,1867, p. 61). Thus five cells are typical of Amphipods but the partial or complete reduction of one of these cells is found in some cases. In exceptional and aberrant cases the number of cells may be further reduced as in some mutants in *Gammarus chevreuxi* (Huxley and Wolsky, 1933-1934, pp. 383, 387) where there are only two or three cells.

Thus among the lower Crustacea the typical condition of the retinula is a five-celled one with a tendency to reduction of one of the cells. The seven-

/celled

celled condition described in <u>Apus productus</u> (Wenke,1908, p.353 et seq) is probably indicative of an ancestral form with a larger number of retinal cells than are found in the remaining lower Crustacea. In the Malacostraca the primitive number is eight, but this is commonly reduced to seven in Leptostraca, Euphausiacea, some Decapods, Mysidacea and Stomatopods. In Amphipods and Isopods the retinal cells have evolved separately from those of the remaining Malacostra and have undergone a series of reductions, so that in Isopods the number varies from seven to four and in Amphipods five to four.

There appear to be no indications of addition to the number of retinal cells. There is no evidence for regarding the cells of reduced size common in Crustacean retinulae, as newly added, by division, or conversion of the original eye cells, or immigration of new cells. Any added cells would presumably be provided with nucleus and nervous connections and probably be of the same size as the original cells.

The rudimentary cells in the cases given above are clearly not newly added but degenerate - they are often without nucleus, nervous connection or rhabdomere.

It is suggested that the ancestor of the Crustacea had a well developed compound eye with eight retinular cells. In the lower Crustacea this number was presumably

/reduced

reduced to produce a five celled type, with a further tendency to reduce to four cells. Hanstrom (1933,p.387 et seq.) related this reduction to the pelagic habit of many of these forms. In the Malacostraca some of the descendants retained the eight cells, but the majority tended to lose one, while some of the Peracarida lost a larger number of cells, and so evolved in this respect along a course parallel to that taken by the lower Crustacea.

Parker (1901, pp.124-127), on the other hand, considered that the five-celled condition of the retinula was the primitive one, and that the Crustacea therefore showed a tendency to increase in the number of retinal cells. He adduced as evidence, that this was the number found in all the lower Crustacea, as well as in some of the higher forms - Isopods and Amphipods. It seems more likely that the five celled condition in the latter is secondary and due to the general degeneration, which appears to have affected these eyes, and which is also reflected, for example, in the loss of the stalk. While he admitted that the five celled condition of the retinula was not more frequently associated with the one condition of the cone or hypoderm, than with another, he considered that the five celled type was more commonly found than any other in conjunction with those conditions of the rhabdom, which he regarded as primitive - that is the five celled condition was generally associated with separate rhabdomeres. He gave as examples of this -

/Argulus,

Argulus, *Gammarus*, *Talorchestia*, *Hyperia*, *Phronima* - (Parker, 1891, p.126). Apart from the fact that the Branchiura are in general aberrant forms, it is clear that the condition in Amphipods is likely to have been due to secondary degeneration. Moreover, fused rhabdomeres are not uncommon in five-celled types as in *Branchipus* (Howland, 1911, p.147) and *Streptocephalus* (see p.75). On the whole it is suggested that Parker's views are not admissable, that the primitive number of cells for the Crustacea as a whole is eight, that there is no general tendency to increase in the number of retinal cells, that a reduction seems to have occurred more than once in evolution and seems to be a fairly rapid process.

There is no anatomical or embryological evidence of the formation of the Crustacean compound eye from separate ocellar units, within the limits of the Class. It remains possible that the eye was formed in some pre-Crustacean ancestor by a coalescence of units each with numerous retinal cells. If this is the case the single reduced cell commonly found in the eyes of Crustacea may be a persistent indication of an archaic tendency to crowding out of over numerous retinal cells. On the other hand the reduction in the number of cells may be attributable to a series of convergent evolutions, due to the lengthening and narrowing of the ommatidium, and the decrease in size of the lower end of the retinal group, as a consequence of the increased external

/convexity

convexity of the eye as a whole.

Primitively in each ommatidium the cells were probably all of equal size, and arranged symmetrically about a single longitudinal axis, parallel to the longitudinal axis of the eye. The great development of the cones and consequent convexity of the external surface, in conjunction with the relatively small tendency of the deeper parts, and especially of the optic nerve, to copy this expansion, results in the radial convergence of the ommatidia at their lower ends, to the point, where they join the optic nerve. The retinal cells therefore typically tend to decrease in size towards the lower end of the ommatidium.

The regularity of this primitive arrangement may be obscured by loss of cells, by their partial coalescence or their differentiation into groups. Partial loss of one cell is very frequent, as pointed out above. In *Ligia natalensis*, for example, there is a partial coalescence of two of the cells towards the base of the eye (see p.42), while the retinal cells also exhibit a tendency to fall into two groups, composed of three cells each. Similarly in *Sphaeroma* (Parker,1891, p. 95) the cells are differentiated into two groups, the one of three smaller cells, the other of four larger. A similar arrangement obtains in *Penaeus* (Patten,1886, p.631-), in which three of the cells are less deeply

/pigmented

pigmented than the remaining four. These conditions are clearly secondary.

The relations between the ends of the rhabdom, the cone, the retinal and cone cells, have already been discussed - see p. 136 At their lower ends the retinal cells pass through the basement membrane, where they are generally slightly constricted, to become continuous with the nerve fibres below. Laterally the cells of adjacent ommatidia are always distinct. Primitively the adjacent cells within an ommatidium are presumably distinct but in general they run together to a greater or lesser degree. Although portion of their contiguous lateral walls may be obliterated, the number of cells is clearly apparent and the ommatidium is corrugated in outline. In transverse sections the individual cells are petaloid and symmetrically arranged about the central rhabdom structures, except in the cases of the individual cells, which are in the course of degeneration. The peripheral ommatidia are frequently slightly longer than the central.

The nucleus varies in position. It is proximal in the following : *Estheria* (Parker, 1891, p. 76); *Gammarus* (Cussans, 1904, p. 31); *Gammarus chevreuxi* (Huxley and Wolsky, 1933-1934, p. 364); *Limnadia* (Nowikoff, 1905, p. 432 et. seq.); *Ligia oceanica* (Hewitt, 1907, p. 24); *Argulus* (Herter, 1928, p. 159 et seq.). It is distal in the following Decapods: *Herbstia*

/Leydig

(Leydig, 1855, p.408), *Paleomonetes*, *Cambarus* (Parker, 1891, p.110), *Cancer* (Pearson, 1908, p. 159), *Eupagurus* (Jackson, 1913, p. 41). Distal nuclei also occur in *Branchipus* (Nowikoff, 1905, p.432), (Howland, 1911, p.147) and in *Streptocephalus* (see p. 74) among the lower Crustacea, as well as in the Decapods mentioned above and in Stomatopods (Parker, 1891, p.106) and some Isopods such as *Philoscia* (see p. 59), among the Malacostraca. A central nucleus is found in *Serolis*(Beddard, 1884, p.21). In *Ligia natalensis* (see p. 43) the position of the nucleus appears to vary even within the cells of a single ommatidium. This is also the case in *Penaeus* (Patten, 1886, p. 631). In some cases the nucleus has been recorded as proximal to the basement membrane as in *Talorchestia* (Watase 1890, p. 396), in *Idotea robusta* (Parker, 1891, Pl. V, Fig. 48) and *Argulus* (Parker, 1891, p. 83). The condition in *Argulus* is not confirmed by Herter, (1928, p.159 *et. seq*). It is not possible to fix a primitive or typical position for the nucleus, nor does there seem to be any constant variation in the size of the cell or rhabdom, which might indicate the primitive position, although the nucleus is frequently located in a swollen region of the cell (Jackson, 1913, p.40), the position of this varies with the position of the nucleus. The displacement of the nucleus below the basement membrane is clearly secondary. The nucleus varies in size and shape. In Stomatopods (Parker, 1891,

/p.106

p.106), as in Eupagurus (Jackson, 1913, p.41), it is large relative to the cell. In most other cases the nuclei appear to be of normal size - that is, of the same order of size as the cone cell nuclei, as in Ligia natalensis and Streptocephalus (see pp.43,74). The nucleus may be reniform and elongated as in Mysidacea (Parker, 1891, p.101), or oval as in Branchipus gelidus (Howland, 1911, p.147) or spherical to ellipsoidal as in Ligia natalensis (see p.43) and Streptocephalus (see p.44). The nucleus is frequently surrounded by an outer, darkly staining layer and contains distinct chromatin material, with one or two large nucleoli, as is usual in sense cells (Huxley and Wolsky, 1933, p. 381). Such a structure has been described in all cases, in which attention has been paid to the details of the nucleur structure of the retinal cells,and are apparent in Philoscia and Streptocephalus (see pp.59,74)

The cytoplasm generally appears to be somewhat coarsely and densely granular as in Ligia, Philoscia and Streptocephalus (see pp.43,59,74) The coarser regions of the cytoplasm consist of pigment granules, for the most part of more or less uniform size, with some larger granules scattered among them. The position of the pigment in the cells varies according to the light. No study of this was attempted. In animals killed in light, without special treatment, the pigment is generally found round the rhabdom, towards the out-

/sides

sides of the cells and along the basement membrane. Such a distribution has been described in Ligia, Philoscia and Streptocephalus (see pp.42,60,74). Hewitt supposes that in Ligia oceanica (1907, p. 24) the pigment, which appears to lie within the retinal cells, is really located in processes of the accessory pigment cells. This does not seem to have been suggested in other cases and does not appear to be the case in Ligia natalensis (see p.44), where the pigment granules clearly lie, within the retinal cells themselves. The pigment contained within the retinal cells is typically a black melanin material. A red pigment usually preceeds this in development. Further particulars of these pigments are given in connection with the accessory pigment cells, in which they also occur (see p~~p~~.190).

Nerve fibrils, continuations of the optic nerve fibrils, are sometimes apparent as longitudinal streaks in the protoplasm of the retinal cells. These have been described in Branchipus and Limnadia (Nowikoff, 1905, p.432 et seq.), in Apus (Wenke, 1908, p.236 et seq), in Branchipus gelidus (Howland, 1911, p.147), in Ligia oceanica (Hewitt, 1907, p.24), in Eupagurus (Jackson, 1913, p.41) and in Argulus foliaceus (Herter, 1928, p.159 et seq). These nerve fibrillae were seen in the retinal cells of Philoscia - see p.64 In Eupagurus and Apus the fibrils are described as running up the cell to form a loop round the nucleus. Whether or not the

/fibrils

fibrils actually enter the rhabdom is questionable. This is discussed further in connection with the structure of the rhabdom - see p. 116 .

Innervation of the eye.

The views of the earlier authors regarding the innervation of the eye have already been dealt with - see pp. 10.13. Some considered the cone, some the retinal cells as the seat of sense perception. Patten (1886, p.641) contributed his evidence in favour of the former view but considered all the cells in the ommatidium as innervated. It is now generally conceded that in all Crustacea only the retinal cells are innervated, in that they are the nerve end cells of the optic nerve fibres. The retinal cells of a single ommatidium run together below the basement membrane and run as a single fibre in the optic nerve. Each nerve fibre is made up of a number of fibrils contained in a pigmented sheath. The pigment is more concentrated near the basement membrane, and is finally continuous with that deposited along the inner side of the membrane - see Parker (1891, p.116).

Ganglion cells

Ganglion cells are occasionally found above the basement membrane and scattered among the retinal cells. Schatz (1929, p.551) and Huxley and Wolsky (1933-[illegible],

/p.361

p.361) have described such cells in Gammarus chevreuxi. Schatz considers that they are ordinary ganglion cells, which have migrated in and degenerated. Their presence is atypical.

Summary.

The retinal cells are of two kinds, the proximal, retinal sense cells, the generating cytons of the optic nerve fibres, and the distal, retinal pigment cells, derivatives of the former. It seems probable that the ancestor of the Crustacea was provided with eight retinal sense cells.

Among the lower Crustacea seven cells remain in Apus sp. Otherwise the cells have reduced in number to five and sometimes to four. Among the Malacostraca, the eight cells may be retained or one cell wholly or partially lost. This loss of cells is carried further in Isopods and Amphipods in conformity with the general tendency to degeneration. The Isopods have from four to seven cells, the Amphipods from four to five. Some instances of exceptionally large and small numbers are given. These are rare and aberrant. There is no evidence of a general tendency to addition of cells by division, conversion, or immigration. The reduced cells are often without nucleus, rhabdomere or nervous connection, and are clearly degenerate. Parker's view of five as the primitive number of cells is rejected. Reduction appears to have occurred more than once and is fairly rapid. The reduction in the number of cells may be due to the persistence of an archaic tendency to reduction if one

/assumes

assumes that the eye was built up of a number of separate units, whose size, on approximation, would require reduction. Alternately the reductions may be a series of convergent evolutions necessitated by the lengthening and approximation of the inner ends of the ommatidia, in relation to an increased external convexity. Primitively the cells are equal in size, symmetrical and arranged about a single longitudinal axis. The convexity of the outer surface of the eye imposes a narrowing on the inner ends of the retinulae. This primitive arrangement is obscured in some cases by the loss of cells, coalescence or grouping with differences in the size or pigmentation of the cells. The relation of the upper end to the cone apparatus has been described on page 136 . At their lower ends they are contracted, pass through the basement membrane, and are continued in the optic nerve, each fibre of which is formed by the running together of the nervous continuations of the retinal cells of one ommatidium. \ Laterally adjacent cells run together, although the number of cells remains apparent in the surface corrugations of the retinula. In large eyes the peripheral ommatidia are longer than the central. The nuclei are very variable in position, shape and size. They frequently lie in a swollen region of the cell. They are provided with a darkly staining wall, densely granular contents, nucleoli and readily visible chromatin material. The cytoplasm is

/coarsely

coarsely and densely granular and contains pigment granules of different sizes both in the cells and their nervous connections. These are distributed according to the illumination. The pigment is typically a melanin. This may be preceded in development by a red material, discussed further below - see pp. 173 In some cases the nerve fibrillae are seen to pass from the nerve fibres through the cytoplasm of the retinal cells. They are not known with any certainty to be continuous with the rhabdomere plates.

The rhabdom.

Each retinal cell secretes along its inner border a rod or rhabdomere. The rods of a single retinal group may become more or less approximated and fused to form a single rhabdom, in which the original parts may or may not lose their identity.

Occasionally these structures have been stated to be absent, for example in Palinurus argus as described by Will (1840, p.15) and Parker (1891, p.110) there is apparently no rhabdom, unless the transparent, axial part of each retinal cell can be regarded as representing a separate and degenerate rhabdomere. Typically a rhabdom is present and its apparent absence may be due to difficulties of preservation or staining.

The number of rhabdomeres must primitively have corresponded to the number of retinal cells, each cell giving rise to a rhabdomere along its inner, longitudinal, axial border. This condition persists only in Ostracods and Branchiura among the lower Crustacea - (see references below). Among the higher Crustacea a similar condition found in some Isopods and Amphipods is clearly a product of the degeneration of these eyes. For the most part there is a tendency to the condensation of the rhabdomeres into a single rhabdom, where the primary division into rhabdomeres is obscured, to a greater or lesser extent, the central cavity being more or less obliterated, while in some cases a secondary segmentation of the rhabdom is set

/up,

up, so that it is divided into units each of which does not comprise a single rhabdomere.

Among the lower Crustacea all the Branchiopoda have eyes with coalesced rhabdomeres. In the Anostraca the rhabdom is a solid rod, in which no structure can be made out, for example in the following : *Branchipus grubei* (Patten, 1886, p. 645); *B. vernalis* (Parker, 1891, p.75); *B. stagnalis* (Nowikoff, 1905, p. 432 et seq.); *B. gelidus* (Howland, 1911, p.147) and in *Streptocephalus* (see p. 76). In these cases, although the retinal cells are themselves equal in size, five in number, and surround the rhabdom symmetrically, the sides of the rhabdom do not correspond simply to the retinal cell with which they are in contact. The rhabdom is squarish rather than pentagonal in most cases except that of *Branchipus stagnalis* (Nowikoff, 1905, p.432) in which the rhabdom is pentagonal with a central cavity. Without a developmental study it does not seem possible to decide, whether the condition in the majority of those described above is due to suppression of one of the rhabdomeres, although the corresponding cell is not in any way suppressed, or whether, as seems most likely, the rhabdomeres have formed a complex structure in which all trace of the original segmentation has been lost. The pentagonal form of the rhabdom, with one side corresponding to each retinal cell, and the presence of a central cavity in *Branchipus stagnalis*, as described by Nowikoff (1905, p. 432 et seq), argues the retention in this

/species

species of the primitive form of the rhabdom.

Among the Notostraca the rhabdomeres are coalesced in Apus productus (Wenke, 1908, p. 236 et seq), among the Conchostraca fused and the rhabdom, as a whole, round or pentagonal in transverse section. This is the case for example in Limnadia (Parker, 1891, Fig. 39). Similarly in Cladocera the rhabdom is solid, as for example in Evadne (Parker, 1891, Pl. 1V, Fig. 45), is solid.

Among the Ostracods, the separate rhabdomeres remain apparent, the rhabdom being longitudinally ribbed (Calman, 1909, p. 66). In the Branchiura the rhabdomeres are unfused, as in Argulus sp.(Parker, 1891, p. 83). In Afoliaceus, Herter (1928, p. 159 et seq) does not appear to have examined the rhabdom in detail, although he mentions the presence of a rhabdom cavity.

Thus among the lower Crustacea separate rhabdomeres are found only among Ostracods and Branchiura. The primitive condition appears to persist in these forms - that is separate rhabdomeres, with a central cavity at least in Branchiura. In the Branchiopods the rhabdoms are fused to a solid rod, in which the central cavity has disappeared in all the cases described except in one Anostracan. This maintains the original shape with one side related to each retinal cell. Generally the rhabdom is rounded or square - so that its sides bear no relation to the retinal cells of a five celled reticular group.

/Among

(Huxley, 1896, p.118), Eupagurus (Jackson, 1913, p. 41). In other forms the rhabdomeres are compressed to form a rhabdom, round in transverse section, without trace of the original segmentation. This is the case in Homarus (Watase, 1890, p. 299); Palaemon sp. (Steele, 1907, p.194); Amphion (Hanstrom, 1933, p. 387 et seq.). In some Acanthephyridae the rhabdomeres remain distinct and project each into its own cell so that the rhabdom as a whole has a seven rayed appearance (Hanstrom, 1933, p. 387). In others the eight original rhabdomeres fuse in pairs so that the rhabdom is cross shaped. The relation of the rhabdom to the retinal cells in Decapods is as follows :- In those in which a square rhabdom is present, Grenacher considered (1877, p. 31) that rhabdomeres were formed by alternate retinal cells within the eight celled retinula. Jackson (1913, p. 41) considered that every two retinal cells, assuming eight as the primitive number, take part in the secretion of one quarter of the rhabdom, each quarter of which is made up by transverse plates, supplied alternately by the two related cells, so that any one retinal cell, if separated out, would have a toothed or cogged appearance. The cogged edge is dovetailed into that of the adjacent cell. In those in which the rhabdom is round or oval in transverse section, all the rhabdomeres appear to have amalgated to form a single rod, in which all trace of segmentation is lost. Where the rhabdom is cross shaped, the rhabdomeres of the eight

/primitive

primitive cells have fused in pairs, one ray of the rhabdom lying between each successive pair~~s~~ of retinal cells. In the seven-rayed form the rays of the rhabdom correspond to the rhabdomeres and preserve their primitive relation to the cells. The condition in Palinurus argus (Parker,1891, p.110,) in which each retinal cell is provided with a transparent, axial part at the inner edge of the cell has been described above. If these parts are to be regarded as remains of the rhabdom, the eye represents a reversion to the primitive condition, in which separate rhabdomeres were arranged about a central cavity. The primitive and typical form appears to be the square type in which a secondary segmentation may or may not be apparent. In some this is further compressed to assume an oval transverse section. The remaining forms, in which the rhabdome consists of separate rays, represent reversions towards the condition in the ancestors. According to Hanstrom (1933, p. 387 et seq.) this is related to a deep sea habitat.

In the Decapods the central cavity is usually obliterated, although the remains of it may be represented by a small pear shaped cavity at the distal end of the rhabdom as in Eupagurus (Jackson, 1913, p.41).

In the Stomatopods the rhabdom is square and divided into four equal segments as in Squilla (Steinlin, 1868, p. 17 et seq.), (Grenacher, 1879, p.175 (Taf.X1, /Fig.122)

Fig. 122) and in *Gonodactylus* (Parker, 1891, p.107). The relations of the cells to the rhabdom are as in Decapods, that is, each rhabdom face is flanked by two cells, or, where one cell is rudimentary or lost, one of the rhabdom faces is flanked by one complete cell and the rudimentary cell (where this is present).

Among the remaining Division of the Malacostraca - the Peracarida - the condition of the Mysidacea is similar to that of the Decapods, there being a four-sided rhabdom divided into four equal parts and bearing the same relation to the retinal cells as outlined in the preceding paragraph. This is the condition in *Mysis flexuosa* (Grenacher, 1879, p.114), and *Mysis stenolepis* (Parker,1891, p.102).

In the Cumacea Burmeister's description of the eye in *Cuma rathkii* (1883, p. 35 et seq.) is the only one available. The eye in this form was degenerate and without well defined structure. No description is available for the Tanaidacea.

In the Isopods and Amphipods the rhabdom is very variable. Among the Isopods there are some forms in which the rhabdom is a solid structure, without a central cavity. This appears to be the case in *Porcellio* (Beddard, 1887, p.443). In *Idotea robusta*, the rhabdom is nearly square in transverse section and does not show even at the proximal end any trace of rhabdomeres (Parker, 1891, p. 88, Pl.V, Fig. 46). This structure is surrounded

/by

by seven cells plus one rudimentary retinal cell and its condition is thus very similar to that in Mysidacea. In *Arcturus furcatus* (Beddard, 1890, pp. 368, 369), the distal part of the rhabdom is solid and marked off by four perpendicular sides, although it is surrounded equally by six cells. Proximally six rhabdomeres are separate, each attached to its own cell. Similarly in *Aega* (Beddard, 1887, p. 443) and in *Serolis* (Beddard, 1887, p.235) the rhabdomeres are fused only in the upper part of the rhabdom. In *Cymothoa* (Beddard, 1887, p.444) the seven rhabdomeres are in contact at their upper ends but do not fuse. Lower down they diverge, each projecting into its own cell. In *Ligia oceniaca* (Hewitt, 1907, p.25) and in *Ligia natalensis* (see p.43) the rhabdomeres are related to their own cells but they are laterally contiguous to form a cylinder with a central canal running through it. In some cases the rhabdomeres are completely separated, so that each lies within its own cell projecting into a central cavity. This is the case in the following : *Porcellio scaber* (Grenacher, 1879, p.30), *Porcellio sp.* (Parker, 1891, p.88), *Sphaeroma* (Bellonci, 1881, p. 98), *Cymothoa* (some spp.) (Beddard, 1887, p.443), *Ligia oceanica* (Hewitt, 1907, p. 25), *Ligia natalensis* (see p.43) and *Philoscia muscorum* (see p.62). In all these cases except in *Sphaeroma* the rhabdomeres project one into each cell. In the latter the rhabdomeres project between the cells, i.e. are formed at the edge of one cell, at the interface between this and the adjacent cell. Occasionally the rhabdomeres may lose

/contact

contact with the retinal cells, through part of their length. This is the case only in *Serolis* (Beddard, 1884, p. 21), where the rhabdomeres are proximally reduced to an axial fibre running between the "hyaline" cells. This, like the rest of the *Serolis* eye structure, is exceptional - see p~~p~~.199

In the Amphipods a similar series can be traced, from a solid rhabdom to a tubular structure and finally to one in which the rhabdomeres are separate(and each related to its own cell) being disposed about a central cavity. Thus in *Hyperia* a solid rod is present (Grenacher, 1879, p.51). In *Phronima* (Claus, 1879, p.128), (Carriere, 1885, p.165, Fig. 128), each rhabdomere is related to its own cell, but they are laterally contiguous so that the rhabdom comprises a hollow rod. In the following forms the rhabdomeres are completely separate and each lies within its own cell : *Hyperia galba* (Carriere, 1885 p.161, Fig. 124), *Gammarus locusta* (Grenacher, 1877, p.114), *Gammarus pulex* (Carriere, 1885, p. 157). In *Gammarus ornatus* (Parker, 1891, p. 71, Pl.1, Fig. 6) each rhabdomere is separate but has the form of an elongated plate, folded along its longitudinal axis into two halves, inclined at right angles to one another, with each retinal cell enclosed along its inner margins by one of these rhabdomere folds. Four cells are arranged in this way with a fifth at the end of one of the rays. A similar condition obtains in *Talorchestia* (Parker, 1891, p. 71). Thus among the Amphipods the rhabdom is primitively presumably

/solid

solid as in the order Mysidacea, the most primitive of the Peracarida. Typically it tends to degenerate, all the intergrades from a coalesced structure to separate rhabdomeres around a central cavity being known.

Primitively the rhabdomeres were presumably of the same length as the retinal cells and extended from the apex of the cone apparatus to the basement membrane, as elongated rods along the inner longitudinal axes of the cells, projecting into the central lumen. Typically the rhabdomeres occupy the same position but are coalesced. There is no marked tendency for the rhabdomeres to extend up round the sides of the cone. They never extend below the basement membrane, but may stop some distance short of this as in Branchipus (Howland, 1911, p.147), where they are only three quarters of the length of the cells. A similar shortening is seen in Stomatopods (Parker, 1891, p.112) and in Philoscia (see p. 6I). The abbreviation is never at the anterior end and the contact with the cone apparatus has been described - see p.I36 .

The function and fine structure of the rhabdom.

The function and structure of the Arthropod rhabdom in general has been considered above - see pp. II,I3 Despite the earlier views to the contrary, some of which have been outlined on pp. I3.I6, it is now apparent that the retinal cells are nerve-end cells and contain the endings of the nerve fibrillae of the optic nerve fibres. Opinion is divided as to the relation of the fibrils to the rhabdom.

Some authors who have been unable to find any

/structure

structure in the rhabdom, or to trace the nerve fibrils into the rhabdom, have considered the latter as a chitinous rod, a secretion of the retinal cells, similar in origin and function to the secretion of the cone and corneal cells. Such a condition was described by Chatin (1877-[illegible], p.1 et seq) in Trypton, Lysianassa, Caprella, Cypridina, by Bullar (1879, p. 513) and Eggert (1931, p.33) in Cymothoa, by Watase in Cambarus (1890, p. 297), by Parker in Palinurus argus (1891, p.110) and by Tschuganoff in Leptodora kindtii (1913, p. 357). A similar condition obtains in Streptocephalus (see p.76). It is possible that the absence of plates in these eyes is to be variously attributed to the inadequate techniques of earlier authors, to degeneration of the eye as a whole, as in Cymothoa, or possibly to the cementing of the plates to one another.

For the most part rhabdom plates are clearly present in Crustacean eyes. This lends itself to the view that the nerve fibrillae run into the rhabdom and end on the plates. In practically all cases, other than the above, in which the rhabdom has been examined with any care, plates have been recognised. These structures were described in some cases by Schultze (1868) and Chatin (1877) among the earlier authors.

The plates are normally arranged in a series parallel to one another and perpendicular to the main axis of the eye and to the incident light. Sometimes the arrangement is more complicated. This is the case in Penaeus (Patten, 1886, p. 630), where the rhabdomeres consist of

/stratified

plates, with the striae of alternate plates perpendicular to one another. In <u>Philoscia</u> the plates appear to form series radiating out from a central axial bar (at different levels) to the outer thickened periphery, (see p.52). These conditions appear to be exceptional and it is not apparent what dioptric or sensory function is subserved by so elaborate a series of differently orientated components.

Occasionally pigment is found between the plates as in some Cymothoidae, as described by Beddard (1887, p.443). This is exceptional and does not appear to have been described in other forms.

Although the plates are present in the majority of Crustacea, there is as yet no real proof that the nerve fibrils, which can be seen in the cytoplasm of the retinal cells, are really continuous with the rhabdom plates. The question of the nature and function of the rhabdom therefore remains an open one. In general the modern view regards the rod as cuticular in material and as skeletal and refractive in function - see Machatschke (1936, p. 90).

<u>Summary</u>.

A rhabdom is typically and primitively present. Primitively this comprises several rhabdomeres, each separate and attached to its own cell, lying along its inner longitudinal axis and projecting into a central cavity. Typically the rhabdomeres are approximated and form a solid rod with the central cavity obliterated. Intergrades between these two types are common. Among the lower Crustacea the

/rhabdomeres

rhabdomeres remain separate [illegible] in Ostracods and Branchiura with the central cavity persisting in the latter. For the rest they are completely fused in all known cases except in one Anostracan. The primitive relation of the sides of the rhabdom to the retinal cells is lost in some cases, with five cells surrounding a four sided rhabdom. In this respect the Branchiopods show an [illegible] advance over the remaining lower Crustacea. Among the Malacostraca a square rhabdom is perhaps to be regarded as both typical and primitive. Primitively each of the four sides is in relation to two of the retinal cells. In some cases a secondary segmentation of the rhabdom into quarters is set up. In this case the original rhabdomeres of two adjacent cells probably have their plates dovetailed together. The fused rhabdom may be round in transverse section. Degenerate rhabdomeres are occasionally found in Decapods, where they may separate completely, or be fused in separate pairs. The remnants of a cavity are occasionally to be seen. In Isopods and Amphipods such degenerations are commoner in the retinal cells, as well as in other features of the eye structure. This may result in the formation of cylindrical rhabdoms, in which a central cavity is apparent, or in the complete separation of the rhabdomeres, within or between the cells.

The fusion of the rhabdomeres may be more marked at one end than at the other. Some exceptional conditions are mentioned. Primitively the rhabdomeres reach from the apex of the cone apparatus practically to the basement

/membrane

membrane. Occasionally the rhabdom structures stop short of the membrane. They do not exhibit any marked tendency to extend up round the cones. The plates appear to be absent in some cases. This may possibly be due to faults in technique, degeneration of the eye, or cementing of the plates. The "Stiftchen" or plates, whether dioptric, cuticular structures or neurofibrillar endings, are typically present and are arranged parallel to one another and perpendicular to the axis of the ommatidium. The exceptional and complicated forms in Penaeus and Philoscia are mentioned. The pigment described as lying between the plates in some Cymothoidae, is exceptional. The nerve fibrils in the retinal cells have not been clearly demonstrated to enter the rhabdom, and the question of the nature of the rhabdom as cuticular or neurofibrillar is still disputed.

The pigment cells.

The pigmented cells of the Crustacean eye, other than the pigmented, retinal sense cells, are of two types - the distal, retinal pigment cells and the accessory, pigment cells. They differ from one another in the following particulars. The distal, retinal cells are derived from the true, retinal cells and lie around the cone in a single layer, seldom made up of more than two cells in each ommatidium. In contrast to this, the accessory pigment cells are not derived from the retinal elements and may not even be of ectodermal origin. They may lie anywhere between the cornea and the basement membrane, where they occupy the inter-ommatidial spaces. They vary considerably in number and position, but there are usually more than two to each ommatidium. Further, the accessory cells differ as a rule from the retinal cells and their derivatives in having a non-nucleolated nucleus - see Parker (1891, p. 119) and Huxley and Wolsky (1933-1[illegible], p. 369).

The distal retinal pigment cells

These cells occur only in some Malacostraca. They have often been confused with the accessory, pigment cells and have been designated "iris" pigment cells by some authors including Korscheldt and Heider (1899, p.169) and Sedgewick (1927, p. 330). This is an unfortunate nomenclature, as they have no relation to the "iris"

/pigment

pigment cells of insects, which are modified corneal hypoderm cells, forming a pigmented sheath about the cone.

The distinction between these and the accessory pigment cells was first clearly pointed out by Parker (1891, p.120), who described the cells in Decapods (Homarus, Paleomonetes, 1891, pp.119-120,) Stomatopods (Gonodactylus, 1891, p. 106) and Mysidacea (Mysis, 1891 Pl. VIII, Figs. 77, 78, 87) as well as in the Isopod Serolis (1891, p. 95) - a form in which the eye is exceptional in many respects(see p. 119) He considered that the pigment cells surrounding the cone in Leptostraca in Nebalia (1891, p. 98) were probably of this type although their number was unusually large. Subsequent authors have confirmed the presence of these cells in the following Decapods : Cambarus (Watase, 1890, p. 299), Paleomonetes (Congdon, 1907, p. 541), (Steele, 1907, p.140), (Welsh, 1930, pp. 386, 459), Eupagurus (Jackson, 1913, p. 41). They are also present in Serolis according to Watase, (1890, p. 284). Although the cells were not found in Amphipods by Parker, they were subsequently described in Gammarus chevreuxi by Huxley and Wolsky (1933 - [illegible], p. 359).

Parker put forward the following evidence that the cells were of retinal origin and not merely accessory pigment cells. The nuclei resemble those of the

/retinal

retinal cells in containing one or two nucleoli in both embryo and adult. In this respect they differ from the accessory cells. (See Parker, 1891, pp. 95, 106, 117). The continuation of the cells through the basement membrane in Homarus and their possession of a vestigeal axial border resembling a rhabdom in Mysis are probably remaining features indicating their retinal origin. (See Parker, 1891, p.120, Pl. V111, Fig. 77). Moreover the confluence of these cells with the retinal sense cells in Gammarus chevreuxi has been held to indicate their common origin (See Huxley and Wolsky, 1933 - 1934, p.367).

These cells may be derived from the retinal cells by migration of whole cells, or by division and upward migration of cells newly divided off from the retinal cells proper. Migration alone accounts for the condition in Serolis according to Parker, (1891, p. 95). There are two distal and four proximal retinal cells as compared with the condition in many other Isopods, in which there are six sense cells and no distal retinal pigment cells.— (Beddard, 1887, p. 443). In Mysidacea, Decapods and Stomatopods the relative numbers of the cells indicate that the distal retinal cells are formed by division of two of the true retinal cells with an upward migration of the newly formed parts. In Gammarus among the Amphipods the distal cells are five in number and thus correspond to the true retinal cells, and are

/formed

formed by division of all of these. (See Huxley and Wolsky, 1933 - 19[illegible], p. 367). In Nebalia there are seven of both the distal and proximal retinal cells. If the former are indeed of retinal origin (of which Parker (1891, p. 98) was in some doubt, on account of their large number), they must be formed as in Amphipods.

The separation of the distal pigment cells from the retinal sense cells appears to accompany an elongation of the ommatidium. It is possible that the absence of these cells in some Malacostraca is a consequence of a secondary shortening of the ommatidium. The cells might well have been secondarily lost in this way in Amphipods, since, where they occur in Gammarus chevreuxi, they show indications of degeneration in the reduction of their nuclei and in the late confluence with the retinal sense cells. (Huxley and Wolsky, 1933-[illegible], p. 369).

Primitively the cells are absent. This is also the typical condition in Crustacea other than Malacostraca. Among the latter the cells occur in Stomatopods, Decapods, Mysidacea, some Amphipods and Isopods and possibly in Leptostraca. Although they are not known to have been distinguished from the accessory pigment cells in other forms, it is probable that they are typical of the Malacostraca as a whole.

Summary.

That the distal retinal pigment cells are of

/retinal

origin is indicated by their nuclear structure, and the occasional persistence of rudiments of nerve fibres and rhabdomeres, and their occasional confluence with the retinal cells. They are to be distinguished from the accessory pigment cells and the "iris" pigment cells of insects. They are primitively absent and do not occur in the Lower Crustacea. They appear to be typical of Malacostraca, where they are formed either by migration of entire retinal cells, or more usually by division of some (or occasionally all) of the cells and upward migration of the newly formed parts. In some Malacostraca in which they are absent, their loss is probably to be accounted for by a secondary shortening of the ommatidium. They form a single layer of cells about the cone and do not as a rule exceed two in number, although five or possibly seven cells are occasionally found.

The accessory pigment cells.

Among the Entomostraca accessory pigment cells are usually absent. They have, however, been noted in Gladocera in Leptodora sp. by Parker (1891, p. 77), although they are not mentioned as present in L. kindtii by Tschuganoff (1913, p.350). They have also been described in Branchiura in Argulus by Parker (1891, p.83) and Herter (1928, p.159 et. seq.).

Among the Malacostraca accessory pigment cells are the rule. These have been described in Leptostraca in Nebalia (Claus, 1888, pp.15 et. seq.). Parker, however, considered that these were more probably distal, retinal pigment cells. They were noted in Euphausiacea in Stylocheiron (Chun, 1896, pls. XVl-XX) and have been described in the following Decapods : Astacus (Carriere, 1885, p.109), Penaeus (Patten, 1886, p.636), Parker, 1891, p.117), Homarus (Parker, 1890, p.25), Crangon, Cambarus, Cardiosoma, Pagurus (Parker, 1891, p.117), Paleomonetes (Parker, 1896, p.493), (Steele, 1907, p.170), (Welsh, 1930, p.459), Palaemon (Moroff, 1911, p.144), Cambarus (Day,1912, p.305-343), Eupagurus (Jackson, 1913, p.41), Amphion (Hanstrom, 1933, p. 387 et. seq.), Acanthephyridae and Sergestidae (Welsh and Chase, 1938, pp.364, 574). They have been noted in Mysidacea (Parker, 1891,p.107), (Korscheldt and Heider, 1899, p.109). Theyooccur in Isopods generally according to Grenacher (1879, p.107) and

/have

have been noted in particular in the following :
Sphaeroma (Bellonci, 1881, p. 99), Idotea (Parker, 1891, p.88), (Peabody, 1939, p.525), Serolis (Watase, 1890, p.294) Ligia oceanica (Hewitt, 1907, p. 25), L. natalensis (see p.46). They are absent in some Isopods as in Philoscia (see p.59). They are known in the following Amphipods : Gammarus sp. (Carriere, 1885, p.157), (Cussans, 1904, p.31), G. pulex, G. ornatus (Parker, 1891, p. 71), G. chevreuxi (Parker, 1891, p. 71), (Sexton and Wing, 1916, p.18), (Ford and Huxley, 1929, p. 67), (Sexton, Clarke and Spooner, 1930, p.204, 1932, p. 308), (Welsh, 1930, p.386), (Sexton and Clarke, 1936, p.694), (Huxley and Wolsky, [illegible]-1934, p. 366). They have been described in Stomatopods in Gonodactylus (Parker, 1891, p.103).

Primitively the cells are absent and this is also the condition typical of the lower Crustacea, in which the occurrence of these cells is rare. They are typical of the Malacostraca.

There is some disagreement as to whether these are of ectodermal or mesodermal origin. In the following cases they have been considered as ectodermal :
In Isopods (Grenacher, 1879, p. 98), in Peneaus (Patten, 1886, p. 673), Serolis and Talorchestia (Watase, 1890, p. 294, 296). They have been considered as mesodermal, in general, by Balfour (1880, p.134) and in particular in the following ; Hyperia (Claus, 1879, p.125), Phronima (Carriere, 1885, p.160); Crangon

/(Kingsley,

(Kingsley, 1886, p. 598), Serolis (Beddard, 1884, p. 21), Mysis (Korscheldt and Heider, 1889, p. 109), (Parker, 1891, p. 103), Gonodactylus (Parker, 1891, p.107), Eupagurus (Jackson, 1913, p. 43), Gammarus chevreuxi (Huxley and Wolsky, 1933-1[illegible], p. 375).

Thus in some Decapods, Amphipods and Isopods both ectodermal and mesodermal origins have been supposed, in Mysidacea and Stomatopods mesodermal only. Other groups in which the cells occur do not seem to have been investigated in this respect.

On phylogenetic grounds Patten considered that these cells were ectodermal and indeed of earlier origin than the "retinophorae" or cone cells. (In this connection he is of course considering the cells, which are now regarded as producing the rhabdom, as of the same nature and origin as the accessory pigment cells). It seems probable, however, that the pigmented cells are not of one kind but of three - the true retinal cells, their distal retinal derivatives and the accessory pigment cells. The retinal cells and their derivatives are certainly ectodermal. The distal derivatives arise, however, only in higher forms and are certainly not primitive. Further, the accessory pigment cells appear to be, at least in some cases, mesodermal rather than ectodermal. Thus Patten's assertion (1886, p.654) that the pigmented cells are all ectodermal and primitive is

/invalid.

invalid. On the contrary they seem to have had a heterogeneous origin and to have arisen at different times in phylogeny.

If the cells are to be regarded as mesodermal it is necessary to demonstrate an extra-retinal origin. The cells could then only enter the eye by one of two methods. Since the basement membrane laid down at the base of all epidermal cell layers is present below the eye, any non-ectodermal cells within the membrane must have found their way in, either through the interstices of the membrane, or by introduction of a band of mesoderm into the eye rudiment, before the formation of the membrane. Both these methods have been described as occurring. In the first case Parker described in Mysidacea (1891, p.103) a nucleus lying in an opening in the fenestrated membrane. This resembled the nuclei of the yellowish pigment cells, which lie on either side of the membrane. This was apparently engaged in migrating into the eye through the basement membrane. Parker considered that this cell had the appearance of passing into rather than out of the retina, and he pointed out that this power of amoeboid movement rendered it probable that these pigment cells were mesodermal. The mesodermal origin of the cells and their migration into the eye has been deduced for other forms on account of the similarity in structure between the retinal acdessory pigment cells and the extra-

/retinal

-retinal, mesoderm, pigment cells below the basement membrane, from which the former seem to originate. Thus in *Gammarus chevreuxi* (Huxley and Wolsky describe (1933-1934, p. 374) the albino eye mutant as containing cells very similar to some, which lie below the basement membrane and which, in this case, ramify outside the head, forming white spots on the body.

The other method of development, which ascribes to these cells a mesodermal origin, has been described by Kingsley (1886, p. 598) for *Crangon*, as follows. After formation of an ectodermal optic pocket "a new element enters the eye at the inner-posterior angle - a thin band of undifferentiated meso-blast. It develops into a single thick layer of connective tissue in which there is an abundant deposition of pigment."

From this it seems clear that, at least in Mysidacea and Decapods, the accessory pigment cells are mesodermal. On the other hand Parker considers (1891, pp. 94, 95) that in *Serolis* the embryology indicates an ecto-dermal origin, which is supported by the general histology of the cells.

If the cells are actodermal, they must either have arisen from actodermal cells, which originally separated the eye units, from which in some distant pre-Crustacean ancestor the eye was possibly formed, or from the ectodermal retinal cells, which, as in the case of the distal retinal pigment cells, were crowded out of the visual axis and lost their sensory function. If these were remains of ectodermal cells originally separating the ommatidia, one would expect their presence to be most marked in the lower Crustacea. This is not the case. On the other hand, if they were differentiated from the retinal cells, it is difficult to see why, unlike the distal retinal pigment cells, they show little similarity to the true retinal cells in their nuclear structure. A difference in the time at which the distal retinal and the accessory pigment cells were differentiated might account for this. In this connection it certainly seems that the accessory cells are more primitive than the distal retinal pigment cells, since they are occasionally found in Entomostraca, where the latter do not occur. If the cells are ectodermal, either of these methods of formation remains possible.

It is possible, indeed, that the accessory cells are not homogeneous among themselves. Whether they are present alone or designed as supplements to distal retinal derivatives, they may be either mesodermal immigations or of ectodermal origin and derived by either one of the two methods suggested above.

Both the number and the position of the cells varies considerably and depend purely on the degree of crowding of the ommatidia. The smallest recorded number is two

/as in

as in *Gammarus chevreuxi* (Carriere, 1885, p.159), *Penaeus* (Patten, 1886, p.643), *Paleomonetes* (Parker, 1891, p. 281) and *Eupagurus* (Jackson, 1913, p. 43). More usually each cell is restricted to a particular region and does not extend as an attenuated band from one end of the ommatidium to the other. The cells may all be massed in one zone or distributed over several such zones.

Examples of the first mentioned configuration are *Paleomonetes* and *Nebalia*, in which the accessory pigment cells are found only in the proximal parts of the retina, (see Parker, 1891, pp. 98, 281) and *Ligia oceanica* (Hewitt, 1907, p. 25) and *Ligia natalensis* (p. 46), where they are restricted to the upper half of the ommatidium. Several zones of pigment cells may occur as in *Hyperia* and *Phronima* (Carriere, 1885, p.161, Fig. 124), where there are three zones, one around the proximal part of the cone, one applied to the distal region of the retinal cells and one near the basement membrane. In *Serolis* there are two such zones, one around the cone and one around the retinal cells, (Beddard, 1884, p. 21). In addition to the main zones of the pigment cells surrounding the cones and the retinulae, there are frequently smaller cells disposed on either side of the basement membrane between the inner ends of the ommatidia and around the nerve fibres, (Parker, 1891, p.14).

Patten (1886, p. 544), considered that typically the pigmented cells were arranged in several zones in a definite pattern of concentric circles, with all the cells extending

/from

from the basement membrane to the cornea. About the nucleus each cell formed a pigmented swelling, while elsewhere it was reduced to a thin hyaline strand-(Patten, 1886, p. 627). He described such an arrangement in Penaeus (Patten, 1886, p. 627). Subsequent descriptions, as quoted above, have not supported his view as to the universal prevalence of such a pattern in the pigment cells. They vary in number and disposition and may lie in one or more zones.

The cells are adapted in shape to fit the interommatidial spaces. The greater the curvature of the surface, the smaller the angle subtended at its centre by an arc of some fixed length. If one supposes that, with increasing curvature, the ends of the ommatidia remain at approximately equal distances apart on the surface of the eye, the angle between the ommatidia becomes more acute and the space to be occupied by the interommatidial pigment cells smaller and narrower. If then the ommatidia become more numerous and their outer ends more crowded, the number and size of the cells will be further reduced. Thus since the number and shape of the pigment cells depends on the external curvature of the eye and the degree of crowding of the ommatidia, they are very variable. In the flattened eye of Gammarus chevreuxi (Carriere, 1885, p.157), (Huxley and Wolsky, 1933-1934, p. 376), the pigmented cells are large and

/goblet-

goblet-shaped, the stem of the pigment cells lying between the upper ends of the conical ommatidia and the proximally expanded part at their base. In *Ligia natalensis*, which has a slightly greater external curvature, the condition is much the same - (see p. 47). In the strongly curved eye of *Penaeus* the cells are reduced to thin strands (Patten, 1886, pp. 631-632). The variation in size, position, shape and arrangement is therefore so considerable that no one condition can be selected as typical.

The boundaries of the cells are not as a rule clear. This is the case for example in *Gammarus chevreuxi* (Cussans, 1904, p. 31), *Eupagurus* (Jackson, 1913, p. 43), *Idotea baltica* (Peabody, 1939, p. 532) and *Ligia natalensis* (p.47). In mutant forms this is exaggerated and the cell boundaries may break down completely as in *Gammarus chevreuxi* white eyed mutant (Sexton and Clarke, 1936, p. 694). The suggestion of Hewitt that the pigment cells in *Ligia oceanica* are prolonged between the retinal cells and the rhabdomeres seems unlikely and has already been discussed, (p. 47)

The nuclei vary in size. They are "readily visible" (Carriere, 1885, p.157), in *Gammarus chevreuxi*, are slightly smaller than those of the retinal cells in *Serolis* and *Sphaeroma* (Beddard, 1887, p. 445), the same size or slightly larger in *Ligia natalensis* (see p.48),

/smaller

of the same eye may contain differant types of pigment. The first and commonest of these is melanin, the black pigment found in all the types of pigmented cells in the eye. This is the light absorbing material which, by its migrations, masks or exposes the sides of the ommatidia and so regulates the amount of light falling upon the sense cells. Secondly there may be a reflector or tapetal material, which is generally white in reflected and yellowish or violet in transmitted light. It appears to increase the amount of light falling on the sense cells by reflection. A third type, a red pigment, is sometimes found. Its function appears to be unknown,

Melanin appears in practically all eyes in the retinal cells, in their distal retinal derivatives, where these are present, and in some of the accessory pigment cells, that is, in those about the cones and retinulae.

The reflector pigment has been described in the following cases : In Amphipods it is known in Gammarus sp. (Cussans, 1904, p. 36), where it is white by reflected and pale yellow by transmitted light, and Gammarus chevreuxi (Huxley and Wolsky, 1933-1934, pp. 375, 378), where a chalky white pigment lies just above the basement membrane. The colourless eye mutant of this species contains refractive non-staining material, which is probably a modified derivative of the substance normally found in these cells: see Sexton and Clarke (1936, p. 694). In Mysidacea a

/fine

fine flaky material, pale yellow by reflected or transmitted light, is described by Parker (1891, p. 93) in *Mysis* sp. and a similar material in Stomatopods in *Gonodactylus* (p.197). In Decapods colourless, transparent crystals, pale yellow in transmitted light, are described in *Penaeus* (Patten, 1886, p. 636) and in *Paleomonetes* (Parker, 1891, Pl. 1V, Fig. 115, 1896, p. 81) as well as in Acanthephyridae and Sergestidae (Welsh and Chase, 1938, pp. 364, 514). The nature of this refractive material is not clear. Patten (1886, p. 637) described it as insoluble in Clove oil, Creosote, Alcohol, Chloroform and Ether. It dissolved in dilute KOH to give a brown solution. He considered that the material resembled certain crystals found in embryonic insects and generally assumed to be of uric acid or its derivatives,

Melanin and the reflector material may be found together in the same eye either in the same or different cells. According to Patten (1886, p. 626) the black material is found in pigmented swellings, while the rest of the pigment cells are thin and reduced and contain, at least in some cases, refractive granules. These colourless bacillar continuations of the pigment cells are not, however, typical and as a rule each cell appears to contain only one type of pigment, the black pigment lying in the cells about the cones and retinulae, and the reflector material in the cells at the base of the eye.

/Red

Red pigment material has been found in some eyes in addition to the types mentioned above. A red carotinoid material has been described in Gammarus chevreuxi by Ford and Huxley (1929, p. 67), by Sexton, Clarke and Spooner, (1930, p. 204, 1932, p. 308) and by Huxley and Wolsky (1[illegible]-193[illegible], p. 373). Sexton, Clarke and Spooner, in their description, pointed out that the first pigment to appear in the embryonic eye was red. Later the rate of deposition of the red pigment falls off rapidly and is gradually obscured or replaced by the black material. It is possible they point out, that the red pigment is being formed all the time, and they suggest that it may even be a necessary chemical precursor of the melanin. The production of the latter is so retarded in some mutants that the eye may retain the red colouring throughout life. (Sexton, Clarke and Spooner, 1932, p. 308).

Sexton and Pantin (1927, p) and Mayer (1943, p.16) point out that the red material is probably of exogenous origin, as are lipochromes in animals generally. Lönnberg (1934-1[illegible], pp. 1-14) extended the knowledge of the presence of this red pigment to almost all orders of Crustacea in which the accessory pigment cells occur. That its presence had not previously been known was due to the masking of the red by the black pigment in the adult and to the fact that this material is soluble in alcohol and has therefore to be investigated in special

/media,

media, such as glycerine.

The exact chemical nature of the carotinoid eye pigment has not been determined. It is possible that this may prove to be related to Kryptoxanthine ($C_{40}H_{56}O$) or β Carotene ($C_{40}H_{56}$), since, in cave animals in which melanin is lost, these are the carotinoids of most frequent occurrence - see Baldwin and Beatty (1941, pp. 143, 151). Whether the red material is a stage in the formation of melanin is still uncertain. Replacement of Lipochromes by melanin deposits in animals, as they grow older, is known in cases other than this, for example, in the epidermis of *Arenicola*, where both McMunn (1886, p. 74) and Fauvel (1899 p. 1273) considered that the change was due to a direct transformation of the lipochrome pigment of the young animal into melanin. It is possible too that the red pigment found in the eyes of young Crustacea, and in mutants and cavernicolous forms, in which the melanin fails to develop, may not be carotinoid in all cases. The formation of melanin (a further stage in the oxidation of 5.6. dihydroxyindole) by the oxidation of tyrosine, involves the formation of red intermediate products of the nature of indole derivatives (Gilman, 1944, p.1128). It is possible that the red material in the eyes may sometimes, at least, be due to the presence of such intermediate oxidation products rather than the presence of carotinoids which are more distantly related to melanin.

/In the

In the same way, the purple colour, which is sometimes seen in the Crustacean eye, is probably due to the presence of an intermediate stage on the formation of melanin, as is the case in Cephalopod eyes (Lederer,1940, p. 306).

Although these cells are very variable and of relatively little importance from the point of view of comparative anatomy, they have attracted a considerable proportion of the interest which has centered on Crustacean eyes, in connection with the physiology of their pigment migration. General aspects of the topic have been dealt with by Exner (1891, pp. 1-206), Parker (1891, p. 281), Frisch (1908, pp. 662-671, 695 - 704) and Buddenbrock (1935, pp. 283-316). Day has worked (1912, pp. 305-343) particularly on *Cambarus*, Welsh (1930, pp. 459-494) on *Paleomonetes* Peabody (1939, pp. 519-533) in connection with *Idotea*, Baldwin and Beatty (1941, pp. 136-143) in connection with *Asellus*. In addition Congdon (1907, pp. 539-548) has dealt with the effect of temperature, ~~and~~ Abramowitz (1937, pp. 407-422) and Brown (1939, pp. 247-355) with the effect of eye stalk hormones on pigment migration and Welsh (1930, pp. 386-395) with the diurnal rythm in the pigment migration. Most of the available information on the anatomy of the pigmented cells of the eyes is to be found in these papers.

/Summary.

Summary.

Although Patten asserted that the pigmented cells were homogeneous and uniformly ectodermal, it seems probable that they are heterogeneous and have arisen at different times. The accessory pigment cells are not primitive and are usually absent in the lower Crustacea. They are typical of Malacostraca. They may lie anywhere between the cornea and the basement membrane and may even extend below this. Their shape, size, number and position are very variable and dictated by the curvature of the eye and the nature of the inter-ommatidial spaces. Patten's elaborate arrangement of the cells in circles and zones is not the typical condition. Each cell is as a rule restricted to a small zone, although in some cases it may stretch throughout the entire length of the ommatidium. Typically there are two zones of cells round the cone and retinulae and another lying just above the basement membrane. The cell boundaries are typically indistinct. The nuclei vary in their size and shape and may be either spherical or irregular in outline. They are typically without nucleoli and lie in a somewhat swollen part of the cell. A black melanin pigment occurs typically in the cells about the cones and retinulae. (It also occurs in the retinal cells and their derivatives). It protects the sense cells and its position is adjusted to admit or

/exclude

exclude light in accordance with the intensity of the illumination. Its migrations are governed partly by a hormone in the eye stalk, partly by a regular diurnal rythm partly by temperature fluctuations. A tapetal or reflector material, usually white in reflected and yellowish or violet in transmitted light, is found in some forms, typically in the cells near the basement membrane, and occasionally in the other accessory pigment cells, together with the melanin but in a separate region of the cell. This is probably a uric acid derivative. In most young eyes, in some mutants and cavernicolous forms, the melanin is absent and a red pigment visible, generally considered to be a carotinoid. Whether the melanin replaces this or is a product of its transformation is uncertain. It is suggested that the red material may sometimes, at least, be other than a carotinoid and, like the purple pigment occasionally seen both here and in Cephalopod eyes, an intermediate product in melanin formation.

Some difference of opinion exists as to the mesodermal or ectodermal origin of the cells. In some cases a mesodermal origin appears to be indicated by the evidence of histology, of immigration of mesodermal cells through the basement membrane, or of their origin from a band of mesoblast in the embryonic eye.

In other cases the embryology and histology appear to indicate an ectodermal origin and a derivation from either interommatidial pigment cells or from very early derivatives of the retinal cells, of the same type as the distal retinal pigment cells, but of earlier formation. Is is probable that the cells are sometimes ectodermal, sometimes mesodermal.

The Hyaline cells and some related structures.

Some abnormal features occur in the eyes of Aegidae, Serolidae and Cymothoidae among the Isopods. In particular the retinal cells may be reduced in number, and the rhabdom peculiarly complicated in structure and development, while so-called "hyaline" cells lie around and below the rhabdom and between the retinal cells.

The retinal cells in Serolidae are reduced to four in number - see Beddard, 1884, p. 21 and Watase, 1890, pl. XXIX, Fig. 1. There are in addition two proximal retinal cells, which according to Parker (1891, p. 95) appear to have been formed by upward migration of two of the retinal cells, of which there must originally have been six. *Aega* and *Cymothoa* (Beddard, 1887, p. 235, p. 444) have a more normal retinal complement of seven cells.

In these forms the structure of the rhabdom is peculiar. In *Serolis schythei* (Beddard, 1884, p.22 : 1887, pp. 234-235, 448) there is a short rhabdom structure in contact with the upper ends of the retinal cells. A transverse section of the rhabdom at this level shows a square outline with a central cavity.

This part ends below in four blunt points projecting into the hyaline cells (see below). Below this the rhabdom appears to be continued towards the basement membrane

/as

as a fine axial filament made up of several fibres not in contact with the retinal cells. In *Serolis cornuta* the upper part of the rhabdom is more complicated - see Beddard 1884, p. 23 - but the essential structure is similar.

The structure in *Aega* appears to be very similar to that in *Serolis schythei* (Beddard, 1887, p. 234). In *Cymothoa* seven rhabdomeres are present, and are in contact with one another although they do not fuse at the upper end of the retinula. Each is conical, projecting down into the hyaline cells. Each is probably continuous with an axial fibre, and although this could not be seen to pass through the hyaline cells, it was thought to be present below the basement membrane.

Two views have been advanced as to the nature of the axial fibrillar structure, running through the hyaline cells to the basement membrane. Beddard (1887, p. 235) pointed out that, although in the adult the axial fibre lies within the hyaline cells and is not in contact with the retinal cells, yet in the young the fibre is square in outline and appears to be derived from the four retinal cells. He considered that the fibrillar structure was to be regarded as an earlier rhabdom, formed by the retinal cells at least in part. This persisted in the adult as a vestige, after the formation of a new adult rhabdom at the upper end of the retinal cells above the hyaline cells. In *Serolis cornuta* (Beddard, 1887, p. 447) the supposed retinal origin of the fibre was considered to be confirmed by the fact that the fibre preceeds the hyaline cells in development while the adult rhabdom was formed later along the sides of the retinal cells.

Parker, on the other hand, (1891, pp. 93-95) considered that the axial structures were continuous with the elongated cone cells. He pointed out that this was in accordance with the fact that the fibrillar structure was differentiated before the rhabdom of the adult.

The transparent hyaline cells peculiar to these eyes, lie below the swollen upper part of the rhabdom, and between the retinal cells. They enclose the lower end of the rhabdom and the axial fibrillar structure.

Two equal cells occur in *Serolis schythei* - (Beddard, 1887, p. 234) and *Serolis* sp (Watase, 1890, pl.xxix). They may be assymetrical as in *Serolis cornuta* (Beddard, 1884, p. 23). They are generally spherical. They appear to be filled with a clear transparent material, which in *Serolis cornuta* is described by Beddard (1884, p. 23), as resembling the cone. Likewise in *Aega* (Beddard, 1887, p. 234) they are clear and homogeneously transparent except that a few pigment granules are deposited on the surface. The Nuclei are irregular granular masses with a nucleolus as in *Serolis schythei* and *S. cornuta* - (Beddard, 1887, pp. 23. 234). The presence of the nuclei renders these indubitably cells and not secretions.

The development of the cells does not appear to have been studied in any detail, most of the attention being devoted to the rhabdom. The fact that they are without continuation below the basement membrane seems

/to

to indicate that they are of other than retinal origin, unless they have secondarily lost their pigment and nervous connections.

The origin and function of the cells is obscure. It was at first suggested by Beddard (1887, p. 450) that the cells might correspond to Patten's colourless visual cells - the retinophorae. It is clear however that the resemblance is superficial, since the hyaline cells do not produce the rhabdom. The similarity to the cone points to a dioptric function, although why a dioptric structure should be necessary or advantageous in such a position is not known. Watase (1890, p. 293) and Parker (1891, p. 96) have considered these as supporting cells. Why such cells should be needed in these particular eyes is not apparent.

Summary

A peculiar formation of the rhabdom in relation to the hyaline cells is found in the eyes of some Aegidae, Serolidae and Cymothoidae. The rhabdom structure is peculiar in that its main part is restricted to the upper part of the retinal cells, where the rhabdom structures are in contact with the retinal cells responsible for their production. This thickened part of the rhabdom projects into the hyaline cells lying below it and between the retinal cells. The rhabdom appears to be continued back as a thin fibre formed by the union of several fibrils which in <u>Cymothoa</u> appear to pass below the basement

/membrane,

membrane. In the adult the fibrillar part is found together with the thickened part of the rhabdom. In the young it preceeds the rhabdom and in some cases the hyaline cells in development. According to Beddard it is produced at least in part by the retinal cells and is a primary rhabdom which persists in the adult together with a new secondary formation. According to Parker this is merely a prolongation of the cone cells. The form and structure of the hyaline cells associated with the rhabdom structure have been described above.

As the hyaline cells do not occur in any other Crustacean eyes, Beddard considered their presence, together with that of the axial fibrillar structure, as sufficient to constitute a new type of compound eye. Parker (1891, p. 97) considered their presence as of no great importance. Whether or not these features represent a fundamental change in the structure or mode of functioning of the Crustacean eye, it is clear that they are highly atypical, while both their origin and function remains unexplained, so that their presence constitutes an isolated departure from an otherwise fairly constant type of eye. The simultaneous occurrence of these peculiarities in a few related types, might argue their assignment to a separate eye-type but this is clearly one isolated in the Crustacea, with no relation to the compound eyes in other Arthropods.

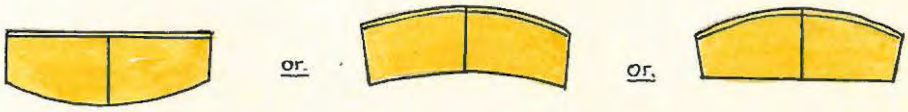
The basement membrane.

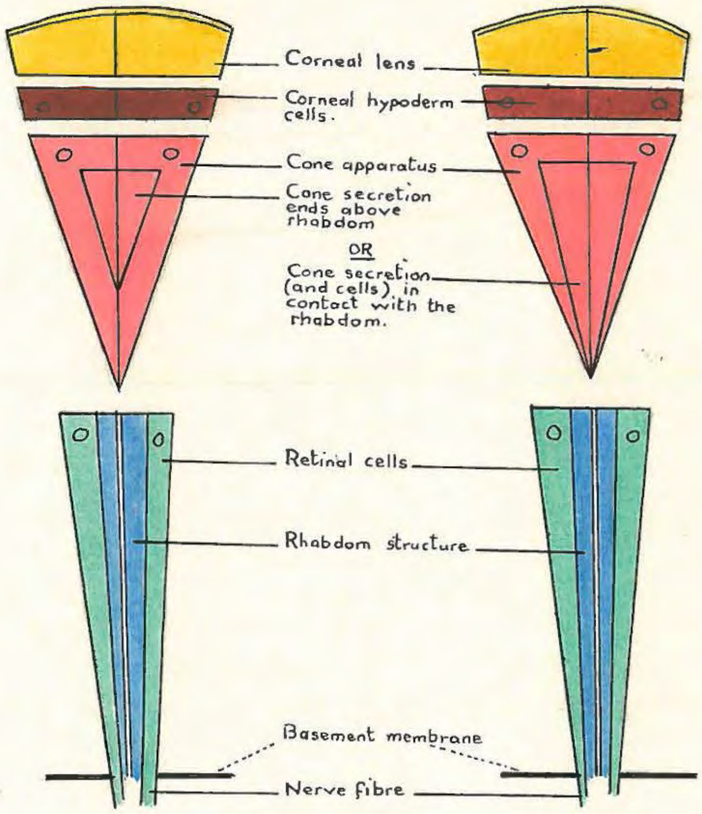
The most detailed description of the structure of the basement membrane appears to be that of Patton in connection with Penaeus (1886, pp. 637-638). He describes the membrane as consisting of connective tissue fibres, fused in part to a hyaline, structureless mass, connected together into a fine network, forming a series of Greek crosses, with the inner surface smooth and compact and the outer more fibrous, with the crosses arranged on a constant pattern throughout the eye. The openings left by the arms of the crosses are bridged by a bundle of diagonal fibres. Through these fenestrations the nerve fibres pass to the ommatidia.

Such an elaborate structure does not appear to have been described elsewhere, and the membrane normally appears as a thin structureless layer formed, like the basement membranes at the base of most ectodermal cell layers, as a simple non-nucleolated membrane. The nuclei, which are sometimes found in the region of the basement membrane, are those of the surrounding pigment cells (Howland, 1911, p. 147).

THE PRIMITIVE FORM OF THE LATERAL COMPOUND EYES OF CRUSTACEA: LONGITUDINAL SECTIONS.

L.S. Corneal lens.





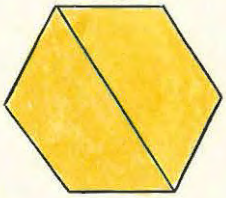
L.S. Entire Ommatidium

(Parts separated somewhat in diagrammatization.)

PLATE 4.

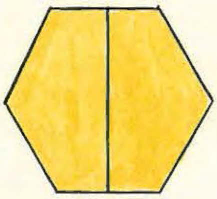
THE PRIMITIVE FORM OF THE LATERAL COMPOUND EYES OF CRUSTACEA. (CONTINUED.)

Transverse Sections.

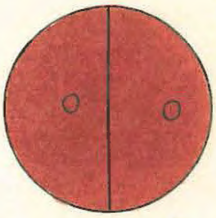


T.S. Facet.

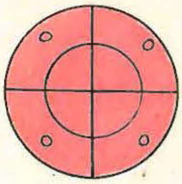
OR.



T.S. Facet.



T.S. Corneal Hypoderm.



T.S. Cone Apparatus.

T.S. Retinal cells.

8-Celled condition.
Primitive for Crustacea as a whole.

5-Celled condition.
Primitively present in the ancestors of many lower Crustacea.

Part III

Conclusions - Crustacea.

1. Occurrence and type.

True lateral compound eyes are typically and primitively present in living and fossil forms with their absence or reduction sporadic and secondary. These may degenerate into a very small number of ommatidia but true lateral ocelli are absent - [illegible]

2. Comparative anatomy.

For comparative purposes an attempt has been made to indicate the range of variation and the typical and primitive condition of each part of the eye. This information has been separately summarised for each section of the Chapter on Crustacea for comparison with similar material appended to the sections dealing with the corresponding structures in the lateral compound eyes of other Arthropods, especially Insects.

3. Basic Plan.

The eyes are typically and primitively built on a common basic plan. (The hyaline cells, found in a few Isopod eyes and in no other Arthropods constitute the [illegible] departure from this). The number of the cells and their arrangement in each of the several parts of the eye show a relatively narrow range of variation. Variations

/within

within an order (except where the eyes are in the course of degeneration) are minor, and within a species are aberrant.

4. Stability and evolution of the eye.

From the stability in the basic pattern of the compound eye, and the absence of evidence for its evolution within the Crustacea, it is clear that the eye was a feature inherited from a distant pre-Crustacean ancestor, where it was already well-developed.

5. Variation of the eye in relation to phylogeny.

The variation in the structure of the eye in different orders bears some relation to that which is generally conceded, on other grounds, to be their phylogentic sequence and relationship. Thus, while the eyes of the lower Crustacea are in many respects heterogeneous, those of the Malacostraca are better developed (especially with regard to the eye stalk, cone cells, retinal cells, rhabdom and pigment cells) and more or less uniform inter se, except in the case of the Peracarida, where the eye has degenerated. Among the Peracarida the eyes of Mysidacea resemble those of the other Malacostrace fairly closely, while those of Isopods and Amphipods have degenerated and altered. This is borne out in detail in each of the sections concerned.

6. Degeneration of the eye.

Where the eye units separate in degenerate eyes of reduced dimension they remain ommatidial in form. Such degenerations (as indicated by a comparative study of some Isopod eyes) results in only some of the changes indicated on p. 23 as necessary to convert a compound eye into a group of ocelli. Thus there is a flattening of the eye as a whole, a reduction in its size and a separation of its units, which become shorter, wider and more cup-like, while the individual lenses increase in size and convexity and become circular and biconvex in form. Corresponding to this change in the dioptric system the pigment isolation of the units decreases in complexity.

The changes in the sense cells and the accessory dioptric structures are not such as to convert the eye into a group of ocelli. Thus the cone is retained, the corneagenous cells showing no tendency to form a vitreous body. The retinal cells generally show no very great increase in number and remain in a retinular group, with the rhabdom structures parallel to the axis of the eye. Although the rhabdomeres may be separated and reduced in size, they are never transferred to the axial faces of the cells. Thus within the Crustacea the lateral compound eyes do not degenerate into a group of ocelli or a single ocellus.

/7.

7. Possibility of the origin of compound eyes from ocelli .

Within the Crustacea there is no indisputable evidence in ontogeny or anatomy of the compound eye having been formed from a single ocellus or a group of ocelli - see appendix on lateral ocelli .

8. General relationships .

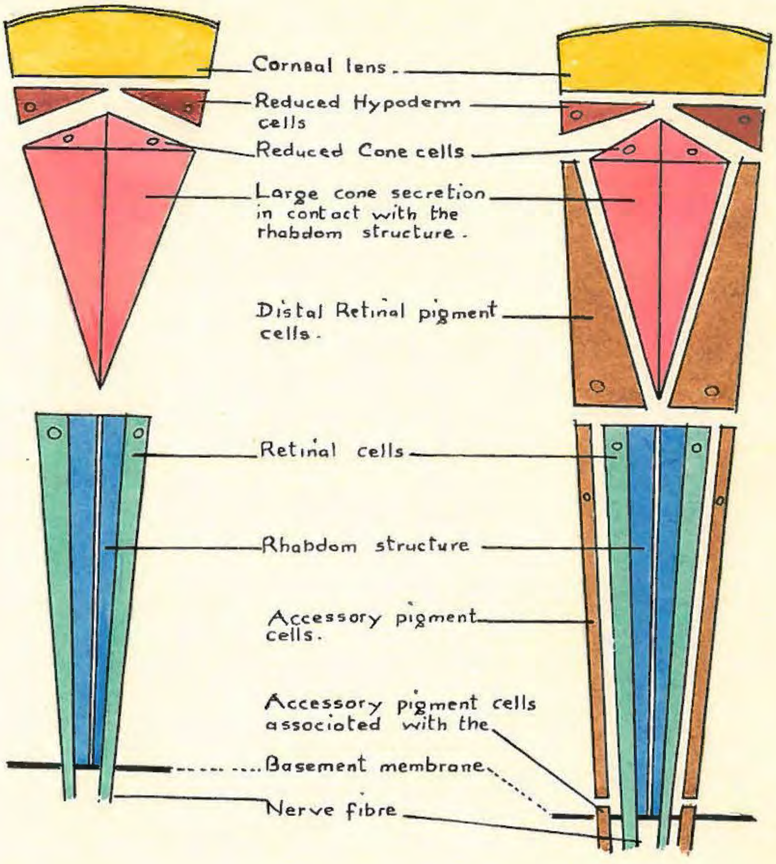
Lateral , compound eyes are typically and primitively present and well- developed.
Their relationships to the eyes of other Arthropods are discussed in the conclusions of the chapters dealing with these.

PLATE 5.

DIAGRAMS ILLUSTRATING AN APPROXIMATION TO A TYPICAL CONDITION IN THE LATERAL COMPOUND EYES OF CRUSTACEA.

LONGITUDINAL SECTIONS

L.S. Corneal Lenses.



In "Entomostraca" as a whole.

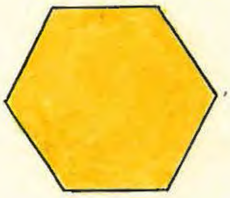
In Malacostraca as a whole.

L.S. Entire Ommatidium
(Parts separated somewhat in diagrammatization)

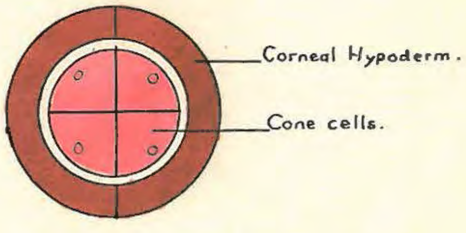
PLATE 6.

DIAGRAMS ILLUSTRATING THE APPROXIMATION TO A TYPICAL CONDITION IN THE LATERAL COMPOUND EYES OF CRUSTACEA.

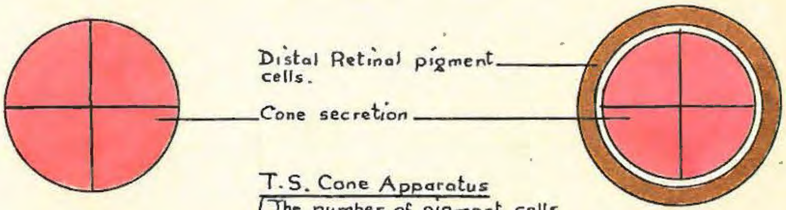
TRANSVERSE SECTIONS.



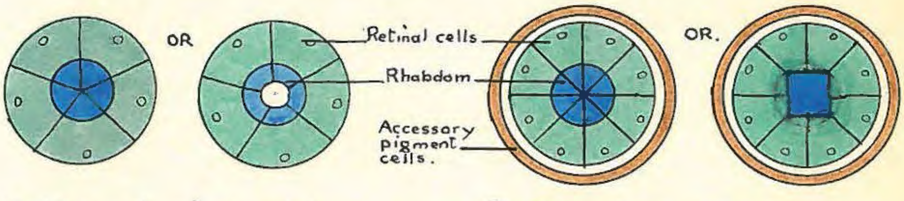
T.S. Corneal lens.



T.S. Hypoderm cells surrounding upper region of Cone cells.



T.S. Cone Apparatus
(The number of pigment cells is variable and they are not shown separately.)



In "Entomostraca" as a whole
5-Celled Condition

In Malacostraca as a whole
8-Celled Condition

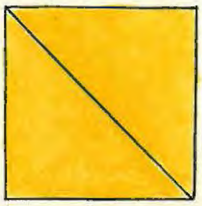
T.S. Retinal Cells and Rhabdom structure
(No one condition of the rhabdom can be selected as typical. The conditions shown are some of the commonest.)

DIAGRAMS ILLUSTRATING THOSE VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYE WHICH OCCUR IN CRUSTACEA BUT NOT IN INSECTS.

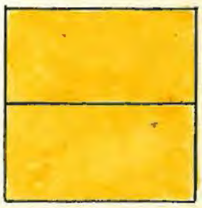
TRANSVERSE SECTIONS.

T.S. Corneal Lenses.

Square (or Rectangular)

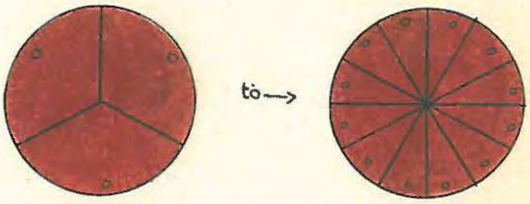


Square diagonally divided



Square transversely divided

2 Cells with opaque Iris diaphragm



From 3 to 12 Cells (irregularly arranged) - associated with unfacetted cornea

T.S. Corneal Hypoderm Cells.

T.S. Retinal Cells showing variation in Number and Arrangement.
(Rhabdom uniformly represented)

Tetragonal + 5 Cells

Pentagonal + 5 Cells

Hollow Pentagon + 5 Cells.

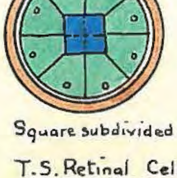
Hollow Cylinder + 5 Cells

5 Lobes + 5 Cells

Circular + 5 Cells

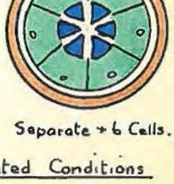
Cross + 8 Cells.

Square + 8 Cells



Square subdivided + 8 Cells

7-Rayed + 7 Cells



Separate + 6 Cells.

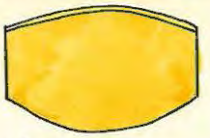
T.S. Retinal Cells showing variations in the Rhabdom, and Associated Conditions of the cells.

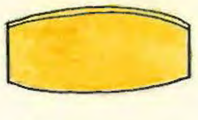
PLATE 8

DIAGRAMS ILLUSTRATING THE COMMONEST VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYE IN CRUSTACEA.

LONGITUDINAL SECTIONS

L.S. Corneal Lenses.

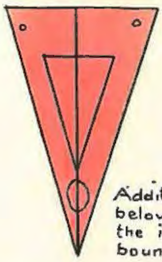

Highly Biconvex

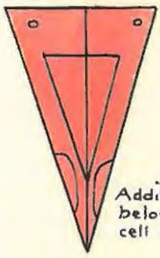

Slightly Biconvex


Flat.

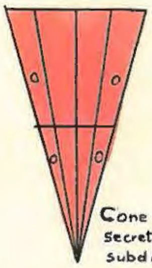

Unfacetted.

L.S. Cone Apparatus.

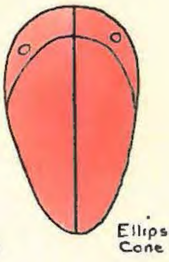

Additional thickenings below the cone on the intercellular boundaries


Additional thickenings below cones on the cell boundaries


Cone segments separate and unflattened.

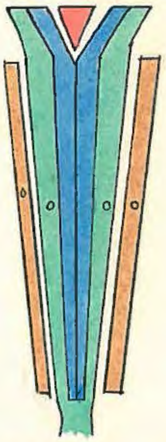

Cone cells and secretions subdivided

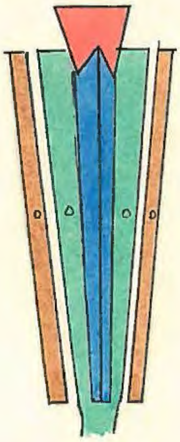

Secretion subdivided

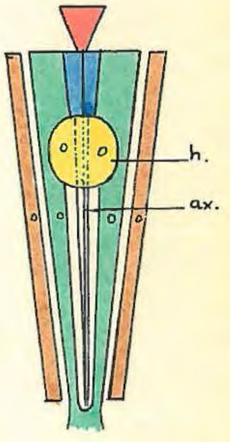

Ellipsoidal Cone.


With Accessory Cone (Isopods)

L.S. Retinal Cells and Rhabdom.


Retinal cells surround cone for a short distance


Cone Apparatus extending between the Retinal cells and the Rhabdom for a short distance



(h) Hyaline cells between the retinal cells
(ax) Axial fibre — See Text.

(N.B. Colours have the same significance as in previous Plates)

Chapter 2 .

INSECTA .

Introduction to the lateral compound eyes of Insects.

The chapter is on the same plan as that dealing with the lateral,compound eyes in Crustacea. The chief interest centres on a comparison of the eyes in the two classes. The first part comprises original descriptions and figures .In the second part the primitive and typical conditions and the range of variation in structure has been indicated for each part of the eye in turn, a summary being appended to each section for readier comparison with the corresponding material on the Crustacean eyes . The third part deals with the conclusions drawn from this chapter on the comparative anatomy, origin and relationships of the lateral compound eyes in Insects.

Part I.

Original descriptions .

I. The anatomy of the lateral eyes of Lepisma sp.

The eyes of *Lepisma saccharina* were described by Hesse (1901). He regarded the earlier work of Carriere (1885) as inaccurate, especially in connection with the retinal cells. These descriptions are not available and no later work on the subject seems to have been published. Hesse's diagram and a few lines of explanation are given by Berlese (1909, p. 660, Fig. 817) and copied elsewhere by Eltringham (1933, p. 35) and Snodgrass (1935, p. 540, Fig. 282B).

As the condition of the eyes in Apterygota and particularly the somewhat problematical arrangement of their retinal cells is here of some interest, a more detailed description of the eyes is given below.

External characters.

Lateral, paired eyes, each consisting of a small group of twelve units, occur on the head near its posterior margin. The eyes are separated by almost the entire width of the head and are dorso-lateral in position. The ocular area is small, even in relation to the head, so that there is some difficulty in obtaining sections at the required angles. The small size of the eye in comparison with that of the Machilida is presumably related to the

/difference

difference in habit. The Machilidae are active hunters while the Lepismata live for the most part in dark crevices among old papers. Each ocular area is irregularly circular in outline. The eyes are of course sessile and immovable and are not as a whole greatly raised above the surface of the head.

__External cuticle__.

The separate units of the eye have facets of a much greater convexity than that of the eye units in Machilidae. The lenses give the upper surface of the eye the appearance of a collection of highly refractive, transparent beads, loosely arranged in more or less regular, alternating rows. Each lens is circular in outline. The lenses are not contiguous, each lens being isolated by a thin area of chitin, through which the deeply pigmented, inner parts of the eye are apparent. The eye surface is colourless and without external decoration. In section each lens is biconvex, with the outer convexity slightly larger than the inner. The lenses are not uniform throughout the eye, those towards the edge being flatter on both sides, although occupying approximately the same area of the head surface as the central elements.

The maximum depth is about 30μ while peripherally each lens is reduced to a depth of about 10μ, the measurements being taken in each case from sections through the centre of the eye unit. The lenses, although continuous with the general body cuticle, are much thicker than the

/latter

latter, which does not exceed 10 μ in depth. Each facet is divided transversely into two parts. The homogeneous outer layer takes up Haematoxylon and other nuclear stains very readily and deeply. The inner part is finely laminated and stains less deeply. Pore canals are absent. The structure of the cuticle over the eye and the body is shown in Figure 23. These two parts differ only in thickness. The facets show no indication of longitudinal division to correspond to their secretion by two separate cells.

Corneal hypoderm.

Two corneal hypoderm cells give rise to each facet. These are shown in Figures 24, 25 and 28 (c. hyp.) Unlike the hypoderm cells in most Insects - [illegible] and like those of Crustacea, these cells do not become pigmented in the adult eye. In the fully formed eye they are in contact with only a small peripheral area of the facet, to the whole of which they must have given rise. During development they are presumably reduced in size and displaced laterally by the development of the underlying cones, which thereby come into contact with the cornea. Laterally the hypoderm cells form a mantle round the upper part of the cone - see Figures 24 and 28. The peculiar relation of the corneal hypoderm (c. hyp) to the cone (c.c.) in Figure 25 is due to the angle of the section. Its obliquity is indicated by the different relative depths of the pigment cells on either side of the cone. The cone and pigment cells, which are shown, are in the same ommatidium and occur below the level of the hypoderm cell-mantle round the cone. The hypoderm cells, which are seen, are those of the anterior adjoining eye unit.

The lateral boundaries between two adjacent hypoderm cells are indistinct. They are separated by the pigment cells from the corresponding hypoderm cells of adjacent eye units. The maximum depth, through which the hypoderm cells extend down the cone, is about 10μ - i.e. about two-thirds of the length of the cone.

The cytoplasm of these cells is coarser and sparser than that of the remaining cells of the eye, possibly in relation to a reduction of the cells. The nuclei are smaller than those of the cone cells, have a thin, darkly staining, outer boundary, with deeply staining, coarsely granular contents without a nucleolus. They are spherical and lie centrally within the cells in the adult.

The cone and cone cells.

The cones are shown in Figures 24 to 28. The cones form the most conspicuous structures across the eye but their size is not very regular. Those at the edge are considerably smaller than those in the centre, i.e. the peripheral cones are reduced in size as are the corresponding corneal lenses in thickness. The cones, therefore, lack the appearance of a uniform layer, which is so striking a feature of their arrangement in the compound eye of most Insects and Crustacea. When unstained they are nearly colourless and highly refractive, in accordance with their dioptric structure.

The cone consists of four segments which must originally have been secreted by four cone cells. In the adult, however, the secretion has entirely filled the cells of which only the four nuclei and the boundaries remain. The nuclei lie, one in each segment, embedded in the outer part of the secretion. They are rather larger than those of the hypoderm cells, have a darkly staining, outer boundary with finely granular, deeply staining contents, without conspicuous nucleoli. Each nucleus is roughly ellipsoidal in shape and lies for the most part along the outer edge of the cone secretion. At its extremities the nucleus leaves the edge of the secretion and lies embedded within this. The shape of the nucleus and the area covered by it are apparent in Figures 24, 25 and 28 (c.c.n). The nuclei have a maximum length of about 15μ and a maximum depth of about 3μ

Each cone segment consists of a refractive, transparent, homogenous mass staining readily and uniformly with the same staining properties as the outer part of the cornea. The four cone segments of each eye unite together to form a concavo-convex structure, crescentic in longitudinal section with a maximum depth of 15μ and ellipsoidal in transeverse section with a major axis of up to 30μ and a minor axis of up to 20μ. The dimensions vary slightly in different eye units. The outer concave surface of the cone is applied to the inner convex surface of the corneal lens, while the lower convex surface of the cone is in contact with some of the rhabdomeres.

The cell boundaries dividing the cone into segments are only roughly at right angles to one another so that the four segments are only approximately equal - see Figure 24. The orientation of the cone segments is not regular throughout the eye, but varies from one unit to the next. In this the eye differs from that of most Insects and Crustacea. The four segments are clearly visible in transverse section. Figure 28C shows a superficial section through the cone passing through only one of the divisions, while Figure 24C is a longitudinal oblique section passing through two of the divisions. Figures 26B, 27 and 28A pass superficially through the cone and outside the nuclei.

Hesse (1901) described the cones of Lepisma *saccharina* as of the acone type. He regarded them as having clear crystalline cells without a true cone secretion.

Carriere (1885) has described a eucone condition. Such eyes are provided with a solid intracellular cone with the cone cell cytoplasm and nuclei lying above the secretion. In this case the cone clearly resembles the eucone type in being a hard secretion (similar in composition to the outer parts of the cuticular structures of

/the

the body) but differs from the eucone type in that the secretion fills the whole of the cells, which are of unusual shape with their nuclei in a position more proximal than that normally occupied in such eyes.

The retinal cells.

These are shown in Figures 24 to 29. The retinal cells differ from those of Crustacea as well as from those of the great majority of Insects, including the related Machilida - see p. 30. They are peculiar in being arranged in two sets - a proximal layer of three cells and a distal of four cells. This is in accordance with the findings of Hesse (1901) and not with those of Carriere (1885), who described only four cells in a single layer - see Berlese (1909, p. 660).

The cells are somewhat assymetrical and irregular in arrangement, being considerably shorter and smaller in the central than in the peripheral eye units. The relative length of upper and lower layers varies as is seen in Figures 28A and 28B. The ratio of their lengths is approximately as three is to seven in the central eye units and as four is to six in the peripheral. The maximum length of the retinal cells combined in one unit is 75µ and the maximum breadth 55µ. In different eye units the cells vary in size. The retinal cells like the cone cells, are unstable in their arrangement, forming no very definite pattern throughout the eye as a

/whole

whole. In this respect they resemble degenerating eyes such as those of the Crustacean Philoscia, and differ from the usual condition in the compound eyes of Insects and Crustacea.

The cytoplasm of the retinal cells is divisible into two parts within each cell. The outer, which occupies two-thirds of the depth of the retinal cells, is densely filled with coarse pigment granules, uniform in size and arrangement, and staining readily with most plasma stains. The inner part of the cell is filled with a finely granular, lightly staining protoplasm. In both longitudinal and transverse section this shows a fine radial striation, converging towards the rhabdomeres. Its appearance is very similar to that of the corresponding region in Machilida. This is Hesse's "Schaltzone" and represents the pigment free region in which the passage of the neurofibrillae could not be traced into the rhabdomere striations. Hesse (1901) described them as continuous with the latter - see Berlese (1909, p. 660).

The nuclei of the retinular cells of the two layers are the same in appearance. They are roughly spherical and rather larger than those of the cone or pigment cells. Each has a darkly staining, outer boundary and finely granular, deeply staining contents, somewhat concentrated towards the periphery of the

/nucleus.

nucleus. A central nucleolus is present. The nuclei vary in position as can be seen from Figures 26 to 29 - (r.c.n.).

The cell boundaries are not very clear. The two layers of cells tend to run together longitudinally, so that it is often difficult to distinguish their exact limits. Some indications of boundaries are apparent, in Figures 26, 27 and 28.

Transverse sections of both upper and lower layers of cells indicate that walls between adjacent retinal cells have, in the main, been lost by coalescence of the cells. Boundaries often persist in the three-celled layer (Figure 29B) although they are poorly represented in the four-celled stratum (Figures 29A, 29C).

Laterally the retinular groups of adjacent units are close together but remain perfectly distinct.

The relation of the upper ends of the retinal cells to the cone is somewhat unusual and differs from that in most Insect compound eyes. Instead of being terminated at, or very slightly above, the level of the lower end of the cone apparatus, they are continued up along the cone to come into contact with the lower surfaces of the hypoderm cells - see Figure 28.

Although the external surface of the eye as a whole is not markedly convex, there is, as in crowded, convex compound eyes, a tendency for the inner edge of the eye units to converge, so that the retinal cells are not uniform in diametre throughout their length but are reduced in width

/towards

towards their lower ends in both upper and lower layers, but more particularly in the latter - see Figure 29.

At their lower ends the retinal cells are continued into nerve fibres which pass to the optic ganglion.

The rhabdomeres.

The rhabdomeres are shown in Figures 27, 28 and 29 (rhb). The three retinal cells of the lower or proximal retinal layer bear three separate rhabdomeres. These show no tendency to coalesce into a compact rhabdom but merely touch one another at their edges to compose a very loosely united structure in the form of a hollow, equilateral triangle - see Figure 29B. The apparently double appearance of the proximal rhabdom part in Fig. 28A and 28B is due to the passage of the section through one of the angles of the triangle, where two adjacent rhabdomeres are in close contact. Throughout its entire width and breadth each rhabdomere - i.e. each side of the triangle - is in the form of a longiginal platelike border applied to the edge of its cell.

The four celled, distal or upper layer of retinal cells has a more complicated rhabdomere arrangement. As in the ~~in~~ proximal layer the rhabdomeres are thin and platelike and arranged along the inner, longitudinal axes of the cells - see Figures 29A and 29C. At their lower ends these rhabdomeres are in very loose contact with those of the proximal layer. At their upper ends these

/rhabdomeres

rhabdomeres, like their subtending retinal cells, pass laterally up round the side of the cone, with which they are in close contact - see Figures 26B, 27, 28A, 28B. This is unusual in Insects, where in most compound eyes the retinal cells and cone apparatus end on more or less the same level, with little overlapping. In transverse section the rhabdomeres are in the form of a hollow square. This is, however, divided into four compartments by two fine lines, at right angles to one another. These can be seen only under high powers and start from the middle of opposite sides of the square. They could not be made out in longitudinal sections but occur in transverse section throughout the length of the distal retinular cell group below the cone. It is possible that they represent the central remains of the boundaries of the retinal cells, from which the rhabdomeres have retracted, either in the course of their formation or artificially. The fusion of the retinal cells in this layer is unfortunately too complete for it to be determined whether the limits of the separate rhabdomeres lie at the corners or along the sides of the square, and therefore it is not possible to see whether the lines within the rhabdom correspond in position to the retinal cell boundaries. They are clearly not a part of the cone cells and there is little doubt that

/they

they must be part of the retinal cells. The lines are apparent in Berlese's copy of Hesse's figure (1909, Fig. 817) but no explanation of them is given.

The peculiar appearance of the rhabdomeres in Figure 27 is due to the obliquely longitudinal angle of the section. The elongated single rhabdomere on the left is apparently one in the upper layer of retinal cells, while the two inclined to one another on the right are apparently of the lower layer of cells.

Both in longitudinal and in transverse sections all the rhabdomeres have a characteristic striated appearance due to the presence of uniform transverse plates arranged in parallel series perpendicular to the edge of the rhabdomere. All the plates are of nearly equal thickness and fairly closely crowded - see Figure 29. These plates are Hesse's "Stiftchen" - see Berlese (1909, p. 660).

The pigment cells.

As has been pointed out above the corneal hypoderm cells are not converted into iris pigment cells as in many insect eyes. In this the eye resembles that of the Machilida [illegible] . The retinal cells are pigmented and, as has been pointed out above, are exceptional in that the upper layer of cells extends up round the cone presumably to supply, at least in part, a substitute for the missing iris pigment cells.

/In

In addition special pigment cells are present. These surround the upper half of each eye unit, and together with the retinal cells form a complete pigment sheath about each unit. At the upper ends the cells are in contact with the cornea and extend down to approximately the level of the end of the first row of retinal cells. They form a complete mantle round the cone, outside that formed by the hypoderm cells about its upper part, and the retinal cells about its lower portion. Figures 26, 27 and 28 show the contact of pigment and retinal cells, (p.c. and p.c.) The retinal cells pass up on the inner side of the pigment cell sheath to make contact round the cones with the hypodermal cells. Thus the pigment cells, with the retinal and hypoderm cells inside these, together form a double sheath about the cone, which extends down from the cornea to the end of the first row of retinal cells.

The upper ends of the pigment cells impinge on small areas of non-lenticular chitin, lying between the lenses. As they are clearly of the nature of modified hypoderm cells trapped between the eye units, it seems not unlikely that they give rise to this chitin between the lenses, which are themselves formed by unpigmented hypoderm cells about the cone. Figure 26A shows these in direct continuation with the hypodermal cells of the body.

Like the retinal cells the pigment cells are crowded towards their bases and become narrower as they

/pass

pass inwards. The maximum length is 40μ.

These pigment cells are very simple compared with the more elaborately arranged, accessory pigment cells found in the eyes of many Insecta and Crustacea.

As in the case of many other eyes, the boundaries of the pigment cells are not always clear. Where they are apparent they are perpendicular to the corneal surface. The cells are somewhat irregularly disposed and common to more than one unit, so that it is not possible to fix a number of cells constantly surrounding each unit.

The cytoplasm is faintly granular and less densely staining than that of the retinal cells. In addition to the fine pigment granules found throughout the cytoplasm, there are larger, [illegible] granules of uniform but sparse distribution. The nuclei are small and spherical, placed high up near the cornea, in a rather irregular line. Each has a dark, outer wall and finely granular, deeply staining contents with no nucleolus apparent.

Basement membrane and associated structures.

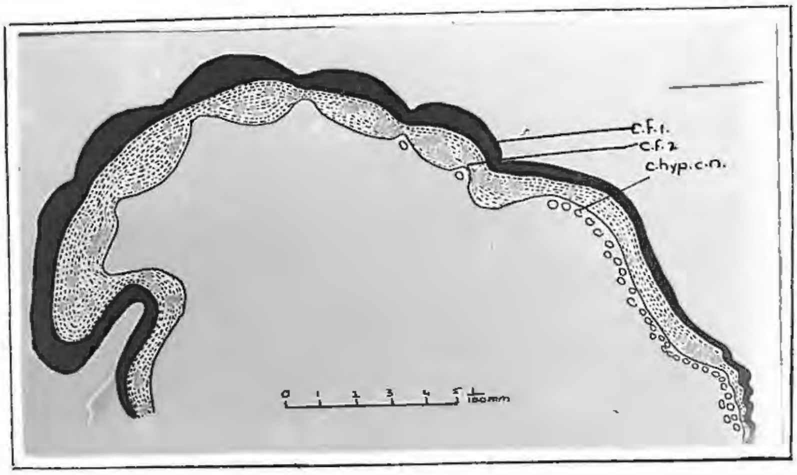
At the base of the eye, where the retinal cells narrow to pass into the nerve fibres, there are a few ragged indications of a basement membrane - see Figure 28 (b.m.). Hesse (1901) described no basement membrane. No tracheae appear to penetrate the eye. They were not described by Hesse (1901) - see Berlese (1909 p. 60).

Figure 23.

c.f.I.	Outer layer of the cuticle.
c.f.2.	Laminated inner layer of the cuticle.
c.hyp.c.n.	Nuclei of the cuticular hypoderm cells.

Figure 23.

A transverse section across the entire cuticle of the eye of Lepisma sp.



Microscopy

8 mm Objective Apochromatic
X 14 eyepiece.
Camera Lucida drawing
3 μ section.

Preparation.

Fixation. Corrosive Sublimate in 96% Alcohol 24 hours.

Embedding: Double embedding in Ether-Alcohol (75/25) solution of cellodion, through chloroform in 50 degrees' melting point wax.

Staining: Heidenhain's Iron Alum Haematoxylon
Light Green (2%) in 96% Alcohol.

Mounting: Through Toluol in Toluol Clarite.

Figure 24.

c.f.2.	Inner part of the corneal facet.
c.c.s.	Crystalline cone segment.
c.c.n.	Nucleus of the cone cell.
c.c.d.	Division between the segments of the cone.
c.hyp.	Corneal hypoderm cell.
c.hyp.n.	Nucleus ofthe corneal hypoderm cell.

Figure 24.

Various sections through the cones and hypoderm cells in the eye of Lepisma.

A. A transverse section through the cone towards its end.

B. Showing a portion of the inner part of the cuticle with the cone and hypoderm cells cut longitudinally with the section passing diagonally through the cone.

C. Showing a portion of the inner part of the cuticle with the section passing rather superficially through the cone~~s~~. Longitudinal section.

Microscopy

4 mm Apochromatic Objective
X 14 Holoscopic eyepiece
Camera Lucida drawing.
2.5-3μ section.

Preparation

As for Figure I.

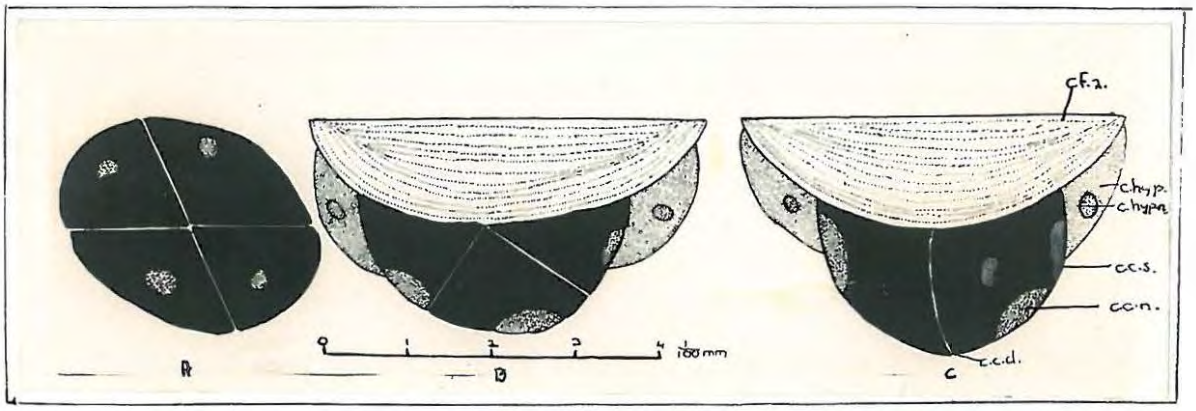


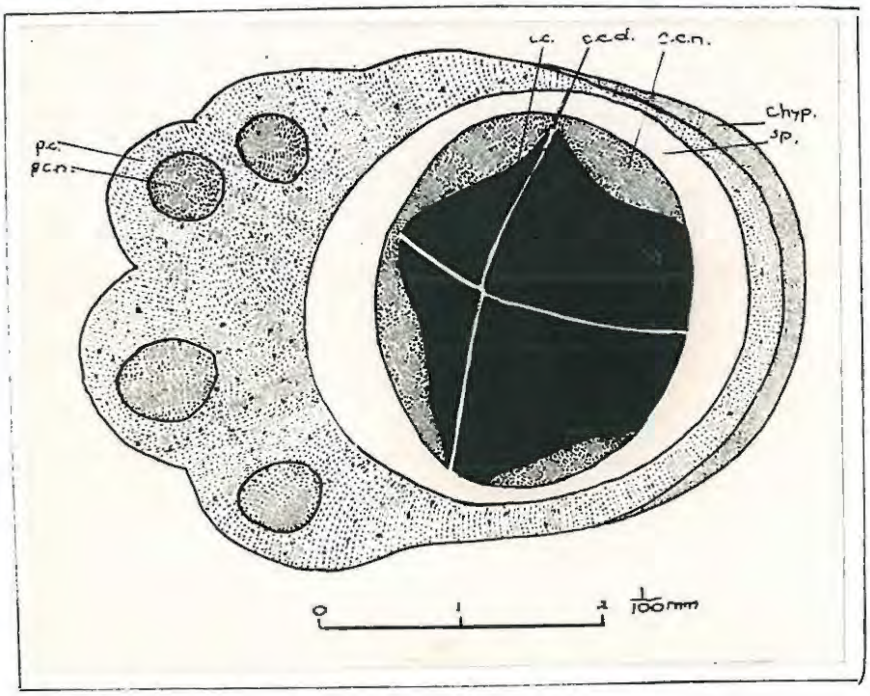
Figure 25.

c.c.s.	One of the cone segments - the cone being seen in slightly oblique transverse section.
c.c.d.	Division between the cone segments.
c.c.~~g~~.n.	Cone cell nucleus.
p.c.	The cytoplasm of several pigment cells which have run together round the cone.
p.c.n.	Nucleus of the pigment cell.
C.hyp.	Cytoplasm of a corneal hypoderm cell.
sp.	Space between the pigment cells and the cone possihly filled in life with the ends of the retinal cells (which here appear to be retracted)

Figure 26.

An oblique section through portions of two eye units through their upper layers. i.e. through the cone and pigment cells of one unit below the level of the hypoderm cells, and through part of the corneal hypoderm cells of the adjacent eye unit.

N.B. The space between the cone and pigment cells may possibly have been occupied by the upper ends of the retinal cells. They were not visible in this section.



Microscopy

2 mm Oil immersion Apochromatic objective
X 14 Holoscopic eyepiece
Camera Lucida drawing.
2.5-3μ section.

Preparation

As for the section in Figure 1.

Figure 26.

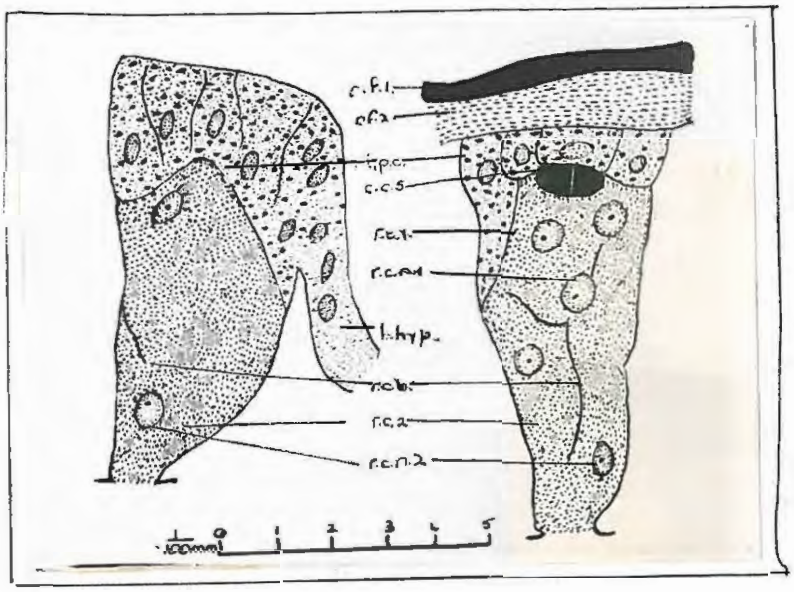
p.c.	Interommatidial pigment cells cut slightly obliquely so that their full length is not seen.
b.hyp.	Hypoderm of the body continuous with~~t~~he the pigment cells.
r.c.I.	Retinal cell of the upper row.
r.c.2.	Retinal cell of the lower row.
r.c.b.	Indication of a boundary separating the two sets of retinal cells.
r.c.n.I.	Nucleus of the upper row of retinal cells.
r.c.n.2.	Nucleus of the lower row of retinal cells.
c.c.s:	Cone segment cut superficially.
c.f.I .	Outer layer of the cuticle.
c.f.2:	Inner layer of the cuticle.

Figure 26.

Two longitudinal sections through the eye units of Lepisma.

A. Through the outermost eye unit to show the direct continuity of pigment cells and hypoderm and showing two of the nuclei of the retinal cells.

B. A longitudinal section showing the remaining five nuclei of the eye unit.



Microscopy

4 mm Apochromatic Objective
X 14 Holoscopic eyepiece
Camera Lucida drawing.
2.5-3μ section.

Preparation

As for the section in Figure I.

Figure 27.

c.f.I.	Outer part of the cuticle.
c.f.2.	Inner part of the cuticle.
c.c.	Cone cut superficially showing only two segments.
p.c.I.	Pigment cell in contact with the cornea and extending down to the first retinal stratum.
p.c.2.	Pigment cell cut through obliquely so that its full ventral extent is not apparent.
p.c.n.	Pigment cell nucleus.
r.c.g.	A section of a retinula group. From the condition of the rhabdom it appears that the section passes through both layers of retinal cells , which have run into one another.
r.c.I.	Upper layer of retinal cells.
r.c.2.	Lower layer of retinal cells.
rbm.I.	A rhabdomere of the upper layer of retinal cells.
rhb.2.	Two rhabdomeres of the lower layer of retinal cells cut obliquely.

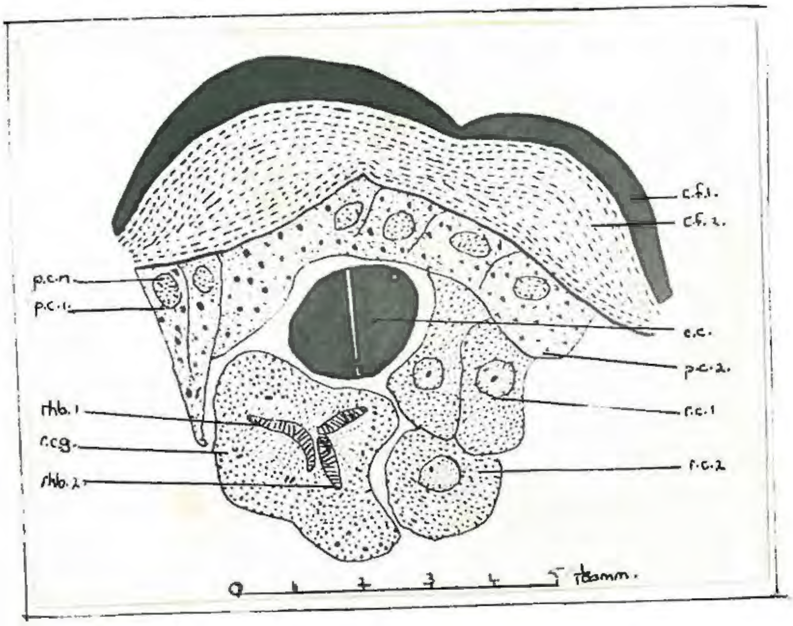


Figure 27.

Oblique section through two eye units in the eye of Lepisma showing relations of the cells.

Microscopy

4 mm Apochromatic Objective
X 14 Holoscopic eye piece.
Camera Lucida drawing.
2.5-3 μ section.

Preparation

As for the section in Figure I.

Figure 28.

c.f.I.	Outer part of the cuticle.
c.f.2.	Inner part of the cuticle.
c.c.s.I.	Cone cut rather superficially.
c.c.s.2.	Cone cut diagonally.
c.c.s.3.	Cone cut very superficially.
c.c.n.	Nucleus of the crystalline cone cell.
c.hyp.	Corneal hypoderm cell.
r.c.I.	Retinal cell of the upper layer.
r.c.2.	Retinal cell of the lower layer.
r.c.d.	Division between the two layers of retinal cells.
r.c.n.	Retinal cell nucleus.
rhb.I.	Rhabdomere of the upper layer of retinal cells
rhb.2.	Rhabdomere of the lower layer of retinal cells.
r.c.p.	Pigmented area of the retinal cell.
r.c.c.	Clear area of the retinal cell.
p.c.	Pigment cell.
p.c.d.	Divisions between the pigment cells.
p.c.n.	Pigment cell nucleus.
b.m.	Indications of the basement membrane.
n.f.	Nerve fibres with which the retinal cells are continuous.

Figure 28.

A longitudinal section through the Lepisma eye showing three units, indicating the rhabdom disposition and the general arrangement of the cells.

A. Longitudinal section slightly more superficial than B.

B. Longitudinal section directly through the centre of the ommatidium.

C. Longitudinal section passing very superficially only through the extreme edge of the cone.

Microscopy

4 mm Apochromatic objective
X 14 Holoscopic eyepiece.
Camera Lucida drawing.
2.5-3 μ section.

Preparation

The same as for the section in Figure I.

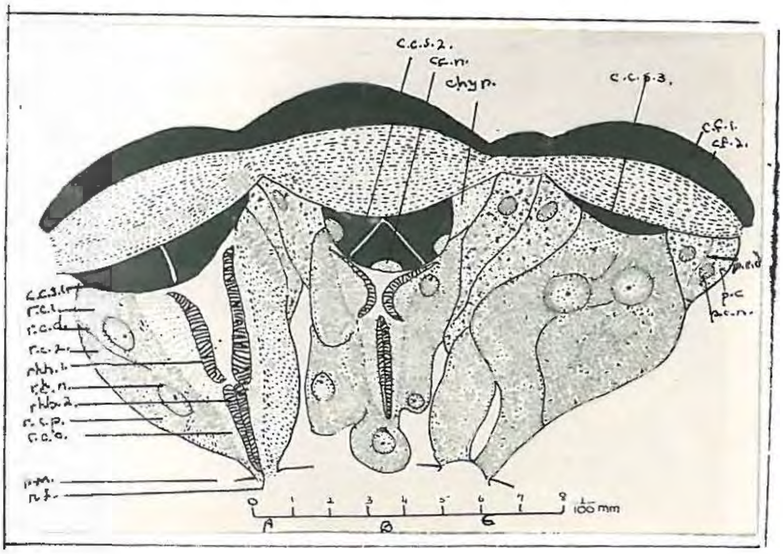


Figure 28.

r.c.p.	Outer part of the retinal cell filled with dense pigment granules.
r.c.c.	Inner clear part of the retinal cell surrounding the rhabdomere.
r.c.n.	Retinal cell nucleus.
r.c.d.	Division between adjacent retinal cells.
rhb.1.	Rhabdomere of the upper row of retinal cells.
rhb.2.	Rhabdomere of the lower row of retinal cells.
r.c.	Cross inside the rhabdom- see text.

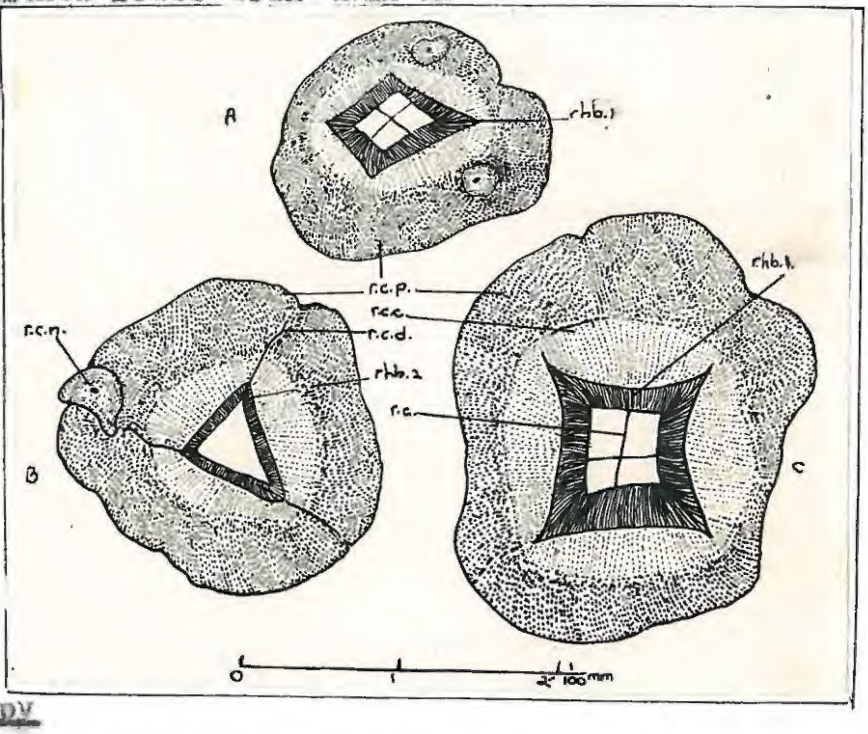
Figure 29.

Three transverse sections through the retinular cells of the two different strata of the retina in Lepisma.

A. Through the four celled distal layer of retinal cells.

B. Through the three celled proximal stratum of the retina.

C. Through the four celled distal layer of cells rather lower down than A.



Microscopy

2mm Oil Immersion Apochromatic objective.
X 14 Holoscopic eyepiece.
Camera Lucida drawing
2,5-3μ section.

Preparation

The same as for the section in Figure 1.

2. The anatomy of the lateral compound eyes of Machilis sp

The eyes of *Machilis maritima* were described by Oudemans (1887) and of *Machilis* sp. by Hesse (1901) and Seaton (1903, pp. 319-329), Berlese (1909, p. 660, Fig. 816), Comstock (1933, p. 140) and Snodgrass (1935, p. 544, Fig. 282D) have given figures and short descriptions of these eyes taken from the work of Hesse and Seaton. None of the original descriptions is available.

A more detailed description of these eyes is given below since the occurrence of complex, compound eyes among the Apterygota (where they are found only in the Machilida) is of some interest, both in regard to the structure of these eyes themselves and for the purpose of comparing them with the peculiar eyes in the Lepismata.

Except where otherwise stated, the description given does not conflict with any of the available particulars on the structure of the eyes of Machilidae but serves to amplify these somewhat, since the available information amounts to little more than a list of the numbers of each type of cell in the ommatidium.

External characters.

There is present one pair of relatively large compound eyes, sessile and immovable. Each is reniform

/in

in shape with the convex part of its outline towards the outer side of the head. Anteriorly the eyes are approximated and touch one another for a short distance along their edges. For the rest the eyes are separate, each lying along one side of the anterior part of the head. The eye is uniformly convex but the convexity is not markedly greater than that of the surrounding surface of the head. The eye is clearly facetted and through the facets the dark, inner, pigmented parts of the eye can be seen.

External cuticule.

The eye cuticle is transparent and colourless, without external decoration and continuous with the general covering of the body surface, from which it does not differ markedly. It is composed of regular, equilateral, hexagonal facets, which are very nearly contiguous, with only a thin area of chitin between adjacent lenses - see Figure 30.

Each eye consists of about three hundred of these facets, which are arranged in regular, alternating, vertical rows. The facets are practically uniform in shape, area, thickness and curvature throughout the eye, with only very slight irregularities towards the periphery. The lenses are not sufficiently convex to give the outer surface of the eye a beaded appearance, yet each facet is itself concavo-convex with the convexity external and the thickness greater centrally (7-8μ) than peripherally (3-4μ). The average diametre of a facet is about 17μ .

/Neither

Neither externally nor in section do the facets show any trace of a double origin, although each is secreted by two separate hypoderm cells. The cuticle stains uniformly and evidence of laminated deposition in successive layers, such as frequently occurs, is not clear.

Corneal hypoderm.

The cells secreting the corneal lenses are clearly derived from the hypodermis responsible for the secretion of the cuticle over the general surface of the body but, unlike these, they do not form a continuous hypodermal layer. Instead, successive pairs of cells, each responsible for the secretion of one of the corneal lenses, are separated by upward processes of the interommatidial pigment cells, which impinge on the thin parts of the cornea between the facets. Along their upper surfaces two adjacent hypodermal cells are in contact with the entire lower surface of the corresponding facet. The cells differ from the corresponding structures in most Insect compound eyes in that they have not become laterally displaced to form "iris" pigment cells. Instead they have remained unpigmented and lie just above the cone and under the facet, in the position in which they occur in the primitive form of the Crustacean eye - see p. 108

The cytoplasm of these cells is thinner than that of any other cell in the eye and is stained and fixed with difficulty. Thus, although the cytoplasm (c.hyp.c.) - was apparent in Figures 31 and 32, it could not be made

/out

out in Figure 33.

The nuclei are relatively large with a thin darkly staining outer boundary - see Figures 31, 32 and 33(c.hyp.n.) They have sparse, deeply staining, coarsely granular contents, are without nucleoli and are rather larger than the cone cell nuclei. They fill nearly the entire length and breadth of the cells, as can be seen in Figures 32 and 33.

The orientation of the hypoderm cells in relation to the cone segments is constant and regular throughout the eye. The division between the hypodermal cells is at right angles to one plane of division between the four cone cells and parallel to the other.

The boundaries of the cells are clearer than in any of the other eyes described, probably due to the fact that the cells themselves seem to have retained their primitive size and position without undergoing great reduction or displacement. The upper surfaces of the cells are applied to the lower surfaces of the cuticle. Ventrally each cell is bounded by the underlying cone cell nuclei, two to each hypoderm cell. Laterally and internally each cell is contiguous with the other member of the pair and the boundary is obliterated, while externally each cell is clearly marked off from the adjacent pigment cells separating the ommatidia.

The hypoderm cells are thicker centrally than peripherally, in accordance with the presence of an apical point on the upper surface of the cone apparatus. The ventral depth of the cells is 3-4 μ and their peripheral depth 9-10 μ.

/Thus

Thus they form a cap over the upper end of the cone apparatus but do not extend round this below the level of its maximum width.

The cone and cone cells.

The cones lie immediately below the hypoderm and form a conspicuous and uniform layer across the eye, each cone being composed of four cells of which the cytoplasm has disappeared - that is, the cells have been entirely converted into, or filled with, the material of their secretions. In this the eyes resemble those of the Lepismata.

The four nuclei are clearly apparent - see Figures 32-35 -(c.c.c.n.) They radiate out to form a cap over the cone segments. They are roughly of equal size and are arranged along two axes, approximately at right angles to one another, as are the underlying and corresponding cone segments. The nuclei are not strictly regular or symmetrical in outline, but can be roughly described as dorso-ventrally flattened structures, with a surface area (on the upper surface of the cone) corresponding to that of a quadrant of a hemisphere. They have a thin, deeply staining, outer wall and take up nuclear stains more deeply than the nuclei of the hypoderm cells, their contents being more finely and densely granular. Like the hypoderm nuclei, they are without apparently a nucleolus. These nuclei lie below the hypoderm cells, with the lower boundary of which they are in contact. They are arranged to form a cap over the raised upper surface

/of

of the cone secretion and as explained above project to some extent between the hypoderm cells - see Figure 32. The nuclei, like the hypoderm cells above them, extend down only as far as the level of the maximum width of the cone. The maximum radius or length of the nucleus, as it lies along the cone, is 13-15µ.

The cone secretions, as mentioned above, occupy the entire cells. In the unstained eye these are refractive, homogeneous and transparent. The cone stains very much in the manner of the cornea and is presumably chitinised. Both the position of the nuclei and the nature of the cone place it in the eucone type - see p. - although the cells as in Lepismata are abnormally reduced.

The entire cone secretion is in the form of two conical solids with their bases firmly fused together, the upper point being short and broad and the lower one tapering to a long narrow point. The maximum width is 19-20µ and the maximum depth 24-25µ. The maximum width is attained about 4µ below the upper apex of the cone.

The cone segments are separated from one another by four walls roughly at right angles to one another. These are deficient or incomplete only in the upper nuclear region - see Figures 33 and 34. The segments are not completely symmetrical but their arrangement throughout the eye is sufficiently regular to form a very definite pattern, which is not present in the eyes in Lepismata.

Laterally the cone segments are surrounded by, but not

/directly

directly in contact with, the interommatidial pigment cells (p.c.), while the lower point of the cone is in contact with the upper end of the rhabdom - see Figure 31.

Retinal cells.

The arrangement of the retinal cells in a single layer resembles that of the great majority of Insects and Crustacea and differs markedly from the peculiar two layered condition of the cells in Lepismata. There are seven retinal cells in each ommatidium in this case. Oudemans (1887) described only six. Hesse (1901) and Seaton(1903), Berlese (1909, p.660) and Comstock (1933, p.140) mention seven.

The cells, like the cones, are fairly uniform in arrangement and size throughout the eyes at any one level. In accordance with the convergence of the ommatidia towards the optic nerve, the cells are reduced in diametre towards their lower ends. They are elongated and rod-like with a maximum diametre of 9-10μ and a maximum length of 70μ. Thus they seem somewhat shorter than those of Lepismata. The comparison is misleading as the retinal cells in the latter extend up round the cone for a considerable distance. The part below the cone in Lepismata is only 50-55μ in length so that the eye unit of the Machilida is, as a whole, much longer and slenderer than that of Lepismata.

In each ommatidium the cells are equal with no tendency to grouping or to the reduction or suppression of any cells. Neighbouring retinular groups are separated by spaces, which

/decrease

decrease in size towards the base of the eye - see Figure 35.

At their lower ends the retinal cells are continued into the nerve fibres which pass to the optic ganglion.

The cytoplasm of the cells takes up most plasma stains very deeply and is fairly uniformly and coarsely granular. The peripheral parts of the cell tend to stain most deeply due to the higher concentration there of the pigment granules, which fill the cell plasma. Surrounding the rhabdom is a clear circle, which shows a fine radial striation and apparently corresponds to Hesse's "schaltzone" - see Berelse (1909, p.651). As in the Lepismata the lines, presumably neurofibrillae, clearly visible where the cell is unpigmented, could not be traced into the rhabdomeres, although Hesse (1901) described this as their termination.

Although the lateral boundaries between the adjacent cells of a retinular group are practically obliterated, the original number of the cells is apparent from the seven-fold marginal lobation.

The nuclei vary somewhat in their level but always occur in the upper third of the retinal cells. They are spherical with a deeply staining boundary and with one or two nucleoli. The contents are deeply staining and granular. The nuclei are of approximately the same size as those of the pigment cells - see below.

<u>The rhabdom.</u>

The rhabdomeres secreted along the inner, axial borders of the retinal cells in the Lepismata, here form a solid rhabdom. The maximum diametre of the rhabdom does not exceed 2μ as compared with a thickness of up to 4μ for the individual rhabdomeres in Lepismata. In longitudinal section the rhabdom appears as a slender rod of uniform size, faintly striated transversely. Thin transverse sections, such as that diagrammatically shown in Figure 37, indicate more clearly the structure of the rhabdom. Each rhabdom has externally along its entire length seven lobes of flutes, four of which are large and three small. Each of these corresponds to one cell, by which it is presumably produced. It is not clear, however, why, if these are rhabdomeres, three of them should be reduced in size, while the retinal cells, responsible for their production, are uniform in size. Although the rhabdom at first glance appears solid, it can be seen to be divided secondarily into four parts, by two lines roughly at right angles to one another. Three of these compartments contain one large and one small part of the rhabdom each, while the fourth contains the remaining single large lobe. It seems possible that after reduction of three of the rhabdomeres, the remaining ones fused as nearly as possible in pairs.

The pigment cells.

Densely pigmented cells surround the upper part of each ommatidium. Their cytoplasm is very similar to that of the retinal cells and contains numerous, uniformly distributed, coarse pigment granules. The cells abut at their upper ends

/on

on the parts of the cornea between the facets. It is possible that they are responsible for a part in the formation of these areas of the cuticle. These cells end below at the level of the upper ends of the retinal cells. They are separated from the cones by a small space. The group of cells between two successive ommatidia, when seen in longitudinal section, is triangular in shape, arranged with a thinly pointed apex and a broad base to fill the space between the upper ends of the ommatidia. As in Lepismata, the limits of the pigment cells are not at all clear, and the lateral walls of the cells, where they lie close to the cones, are the only sharp boundaries. Because these boundaries are indistinct and because cells are shared between adjacent ommatidia, it is not possible to assign a definite number of cells to each eye unit.

The nuclei lie at different levels and are roughly spherical with a darkly staining boundary, with densely granular, deeply staining contents and one or two nucleoli.

Basement membrane and associated structures.

A thin basement membrane is distinctly seen throughout the eye at the base of the eye, through which the nerve fibres are continuous with the retinal cells. The Tracheae were not seen beyond the basement membrane. Their demonstration requires special and critical staining, and their arrangement is of relatively little interest in comparison of their anatomy with the eye of other Arthropods.

<u>Figure 30.</u>

c.f.	Hexagonal cuticular facet - takes up Haematoxylin stain.
c.f.I.	Thin cuticlula between the facets - takes up the Eosin stain.

Staining : Heidenhain's Haematoxylon Iron Alum
Aqueous Eosin
Mounting : Through Toluol in Toluol Clarite.

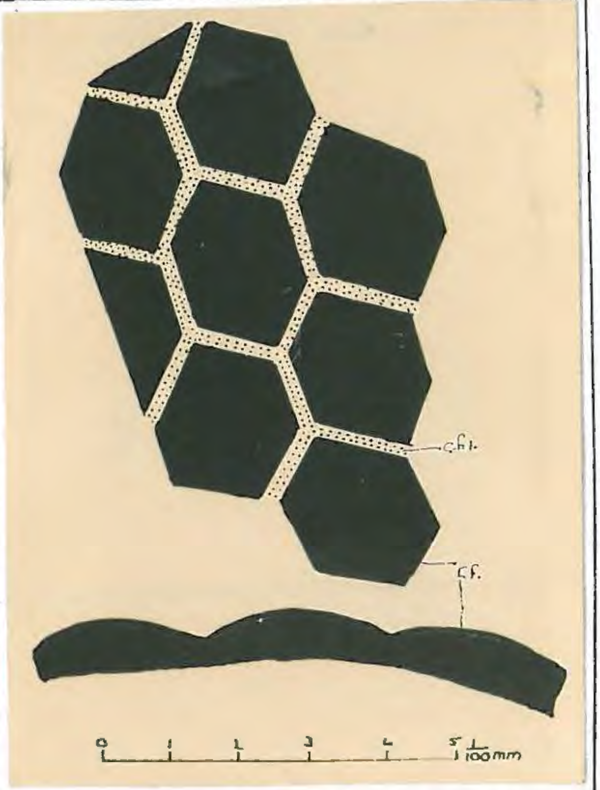


Figure 30.

A. Surface view of the corneal facets of the eye of Machilis.

B. Sectional view of three facets of Machilis eye.

Microscopy:

4mm Apochromatic Objective
X 20 Holoscopic Eyepiece
Camera Lucida drawing
3μ section . B.

Preparation

Fixation: Bouin 24 hours

Embedding Double embedding through Alcohol-Ether (25:75) Celloidin Solution and Chloroform in 60 degrees M.p. Wax

Figure 31.

c.f.	Corneal facet.
c. hyp. c.	Cytoplasm ofcorneal hypoderm cell.
c.hyp.n.	Corneal hypoderm cell nucleus.
c.c.	Crystalline cone filling the entire cone cell.
p.c.	Iris pigment cell round the cone.
p.c.n.	Pigment cell nucleus.
rhb.	Rhabdom in contact with the lower end of the cone.
r.c.	Pigmented cytoplasm of the retinal cell
r.c.n.	Retinal cell nucleus.
c.c.c.n.	Cone cell nucleus
b.m.	Basement membrane
n.f.	Nerve fibre

Figure 31.

Longitudinal section of four of the central ommatidia of the eye of Machilis.

Microscopy

4mm Apochromatic Objective
X 14 Holoscopic eyepiece
Camera Lucida drawing
3μ section

Preparation

Fixation : As for Figure 30.

Embedding: As for section in Figure 30.

Staining : Depigmented in Howland's fluid,
Heidenhain's Iron Alum Haematoxylon

Mounting : Through Toluol in Toluol-Clarite.

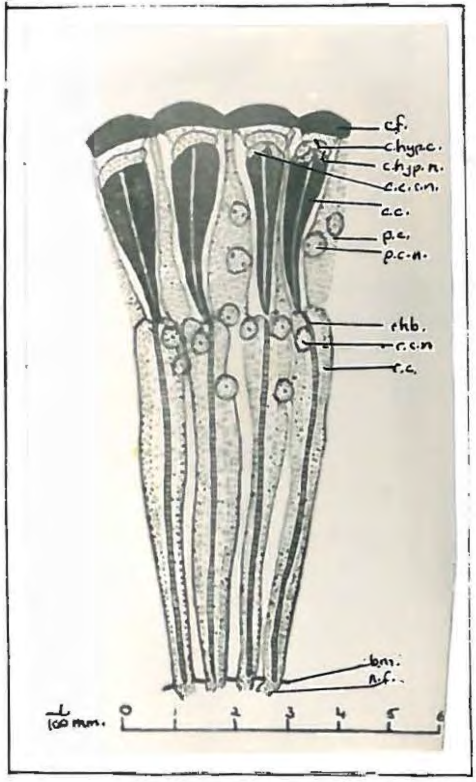
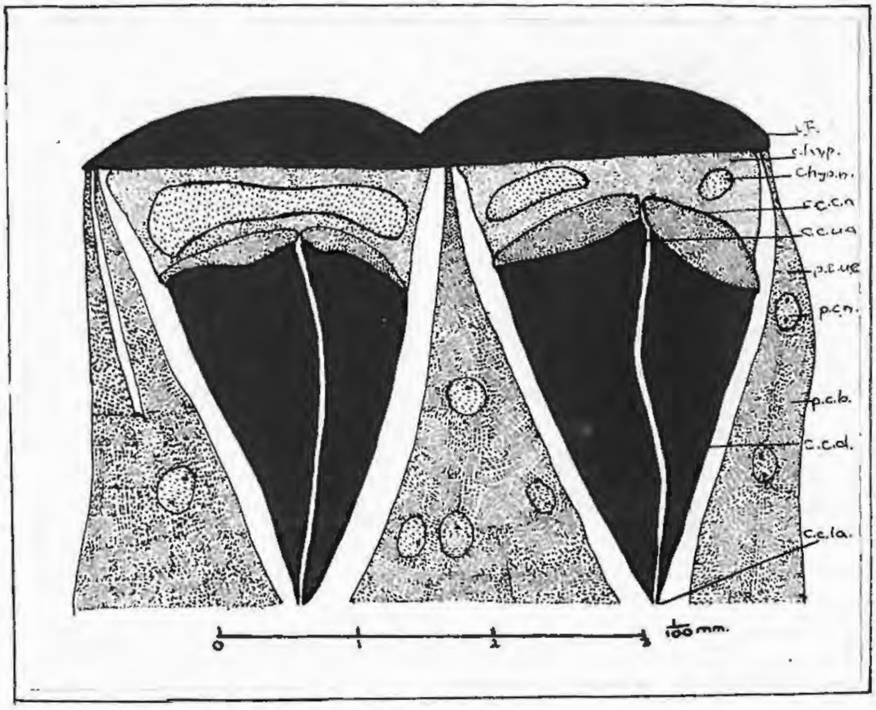


Figure 32.

c.f.	Corneal facet.
c.hyp.	Corneal hypoderm cell cytoplasm
c.hyp.n.	" " " nucleus
c.c.c.n.	Crystalline cone cell nucleus
c.c.u.a.	Crystalline cone upper apex
p.c.u.e.	Attenuated end of the pigment cells between the upper ends of the ommatidia
p.c.n.	Pigment cell nucleus.
p.c.b.	Expanded base of the pigment cells
c.c.d.	Division between the segments of the crystalline cone - one of two divisions
c.c.l.a.	Lower apex of the crystalline cone.

Figure 32.

Longitudinal section through the outer ends of two ommatidia of the eye of Machilis.



Microscopy

4mm Apochromatic Objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
3-4 μ section

Preparation

Fixation : As for section in Fig. 30

Embedding : As for section in Fig. 30

Staining : Depigmented in Howland's fluid.
Heidenhain's Iron Alum Haematoxylon

Mounting : Through Toluol in Toluol-Clarite.

Figure 33.

p.c.	Pigment cell
c.hyp.n.	Corneal hypoderm cell nucleus filling practically the whole cell. (Cytoplasm did not show up in this section: stains poorly.)
c.c.	Extreme tip of the crystalline cone
c.c.c.n.	Crystalline cone cell nucleus
c.c.c.n.d.	Division between the nuclei of the cone cells.

Figure 33.

Transverse sections of cells in the outer regions of the eye of Machilis, showing the relations of the corneal cells to the outer ends of the cone.

Microscopy

3mm Apochromatic Oil immersion objective
X 14 Holoscopic eyepiece
Camera Lucida drawing
3-4 µ section.

Preparation

As for section in Figure 30

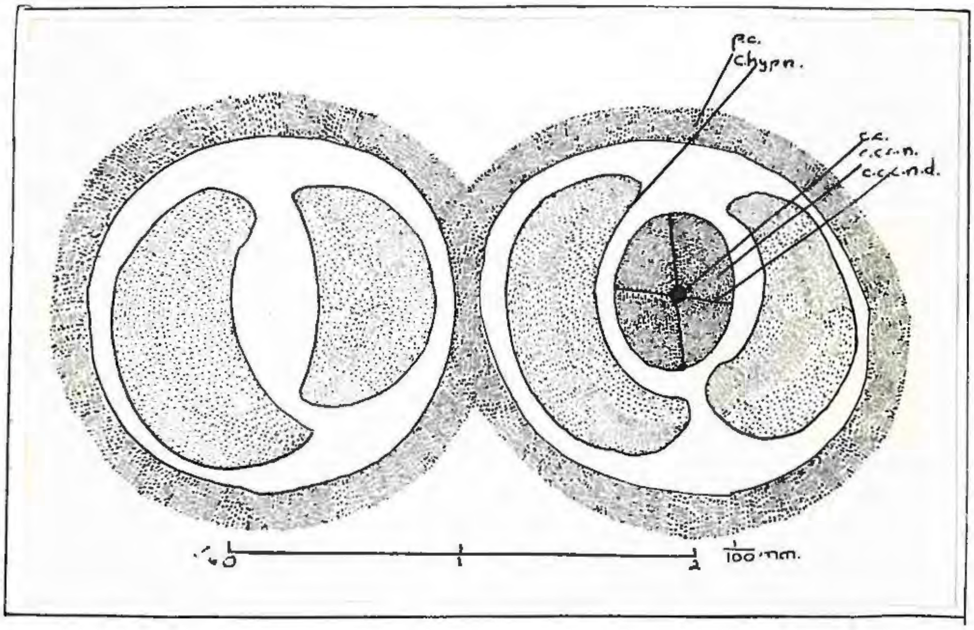


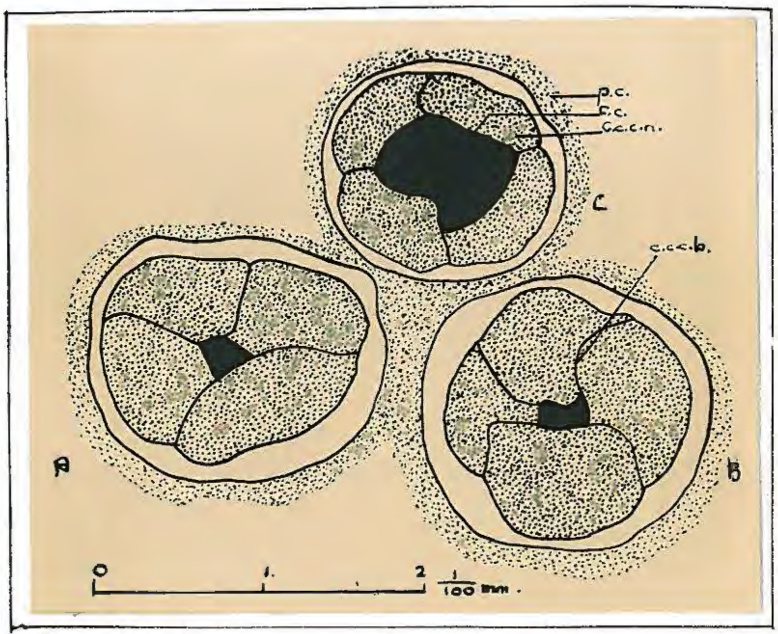
Figure 34.

(A, B, C represent successively deeper levels.)

p.c.	Pigment cell
c.c.	Upper of crystalline cone with the division into segments not clear.
c.c.c.n.	Nucleus of the crystalline cone cell
c.c.c.b.	Somewhat irregular boundaries of the crystalline cone cell nuclei.

Figure 34.

Transverse sections through the cone cell nuclei and upper parts of the crystalline cone in Machilis.



Microscopy

2mm Apochromatic Oil immersion objective
X14 Holoscopic eyepiece
Camera Lucida drawing
3-4 μ section.

Preparation :

As for section in Fig.30.

Figure 35.

p.c.	Pigment cell
s.	Space separating the cone from the surrounding pigment cells.
c.c.s.b.	Basal portion of the crystalline cone segments still separate
c.c.b.	Somewhat asymmetrical boundaries between the crystalline cone segments
p.c.n.	Pigment cell nucleus
c.c.c.n.	Crystalline cone cell nucleus
c.c.u.e.	Upper end of the crystalline cone
c.hyp.n.	Corneal hypoderm nucleus - Cytoplasm of the cell very faintly stained and not shown.

Figure 35.

Transverse sections through the cones - "crystalline" - at successively deeper levels - I, II, III.

Microscopy

3mm Apochromatic Oil Immersion Objective
X 14 Holoscopic eyepiece
Camera Lucida drawing
3 μ section.

Preparation

As for the section in Figure 30.

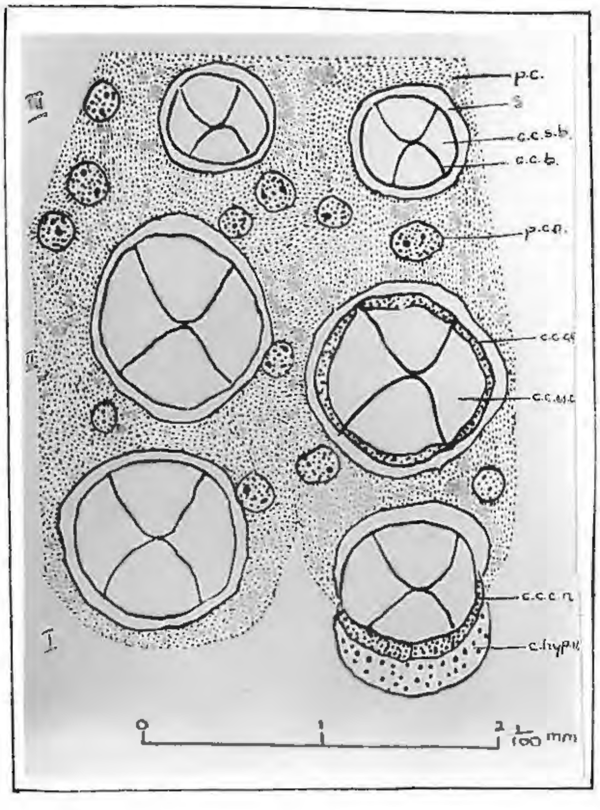


Figure 36.

I-VII are sections at successively deeperlevels

r.c.n.	Retinal cell nucleus
r.c.7.	Seven retinal cells to each unit in I-VII
rhb.	Rhabdom mass
r.cp.	Outer densely pigmented part of the retinal cell- thelobation of the outer edges of these parts anables one to count the number of retinal cells.
r.c.c.	Clear region of the retinal cell surrounding the rhabdom . The cytoplasm here is very fine , stains faintly and is marked by faint, radiating striations.

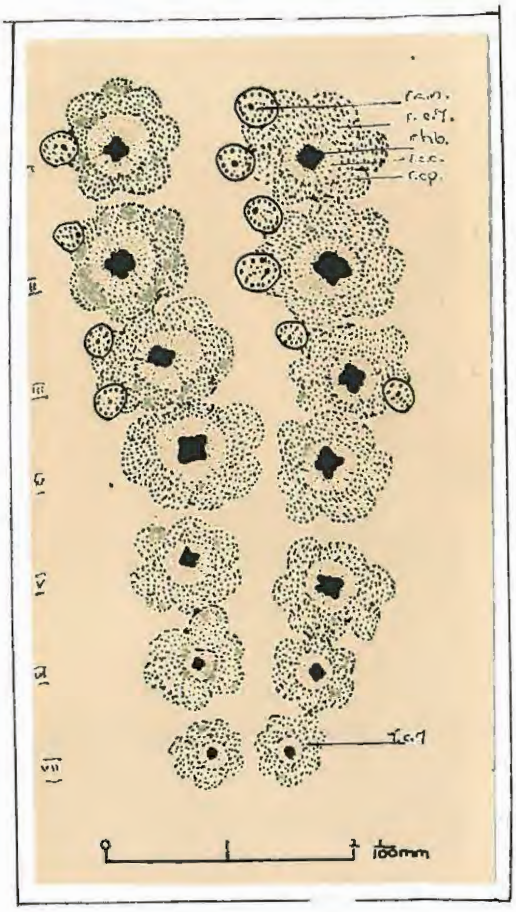


Figure 38.

Transverse sections through groups of retinular cells at successively deeper levels to show the constant number and decreasing size of the cells throughout the length of the ommatidia.

Microscopy

2mm Apochromatic Oil immersion objective
X 14 Holoscopic eyepiece
Camera Lucida drawing.
3 μ section.

Preparation

As for section in Figure 30 .

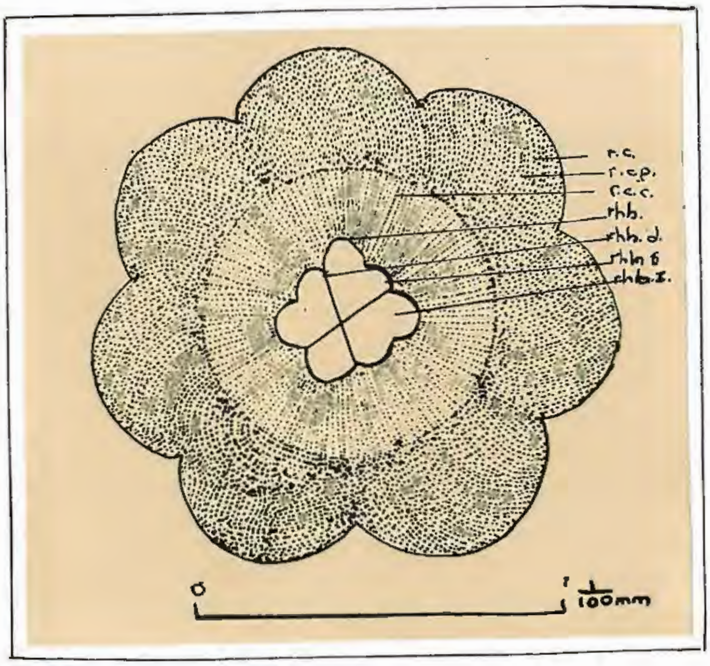
Figure 37.

r.c.	One of the seven retinal cells.
r.c.p.	Outer pigmented part.
r.c.c.	Clear inner region round rhabdom.
rhb.	Rhabdom.
rhb.d.	One of the two divisions which secondarily divide an originally seven parted rhabdom into a four parted structure.
rhb.I.	One of the large lobations of the rhabdom presumably corresponding to an original rhabdomere.
rhm.s.	One of the small lobations of the rhabdom presumably corresponding to a reduced rhabdomere.

Figure 37.

A Semi-diagrammatic transverse section through either end of the retinula of an ommatidium of the eye of Machilis.

The diagram was constructed from the section from which figure 7 was taken, seen under oil immersion.



Part II.

Comparative anatomy of insect lateral compound eyes.

Occurence.

Among the Pterygote Insects a single pair of lateral compound eyes is typically and primitively present in the adults. Among those with an incomplete metamorphosis, the eye is gradually developed by growth of the nymphal compound eye. Among those with a complete metamorphosis, the larva, with few exceptions, is provided with simple, unaggregated, lateral eyes, which are usually ocelli, but sometimes very nearly ommatidial in structure - see appendix. These larval eyes regress and the compound eyes are formed anew in the pupa. In a few cases compound eyes are precociously differentiated in the larva. Among Diptera this is the case in the active aquatic larvae of Culicidae and Chironomidae, in which the growth of the eye is described in detail by Zavrel (1907,p.248). Larval compound eyes are also found in Mecoptera and among the Lepidoptera in Micropterygidae according to Tillyard (1926, p.13).

In some Pterygote Insects the compound eyes may be greatly reduced or even lost either sporadically, in those species of cavernicolous, burrowing or parasitic habit, or throughout an entire order, where parasitic habits prevail.

/They

They are clearly lacking in some female Embioptera, in some Coccidae, in wingless Zoraptera, in certain castes of some species of Isoptera and social Hymenoptera, in female Strepsiptera and in some Coleptera - see Raffray (1895, pp. 20-22).

Occasional cases of extreme reduction of the compound eye have been listed by van Rosen (1916, p. 625) in Isoptera, by Weber (1937, p. 35) in Coccidae and Psocidae, by Raffray (1895, pp. 20-22) and Lea (1905, pp. 356-358) in Coleoptera. Imms (1938, p. 80) mentions the reduction of the eye to a single ommatidium in a worker ant of the species *Ponera punctissima*. In these cases the remaining units, except where they are so far degenerate as to be practically pigment spots, are clearly ommatidia, and not ocelli.

In some the reduction of the eye to a single unit is not sporadic, but characteristic of an order as a whole. This is the case in Mallophaga and Anopleura. Although the eyes in these cases are sometimes referred to as ocelli, Weber (1937, p. 75) points out that they are connected with the optic ganglion and are clearly, as in the cases cited above, a product of the degeneration of the compound eye, with a reduction in the number of ommatidia.

The conditions obtaining in the eyes of Aphaniptera and Strepsiptera are unusual. In Aphaniptera Hesse (1901) pointed out that the eye was very similar to

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the dorsal ocelli of many Insects, being composed of a biconvex lens, with unorganised retinal cells, without rhabdomes, and with no crystalline cone. Snodgrass (1935, p. 541) quoting Hesse's description, considered that these are possible transposed dorsal ocelli. As this theory was not confirmed by observations on the innervation of the eye, it seems safer to suppose that this eye is a product of reduction of the compound eye in accordance with the parasitic mode of life. If this is the case, degeneration has here resulted in the production of an ocellar rather than an ommatidial unit and the reduction has been carried further than in any Crustacean or other Insect eye in which it has been described.

(If Snodgrass is correct in suggesting the eye a migrated dorsal ocellus, a precedent for his case could be traced in the migration of the dorsal ocelli, which Calman (1909, p. 85) supposes to have occurred in some Copepods).

Strepsiptera appear at first sight to be possessed of an ordinary compound eye, and in text books the eye is usually referred to in this way - see Imms (1938, p. 538). Strohm, however, (1910, p. 156), who described the eye of *Xenos rossi*, regarded this as an "ocellar compound eye", in which each unit was composed of a biconvex lens with an underlying, thickened, continuous hypodermal layer, forming a vitreous body, and with about fifty to fifty-five ungrouped retinal cells, with distal rhabdom-

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-eres. There is no reason to suppose that these are migrated and multiplied dorsal eyes, nor any precedent for assuming that such well-developed ocelli would result from the degeneration of a compound eye. (The eye as a whole is fairly well developed, with about fifty units). It seems probable that the eyes are to be regarded as aberrant and unique among Insects and that they represent the product of a retention and multiplication of larval eyes such as those mentioned by Kirkpatrick (1937, p. 40) in *Coricmnos antestii*.

Among the Apterygotous Insects, Campodeidae and Japigidae are blind, while the "pseudo-ocelli" in Myrientomata are not really eyes but, as Imms points out (1938, p. 223) correspond to the postantennal sense organs of Collebola, which are of uncertain function. There seems no reason, however, to regard blindness as a primitive character of the Apterygote stock. The eyes of Machilida are fully as well developed as those of many Crustacea, which in some respects they resemble more than Insects. It is probable that the loss of the eye in the blind forms is secondary and related to the habits of living.

Among the remaining Apterygota lateral eyes, here regarded as compound, but sometimes referred to as ocellar, are present in Collembola and Lepismata. These eyes differ markedly in structure from the compound eyes of other Insects.

In Lepismata - see pp.211,212-the eye consists of a small number of loosely grouped units, each with a biconvex lens, a cone of four segments, and a small number of grouped retinal cells with axial rhabdomeres, The eyes differ from a typical ommatidial structure only in the marked division of the retinal group into two superimposed layers of cells, and in some minor points.

With regard to the Collembola, Willem writing in 1897 (pp. 225-226) pointed out that their eyes had, until that date, been regarded as ocelli. He investigated *Sminthurus*, *Papirus*, *Tomocerus*, *Orchesella*, *Podura*, and *Anurida* spp. and described their eyes as made up of scattered, eucone ommatidia with planoconvex facets, a layer of rudimentary corneagen cells, four cone cells, two pigment cells, and four retinal cells. Hesse (1901) working mainly on *Orchesella*, corrected the description of the retinal cells and pointed out that the retinal group was, as in Lepismata, arranged in two rows of cells. This description is quoted by Snodgrass (1935, p. 540-541) and corresponds closely to that given by Berlese (1909, p. 659) for *Podura*. In some of the Collembola, as pointed out by Imms (1906, p. 41, Fig.34) in the case of *Anutida Maritima*, the eyes degenerate into a pigment spot, the retinal structure and the cones being lost. While both Snodgrass (1935, p. 540) and Imms (1935, p. 227) refer to the eyes of Collebola rather loosely as ocelli, it is clear that they, together with

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the eyes of Lepismata, should be regarded as separated ommatidia, in some cases very degenerate.

External characters.

There is a great variety in the shape and size of the eyes and the position relative to other head structures. These features may differ greatly in nearly related forms or even in male and female of the same species. References to details of such variations in relation to habit are numerous and scattered but the interest attaching to them is somewhat specialised.

As a rule the eyes are separate but where the head is narrow or the eyes large they may touch along a part of their boundaries. This is the case in many Odonata, Ephemeroptera and Hymenoptera. Occasionally the eyes run together completely on the top of the head with no boundary perisisting between them - see Lucas (1868, p. 737)- but this is aberrant and restricted to a few specimens. There is nothing in Insects comparable to the fused eyes of some Crustacean orders - see p.

Although the eyes vary somewhat in position they maintain a general relation to the head sutures and always lie on the parietal area sclerite either on the vertex or on the gena - see Snodgrass (1935, p.111). The compound lateral eyes and their derivatives are always innervated from the protocerebral part of the brain arising in the pre-antennal segment (while the median eyes are innervated from the

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deutocerebral part arising in the next or antennal segment- see Tillyard , 1926 , p. 13.

Where the eyes are large and well developed, a collar-like ridge or apodeme, surrounding the eye , cuts off a narrow ocular sclerite - see Snodgrass (1935,p.343). The ridge acts as a skeletal ring supporting the eye and serving for the attachment of the head muscles.

The convexity of the eye varies considerably. Primitively and typically , although the eye convexity is greater than that of the head, the eye is not as protuberant as in the majority of Crustacea. Stalked forms are rare and of scattered occurrence. They are found in some male Ephemeroptera and in Diopsidae. In no case is the stalk jointed. It is merely a head lobe Occassional cases in which the eye has been borne on a stalk are noted by Cockayne (1926, pp. 204-216, 1930, p.209). He points out that such eyes are found in the squat mutation of *Drosophila melanogaster* , while *Tenebrio molitor* and *Stylopyga orientalis* occasionally regenerate an antenna after removal of the eye . In *Cerambyx scopoli* the eye surface may bear an antenna like appendage In *Syrphus perplexus* an eye has been known to occur on the abdomen its place being taken by a small, antenna-like structure. Cavillee (1942 , p,497) has described a *Drosophila* mutation with an antenna instead of an eye or in connection

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with a rudimentary eye. Apart from sporadic abberrations or teratological cases of this kind, there is nothing in Insects to suggest that the eye is primitively stalked, nor any suggestion that, where the stalk occurs, it is appendicular in nature. Primitively and typically the eye is unstalked.

Divided and Double Eyes.

Among Crustacea and Insecta, coalesced eyes are commoner in the former and double or divided eyes in the latter. In Insecta eyes, which are either incipiently or completely divided, occur in Odonata, Ephemeroptera, Psocoptera, Dictyophora (Mantida), Hemiptera (Aleurodidae, Aphidae, Coccidae), Diptera, Coleoptera and Hymenoptera.

The sharpness of the separation of the two parts of the eye varies considerably. In Odonata, Dictyophora and Hymenoptera the eyes are in some cases made up of areas differing in size and arrangement of the facets and in the internal structure and pigmentation of the ommatidia. These parts of the eye may grade into one another or be separated by a sharp line but they always remain contiguous and form "divided" eyes. Examples of such differentiations of the eye are given in the case of Odonata by Zimmerman (1913, p.1 et seq) Mallock (1922, p. 770), Comstock (1933, p.144) and Eltringham (1933, p.34); in the case of Mantida by Wigglesworth (1933, p. 114) and in the case of Hymenoptera by Geyer (1912, p. 379).

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In Coleoptera, Diptera and Ephemeroptera the division of the eye is much more marked and many series ranging between single, divided and double eyes can be traced. In Psocoptera, Aphidae, Aleurodidae and Coccidae the division is complete, and the eyes "double". Among Coleoptera division of the eye is a fairly common feature and as pointed out by Hatch (1926, p. 343) is to be found in ten unrelated groups representing six different families. He gives numerous series showing all conditions from slight emargination of the eye to a complete separation of two parts. These illustrations are drawn mainly from Cerambycidae, Meloidae, Scarabidae, Tenebrionidae, Hydrophilidae and Gyrinidae, with some other scattered examples. In some Meloidae and Hydrophildae the eye is emarginate but the two parts always remain connected. Cerambycidae, Scarabidae and Tenebrionidae show long series from a slightly emarginate eye to one divided into two parts, usually connected by an isthmus formed by a constriction and drawing out of the chitinous rim which surrounds the eye. The occasional presence of facets on the isthmus points to the relatively recent origin of the divided and double forms. The double condition in Gyrinidae represents the culmination of the development of divided eyes in Coleoptera. Hatch considers that this is the only family in which the divided nature of the eye is related to the life habits - the upper part being used for aerial vision and differing in structure from

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the lower part, used for aquatic vision. He points out that in all other cases in Coleoptera the two parts of the eye do not differ in structure, and that their seperation is a mechanical consequence of movement of the antenna or frontal ridge or the extension of a canthus across the eye.

Carriere (1886, p.142), Wesche (1900, p. 367), Zavrel (1907, p. 248) and Dietrich (1908, p. 470) have pointed out similar series in male Diptera, ranging from the faintly divided eyes of *Tabanus* to the double eyes of *Bibio* and *Simulium*. Apart from those mentioned, examples of double and divided eyes in the Diptera (adults) are drawn mainly from Stratiomyidae, Empidae, Leptidae and Asilidae.

The order in which the double eyes reach their greatest specialisation is Ephemeroptera. In some cases two parts differing in the form of the facets and the pigmentation of the ommatidia are merely separated by a groove. In others, such as *Siphlonurus*, the upper part of the eye is separate, enlarged and expanded. In Beatinae this assumes a mushroom-like shape and stands well out from the head surface, and in *Chloeon* and *Potamanthus* the upper part is raised on an unjointed pillar, widely separated from the rest of the eye and highly elevated. (These examples are given by Needhan Traver and Tsu, 1935, pp. 30, 109).

In Aleurodidae the eye is sometimes divided into two areas differing in the size and arrangement of the

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facets as described by Mallock (1922, p. 770), Williams (1930, p. 56) and Eltringham (1931, p. 431). In some Aphidae the eye, although small, is divided, a few lenses being found on the summits and side of a small, conical projection towards the hind end of the head. This is described in <u>Phylloxera quercus</u> by Berlese (1909, p.663 Figs. 826, 827) Reduction of the eye to a few ommatidia falling into two separate groups has been described in some Psocoptera - <u>Troctes spp.</u> - according to Imms (1938, p. 341) and is obvious in some male Coccidae as in <u>Aonidiella aurantii.</u>

The commonest differences between the two parts of the eye are in the shape and arrangement of the facets. Such differences have been noted in Odonata by Zimmerman, (1913, p. 539), Mallock (1922, p. 770) and Eltringham (1933, p.34), in Ephemeroptera by Needham, Traver and Tsu (1935, p.30) and in Mantida by Wigglesworth (1934, p. 114). The Upper facets are here larger and the lower smaller. The reverse is the case in the divided eyes of Aleurodiae, according to Eltringham (1931, p. 431) and in those of Hymenoptera according to Geyer (1912, p. 379). In Diptera the upper facets are the larger in Tabanidae - see Imms (1938, p. 80) - and the smaller in many other forms - see Wesche (1909, p. 367) and Dietrich (1908, p. 470). In Gyrinidae the upper facets are larger but it appears that in other Coloeptera there is no difference in the size and arrangement of the facets in the two parts of the eye.

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In many Diptera the two parts of the eye differ in pubescence. Both in Bibionidae and Tipulidae the upper eye is more strongly pubescent - according to Carriere (1886,p.142) and Wesche (1909,p.367).

In some cases there is a regional difference in the distribution of pigments in these eyes, associated with differences in the retinal cells. This is the case in Odonata according to Zimmerman (1913,pp.1-36), and in Ephemeroptera according to Carriere (1886,p.143) and Needham, Traver and Tsu (1935,p.30), in Mantidae according to Wigglesworth (1934,p.114), in Hymenoptera according to Geyer (1912,p.379), in Diptera according to Carriere (1886,p.142) and in Gyrinidae according to Hatch (1926,p.343). These differences in pigmentation are associated with a separation of the eye into two parts, one concerned with apposition vision in strong light and the other with superposition vision in dim light. In apposition eyes the ommatidia are densely isolated by pigment and the rhabdom and cone apparatus are in direct contact, while in superposition eyes the ommatidia are poorly isolated by pigment and the rhabdomes and cones are separated by a long, clear part of the ommatidia.

In some cases the difference in the structure of the two parts of the eyes is greatest in the cornea and cone, which differ in size and form. This is the case in many Hymenoptera according to Geyer (1912,p.379) as well as in many Diptera, according to Carriere (1886,p.142).

In some cases the division of the eye is found only in the male sex, as in Ephemeroptera and Diptera where the eye in the female generally corresponds to the ventral part of the male eye.

The main purpose served by the division of the eye appears to be the formation of two parts in which apposition and superposition vision is separately accomplished.

It has been suggested that the differentiation is in some cases associated with a division of the eye function, partly for the perception of movement at a distance and partly for the perception of near detail. This was suggested by Geyer (1912,p.380) for the divided eyes in Hymenoptera and by Mallock (1922,p.770) for those of Odonata.

Where the division of the eye occurs in one sex only, this is presumably correlated with the mating habit. Needham, Traver and Tsu (1935,p.109) have pointed out that the elevated eye in male Ephemeroptera is correlated with the habit of the male of approaching the female from below. In Palingenia, where the male approaches the female on the surface of the water, the eyes of the male are not divided and are smaller than those of the female. The specialised function of the two parts of the eye in Gyrinidae has already been mentioned.

Zavrel (1907,p.248) has shown that in many Diptera, in which the adult eye is single, the eye arises from double or triple rudiments. On these grounds he supposes that the Insect eye is primitively double or triple. The double nature of the eye is clearly a special feature of larval life in a highly developed group and this is not a criterion of the primitive

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condition. A tendency to division is certainly commoner than in Crustacea, but is not a general feature of Insect eyes. The fact that the optic ganglion undergoes no division and that the two parts of the eye are frequently joined by a facetted bridge indicates a relatively late, secondary origin of divided and double eyes

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External Features - Summary.

Fairly large compound eyes are a primitive and typical feature of the Insect stock. Among the Pterygota they are more or less universally present in adults, nymphs and pupae but rarely in larvae, where their place is taken by simple lateral eyes. In many orders there are cases in which they are sporadically reduced or lost in accordance with cavernicolous, burrowing or parasitic habit. Reduction to a single ommatidium is characteristic of the orders Mallophaga and Anopleura. The lateral simple eyes of Aphaniptera are possibly transposed dorsal ocelli, but more probably products of extreme degeneration of the compound eye, where the process is carried further than in the sporadic reductions of the eye, which result in the formation of reduced numbers of ommatidia. The eyes of Strepsiptera are unique and are probably to be regarded as formed by the retention and multiplication of the larval ocelli, where compound eyes have failed to develop.

It is probable that the Apterygota are primitively eyed with Campodeidae, Japigidae and Myrientomata secondarily blind. Machilida have typical and well developed compound eyes, resembling those of some Crustacea. The eyes of Collem-

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-bola and Lepismata, here regarded as compound, are of a different type, degenerate in some cases.

Externally there is considerable variation in the shape, size and relative position of the eyes and these features are related to the habits of life. The eyes are typically and primitively clearly separate on the sides of the head but occasionally approximated to encircle it. They are only rarely or aberrantly fused along a line of contact. Nothing comparable to the completely fused eyes of some Crustacea occurs in Insects. The eyes maintain a general relation to the head sutures and belong to the pre-antennal segment, innervated from the protocerebral part of the brain. A ridge for attachment of the head muscles commonly surrounds the larger eyes and cuts off the adjacent ocular sclerite. The convexity varies with habit but is primitively and typically greater than that of the head. In some Ephemeroptera and Diopsidae, where the eyes are borne on a stalk or lobe of the head, these structures are unjointed and immovable. In other forms stalks are of aberrant or teratological occurrence and generally attributable to heteromorphic regeneration. There is nothing to indicate that the eye stalk is primitive or, where it occurs, appendicular in origin.

Double or divided eyes are commoner than in Crustacea. In some Odonata, Mantida and Hymenoptera the eyes are differentiated into contiguous areas, differing in external and internal structure. The separation of these areas varies in sharpness. Coleoptera, Diptera and Ephemeroptera show

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several series ranging from single eyes through divided eyes to double eyes. In some Psocoptera, Aleurodidae, Aphidae and Coccidae, the eyes are completely divided - i.e. doubled. Differences between the two parts are commonly found in form and arrangement of the facets and pubescence of the eye, in form and structure of the cone and cornea and in the disposition of the pigment and structure of the retinal cells. The last two factors are concerned with the division of the eye into one area for apposition vision and one for superposition. Examples of such differences are given. In Ephemeroptera and Diptera divided and double eyes are restricted to the males, the female eyes corresponding to the lower eyes in the male. In many Coleoptera the two parts of the eye do not differ in structure, the division being a mechanical consequence of the emargination dependent on the backward movement of the antenna or frontal ridge or the extension of a canthus across the eye. Generally the two parts differ, one being associated with apposition vision and one with superposition, or one with perception of movement at a distance and one with perception of near detail, or one with aerial and one with aquatic vision (Gyrinidae). Where the division is restricted to the male the form and position of the eyes is correlated with the mating habits. Although the eye in some cases arises from double or triple rudiments, there is no reason to suppose that the eye is primitively other than single in origin. The tendency to division or division and separation, although not uncommon, is secondary, has arisen more than once, and is relatively recent (as is indicated especially by the single form of the ganglion and the occasional presence of facets forming a bridge between the two parts of the eye).

The cuticle.

As in Crustacea the eye, like the body, is covered by a cuticular secretion of the hypoderm cells, which forms a protective covering. In the case of the eye, in accordance with its special function of admitting and concentrating light, the cornea is as a rule transparent, colourless and lenticular.

As in Crustacea the cuticle of both the body and the eye consists, except in specialised cases, of two main layers, an outer, very thin, readily staining part, without chitin or calcium, about 1µ in depth and an inner, thicker part, usually deposited in successive laminae for the greater part of its thickness, not staining as readily as the outer layer, chitinised and sometimes calcified. These two parts correspond to the epidermis and dermis of Ber~~e~~lese (1909,p.650) and the first to the epicuticle, the second to the combined exo- and endo-cuticle of Wigglesworth (1939,p.17).

The outer epicuticle, as pointed out by Wigglesworth (1933,p.270, 1938,pp.1-3, 1939,p.17) is a thin,impermeable membrane composed of "cuticulin", a mixture of complex fatty and waxy substances allied to cutin and suberin, which may be colourless, amber coloured, or more or less deeply tinged with melanin.

In the Insect eye the epicuticle has been described in the case of Lepidoptera by Nowikoff (1931,p.8)

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This could not be seen in the forms examined and does not appear to have been described in other Insect eyes. It is probable that an epicuticle in the eye in Insects is normally present as in Crustacea and as described by Wigglesworth in the typical insect cuticle. Its apparent absence is probably in many cases is to be attributed either to the fact that it has been dissolved in the material used in preparing sections or to the fact that - due to the similarity between its constitution and that of the exocuticular part of the inner layer - it is readily overlooked and mistaken for a part of the latter.

The epicuticle in Lepidoptera is often specialised according to Nowikoff (1931,pp.18-19). In apposition eyes it passes inwards for some considerable distance through the lens at its periphery and in many cases is sufficiently pigmented to form an opaque barrier round each lens. This is faint in Pieris, clear in Epinephele and very well developed in Zygaena. It renders the pigment isolation of each ommatidium, characteristic of apposition eyes, complete. It is clearly adapted to this specific end. A similar structure is present in superposition eyes but is refractive and remains unpigmented.

Wigglesworth points out (1933,p.270, 1938,pp.1-2) that the inner layer in Insects is often subdivided into two parts, of which the outer is termed exocuticle and the inner endocuticle. The exocuticle resembles the epicuticle in its homogeneity, staining properties and range of coloration.

It is fairly thick and composed of cuticulin continuous with that of the epicuticle and chitin and protein continuous with that of the endocuticle, together with a certain quantity of polymerised carbohydrates other than chitin. The inner part or endocuticle he describes as a colourless elastic layer, horizontally laminated and pierced by vertical pore canals, corresponding to infoldings of outer parts of the cuticle, and filled, according to some, with fluid or protoplasmic substances and, according to others, with chitinised material. Wigglesworth (1933,p.271) points out that the exo- and endo-cuticular parts of the inner layer correspond respectively to the parts formed before and after the last moult.

Due to the readiness with which the epicuticle is overlooked, the eye cornea generally appears to consist of an outer homogeneous part followed by a thicker, less refractive, inner, laminated part - the exo- and endocuticle - which have the properties indicated above. Such a structure has been almost universally described or figured. The apparently uniform facet in Machilida - see p.236 - is unusual.

Nowikoff (1931,pp.33-34) described only two layers in the unspecialised lenses of superposition eyes in Lepidoptera. These correspond to the epicuticle and a fused exo- and endo-cuticle.

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In some cases the endocuticle is enlarged to form a smooth, downwardly projecting "processus corneae" which may exceed the rest of the cornea in depth. Functionally this supplements the cone. Nowikoff (1931,p.10) described this process as laminated throughout and faintly granular, with the refractive power decreasing from the centre to the periphery - an optical property which it shares with the normal cone apparatus. This "processus corneae" is characteristic of the apposition eyes of Lepidoptera according to Nowikoff (1931,p.10) and Eltringham (1933,pp.4-5, 17-18).

Similar prolongations of the lower side of the cornea are found in the exocone eyes of some Insects. In these cases however the cone apparatus is very much reduced and the process of the cornea much deeper than in the above case. Such "exocone" eyes have been described by Kirchoffer (1908) in many Coleoptera of the families Staphylinidae, Silphidae, Histeridae, Malacodermidae, Cleridae, Byrrhidae, Elateridae and Dermestidae and by Eltringham (1933,pp.29, 32) in _Lampyris_ and _Cantharis_. Exocone eyes of an intermediate type with an enlarged lens and somewhat reduced cone apparatus have been described in Dermaptera by Eltringham (1933,p.28).

Although the lenses are primitively and typically either colourless or of a very faint chitin-yellow tint, there are some eyes in which they are pigmented. Eltringham (1919,p.4) points out that the lenses in the eyes of _Vanessa urticae_ are colourless centrally but yellowish-brown at the periphery of the eye. In _Aleorodes brassicae_ and _A. proletella_, according to Williams (1930,p.56) and

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Eltringham (1931,p.433), the lenses are arranged in rosettes, with six thick yellowish-brown lenses surrounding a central, thin, colourless lens. The underlying ommatidia are identical and lenses are as nearly as can be seen, of the same focal length. It is possible that there is some difference in the refractive power of the coloured lenses which may render the feeble eyes especially sensitive to the yellowish-green colour of the leaves, which they inhabit - see Butler (1938,p.300).

Unfacetted eyes are much rarer than in Crustacea and it is probable that the primitive and typical forms were provided with lenses. Phillips (1906,p.130) has suggested that Parker's idea of the Crustacean eye as primitively unfacetted should be extended to apply to Insects, but he gives nothing other than the precedent he quotes in support of this. Although the facets are sometimes formed late in development as in Periplaneta and Agrion (Lowne 1884,p.401) and in Tribolium confusum (Marshall, 1927,p.620), the very rare occurrence of unfacetted adult eyes suggests that this does not represent the primitive condition but is a secondary consequence of crowding of the outer parts of the eye in early development. That a very crowded condition obtains in the outer parts is to some extent borne out by the fact that, as the lenses form their individual thickenings, the cones, being compressed, decrease in size. This is a frequent feature in development - see Marshall (1927,p.622). Facets are occasionally absent in mutant forms, as in the case of bar eyed Drosophila. Huxley and Wolsky (1936,p.485) point out,

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however, that the regions in which facets are absent in this case have a very degenerate ommatidial structure. They consider that the normal formation of the retinal cells is necessary to the formation of facets. The absence of facets in some Dorylinae as described by Werringloer (1932,p.432) is a degenerate feature of a degenerate eye.

As in Crustacea a wide variation in the convexity of the facets is apparent, so that the outer surface of the eye may appear either smooth or granular. Here too the various facet forms are scattered irregularly among the different orders. A highly biconvex form as in Crustacea is associated with a circular shape of the facets and other evidences of the reduction of the eye and the separation of the units (except where the biconvex form is due to the specialised development of a "processus corneae" or an exocone process). *Lathridium* and *Batocera* (Col.) are given by Packard (1903,p.250) as examples of highly biconvex, circular lenses in reduced eyes. Such lenses occur in Aphides, are figured by Berlese (1909,p.664, Fig.826) in *Phylloxera quercus* and described in Thysanoptera by Imms (1938,p.341). Most of the variations in facet form are represented in each order. The following examples are drawn from Geyers' work on Hymenoptera (1912,pp.373, 378, 380). Biconvex lenses with slight convexity occur in some Sphegidae, and in Pompilidae and Chalcididae. Planoconvex lenses with an external convexity occur in Sphegidae, with an internal convexity in Apidae, Vespidae, Formicidae, Brachonidae and Siricicdae.

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Although the concavo-convex form is not known in Hymenoptera it occurs in other orders such as Diptera where it is present for example in <u>Drosophila melanogaster</u> (Huxley and Wolsky, 1936, p. 485). The form of the facets may differ widely in nearly related types or even within different areas of the same eye, especially towards the periphery of the eye.

In <u>Aleurodes brassicae</u> (Eltringham 1931, pp. 433-434) the variation is more elaborate. Here the facets are arranged in rosettes with the central facet considerably less convex than the outer ones. In view of the variability of the facets no one form can be selected as primitive or typical.

As in Crustacea the commonest form of the facet is the hexagonal, With a few exceptions it has been practically universally described or illustrated in all Insect species, in which the eye has been investigated. In a few cases circular or oval facets are present - in degenerate eyes Phillips (1906, p.130) has argued that the primitive arrangement of the eye units as a whole is on a tetragonal rather than a hexagonal plan, since he considers that this is the case in the lower parts of the eye, where the units are less closely appressed and less likely to have been displaced from their primitive plan. There are, however, no Insect eyes with facets arranged on a tetragonal basis. It is clear that the primitive and typical arrangement of the facets is hexagonal, as in Crustacea and that the circular facets are secondarily derived from these, where the eyes

/degenerate

degenerate and the ommatidia separate.

No division of the facets such as is found (as a transverse of diagonal line) on the facets in some Crustacea - see p. 105 - is apparent in Insect eyes. Although the facets are secreted as a rule by two hypoderm cells, each lens is primitively and typically a single structure.

As in Crustacea the facets are typically and primitively arranged in regular, alternating, vertical rows, and are equal in size, identical in form and regular in arrangement as far as is mathematically consistent with the distribution of hexagons on a curved surface - see p. 106 Areas of disturbance in the regularity of the arrangement are not uncommon towards the eye periphery. A disturbance in the arrangement is sometimes found in mutant forms, as in the bar-eyed mutant in Drosophilia melanogaster, where the facetted area of the eye is interrupted by a degenerate unfacetted strip, the ommatidia being reduced in number and restricted to a band- see Zeleny and Matoon (1915, p. 516) and Huxley and Wolsky (1936, p. 485). The facets are generally contiguous or very nearly so. Separation of the facets is common in degenerate eyes. In those Hymenoptera and Lepidoptera in which hairs are present, these are inserted between the facets, which are slightly separated from one another. The slight separation of the lenses in Machilida, a feature more marked in Collembola and Lepismata, possibly indicates that the primitive eye was rather less closely aggregated than the typical form with its crowded and contiguous facets, (although the tendency

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to separation in many Collembola is probably complicated and increased by degeneration of the eye.)

The eye is typically large but the actual number of facets varies in relation to the habits of life and differs in nearly related forms, or even in the two sexes of the same species. Thus Lienemenn (1906, p.191 et seq) points out that there are two thousand five hundred lenses in the eye of the male *Lampyris splendidula* as compared with three hundred in the female, five-thousand three hundred in the male, *Melolontha vulgaris* with four thousand eight hundred and fifty in the female. The facet number is not precisely fixed for the species. Lienemenn has pointed out from his counts of the facets numbers in one hundred and fifty species in Coleoptera that there is a tendency to increase in the number of facets as the body size of the individual specimen increases. Driver (1926, p.317) has pointed out that in the development of *Drosophola melanogater*(a bar eyed mutant)the facet number varies inversely with the temperature of larval development, while Bodenstein (1941, pp.87-) has shown that the facet number depends on the duration of the pre-imaginal stages in development. There is no record that the number of facets and their individual area increases throughout the life of the Insect, but it is possible that this will prove to be the case in Insects as in Crustacea. Generally the number of the facets is largest in active forms. It is often but not always

/reduced

re reduced in noctornal species. As pointed out by Linnemann (1906, p.191) there are twenty-four thousand facets in the nocturnal beetle <u>Necrophorus germanicus</u>. Some examples are given below to illustrate the range of variation of the facet number in different orders. Among the Hymenoptera (in the ants) one ommatidium only is found in <u>Ponera punctissima</u> (Imms 1938, p. 80), six to nine in the worker ant <u>Solenopis fugax</u> (Sharp, 1901, p.92) fifty in many worker ants (Packard, 1903, p. 248) and from one hundred to six hundred in others, with two to three hundred in most female ants and about four hundred to about eight hundred and fifty in most male ants (Snodgrass, 1926, p. 75). A similar series can be found in Coleoptera, seven facets being present in <u>Lathridius</u> (Packard, 1903, p. 248) two thousand to three thousand in <u>Saperda</u>, two thousand five hundred in <u>Carabus</u> species,and the male <u>Lampyris splendidula</u>, five thousand three hundred in the male <u>Melolontha vulgarus</u> (with four thousand eight hundred and fifty in the female (Lienemann 1906, p. 191 et. seq.) nine thousand in <u>Dytiscus Marginalis</u> (Korscheldt, 1924, p. 432), twenty-four thousand in <u>Necrophorus germanicus</u> (Linnemann, 1906,p.191) twenty-five thousand in <u>Mordella</u> (Packard, 1903, p. 249). In Lepidoptera the variation is less and the number of facets on the whole larger. Five thousand to six thousand are present in <u>Vanessa urticae</u> (Eltringham, 1919, p. 4), twelve to seventeen thousand in many Lepidoptera (Packard, 1903, p. 249), twelve thousand in <u>Acherontia atropos</u>,

/seventeen

seventeen-thousand in *Papilio* and twenty-seven thousand in *Sphinx convoluta* (Packard, 1903, p. 249) Similar numbers are found in most Odonata with fifteen thousand to twenty thousand facets in most *Aeschna* species, with a maximum of thirty thousand in other species (Snodgrass, 1935, p. 532).

Hairs and scales, absent in the eyes of Crustacea, are occasionally found in Insects. Their occurrence is neither primitive or typical. These hairs are elongated, straight and unbranched, being inserted between the facets and radially arranged, so that they presumably interfere as little as possible with the vision of the ommatidia, which they surround. In the older specimens they are often partly brushed off. They are frequently found in Hymenoptera and among Lepidoptera are fairly common, as pointed out by Nowikoff (1931, p.10). In Coleoptera the hairs are occasionally replaced by small scale-like structures as in *Trachypholis* - as described by Waterhouse (1889, P.XXlV). The hairs are the product of small hair cells, hypodermal cells interposed between the ommatidia as described by Johannsen (1892, p. 354), Phillips (1906, p. 132) and Nowikoff (1931, p. 10). Phillips mentions that these cells are binucleate, with a protoplasmic part projecting into the hair. The function of the hairs is uncertain. It is possible that they serve to protect the cornea and keep it free of pollen particles, etc. since the hairs are found mainly in flower frequenting forms.

External features (Summary)

As in Crustacea the eye is protected by a cuticular secretion of the corneal hypoderm cells, continuous with the body cuticle, normally colourless, transparent and lenticular and composed of two main layers, an outer, very thin, portion staining readily, containing no chitin or calcium and an inner, thicker, laminated part, chitinised and sometimes calcified. These correspond to the epidermis and dermis of Berlese and to the epicuticle and combined exo- and endo-cuticle of Wigglesworth. The epicuticle is thin, made up of "cuticulin", a mixture of fats and waxes, and is colourless to amber, or occasionally tinged with melanin. The layer has only been described in Lepidotera but is probably typically present and either destroyed in preparation or mistaken for a part of the exocuticle. In Lepidoptera the epicuticle may be modified into an inwardly projecting sheath, surrounding the rest of the cornea and pigmented in apposition eyes, refractive in superposition forms. The inner part is generally not so uniform as in Crustacea but subdivided into an outer exocuticle, staining homogenously, coloured like the epicuticle where this is pigmented, composed of a mixture of cuticulin, chitin, protein and polymerised carbohydrates, and an inner endocuticle colourless, elastic, laminated, pierced by longitudinal pore canals, and composed of a mixture of chitin and protein.

The exo- and endo-cuticle correspond to the

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parts formed before and after the last moult. As the epicuticle is readily overlooked the eye has generally been described as having a two layered cornea made up of exo- and endo-cuticle. Nowikoff found no exocuticle in Lepidoptera but defined the epicuticle and endocuticle. In some Lepidoptera the endocuticle is greatly enlarged and projects inwards to form a "processus corneae". In exocone eyes a much larger projection of the cornea occurs and the cone is reciprocally reduced, the refractive properties of the "processus corneae" and exocone process approximate to those of the cone apparatus in other forms. In some Dermaptera and Hymenoptera there is an intermediate condition with a fairly large exocone process developed and the cone partially reduced. Primitively and typically the lenses are colourless or a very faint chitin yellow or amber. The occurrence of melanin in the outer parts of the cornea is exceptional, as is the peculiar pattern of coloured and colourless lenses in Aleurodes. The eyes are primitively and typically facetted, the late origin of the facets in some cases in development being due to a crowded condition of the outer parts of the eye. Loss of the facets occurs in some mutant and degenerate forms. The convexity and form of the lenses varies greatly and in nearly related forms or even different areas of the same eye. As in Crustacea highly biconvex forms are usually separated, circular and associated with a general degeneration of the eye. In view of the variability in convexity of the facets, no one condition can be singled out

/as

as typical or primitive. The hexagonal facets are primitive and typical. A circular form is associated with reduction of the eye and tetragonal facets are absent. Although Phillips contends that the arrangement of the ommatidia is primitively on a tetragonal pattern there is nothing to indicate that this applies to the facets. The facets are not divided as in some Crustacea into two parts corresponding to the hypoderm cells secreting them. As in Crustacea, they are typically and primitively arranged in regular, alternating, vertical rows, equal in size, identical in form, and regular in arrangement, as far as possible,with areas of irregularity at the periphery or in mutant forms. They are typically contiguous or very nearly so, but are separated in degenerate forms , and where hairs occur. The separation of the facets in Apterygota possibly indicated that the primitive form was rather less closely aggregated than the typical. Typically the facet number is large but varies in nearly related forms and in the two sexes of the same species. It is not fixed for the species but increases with body size and varies with the temperature and duration of development. Whether the number of facets and their individual area increase during life, as in Crustacea, is not certain, but is quite possible. The number is largest in the most active forms. It varies, for example, in Ants from one to eight hundred and fifty, in Coleoptera from seven to twenty-five thousand.

/Other

Other examples are given and the maximum number reached appears to be thirty-thousand in Odonata. Hairs and scales are occasionally present. They are radially arranged to interfere as little as possible with the vision of each ommatidium. The hairs are straight, elongated, unbranched and secreted by underlying hypodermal hair cells. They are sometimes brushed off in the older forms and are probably protective in function.

Corneal hypoderm.

The cornea is secreted by hypodermal cells corresponding to those producing the body cuticle, these structures being continuous at the edge of the eye. Berlese (1909, pp.660-662) has pointed out that the occurrence of these cells, as in Crustacea, is to be regarded as a hallmark of the compound eye and in this connection he described their presence in several forms, in which they had previously been regarded as absent. That these cells have sometimes been overlooked, is due to the fact that in some of the lower orders they are reduced in the adult and demonstrated with difficulty in thin sections only, while in the rest of the Insects they are converted into pigment cells, which have migrated from their primitive position.

Primitively two small, colourless cells are present, interposed between the cornea and the cone. Although fairly well developed in the young, there is a tendency for these to be reduced in the adult, where they may be slightly displaced and separated from one another laterally. This is probably an indication that here, as in Crustacea, the cells were once more conspicuous than at present. Snodgrass (1935, p.351) has pointed out that at the beginning of each

/instar

instar the cells assume a position immediately below the lens, which they have to secrete. (Their permanent occurrence in this position in Crustacea is correlated with the habit of moulting throughout life).

This primitive condition of the corneagenous cells has been described in many Collembola (Willem,1897,p.225), in Lepismata (see p.216), in Machilida (see p.222), in Ephemeroptera (Needham, Traver and Tsu, 1935,p.48), in <u>Mantis religiosa</u> (Patten,1886,p.646) and in <u>Periplaneta</u> (Berlese,1909,p.655). This arrangement, corresponding to that in many Crustacea, is in general characteristic of all the Apterygota and a few members of the lower Pterygota (mentioned above) and of the early stages of development of the eye in other forms. Berlese (1909,pp.665-666) pointed out that in all cases, in which the development of the eye had been studied, the corneagenous cells exist first in the primitive position and are only later and secondarily displaced and pigmented.

Among the remaining Insects, as Hesse (1901) has pointed out, the corneal hypoderm cells, after the secretion of the adult cornea, are converted into "iris" pigment cells. These are typically two in number in each ommatidium and are laterally displaced to surround the cones. This is the typical condition in all cases except those mentioned above. The fate of the displaced cells was unknown however, before the work of Hesse (1901) and the formation of the cornea was attributed to the upper surface of the cone cells as in Johannsen's work (1892,p.353) on the eyes of Lepidoptera.

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The eye is typically and primitively facetted and the hypoderm cells arranged in pairs, one pair under each facet. An exceptional number is found by Imms (1906, p.41) who described four cells in the degenerate eyes of *Anurida* and by Lowne (1884, pp.401-402) who described only one cell in the eyes of *Agrion sp.* and *Periplaneta sp.* There appear to be no other exceptions to the two celled condition.

As in Crustacea the boundaries of these cells are in general not clear and the cells of adjacent ommatidia tend to run together, both in the pigmented and the unpigmented forms. In no case does a central displacement of the cells, such as occurs in some Crustacea, seem to have been described. Lateral displacement is, however, very common, being slight where the cells are unpigmented, and marked where they form an "iris" pigment sheath round the sides of the cone.

As in Crustacea the nuclei are regularly arranged throughout the eye. They have seldom been described but where figured seem to resemble those of Lepismata and Machilids, being spherical, with a regular wall, with deeply staining, coarsely granular contents without a nucleolus. In most adults except Lepismata they are small where the cells are unpigmented and, where the cells are pigmented, the nuclei are so closely surrounded by coarse pigment granules that their structure is difficult to make out.

The pigment is black or brown in colour and appears

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to be of the nature of a melanin. The granules are densely and regularly packed in the thin clear cytoplasm of the cells. The pigment like that of the rest of the eye - [illegible] - is subject to migration.

Corneal hypoderm - Summary.

Hypoderm cells, corresponding to those secreting the body cuticle, give rise to the eye cornea. Their apparent absence in some cases is due to this small size or to their displacement to form "iris" pigment cells. Primitively two. small, colourless cells occur between the cone and cornea, reduced in size in the adult and often slightly displaced laterally, although they lie immediately under the cornea when this is in the course of formation. As in Crustacea they were probably once more conspicuous. The primitive condition obtains in all Apterygota, in some of the lower Pterygota (Ephemeroptera, Mantis and Periplaneta) and in the young of all Insects. According to Hesse, in the remaining Insects, these cells, after the formation of the cornea, are displaced and pigmented to form an "iris" pigment sheath round the cone. In such eyes the formation of the cornea had previously been attributed to the upper surface of the cone cells. Typically and primitively the eye is facetted and the hypoderm cells regularly arranged throughout the eye, one pair to each ommatidium. In a few exceptional cases four cells or one cell have been recorded. As in Crustacea the boundaries are not clear and the cells tend to run together. They undergo no

/central

central displacement but lateral displacement is common and marked where the cells are pigmented. The nuclei are typically small, spherical, with a regular wall, coarsely granular, densely staining contents and with no nucleolus. The cytoplasm is thin and clear. The pigment granules, where present, are dense and regular in arrangement, composed of melanin, typically black or brown in colour and subject to migration.

The cones and cone cells .

The dioptric cone apparatus lies immediately below the cornea and the corneal hypoderm cells, where these cells remain in their primitive position. This apparatus consists of the cone cells and of their secretions except in acone and exocone eyes (see below) where the secretions are absent . Each segment of the cone secretion is related to one of the cone cells and these segments are typically and primitively flattened against one another to form an axial structure, enclosed centrally within the cells. In some exceptional cases the cone segments do not come into contact with one another and each remains rounded off within its own cell. Marshall points out (1927, p.61) that this is characteristic of the early stages of development and according to Patten (1886, p.646) the condition persists in the adult eye of Mantis. Such mutant irregularities as result in the separation of the cone segments in some Crustacea, do not appear to have been noted in Insects.

As in the eyes of Crustacea the cone segments are typically and primitively regular and symmetrical in form and constant in orientation throughout the eye as a whole, although minor peripheral irregularities occur, as in the eyes of Lepismata - see p. 213

As in Crustacea the size of the cone

apparatus/

apparatus is very variable and bears no fixed relation to the size of the retinal cells, although, where one is poorly developed, the other is never large or elaborate.

As far as is known the cone secretion is formed directly within the cytoplasm of the matrix cells - that is, it is not extruded from the nucleus as is sometimes the case in Crustacea. Such an intracellular cone has been described in Apis mellifica by Phillips (1906, p.126) and in Tribolium confusum by Marshall (1927, p.619).

Secondary transverse division of the cone cells or their secretions, such as is occasionally found in Crustacea, does not occur in Insects.

As in Crustacea the cone secretion is primitively and typically colourless. Very rarely the cones are coloured as in Melolontha, where they are described by Eltringham (1933, p.21) as of a faint pinkish tint. (Lowne (1884, p.405) pointed out that the occasional pigment granules, which he had described as embedded in the cones in the eyes of Lepidoptera, must have been artificially deposited there by shrinkage of the surrounding pigment cells)

The cone secretions are typically and primitatively highly refractive and homogeneous. Exner pointed out (1891) that the refractive index within the cone apparatus as a whole tended to decrease

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from the centre of the secretion to the periphery of the cells, so that oblique light rays were totally reflected and the main ray left the cone parallel to its long axis. In the apposition eyes of some Lepidotera as described by Nowikoff (1931, p. 11) a peripheral decrease in the refractive index is not confined to the cytoplasmic part but found within the cone secretion itself, so that both in *Epinephele* and *Zygeana* the central part of the secretion is denser and of a higher refractive index than the outer part. Such non-homogeneity of the cone secretion itself does not appear to have been described elsewhere.

The cone apparatus is typically and primitively conical in form with the expanded base outwards and the long axis corresponding to that of the ommatidium. The precise contour of the upper surface of the cone apparatus is determined by the form of the cornea and hypoderm cells. Where the upper surface of the cone apparatus is partially or entirely capped by hypodermal cells, this may be convexly rounded as in Lepismata or pointed as in Machilida - see pp 214, 229 Where the hypoderm cells are displaced the upper surface of the cone apparatus conforms to the shape of the inner surface of the corneal lens. The inner end of the cone apparatus is typically drawn out into a point which makes contact with the sensory structures below/

below. The length of this point and the degree of its attenuation are determined by the length and attenuation of the ommatidium, and, in cases in which the ommatidia are short and the eye small, as in Collembola (Willem, 1897, p.225) and Lepismata (see page 214), the lower surface of the cone apparatus is rounded rather than drawn out to a point. The hourglass shape of the cone in Scarabeus vermiculosus as described by Elringham (1933, p.34) is clearly exceptional.

The number of cone cells and segments is typically and primitively four. The two celled condition in the degenerate eye of Anurida, as described by Imms (1906, p.41), is exceptional as is the variability in the number of cone segments shown in some Lepidoptera. Among the latter, according to Nowikoff (1931, p.35) , the number of cone segments varies from three to five in the case of Trimandria sp, while, in the case of Ephestia kuhniella as described by Umbach (1934, p.561), the number of segments varies from two to five. Otherwise four cone sells and segments have been universally mentioned and figured in the available literature.

The cone apparatus is the most variable

part/

part of the Insect eye. The first classification of the eye was that of Grenacher (1879), who defined three cone types/eucone, pseudocone and acone - which differed in the presence or absence and the nature of the cone secretion, as well as in the position of the nuclei. Kirchoffer (1908), working on beetles, described an additional exocone type. These types have been admitted in all later work. (Although Lowne,(1878, p.577) at first classified the cones according to their contents as "hydroconic", with a fluid content contained in an elastic capsule, or "tetraconic", with a solid content, he later abandoned this (1894, p.404) in favour of the current classification).

It seems probable that eucone eyes, resembling those of the Crustacea, are to be regarded as the primitive type. No one type is typical of the Insects as a whole, but the eucone form is the commonest and most widely spread. Although Phillips (1906, p.131) has suggested that the acone eye is more primitive than the eucone there is little to support this view. He based this suggestion on the fact that an acone condition preceeded the eucone condition in the development of some Hymenoptera. It seems unlikely that this is a reliable guide to

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the phylogenetic sequence of the cone types.

The definition and occurrence of the cone types is as follows. Eucone eyes are provided with a solid, chitinous secretion of the cone cells, the four segments being closely appressed, highly refractive, transparent and colourless, with the nuclei placed in front of the secretion. Such cones have been described in Collembola by Willem (1897, p.225) and Berlese (1909, p.659); in Lepismata (slightly modified - see p. 216); in Machilida (see p. 219) ; in Ephemeroptera by Needham Traver and Tsu (1935, p.47); in Odonata by Imms (1942, p.82) ; in Orthoptera by Lubbock (1899, p.151), Packard (1903, p.253), and Imms (1942, p.82) ; in Tricoptera by Imms (1942, p.82) ; in Neuroptera by Lubbock (1899, p.151) and Packard (1903, p.253) ; in Hemiptera by Packard (1903, p.253) and Imms (1942, p.82) ; in Lepidoptera by Lubbock (1899, p.151), Packard (1903, p.253), Eltringham (1919, p.15) and Nowikoff (1931, pp.11,34); in Diptera by Lubbock (1899, p.151); in Hymenoptera by Phillips (1906, p.145) and Geyer (1912, p.382) and in Coleoptera, in Carabidae, Scarabidae, Dytiscidae and Cicindelidae by Kirchoffer (1910) and in Dytiscidae by Korschelt (1924, p. 427) and Fischer (1933, p. 17).

Pseudocone eyes/

Pseudocone eyes contain a transparent fluid or semifluid secretion within the cone cells with the nuclei lying behind this. Carriere (1885, p.143) has emphasised that the pseudocone and eucone types grade into one another as far as the consistency of the cone secretion is concerned and that they differ most markedly in the position of the nuclei. According to Grenacher (1879), who defined the type, pseudocone eyes were confined to some of the Diptera. Lowne (1884, p.405) and Zawarin (1914, p.186) described a similar cone in some Odonata. Patten described them in Mantis (1886, p.647), and Eltringham in Aleurodes (Hemiptera) (1931, p.431). Packard (1903, p.253) described them as present in a few Coleoptera. Since Grenacher's time their presence in many Diptera (Bradcycera and Clyclorrapha) has been confirmed by Fischer (1933, p.17) , Imms (1942, p.82) and Huxley and Wolsky (1936, p.485).

Acone eyes have elongated, clear, transparent cells, with no secretion solid or fluid. These occur in Dermaptera according to Packard (1903, p.253), Fischer (1933, p.17), Eltringham (1933 p.17) and Imms (1942, p.82). They are known in He~~r~~miptera as well as in Nematocerous Diptera and in some Coleoptera especially Cleridae, Coccinnellidae, and Curculionidae and some Staphylinidae, Histeridae and Silphidae according to Eltringham (1933, p.17).

In exocone eyes the cone cells are reduced in ~~from~~ size and degenerate in structure. They do not form a cone secretion and are functionally replaced by an enlargement of the inner part of the corneal lens resembling the processus corneae of Lepidoptera - see page 264 . This is an extracellular product of the hypoderm cells, is bluntly rounded and, like the rest of the endocuticle, faintly laminated. Its refractive index, like that of the cone apparatus, decreases towards the periphery, so that it has much the same optical properties as the latter. The peripheral part is less highly chitinised than the central. Such a structure is common in Coleoptera, in some Silphidae, Staphylinidae and Histeridae and in Byrrhidae, Elateridae, Dermestidae, Malacodermidae, and Cantharidae according to Eltringham (1933, p.17). Marshall (1927, p.619) has described exocone eyes in the adult beetle Tribolium confusum replacing a eucone condition in the young.

The nuclei are more variable in position than those of Crustacea, which are characteristically distal. In Insects in eucone eyes the nuclei are in front of the secretion, in pseudocone eyes behind it, while in acone and exocone eyes their position is not fixed. The nuclei may be oval, ellipsoidal, spherical or slightly flattened against one another, where they

form /

form a cap over the cone apparatus, as in the case of Machilida - see p. 218. Where the nuclei are figured, they are without exception densely granular, with a distinct boundary, and are larger than the hypodermal nuclei. No nucleolus appears to have been described.

As in Crustacea it is probable that there is no constant or characteristic structure for the cytoplasm of the cone cells and that its condition varies with the secretory activity of the cell. No detailed descriptions of the cytoplasm are available but in the majority of figures it appears uniform and clear or very faintly granular. In the case of acone eyes it is highly refractive. Marked thickenings, other than the cone secretions, such as are sometimes found on the walls of the cone cells in Crustacea, have apparently not been described in Insects. Slight local differences in the cytoplasm may occur as in *Epinephele* where the cytoplasm is more dense at the upper than at the lower end of the cells - see Nowikoff (1931, p.12). In some cases as in Lepismata and Machilida - see pp 216, 229 - the cytoplasm is practically eliminated, the entire cell being filled by the cone secretion.

At their lower ends either the cone cells or their secretions, or both of these, are in contact

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the upper end of the rhabdomeres or rhabdom. The variable relative lengths of the cone cells and their secretions, determines which of these come into contact with the retinal structures. In all apposition eyes [illegible] a clear, transparent prolongation of the retinal cells makes contact with cone apparatus. The contact between the two structures is so close that they have been described as continuous by Patten in the case of *Vespa* and *Mantis* (1886, p.646), by Phillips (1906, p.138) in the case of *Apis mellifica* , by Johnas (1911, p.215 et seq.) in the case of many Lepidotera, and by Jorschke (1914, p.153) in the case of the eyes of many Orthoptera and Termites. The apparent continuity is only a close contact since the two structures are secreted by cells of a totally different type.

Primitively and typically retinal cells and rhabdoms or rhabdomeres end at the level at which the cone apparatus is in contact with the retinal structures. As in Crustacea there are however exceptions to this, and in some cases the cone apparatus extends down between the rhabdom structures and retinal cells for a short distance. This condition is described by Nowikoff (1931, pp.11, 12) in the eyes of *Panorpa~~dae~~* as well as in those of the Lepidoterous forms *Epinephele*

and/

and *Zygaena* and by Korschelt (1924, p.427) in *Dytiscus marginalis*. With a few exceptions ([illegible] . there is little tendency for the retinal cells to project up round the cone apparatus for any considerable distance. Laterally the cone apparatus is in contact with or separated by only a small distance from the surrounding pigment cells. The two always remain perfectly distinct.

Primitively the cone cells and segments, although appressed, are separated from one another by the original cell boundaries, which are roughly at right angles to one another. Typically the boundaries tend to be partially at least obliterated. This is the case in *Mantis* as described by Patten (1886, 646p.) where only one of the two planes of division persists towards the inner end of the cone apparatus. In many other cases as described in general by Berlese (1909, p.657) and especially in Lepidotera by Nowikoff (1931, p.34) the boundaries are very difficult to make out and often completely absent.

The cone and cone cells - summary .

The dioptric cone apparatus comprises the cone cells and their secretions (when these are present). It lies between the cornea or the hypoderm cells (where these remain distal) and the sense cells. The segments of the cone correspond to the cells secreting them and are primitively and typically symmetrical in arrangement throughout the eye with only minor, peripheral irregularities. The size of the cone varies without strict relation to that of the sense cells. The cone secretion is of intracellular rather than of intranuclear origin (as in some Crustacea). The cone segments are typically and primitively in close contact with one another and are separate only in early development and in the adult Mantis as described by Patten. The cone apparatus is, with rare exceptions, colourless and universally transparent and refractive, with a peripheral decrease in refractive index in the cytoplasm, or in some cases the cone itself, ensuring that the rays passing out are parallel to the axis of the ommatidium. Typically and primitively however the cone secretion itself is homogeneous, with its basic form conical, the upper contours being specifically determined by the form of cornea and hypoderm cells and the lower end being drawn out with

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an acuity dependant on the elongation and degree of crowding of the ommatidia. The "hourglass" form in Scarabeus is exceptional. Neither cells nor secretions show any tendency to traverse division such as occurs in some Crustacea and they are primitively and typically four in number with the two celled type in Anurida degenerate, and the variable number (from two or three to five) in some Lepidoptera exceptional. Grenacher's classification of the cone types, modified by Kirchoffer, is that in general use. In eucone eyes the secretion is chitinous and solid and the nuclei distal. Examples are common among Collembola, Lepismata, Machilda, Ephemeroptera, Odonata, Orthoptera, Neuroptera, Hemiptera, Tricoptera, Lepidoptera, Diptera, Hymenoptera and Coleoptera. In pseudocone eyes the secretion is fluid or semifluid and the nuclei proximal. Such cones appear in Odonata, Orthoptera, Hemiptera, Coleoptera and Diptera (Brachycera and Cyclorrapha). Acone eyes, with clear transparent cells with no secretion occur in Dermaptera, Hemiptera, Diptera (Nematocera) and Coleoptera. Exocone eyes with a degenerate cone aparatus functionally replaced by an enlarged corneal lens are restricted to Coleoptera. The eucone type resembling the Crustacean form is regarded as primitive and is the commonest and most widely spread. The nuclei vary in position, may be oval, ellipsoidal, or flattened to form a cap over the cone apparatus. They are densely granular, larger than the hypoderm nuclei, with a distinct boundary and no nucleoli. The cytoplasm shows occasional local variations in consistency but forms no thickenings other than the cone secretions. It may be practically eliminated and has no very characteristic structure. Proximally the cone apparatus (cells, secretions, or both depending on their relative lengths) makes contact with the rhabdom structure (except in superposition eyes), at a level on which both retinal cells and rhabdoms end. This primitive and typical arrangement is occasionally disturbed by the penetration of the cone apparatus below this level or the extension of the retinal cells above it. The cone apparatus shows no tendency to coalescence with the pigment cells surrounding it. Primitively the intracellular boundaries are apparent at right angles to one another but typically tend to disappear at least partially.

The retinal sense cells.

As in Crustacea the retinal sense sense are unipolar, pigmented, nerve end cells, bearing axial, sensory rods and associated into retinula groups. The distal, retinal, pigment cells, found in some Crustacea, are not represented in Insects.

As in Crustacea the retinal sense cells vary in number and in the great majority of cases this number lies between four and eight. The two or three celled types, found as occasional mutants in some Crustacea, are not represented in Insects. Retinulae containing more than eight cells are comparatively rare, although of more frequent occurrence than in Crustacea. The cells never exceed twelve in number, the maximum number in Crustacea being fourteen.

Cases in which more than eight cells are present are restricted to Lepidoptera and Hymenoptera. Among Lepidoptera ten cells have been described by Johnas (1911, p.218 et seq.) in *Cedaria* and *Agrotis*. Nowikoff (1931, p.37) points out that an increase in the number of retinal cells as in some Crustacea - see p.148 - is an adaptation to vision in dim light. He described ten cells in the superposition eyes of *Agrotis* and twelve in *Trimandria*. Umbach (1934, p.561) found ten cells (of which one was somewhat reduced and displaced towards the base of the eye) in *Ephestia kuhniella*.

Phillips pointed out (1906, p 126) that, although eight cells were typically present, there were some ommatidia in the eye of *Apis mellifica*, which were provided with nine retinal cells. Nowikoff (1931) p. 15) described nine cells, of which one was clearly a reduced and degenerate remnant at the base of the group, in *Pieris* and *Epinephele*.

Eight cells are of very common occurrence. They have been described by Zimmerman (1913 p. 1 et seq.) in Libellulidae, Phasmida and Mantida. In all of these cases one of the cells is reduced to a nucleus surrounded by a small amount of protoplasm and is displaced to the base of the eye. Dietrich (1909, p.465) found eight cells in Odonata nymphs, although Zavarin (1914, p.186) found only four cells in the adult retinula in *Aeschna sp.*

Eight retinal cells, with seven in some of the ommatidia were described by Jorschke (1914. p. 158) in many Orthoptera and Termites and by Uchida (1934 p. 520) in the Longicorn forms *Euconocephalus nasutus* and *Homocoryphus lineosus*. Among the Hemiptera Heteroptera eight cells have been described as typical of the Cryptocera by Bedau (1911, p.417) and the same number occurs in *Aleurodes brassicae* among the Homoptera according to Eltringham (1931, p. 433). Ast (1930) described eight cells as typical of Neuroptera. Eltringham (1919, p.5) found the same number in the Lepidopteran _Vanessa urticae_, although he pointed out later (1933, pp. 21, 22), that the number in this case might vary from six to eight. Johnas (1911, p. 218 et seq) regarded eight to ten cells as typical of Lepidoptera, while Nowikoff (1931, p.14) described eight cells as typical of the apposition eyes of this order and in particluar mentioned this as the number in _Epinephele_ and _Macroglossa_, where, in both cases, one of the cells is reduced in size and restricted to the base of the eye. Kirchoffer (1908, p. 237 et seq.) regarded eight as the commonest number of retinal cells in Coleoptera as a whole. (Some exceptions are pointed out below.) Among Diptera eight cells have been described in _Drosophila melanogaster_ by Huxley and Wolsky (1936 p. 485). Eight cells appear to be typical of Hymenoptera where they have been described in Apidae by Phillips (1905, p. 126) and in Sphegidae, Pompilidae, Vespidae, Formicidae, Chalcidae, Siricidae and Tenthredinidae by Geyer (1912, pp. 377 -383). Werringloer (1932, p.432) found eight cells in some of the ommatidia of _Dorylus sp._ and six in others.

Thus eight cells were found in Odonata Isoptera, Longicornuta, Mantida, Hemiptera Heteroptera and Homoptera, Neuroptera, Lepidoptera, Diptera Coleoptera and Hymenoptera and have been regarded as typical of the Insects as a whole by Grenacher (1879), Carriere (1886, p. 142), Hesse (1901), Nowikoff (1931 p. 14) and Eltringham (1933 p. 123).

Others including Patten (1885, p. 647) Zawarin (1914, p 186) and Imms (1938, p. 81) have regarded seven as the typical number. A peculiar arrangement of seven cells in two layers, one of three and one of four cells, has been described in Collembola by Berlese (1909, pp. 659 - 660) and in Lepismata - see p. 216 . In the seven celled retinulae of Periplaneta and Mantis four of the cells are somewhat longer than the others and project up round the cone.

Seven celled retinulae with equal cells disposed in a single row have been described as typical of Ephemoptera by Needham, Traver and Tsu (1935 p. 49). and in some of the ommatidia of Euconocephalus nasutus and Homocoryphus lineosus by Uchida (1934 p. 520) Seven cells have been described in Cicadidae by Kuhn (1926, p. 489 et seq.). In Lepidoptera the same number has been described in Vanessa urticae by

Johannsen (1892, p. 353). Johnas (1911 p. 218 et seq) stated that this was a fairly common number of cells in Lepidoptera. In Diptera Carriere (1886, p. 143) described seven cells, six peripheral and one central (see below) in the retinula of *Musca*, *Bibio* and *Culex spp*. Vigier (1907 p. 532) regarded this as the number typical of Muscidae and Eltringham (1933 p.28) described seven cells (including one central cell) in *Tipula*. The same arrangement has been described in Coleoptera in *Dermestes vulpinus* by Kirchoffer (1901, p. 1 et seq.) and in *Clerus formicarius* by Eltringham (1933, p. 27). Seven cells are present in *Melolontha* according to Eltringham (1919, p.5) and in *Dysticus marginalis* according to Korschel~~d~~t (1924 p. 443), with one of the cells degenerate in the latter case.

Six cells are of comparatively rare occurrence. In many cases, in which six cells were originally thought to be present, other reduced cells at the base of the eye were subsequently located. Thus Grenacher (1879) described six cells in *Epinephele* but Nowikoff (1939, p.13) afterwards found two additional cells at the base of the ommatidium. Similarly six cells were described by Grenacher (1879) in *Dermestes*, where an additional one was later described by Kirchoffer (1911, p.1 et seq.). Six

Cells are however present in some ommatidia in *Vanessa antiopa* and *Vanessa urticae* according to Eltringham (1933, p. 32). Among Hymenoptera Werringloer (1932, p. 432) has described a six celled condition in some ommatidia in *Dorylus*. Among Diptera six cells have been described in *Musca spp.* by Lowne (1884, p 399), Packard (1903, p. 253) and Dietrich (1909, p. 465). There is no reason to suppose that six cells are primitive or typical. When present, they appear to have been formed by the reduction of a seven or eight celled retinula.

Fewer cells than six are rare. Willem (1897 pp. 225-226) described four cells in Collembola. This was subsequently corrected when an additional row of three cells was described by Berlese (1909 pp. 659, 660) The four cells described by Imms in *Anurida* (1906, p. 41) are presumably degenerate like the rest of the eye. Zawarin (1914 p. 186) found four cells in *Aeschna spp.* sometimes with indications of a fifth reduced cell.. Dietrich (1909, p. 465) had described eight cells in the nymphs and it is possible that the four celled type originated secondarily by the fusion of the cells in pairs, possibly induced by crowding of the ommatidia in a large eye.

In *Periplaneta* four cells were described by Grenacher (1879) who apparently examined only the upper region

Seven cells were later made out by Berlese, (1909, p. 662). Grenacher (1879) described four cells in *Dytiscus marginalis*. This was repeated by Hesse (1901) and Eltringham (1919, p.5) but Korschelt (1924, p. 443) described seven cells. The fact that the rhabdom was four armed had led the earlier author into the error of supposing that there were four retinal cells. This error is similar to that which appears to have been made in connection with some of the Crustacea - see p. 147 Four cells, described by Eltringham (1933, p. 27) in the beetle *Trichodes apiarius*, are presumably degenerate and reduced as are the rhabdom and the cone structures in this type.

Thus more than eight or less than six cells are of rare occurrence. An increase in the number of cells up to twelve appears to be an adaptation to sight in dim light. A degenerative increase - such as occurs in some Crustacea - see p. 148 has not been described in Insects. Six celled forms appear to have arisen by degeneration of one or two cells in a seven or eight celled retinula, types which are often found existing in the same eye as the six celled form. The five and four celled types, common in Crustacea, are very rare in Insects and degenerate except in Odonata (where the four celled condition has possibly arisen by a fusion of the cells in pairs, which, when incomplete, results in a five celled retinula.) Either the seven or the

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eight celled form must be regarded as primitive and typical. The eight celled condition is probably the more widespread of the two. Reduction of one or two cells, which are pushed out of the optical axis of the ommatidium, is a very common phenomenon. It is, therefore, probable that the eight celled is the more primitive type and that the remaining forms with fewer cells were derived from this by reduction of one or two or occasionally more of the cells, and in Odonata by an early and isolated tendency to fusion of the cells in pairs.

As in Crustacea the reduced structures at the base of the eye are often without nuclei or nervous connections or a share in the formation of the rhabdom. This tendency to reduction, as in Crustacea, may be the remnant of an ancestral tendency to a loss of retinal cells occasioned by the appression of units with large numbers of retinal cells in the course of the formation of the compound eye. The formation of the compound eye was, however, clearly pre-Insectan and the loss of the retinal cells is probably secondary and repeated more than once in evolution as a fairly rapid process, accompanying the lengthening and narrowing of the ommatidia and exaggerated by an increased external convexity of the eye. Reduction may apparently occur even where the cells have undergone an initial increase in number, as in the case of

Ephestia, *Pieris* and *Epinephele* - see p. 288.

As in Crustacea the position of the nucleus is very variable and no one location can be selected as primitive or typical. The nuclei may be proximal, distal, central, scattered or even below the basement membrane. Thus among Lepidoptera they may lie in the distal region as in *Hadena*, a little lower as in *Trimandria*, centrally as in *Agrotis*, proximally as on *Saturnia* and *Macroglossa* or in two layers as in *Epinephele* and *Zygaena*. These examples are drawn from Nowikoff's descriptions (1931, pp. 14, 15, 32). Similar variations are apparent in many Hymenoptera, as described by Geyer (1912, pp. 377-383) where, in addition to occupying the positions indicated above, the nuclei may be irregularly scattered as in Siricidae and Formicidae. A similar range of variation is apparent in Diptera as is clear from the work of Carriere (1886, p. 142 et seq), Hesse (1901), Dietrich (1909, p. 465 et seq.) and Constantineanu (1930, p. 253). Constantineanu pointed out that in some Diptera the nuclei, although above the basement membrane in the pupa, migrated below this in the adult. This condition is clearly exceptional.

The nuclei are commonly, although not universally, found in local swellings of the retinal cells. These occur in *Mantis religiosa* according to Patten (1886, p. 647) in many Hymenoptera according to Geyer (1912, p. 383) and in many Lepidoptera according to Nowikoff (1931, p. 32).

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As in Crustacea the nuclei are of about the same size as those of the cone cells. They are always depicted as spherical or ellipsoidal with a distinct outer wall with dense chromatin granules and usually with nucleoli - see Hesse (1901), Geyer (1912, p. 378) and Nowikoff (1931, p. 39).

As in Crustacea the retinal cell cytoplasm is coarsely and densely granular, with pigment granules of different sizes scattered throughout the cells in accordance with the illumination and other factors - see p. 157 As in Crustacea, where the animals are killed in light, the pigment is concentrated chiefly round the rhabdom, round the edges of the cell and in the region of the basement membrane. A concentration of pigment about the nucleus is not uncommon and has been described in *Aeschna* by Zawarin (1914, p. 186), in *Apis mellifica* by Phillips (1906, p. 143) and in *Tribolium confusum* (Col.) by Marshall (1927, p. 624)

The pigment appears to be of the melanin type, see p. 331 . There is some doubt as to its origin - see p. 328 . Retinal cell pigment is occasionally absent in the superposition eyes of some Lepidoptera, as described by Nowikoff (1931, p. 32). This is clearly a secondary loss in accordance with the superposition mode of vision.

The structure of the retinal cell cytoplasm itself, apart from that of the pigment granules, does not seem to have been described in any detail except

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in Lepidoptera - see Nowikoff (1931, pp. 38-40) and these observations are too isolated to be of comparative interest.

Typically the retinal cells as in Crustacea run parallel to the axis of the ommatidium from the apex of the cone apparatus to the basement membrane forming a regular rosette about a central, axial rhabdom structure.

Since the optic nerve does not copy the expansion and convexity of the external surface of the eye, the retinal cells decrease in diametre towards the base of the eye. For the same reason one or two cells may be squashed out of the main axis of the ommatidium to become displaced and reduced - see below.

Adjacent ommatidia are perfectly distinct but the component cells of a single retinula group tend to run together in many cases. The retinula may vary from a practically continuous sheath to one in which the divisions between the cells reach practically to the rhabdoms. Examples of such variations in nearly related forms in Hymenoptera are given by Geyer (1912, pp. 379-382). Typically and primitively the outline of the retinula is corrugated and the demarcation of the cells fairly clear.

Anteriorly the cells may extend up for a short distance round the cone - see p. 282 . The typical and primitive relations between the ends of the retinal cells and the rhabdom and cone structures have been

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dealt with in connection with the cones - see pp 282.283.

Proximally the cells pass through the basement membrane to become continuous with the nerve fibres, of which they are the generating cytons. At this point they are usually slightly constricted. The condition in the male *Simulium* described by Dietrich (1909, pp. 491-492) in which the basement membrane is deficient, so that the retinal cells protrude at the base of the eye in a series of irregular processes, is clearly secondary and exceptional.

The retinal cells are typically uniform in content throughout their length. In Superposition eyes,however, the retinal cells are differentiated into an anterior and posterior region. A thin, elongated, transparent, distal part without pigment, is in contact with the lower end of the cone apparatus. The proximal part of the retinal cells contains the nuclei and the rhabdom structures together with the pigment, when present. The exact form of the two parts in the retinal cells of the superposition eyes in Lepidoptera has been described by Nowikoff (1931, pp. 38-41). The rhabdom structure is longer in apposition eyes but the length of the cells in front of this in superposition eyes more than compensates for the difference (in types of comparable size.)

Neurofibrillae passing through the retinal cells have been commonly described in Crustacea - see p. 157 They have been traced from below the basement membrane

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into the retinal cells where they are seen as fine lines in the cytoplasm, often especially clear in the neighbourhood of the nucleus, the basement membrane or the rhabdom structure. Elsewhere in the cells they are apt to be masked by pigment. In Insects these structures have not been as widely described as in Crustacea. Imms (1906, p. 41) described them in Collembola, in *Anurida*. Zavarin (1914, p. 186) found them in Odonata but could trace them only from the basement membrane to the nucleus. Hesse (1901) described them in *Periplaneta* and considered that they could be traced from below the basement membrane into the retinal cell cytoplasm, through the "Schaltzone" or clear region surrounding the rhabdom (in which region they were particularly apparent). The neurofibrillae of the cell were finally continuous with the "Stiftchen" or rhabdom plates or striations. In other cases in which he was not able to follow the fibrils, even in very thin sections, he assumed that this was due to the masking action of the pigment. Nowikoff (1931, p. 20) points out that Hesse (1901) was unsure of himself and inclined to speak with very great care. Phillips (1906, p. 144) described a condition in *Apis mellifica* corresponding very closely to Hesse's description of *Periplaneta*. Constantineanu (1930, p. 322) inclined to Hesse's views and considered that he was able to trace the fibrillae well up into the cells and on to the rhabdom in the compound eyes of Dipterous

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larvae. Machatschke (1936, p. 91) working on Diptera (Tabanidae and Syrphidae) traced the neurofibrillae for a short distance into the retinal cells, parallel to the rhabdom, but could not find them beyond this. Bedau (1911, p. 417 et seq.), working on Cryptocera, and Eltringham (1919, p. 5) and Nowikoff (1931, p.10) working mainly on Lepidoptera, were unable to trace neurofibrillae for any appreciable distance into the retinal cells. Although the clear striated "Schaltzone" could be seen in the eyes Lepismata and Machilids, no continuity could be traced between neurofibrillae in the cells and the rhabdom plates or "Stiftchen". The nature of the "Stifchen" and the ending of the neurofibrillae is discussed further in connection with the rhabdom structure - see p.319 .

In Insects as in Crustacea the fibres proceeding from the cells of a single retinula group pass out of the eye together enclosed in a common pigmented sheath. Only the retinal cells are now believed to be innervated. Some earlier views on the innervation of other parts of the eye are mentioned in the introductory part - see p.13.

The single layered arrangement of the retinal cells, with each of the cells extending equally and uniformly from the cone apex to the basement membrane, is often disturbed. Displacement or reduction of one of the cells towards the base of the eye is a common feature. In other cases one of the cells may be displaced to lie in the

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centre of the group with the remaining cells surrounding it. In others the cells may be differentiated into groups differing in length, size and pigmentation. In a few cases the retina may be stratified and the cells disposed in two superimposed layers. Some examples of these arrangements follow.

Where cells are pushed out the base of the ommatidium, these are reduced in size and no longer participate in the formation of the rhabdom. Examples have been given by Zawarin (1914, p. 186) in Odonata, by Zimmerman (1913, p.1 et. seq) in Odonata, Phasmida and Mantida, by Nowikoff (1931, pp. 14-15) and Umbach (1934, p. 561) in Lepidoptera, by Carriere (1886, p. 145) and Dietrich (1909, p. 465) in Diptera and by Korscheldt (1924, p. 443) in Coleoptera.

The arrangement of the retinal cells about a single proximally or distally displaced, central cell is found in some Dermaptera, Diptera and Coleoptera. In Dermaphera as described by Eltringham (1933, p. 28) there is a single, distal, central cell surrounded by the remaining retinal cells in each group. Among Diptera Grenacher (1879) and Eltringham (1933, p. 27) have described six cells surrounding a seventh distal, central cell, in *Tipula*. Carriere (1886, p.145) and Dietrich (1909, p. 465) have described six cells surrounding a central basal nucleus in *Musca*, *Bibio* and *Culex spp.* Machatschke (1936, p. 98) has described the same arrangement in Tabanidae and Syrphidae. In

/Coleoptera

Coleoptera six cells surrounding a distal, central cell have been described in Dermestes vulpinus by Kirchoffer (1910, p.1 et seq.) and in Clerus formicarius by Eltringham (1933, p. 27). Where one cell is centrally displaced the rhabdomeres are separated and reduced in length, so that the arrangement is probably degenerate.

The arrangement of the cells in groups differing in length, size and pigmentation is found in Periplaneta, Mantis, Apis and Pieris. In Periplaneta as pointed out by Hesse (1901,) Berlese (1909, p. 662) and Jordan (1929, p. 624) four of the cells are longer than the remaining three and together with their rhabdomeres surround the lower part of the cone (for about one third of its total length). Below this there is the usual seven celled arrangement with all the cells participating in the formation of the rhabdom. In Mantis religiosa as described by Patten (1886, p. 647) three of the cells are somewhat longer, thicker and more deeply pigmented than the remaining four and project up round the base of the cone to a very small extent. Phillips (1906, p. 123) described four of the cells in Apis mellifica as being very slightly longer and also thicker than and more deeply pigmented than the rest.

Nowikoff (1931, p.15) has described a very peculiar grouping of the cells in Pieris. He found two layers of retinal cells, each composed of four, narrow elongated cells, (with an additional cell crowded out at the base of the eye). As most of the related forms have eight

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cells it would seem that the retinula is normally formed by three divisions of the parent cell. It seems possible that the last division has in this case been in a plane ~~position~~ perpendicular to that in which it normally occurs. There is very little overlapping of the cells of the two layers and no tendency for those of the upper layer to project up round the cone. This is a late, isolated and highly modified type of eye and the arrangement of the retinal cells appears to be aberrant and without phylogenetic significance.

A stratification of the retinal cells into a distinct upper and lower layer - the upper layer surrounding the whole length of the cone - is present in Collembola and Lepismata. In Collembola the seven retinal cells are, as Hesse (1901) and Berlese (1909, pp. 659-660) have pointed out, arranged in two superimposed layers, the distal of four and the proximal of three cells. The same arrangement has been described in the eyes of Lepismata - see p.216 . (A similar form is described in the lateral, larval eyes of Tricoptera and Lepidoptera and some Coleoptera by Landois (1886, p.27 et seq.), Pankrath (1890, p. 696), Hesse (1901) and Berlese (1909, p. 653-654, Figs. 804, 805, 806). In these cases the distal layer consist of four and the proximal of three cells. They are mentioned further in the appendix). There is nothing in Crustacea corresponding to such an arrangement.

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The peculiar eyes of Collembola and Lepismata must be considered separately from those of the rest of the Insects. Two main possibilities as to the origin and relationships of these eyes present themselves. Their retinal peculiarities and relatively low grade of development and organisation (as exemplified by the small number of units, their abbreviated form and somewhat irregular arrangement, as well as their small cone apparatus and ill-coordinated rhabdom structure) may be either primitive or degenerate features. These two possibilities are considered in turn.

A view of these eyes as primitive is in accordance with the fact that the Lepismata and Collembola are among the earliest known Insects. If these eyes are primitive, the condition of the retinal cells would best be accounted for by supposing that the eye arose by an approximation of units, in which some of the retinal cells were crowded out and pushed upwards to surround the cone. The pushing up of some of the retinal cells in *Periplaneta* could then be regarded as a remnant of this tendency, preserved in some of the lowest Pterygote forms. (Something of this kind appears to have occurred in the eyes of Scutigeromorpha - see p.449). There is, however, no indication of such an origin of the eye or of such an arrangement of the retinal cells in any of the remaining Insects (excluding some larval eyes which are discussed in the appendix) or in any Crustacea. The eyes of the remaining Insects and those of Crustacea are

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very obviously formed on a common basic plan, while among the Apterygota the eyes of Machilida are so strikingly Crustacean in character that it seems clear that the Insect eye must have been derived from a well developed and stabilised Crustacean or pre-Crustacean form. There is no clear indication in these eyes in anatomy or ontogeny of their formation from separate units. If this ever occurred it was clearly in a very distant ancestral form. It is difficult to see why traces of any such process should have been preserved in Collembola and Lepismata and lost in other forms.

On the whole it seems more probable that these eyes are degenerate than that they are primitive forms representing an early stage in the formation of the compound eye by the approximation of separate eye units. The eyes are, on the whole, poorly developed and of little use. An extension of the retinal cells round the cone is not unknown in degenerate eyes (as in Philoscia) and it is possible that this, carried to an extreme, would produce the condition of a double retinula. The small, rounded cone and the separate rhabdom structure might well be degenerate features. (If these eyes are degenerate the pushing up of the cells round the cone in the well developed eyes of Periplaneta is presumably secondary and without real relation to the condition in Collembola and Lepismata.)

It is probable that some of the earliest Insects were secondarily blind. While the eyes of Machilida

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and the rest of the Insects appear to be derived in a direct file from a Crustacean stock it seems probable that the eyes in the ancestors of the Collembola and Lepismata were temporarily lost or very severely reduced and that these peculiar and partly degenerate eyes were developed in response to habits involving an increase in illumination, from the remaining rudiments of the compound eye, along lines corresponding to the original structure but modified by its degeneration.

Summary - the retinal sense cells.

The unipolar, pigmented, nerve end cells are arranged in retinula groups comprising from four to twelve retinal cells. Distal, retinal, pigment cells are absent. The two or three celled forms occasionally found in Crustacea are not represented. More than eight cells occur only in some Hymenoptera and in Lepidoptera, in adaptation to superposition vision. The number never exceeds twelve, as it does in some degenerate Crustacean eyes. Eight celled types occur in Odonata, Isoptera, Phasmida, Longicornuta, Mantida, Hemiptera Homoptera and Heteroptera, Neuroptera, Lepidoptera, Diptera, Coleoptera and Hymenoptera. (This is the number regarded as typical of Insects by Grenacher, Carriere, Hesse, Nowikoff and Eltringham). Seven celled retinulae (with a peculiar double layered arrangement of the cells) occur in Collembola and Lepismata; seven cells, some projecting round the cone for a short distance, occur in Periplaneta and Mantis. Seven cells, typically disposed, are present in some Ephemeroptera, Homoptera, Lepidoptera, Diptera, Coleoptera and Hymenoptera. (This number was regarded as typical of Insects by Patten, Zawarin and Imms). Six celled types are known in some Lepidoptera, Hymenoptera and Diptera. In some cases this number has been reported in error and additional cells have

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later been discovered at the base of the eye. The six celled type appears to arise from the reduction of one or two cells in a seven or eight celled retinula. The four and five celled types, found in some Crustacea, are rare. Four cells have been described in error in Collembola, *Periplaneta* and *Dytiscus*. The stratification of the retina and projection of some of the cells round the cone proved confusing in the first two cases and the four sided nature of the rhabdom was misleading in the last case, as in some Crustacea. The four celled condition in *Anurida* and *Trichodes* is degenerate and that in some Odonata probably formed by an early and isolated fusion of the eight nymphal cells in pairs. This, when incomplete, results in the formation of the only five celled retinula known in Insects. Eight would appear to have been the primitive number and is the commonest and most widespread one. Reduction of one of the cells is very frequent. It appears to have occurred more than once and to be a fairly rapid process, accompanying the elongation and narrowing of the ommatidium. It may occur even where the cells exceed eight in number and have presumably undergone an initial secondary increase.

The nuclei may be proximal, distal, central or scattered and may even lie below the basement membrane in a few cases. They are not infrequently located in local swellings of the cells, are usually about the same size as the cone cell nuclei, spherical or ellipsoidal with a

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distinct boundary, with granular contents and nucleoli.

The cytoplasm is coarse and densely granular, containing scattered pigment granules, distributed in relation to illumination and other factors. The pigment, typically a melanin derivative, is probably as a rule formed in situ, although it may in some cases be derived from the larval eyes, at least in part. Pigment is absent only in some super-position eyes.

As the retinulae converge to the optic nerve, the retinal cells decrease in size proximally and tend to be squashed out at at the base of the ommatidium. Adjacent cells run together laterally, but the retinula remains corrugated in outline. The typical and primitive relations of the ends of the retinal cells, their rhabdom structures and the cone apparatus, have been discussed elsewhere. The retinal cells project up round the cone apparatus only in Collembola, Lepismata and *Periplaneta* and to a lesser extent in a few other cases. At their lower ends the cells are constricted, where they pass through the basement membrane, to become continuous with the nerve fibres. (The irregular arrangement at the base of the eye in *Simulium* is very exceptional). The nerve processes arising from a single retinula group pass together in a pigmented sheath to the optic ganglion.

Superposition eyes are characterised by a division of the retinal cells into an elongated, transparent, non pigmented part, in contact with the cone apparatus, and

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a posterior part, containing nucleus and rhabdom, with (or sometimes without) pigment granules. Although the rhabdom is longer in apposition eyes, the whole ommatidium is longer in superposition forms.

Neurofibrillae in the retinal cell cytoplasm have not been as widely described as in Crustacea. They have been found in some Collembola, Lepismata, Machilida, Blattida, Diptera and Hymenoptera. Only Hesse, Constantineanu and Phillips have definitely claimed a continuity between the fibrillae in the cell and the "Schaltzone" and the rhabdom plates or striations. Machatschke, Bedau, Eltringham and Nowikoff have denied this. Cells other than retinal cells are not innervated. (Lowne's and other earlier views on the innervation are mentioned elsewhere)

Disturbances of the single layered arrangement of equal retinal cells are not uncommon. Displacement and reduction of one of the cells at the base of the eye has been described in Odonata, Phasmida, Mantida, Lepidoptera, Diptera, and Coleoptera as in many Crustacea and is apparently due to a crowding of cells at the base of the eye. The arrangement of the cells about a central cell - either basically or distally placed, is found in some Dermaptera, Coleoptera and Diptera and is associated with a degenerate rhabdom structure. Arrangements of the cells in groups, differing in length, size and pigmentation, are known in *Periplaneta*, *Mantis*, *Apis* and *Pieris*. In the first three, some

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of the cells are longer than others and project up round the cone to a small extent (greatest in *Periplaneta*). The double layered arrangement of the cells in *Pieris* is apparently secondary and aberrant. A stratification of the retinal cells into two layers of four and three cells respectively has been described in Collembola and Lepismata. The upper layer surrounds the cone throughout the entire length of this structure. (Such an arrangement is found elsewhere in Insects only in some larval eyes - see appendix). It is possible that the eyes in Collembola and Lepismata are either primitive, representing an early stage in the formation of the compound eye from separate units) or degenerate. The latter seems more likely. It is suggested that these eyes have been re-developed from a partly degenerate compound eye rudiment, while the eyes in the rest of the Insects, including Machilida, have been derived directly from a Crustacean or pre-Crustacean stock with well developed compound eyes.

The rhabdom.

As in Crustacea a sense rod or rhabdomere is borne along the inner, longitudinal, axial border of the retinal cell. In each retinular group these rods are more or less approximated to form a rhabdom. The rods are universally present and typically extend throughout the length of the retinal cells from the apex of the cone apparatus to the basement membrane. Distally the retinal cells and their rhabdom structures may extend up into the region of the cone apparatus to a small extent as in *Apis mellifica* (Phillips, I906, p. I26). It is only in Collembola (Berlese, I909, p. 659), Lepismata (see description above) and *Periplaneta* (Hesse, I90I) that this is in any way marked.

Primitively and typically the cone apparatus is in contact with the rhabdom structure. This is apparently designed to allow the ready passage of light from one to the other and the contact is sometimes so close that the two structures have been described as continuous - see p. 292. In some cases however the cone apparatus is not in contact with the rhabdom. In numerous superposition eyes in Lepidoptera and Neuroptera (see Nowikoff, I93I, pp. 38-4I) and in some cases in Hymenoptera (see Werringloer, I932, p. 432)

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the rhabdom is confined to the lower third or quarter of the retinula group and is separated from the cone apparatus by a long , clear , transparent part of the retinal cells. Isolated examples of superposition ommatidia of this kind are found in parts of the double eyes of Odonata , Ephemeroptera, Diptera , Hymenoptera and Coleoptera- see p. 241 . The physiological importance of the structure of the superposition eye is very well known - see Imms (1938 ,pp. 86-88). It is clearly adaptive and neither primitive nor typical. Approximately the same effect is temporarily attained in eyes with the apposition structure (with the cone and rhabdom structures in contact) by migration of the pigment . In the functionally apposition state the ommatidia are isolated by pigment . In the functionally superposition state the isolation is incomplete in the region of contact between the cone and rhabdom structures so that the light passes from the tip of the cone into all the neighbouring retinulae and not only into the one immediately below .

At its lower end the rhabdom structure never extends below the basement membrane but , as in Crustacea may end a considerable distance above this. Where a large tracheal distributor - see below - is present between the retinal cells but above the basement membrane as in Lepidoptera , the rhabdom rests on this and does not reach the basement mebrane

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(see Eltringham , I9I9, p. 5 , I933, p. I23) . Abbreviation of the rods is characteristic of those cases in which a group of retinal cells surrounds a central cell - see p. 401 . The rhabdomeres in these cases remain separate and isolated within the distal regions of their own cells. In very small eyes such as those of <u>Aleurodes brassicae</u> as described by Eltringham (I93I , p. 443), the rhabdomeres are reduced and extend along only a part of the retinal cells.

Primitvely the rhabdomeres were presumably separate and disposed about a central cavity. Degenerate eyes , as in some Crustacea, show a tendency to revert to the primitive condition in this respect. The central cavity in <u>Periplaneta</u> (Hesse , I90I), (Berlese , I909, p. 663 , Fig. 8I8) and its separate or very loosely grouped rhabdomeres are apparently primitive. The separate rhabdomeres found in those cases in which the retinal cells are grouped about a central cell are clearly degenerate in arrangement as they are in extent.

Typically ,as in Crustacea, the rhabdomeres show a tendency to coalesce , which results in the partial or complete obliteration of the central cavity and the more or less complete fusion of the rhabdomeres. Examples of some of the intermediate stages in this process are given below .

A secondary segmentation , set up after

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may occur
the formation of the rhabdom, as in Machilida - see p.232 - where a seven -parted rhabdom is divided into four secondary segments. This is commoner in Crustacea than in Insects.

The transvserse section of the rhabdom structure assumes a number of shapes . These are not perhaps quite as varied as in Crustacea. No one form can be regarded as typical but the lobate or rosette form is perhaps the commonest. In this case the lobes correspond to the original rhabdomere segments This rhabdom type is found in Machilida - see p.232 , in many Lepidoptera (Nowikoff , I93I, p. 40) and Hymenoptera (Geyer (I9I2, p. 383) . A trapezoidal form has been described by Zawarin (I9I4, p. I86) in *Aeschna* sp . A stellate type has been described by Carriere in *Musca* (I885, p. I45) . An X shaped type with the arms of the cross projecting between the cells has been described in *Dytiscus marginalis* by Korschelt (I924, p. 425) and in some Lepidoptera by Nowikoff (I93I, p. 40). The condition in *Pieris* is very unusual. Nowikoff (I93I , p. I5) points out that the rhabdom is distally rounded, then becomes square , then hexagonal and again square in successive sections. This peculiarity is due to the singular arrangement of the retinal cells. The rounded or square parts of the rhabdom are surrounded by the four cells of the upper or lower layers . The hexagonal form is found in the small

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region in which the layers meet - see p.302 .

The longitudinal form of the rhabdom also varies . The size of the rhabdom structure , like that of the retinal cells , commonly decreases towards the base of the eye . It is usually in the form of a rod decreasing in diametre basally. In some cases however it is spindle shaped and considerably thickened centrally . This is the case in _Mantis religiosa_ (Patten , 1886, p. 646) and in _Calliphora_ and others according to Lowne (1884, p. 416 and 1890, p. 413) and in many Lepidoptera according to Nowikoff (1931, pp. 39-40). Patten and Lowne considered that this was the typical form and referred to the rhabdom as the "spindle".

Primitively each retinal cells is associated with a single rhabdomere, which lies along its inner edge, and typically with a single element of the rhabdom (where they are sufficiently clear to be made out). The arrangement as described by Korschel~~d~~t (1924, p. 436) in _Dytiscus marginalis_ is exceptional. In this case the rhabdom is roughly X shaped, with each ray projecting between two adjacent cells. The arms of each of the two members of the smaller pair of opposite angles lie along the borders of a single cell , while the arms of each of the remaining pair of angles embrace two adjacent cells. Thus the four arms of the rhabdom are subtended by six cells.

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The peculiar relations of the retinal cells to the rhabdom structure seen in some Crustacea , do not seem to be paralleled in Insects . In all cases the rhabdom structures are in close contact with the retinal cells and do not separate from these as is the case in a few Crustacea - see p.200 .

Pigment granules , which have been described a few times in the rhabdoms in Crustacea are absent from the Insect rhabdom .

A small refractive structure has been described by Kirchoffer (1908,) in Lampyris. He claims that by suitable staining methods this can be differentaited from the rhabdom structure. He suggests that it is a special refractive apparatus. Eltringham (1933 , p. 32) points out that it is very peculiar and rare and its function obscure.

Whether the rhabdom is a cuticular secretion of the cell with a dioptric function , or a clear differentiation of the protoplasm, in which the neurofibrillae terminate , has long been a matter of dispute . This has ben discussed elsewhere - see pp 11, 13. The "Stiftchen " or rhabdom plates or striations, described by Hesse (1901) as neurofibrillar endings in therhabdom have been described in several instances but are not as common as in Crustacea. Where they have been observed, they are simple and perpendicular to the axis of the ommatidium. None of the complicated arrangements of the plates described in some Crustacea

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- see p. 173 - appear to have been noticed in Insects. A striated rhabdom structure has been recorded in Lepismata and Machilida (see pp. 221 , 232), in Cicadidae (Kuhn , 1936, p. 489 et. seq) , in Apis mellifica (Phillips , 1906, p. 144), in many Lepidoptera according to Johnas (1911, p. 218 et seq.) and in the compound eyes of larval Culicidae according to Constantineanu (1930, p. 253 et . seq .) . Hesse (1901) described this in detail in Periplaneta and regarded it as typical of the Insect compound eye . These structures are absent in the superposition eyes of some Lepidoptera and Neuroptera according to Nowikoff (1931 , p. 31) and in those of some Hymenoptera according to Werringloer (1932 , p,432) and in superposition eyes in general according to Hesse (1901) .

In some Muscidae as described by Vigier (1907, p. 532 et seq .) the rhabdom is divided into an anterior , refractive , homogeneous part and a lower part, finely striated transversely. The upper part resembles a typical apposition rhabdom (Nowikoff 1931, p. 43) and the lower part a typical superposition rhabdom . This is a very exceptional arrangement.

A definite continuity between the neurofibrillae in the cell - see p. - and those in the "Schaltzone " with the rhabdom striations has been /claimed

claimed in general by Hesse (I90I) and described in particular by Phillips (I906, p. I44) in *Apis mellifica* by Johnas (I9II, p. 268 et. seq) in Lepidoptera , by Korscheldt (I924, p. 438) in *Dytiscus marginalis* and by Constantineanu (I930, p. 253 et seq.) in the compound eyes of larval Culicidae.

Most other authors, who have touched on the problem, have claimed a pure cuticular structure for the rhabdom and not a neurofibrillar one. This is the opinion of Grenacher (I879), Watase (I890), Exner (I89I) , Jorschke (I9I4) , Nowikoff (I93I) and Machatschke (I936). The cuticular nature of the rhabdom is , according to Nowikoff (I93I) , apparent from its staining and optical properties, its resistante to physical strains and its resemblance to developing chitin. Machatschke (I936, p.90) concurrs in this and ilustrates in detail the resemblance between the striated rhabdom and the newly formed chitin deposits.

There is no real aggreement as to the nature of the rhabdom but in Insects the evidence weighs in favour of the view that this is a skeletal and dioptric structure, formed as a cuticular secretion, and serving typicaly to disperse the light, condensed by the cone and corneal lens, onto the sensitive ends of the neurofibrillae in the pigmented cytoplasm of the retinal cells.

/Summary

Summary - the rhabdom.

Primitively the rhabdomeres lie along the inner, longitudinal , axial borders of the retinal cells from the cone apparatus to the basement membrane. Extension into the cone region is marked only in the eyes of Collembola, Lepismata and *Periplaneta* . The typically close contact with the cone apparatus is lost when the rhabdomeres separate and degenerate and in superposition eyes, where the cone and rhabdom structures are separated by a clear, distal part of the retinal cells . The rhabdom structure never extends below the basement membrane but is often abbreviated, where a tracheal distributor or a central cell is present, or where the cells are very small. Primitively the rhabdomeres are arranged about a central cavity as in *Periplaneta* . Typically the rhabdmeres coalesce to a greater or lesser extent, with a loss or decrease in the size of the cavity. Degenerate forms , as in Crustacea , may revert to the primitive type. Secondary segmentation is not as common as in Crustacea and the transverse section is not as varied . This is commonly lobate but may be trapezoidal, square , stellate , X shaped , cruciform or hexagonal. It may vary thoughout the length of therhabdom but the extreme variability in *Pieris* is exceptinnal and related to the peculiar arrangement of the retinal cells

A spindle shaped rhabdom is not uncommon and there is a general tendency to decrease in size at the base of the eye. Division into two parts as in some Diptera, is rare. Primitively and typically each rhabdomere (as far as it can be distinguished) is related to a single cell. The exceptions to this are not as numerous as in Crustacea or as complicated. The rhabdom is always in contact with the cell and always without pigment. The plates or striations, regarded as typical by Hesse, have been described by other authors in some Lepismata, Machilida, Hemiptera, Hymenoptera, Lepidoptera and Diptera. They are not as common or as complicated as in Crustacea and are characteristically absent in superposition eyes. A direct continuity of the neurofibrillae with the rhabdom plates has been claimed in general by Hesse and by other authors in some Hymenoptera, Lepidoptera and Coleoptera. Grenacher, Watase, Exner, Jorschke, Nowikoff and Machatschke have regarded the rhabdoms as cuticular and without relation to the neurofibrillae. The rhabdom resembles other chitinous structures in staining and optical properties and in resistance to stains, while the striated appearance is common in developing chitin. The nature of the rhabdom is still a matter of some doubt but it is probably to be regarded as a cuticular structure dioptric and skeletal in function.

The pigmented cells.

The pigmented cells of the Insect eye are of three types, the so-called "iris" pigment cells surrounding the cone, the retinal, sense cells and the accessory pigment cells. The distal, retinal, pigment cells found in some Crustacea are not represented in Insects. (Although these are sometimes termed "iris" pigment cells, in view of their position round the dioptric apparatus, they bear no morphological relation to the "Iris" pigment cells in Insects)

The pigment cells surrounding the cone in Insects are modified corneagenous cells. These are "le cellule pigmentari principale" of Berlese (1909, p. 662) or "Hauptpigmentzellen" of many German authors. Primitively in Insects, as in Crustacea, they lie immediately below the cornea and are not pigmented. As previously pointed out, (see p. 267) this condition persists only in Apterygota, Ephemeroptera and some Orth~~r~~optera and in the early stages in the development of other forms. Among the rest of the Insects the cells are displaced laterally around the cone and are pigmented. The occurrence, number, form and position of the cells and the structure of their nucleus, pigment and cytoplasm has been dealt with in connection with the corneal hypoderm cells (see p.267 et seq). The retinal cells are typic-

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typically and primitively pigmented and their structure is dealt with elsewhere (see p.).

The accessory pigment cells.

Inter-ommatidial, accessory, pigment cells are typically and primitively present in Insects. (In Crustacea these cells are primitively absent and typical only of the higher Crustacea). Although there is considerable disagreement as to whether the cells are of ectodermal or mesodermal origin in Crustacea, they are almost universally regarded as of ectodermal origin in Insects. Although Balfour (1880, p.134) described the penetration of a meso-dermal pigment strip into the eye in development, similar to that later described by Kingsley (1886, p. 598) in Crangon his views on the origin of the pigment have not been supported by other authors, who regard the accessory pigment cells as ectodermal cells trapped between the ommatidia in development.

As in Crustacea the number, position, arrangement and form of these cells, is determined by that of the inter-ommatidial spaces and this in turn depends on the degree of crowding of the ommatidia. The group of cells between successive ommatidia, seen in longitudinal section, is roughly triangular in shape with the dimensions and angles depending on the degree of approximation of the ommatidia. Berlese (1909, p.657)

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affirms that the number round each ommatidium is constant and characteristic for each species but since the boundaries of the cells are not as a rule clear, and since contiguous cells are shared between neighbouring ommatidia, the numbers are difficult to count and most authors merely describe the number as large and variable. Where actual counts have been made, the numbers appear to vary from about two to about twenty in each ommatidium. Thus two cells are common in Lepidoptera in both apposition and superposition eyes according to Nowikoff (1931, pp. 24, 44), although he points out the number may rise to six or eight in *Pieris* and *Epinephele* or even twelve in *Zygaena*; eight cells are common in Ephemeroptera, according to Needham Traver and Tsu (1935, pp. 48, 49); six to eight are described in *Mantis religiosa* by Patten (1886, p. 646), eight to twelve in *Drosophila melanogaster* by Huxley and Wolsky (1936, pp.485-486). Among the Hymenoptera there are six in Chalcididae, nine in Formicidae, nine to eighteen in Sphegidae and eighteen to twenty in Vespidae, according to Geyer (1912, pp.377, 380-382).

As in Crustacea the accessory pigment cells vary in their extent. In some rarer cases each cell may form a long, attenuated strand running from the cornea to the basement membrane. This is the case in *Mantis religiosa* as described by Patten (1886, p. 646) and in

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some Hymenoptera - for example in Apidae as described by Phillips (1906, p.126) and Geyer (1912, p.377) and in Brachonidae as described by Geyer (1912, p. 3801).

More usually, however, the cells are reduced in length and each restricted to a particular zone. Such zones may be present about the cone or the retinal cells or along the basement membrane or even along the nerve fibres below this. The zones are, however, somewhat irregular and are not disposed in the form of concentric circles, which is described by Patten (1886, p. 666) as the general arrangement in the Arthropod. compound eye.

In some cases accessory pigment cells are limited to the upper part of the ommatidium, round the cone, They extend at least to the level of the upper ends of the retinal cells, so that together with the latter they form a pigment barrier round the entire ommatidium. This is the position in Collembola (Willem, 1887, p.226) and in Lepismata and Machilida (see p.222,223) as well as in Ephemeroptera (Needham, Traver and Tsu, 1935, pp. 48, 49) and some Orthoptera (Uchida 1934, p. 518), that is, in those cases in which "iris" pigment cells are absent. In all other cases the main accessory pigment cells occur round the retinal cells, with or without smaller cells surrounding the basement membrane and nerve fibres. Pigment cells surrounding the retinal cells have been described in the following cases : - In Odonata (Zawarin, 1914, p. 185), in Ephemeroptera (Needham Traver and Tsu, 1935, pp. 48/49)

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in many Lepidotera (Nowikoff, 1931, pp. 24, 44), (Eltringham, 1933, p. 34), (Umbach, 1934, p. 516), in many Hymenoptera (Geyer, 1912, p. 377) and in Coloeptera in Tribolium confusum (Marshall, 1927, p. 624). Apart from these specific cases they are very widely figured throughout the Insects. Additional accessory cells have been described in the neighbourhood of the basement membrane in Lepidoptera, by Nowikoff (1931, p.24) and by Eltringham (1933, p. 34) and in Hymenoptera in Apidae by Phillips (1906, p.126) and Geyer (1912, p. 377), and in Chalcididae by Geyer (1912, p. 381). In some cases these cells may penetrate the basement membrane and come to lie below it as well as above. This is the case in Apidae according to Phillips (1906, p. 126) and Geyer (1912, p. 377) and in many Lepidoptera according to Nowikoff (1931, pp. 26, 46). Nowikoff maintains that these cells, in spite of their position, are epithelial cells and not of mesodermal origin.

As in Crustacea the cell boundaries are not, as a rule, clear. This is the case in Lepismata and Machilida as well as in many Lepidoptera according to Nowikoff (1931, p. 26) and in Tribolium confusum according to Marshall (1927, p. 624). These cells tend to run into one another and into the retinal cells at the base of the eye.

The cytoplasm of these cells is, as in Crustacea, finely granular and contains variously distributed pigment granules of different sizes. As a rule it stains less

/deeply

deeply than that of the retinal cells. The differentiation into a swollen, deeply pigmented part, surrounding the nucleus, and an attenuated, non-pigmented bacillus (described by Patten,(1886, p. 666) as a typical feature of the compound eye) does not seem to be common,although described by Berlese (1909, p. 667) as occasionally present. Typically the cells are roughly uniform in content throughout their length except with regard to local differences occasioned by pigment migration.

The nuclei, like those of Crustacea, vary somewhat in shape but are generally figured as spherical or ellipsoidal, with no tendency to an irregular outline as in some Crustacea. They are surrounded by a thin, clearly staining membrane and have densely granular, deeply staining contents, usually without nucleoli, although these are present in Machilida. They are sometimes surrounded by dense masses of pigment as in _Zygaena_ and other Lepidoptera, as described by Nowikoff (1931, p.44).

Nowikoff (1931, p. 34) has emphasised that the pigment is usually thicker in the centre of the eye than at the edges, since this part usually receives the most light. In some specialised cases the pigment within the eye is distributed in zones which are usually arranged in a definite pattern, clearly visible externally. In Orthoptera Jorschke (1914, p. 153) mentions the frequent occurrence of eyes in which zones of yellowish ommatidia, practically free of pigment, alternate with zones of

/darkly

pigmented ommatidia. Uchida (1934, p. 518) has described a more elaborate arrangement in the Longicorn forms *Euconcocephalus nasutus* and *Homocoryphus lineosus* with four zones of pigment differing in their colour and reaction to illumination. Girschner (1888, p.155) points out that among the Diptera spotted or banded eyes are common, especially among the Dolichopidae, Bombyliidae and some Tabanidae, where bright metallic colours are sometimes found. The physiological significance of the spots or bands, sometimes present in one sex only, remains unexplained.

It has been suggested that the pigment in the cells of the adult eye is derived from that of the larval ocelli. Johannsen considered (1872, p. 353) that the pigment in Lepidoptera travelled via leucocytes from the ocelli to the compound eye. Kirchoffer (1910) considered that the pigment granules of the larval eye of Coleoptera migrated along the nerve fibres into the retinal cells and thence into the remaining pigmented cells of the eye. Marshall, however, in his study of the development of the beetle *Tribolium confusum* points out (1927, p. 614) that the larval ocelli do not contain sufficient pigment to supply the compound eye and that they remain fully pigmented in the adult, although withdrawn from the surface of the head. He considered that the pigment is formed in the separate cells of the pupal compound eye, first in the retinal and then in the remaining cells.

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As is the case in Crustacea, more attention has been paid to the phenomenon of pigment migration within these cells, than to their structure. Pigment migration seems to be determined primarily by the conditions of illumination. The pigment assumes the apposition configuration in bright light and the superposition in dim light. These conditions are illustrated in most text books - see Imms (1938, pp. 86-88). In darkness or dim light the ommatidia are not completely isolated and the oblique components of light rays entering one ommatidium are not lost in the pigment cells but pass from the apex of the cone apparatus into neighbouring ommatidia so that the maximum stimulation is obtained. In strong light the pigment is arranged to separate the ommatidia completely so that each receives only the rays entering perpendicularly to its own lens. There is a gain in clarity of vision at the expense of the loss of the oblique light rays absorbed by the pigment cells.

The general nature of the pigment movement in relation to illumination has been worked out by Exner (1891), Frisch (1908, p. 663) and Eltringham (1933, pp.123-124). Demoll (1911, p.169) suggests that the pigment is maintained in the dark position by a tonus from the brain overcome by sleep, narcotics or strong illumination. Horstman (1935, p. 93) considers that there is an inherent diurnal rythm independent of artificial changes in

/temperature

The colour of the eyes varies very considerably. Purple, black and brown colours are commonly found in the retinal and accessory pigment cells, and lend their colour to the eye as a whole.

As Berlese points out (1909, p. 658) yellowish red and greenish-brown granules are present in some cases. Their presence in the "iris" pigment cells is confirmed by Nowikoff (1931, p. 34) in Epinephele and Pieris but even in these cells darker pigments are commoner.

The colour of the eye may vary considerably during the life of a single specimen. Thus Ludtke points out that in some Hemiptera Heteroptera (1941, p.1 et seq) it is successively yellow, rose, red, carmine, brown and black during development. Within a single species there may be many different colour mutations, eg. in Drosophila melanogaster - see Bridges (1919, pp. 265, 337), Beadle (1937, p. 120), Mainx (1937, p.470) and Euphrussi (1942, p. 40). These authors have described no fewer than twenty seven mutations varying from light brown to orange red.

Dickler (1943, p. 287) has described similar variations (including a white eyed strain) in Simulium, Psychoda and Lucilia cuprina and Becker (1939, p. 597) in Ephestia kuhniella. David (1938, p. 574) had pointed out that at least in the case of Habrobracon juglandis (Diptera) the depth of pigmentation of the eye varies inversely with the temperature of development.

No ~~AB~~

~~temperature or illumination.~~ No hormonal control of pigment migration, such as that suggested in some Crustacea, is known in Insects.

In Insects, as in Crustacea, all the accessory pigment cells and the retinal cells contain, as a rule, a dark pigment which according to the density of its distribution, appears brown, purple, or black. This is presumed to be a melanin derivative or related to these substances (see Becker, 1939, p. 597). Its function is apparently that of light absorbtion in the case of the accessory pigment cells, while in the retinal cells in the neighbourhood of the nerve endings it is presumably concerned in the photochemistry of the visual processes. The refractive substance found in some Crustacean eyes does not appear to be represented in Insects, where the air-filled tracheae and tracheal distributors at the base of the eye appear to fulfil its tapetal function in nocturnal forms. The presence of the red pigments, found in the eyes of some Crustacea, and especially in the young, does not seem to have been widely demonstrated in Insects.

Becker (1939, pp. 597-598) has described in Lepidoptera in *EphestiaKuhniella* a red material, possibly an ommine, which he describes as occurring in many Lepidotera, Hemiptera Heteroptera, Coleoptera and Nematocerous Diptera. More weakly coloured ommatines are described in many other Diptera as well as Odonata

/and

and Orthoptera. He suggests that these ommatines are chromoproteins allied to melanin. The red pigments are apparently not as widely known as in Crustacea, and their chemical nature is very obscure. The origin of the metallic sheen of some Insect eyes does not seem to have been explained.

The pigmented cells - Summary.

The pigmented cells of the Insect eye are of three types. The corneagenous or "iris" pigment cells surrounding the cone are primitively distal and not pigmented but typically displaced and pigmented in all adults except Apterygota, Ephemeroptera and some Orthoptera. The retinal sense cells and the accessory cells are typically and primitively present and pigmented. The retinal and corneagenous cells are dealt with elsewhere. The distal retinal pigment cells of some Crustacea are not represented.

The accessory pigment cells.

The number, position, arrangement and form of the ectodermal, accessory pigment cells are such as are adapted to fit the interommatidial spaces. Since the boundaries of cells shared between neighbouring ommatidia are indistinct these are difficult to count and generally described as numerous and variable. Their number ranges from two to twenty, reaching a maximum among the Hymenoptera.

In some cases the individual cells extend throughout the length of the ommatidium. Primitively (among those forms in which the hypodermal cells retain the primitive position) there is a single zone of cells surrounding the cone. Typically the cone is surrounded

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by corneagenous pigment cells with the accessory cells mainly around the retinal cells. In some cases smaller cells lie upon the basement membrane and may penetrate this to surround the nerve fibres.

The finely granular cytoplasm contains numerous, variously distributed pigment granules of different sizes. The contents of the cells are uniform throughout. The nuclei are not irregular as in some Crustacea but spherical or ellipsoidal, densely granular, and deeply staining with a thin membrane and usually without nucleoli.

The pigment is generally denser towards the centre of the eye, since this usually receives most light. In some Diptera and Orthoptera it is distributed in spots or bands of unknown physiological significance.

Although it has been suggested that the pigment of the adult eyes is derived from that of the larval forms, this is not always the case. Where pigment is formed in the eye itself, it is developed first in the retinal cells and later in the accessory cells.

The eyes are commonly brown, purple or black, in accordance with the density of the pigment, presumably related to melanin, which typically and primitively occupies the retinal and accessory cells. The iris cells sometimes contain lighter materials,

/yellowish-

yellowish-red or greenish-brown in colour. The colour is very variable, even in individual development where it may change from yellow to black; in some forms its intensity is known to vary inversely with the temperature of development; In some cases, as in Drosophila, there are several mutant variations.

Pigment migration results in apposition vision in bright light and superposition vision in dim light and is mainly in response to conditions of illumination but may in part be governed by a nervous tonus or an inherent diurnal rhythm. No hormonal control (such as occurs in some Crustacea) is known.

The pigment of the accessory cells is light absorbing in function, while that of the retinal cells is concerned with the photochemistry of vision. The tapetal material of some Crustacean eyes - see p. 191 is functionally replaced by refractive, air-filled tracheae.

Red pigments such as those common in many Crustacea are known in several orders but their chemical nature is very uncertain. The origin of the metallic sheen of some eyes appears to be unknown.

Basement membrane.

As in Crustacea a basement membrane (corresponding to that at the base of the hypodermal cells of the body wall) is typically and primitively present at the level at which the nerve fibres become continuous with the retinal cells. It is occasionally poorly developed or practically absent as is the case in the eyes of Lepismata (see p.123) and those of the male of Simulium as described by Dietrich (1909, p.465).

As in Crustacea the membrane is a structureless secretion of the inner ends of the layer of hypodermal cells from which the eye is developed. Patten's suggestion (1886, p.647) that the membrane in Insects and Crustacea is made up of an intricate web of connective tissue fibres is not supported elsewhere.

The retinal cells of a single ommatidium are continuous through the fenestrations of the membrane with the nerve fibres of one nerve fibre bundle. Lowne (1875, p.517, 1890, p.406) was unable to trace this continuity and he therefore considered all structures above the membrane as merely dioptric - the "Dioptron"- and all below as sensory - the "Neuron". At the time when Lowne's views were being put forward, the relation between the retinal cells and nerve fibres was a subject of very controversial correspondence in "Nature" - (1885, pp.341,433).

/The

The argument was settled in favour of Lowne's opponents, and the continuity of the retinal cells and nerve fibres is now universally admitted.

Small pigment cells lying on either side of the basement membrane and along the course of the nerve fibres are of very common occurrence according to Nowikoff (1931,pp.39, 46) and Eltringham (1933,p.127). A second "basement membrane" has been described by Bedau (1911) and Kuhn (1926, p.489) in some Hemiptera, by Ast (1920) in *Myrmelion* among the Neuroptera. Among Lepidoptera this has been described by Hesse (1901) in *Sphinx* and *Plusia*, by Nowikoff (1931,p.45) in several superposition eyes, and by Umbach (1934,p.561) in *Ephestia kuhniella*. Where there appear to be two membranes, one is in the normal position and one slightly above this. The appearance of an additional "membrane" is due to the abrupt ending of the pigment cells all on one level. Nowikoff (1931,p.45) emphasises that no morphological membrane is present in these cases.

Miscellaneous structures associated with the compound eye in Insects.

Tracheae.

Primitively and typically the retinulae of the Insect eye are supplied with fine tracheal branches. These are absent only where the eyes are very small. Their typical occurrence has been pointed out and references to their presence have been given by Lowne (1890,p.411), Exner (1891), Hesse (1901), Eltringham (1919,p.7, 1933,p.22) and Nowikoff (1931,pp.29,30, 47,48). Eltringham pointed out that in Lepidoptera each branch on penetrating the basement membrane enlarged to form a cylindrico-conical structure, lying between the end of the rhabdom and the basement membrane, with the walls thickened by a spiral chitinised thread. This so-called tracheal distributor is divided internally by a cruciform septum into four primary chambers, each of which is eventually subdivided to form in all eight compartments, from which eight small tracheae arise to pass forward and supply the same number of retinal cells. Nowikoff (1931, pp. 30, 31, 32) described a similar arrangement of "tracheenblasen" (corresponding to the tracheal distributors of Eltringham) and tracheae in *Epinephele* and *Zygaena*. He points out that the fine tracheae of the eye run up between the inner ends of the retinal cells, where these join the nerve fibres and then pursue their

/course

course for some distance along the retinal cells, losing their spiral thickening as they decrease in diametre.

The air filled tracheae in nocturnal insects, especially lepidoptera, are abundant and highly refractive, and form a tapetal structure, reflecting the light back into the retinal cells. In many large eyes the tracheae are also probably skeletal in function as in Odonata according to Zawarin (1914, p.187). As the tracheae are of very little interest in comparative anatomy of the eyes of Arthropods as a whole, detailed consideration of them is omitted.

Lymph sinuses.

The lymph sinuses in and about the eye are described in detail by Lowne (1890, p. 373) in Odonata. Otherwise these have attracted little attention. As their arrangement appears to be determined by the shape of the individual eye, their form is here of little interest.

Focussing mechanisms.

The possible presence of a focussing mechanism within the Insect eye has long been a matter of some doubt. Cole (1944, pp. 228, 324) in his history of comparative anatomy, mentions some of the early speculations on the subject. He points out that it was supposed that the filling and emptying of the tracheae served to focus the eye by altering its external convexity. Lubbock (1889, p. 169) pointed out that Leydig (1857) considered that there were muscle fibres running between the cornea and the cone which served to

/regulate

regulate the distance between the two. Vigier (1904, pp. 775-777) claimed to have seen in the eyes of Odonata striated muscle fibres running in connection with the ommatidia. He considered that their contraction led to a shortening and widening of the cone, while pressure of air on the walls of the tracheae compressed the cone and led to its elongation. Imms (1931, p. 94) commented on this "isolated" observation, and called notice to the matter as deserving further attention. Eltringham (1933, p. 45), however, pointed out that a focussing mechanism in such an eye would be of no real use, the clarity of vision depending not so much on the correct focus as on the number of units engaged.

It is clear that focussing mechanisms, whether tracheal or muscular, if present at all, are neither primitive or typical.

Ganglion and hyaline cells.

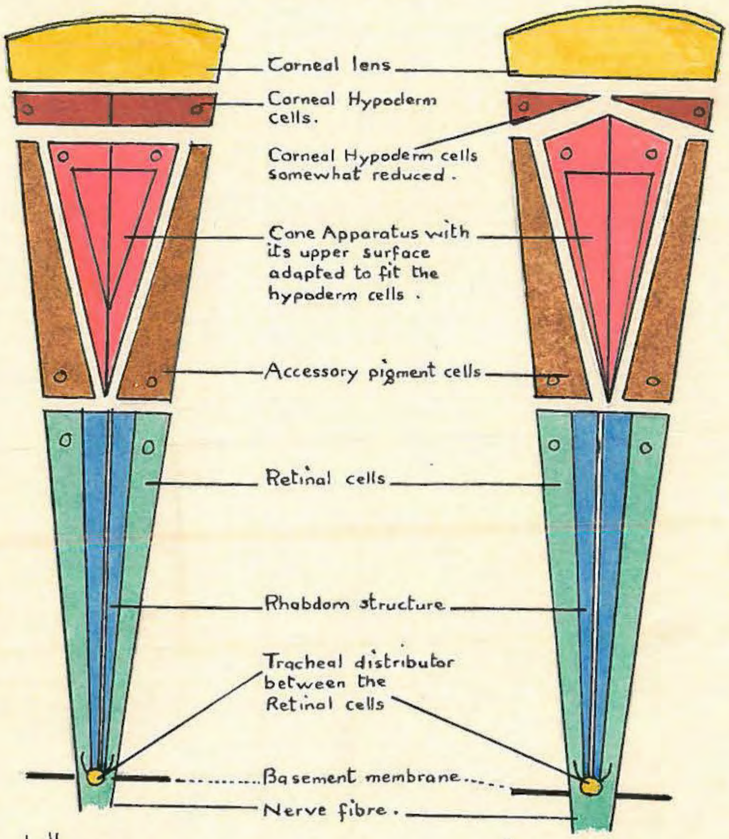
Intrusive ganglion cells, such as are found in some Crustacea above the basement membrane, do not occur in Insects. The hyaline cells described as an aberrant feature of the eyes of some Isopods, are absent in Insects.

PLATE 9.

DIAGRAMS ILLUSTRATING THE PRIMITIVE FORM OF THE LATERAL COMPOUND EYES IN INSECTS.

Longitudinal Sections

L.S. Corneal lenses



In the young

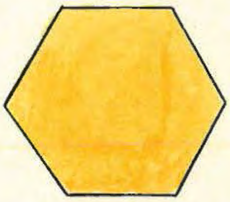
In the adult

L.S. Entire Ommatidium

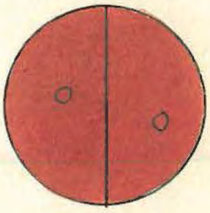
PLATE 10.

DIAGRAMS ILLUSTRATING THE PRIMITIVE FORM OF THE LATERAL COMPOUND EYES OF INSECTS. — CONTD.

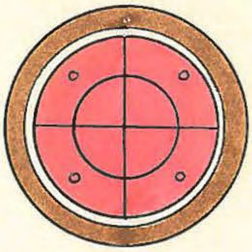
Transverse Sections



T.S. Corneal lens



T.S. Corneal Hypoderm.



T.S. Cone Apparatus

T.S. Retinal cells

Conclusions - Insects.

1. Occurrence and type.

True, lateral, compound eyes are typically and primitively present with their absence or reduction secondary. They are almost universally present in adults, nymphs and pupae, but are only occasionally differentiated in the larvae. The eye may be reduced to a single ommatidium (Mallophaga and Anopleura) or even degenerate so far that it is represented by a single ocellus (Aphaniptera). Blindness in the primitive orders Campodeidae, Japididae and Myrientomata is presumably secondary - (a compound eye being well developed and well established in related Apterygota). Sporadic blindness and reduction in other orders is not uncommon. The larvae are typically provided with lateral ocelli. These do not occur in the young of other Arthropods as functional precursors of the compound eye.

2. Comparative anatomy.

For comparative purposes an attempt has been made to indicate the primitive and typical conditions and the range of variation of each part of the eye. This is summarised for each section for comparison with similar material appended to the sections dealing with the corresponding structures in other compound

/eyes -

eyes - notably those of Crustacea. Conditions in Insects and Crustacean eyes differ in the following main respects :-

(i) The corneal hypoderm cells in Insects, while primitively resembling those in Crustacea, are typically displaced and pigmented to form "iris" pigment cells surrounding the cone ;

(ii) The cones in Insects, while primitively of the eucone Crustacean type, and very commonly retaining this form, are sometimes modified to give rise to the pseudocone, acone or exocone condition;

(iii) The retinal cells in Insects never exceed twelve in number as they do in some Crustacea; the four and five celled retinulae not uncommon in lower Crustacea are very rare in Insects, while the two and three celled types, occasionally found in Crustacea, are not known in Insects; (eight cells appear to have been the primitive condition as for Malacostraca and probably for the whole of the Crustacea);

(iv) The double layered condition of the retinula in Collembola and Lepismata and the presence of central cells in some retinulae, are features not found in Crustacea;

(v) The superposition mode of vision, associated with a permanent modification of the retinal cells in Insects, is accomplished in Crustacea by a temporary migration of the pigment;

/(vi)

(vi) The distal, retinal pigment cells in some Crustacea have no morphological equivalent in Insects;
(vii) The rhabdom structures are not as commonly or as clearly striated as in Crustacea;
(viii) The tracheae and tracheal distributors, which may form a tapetum in the Insect eye, are absent in the typical Crustacean eye where they may be functionally replaced by a reflector pigment at the base of the eye;
(ix) On the whole the eyes of Insects resemble those of Malacostraca more than those of the Lower Crustacea, in the structure of their cones and retinal cells, although differing from them in the primitive and typical absence of a stalk and of distal, retinal pigment cells (in which respects they approach the conditions found in lower Crustacea). In spite of the differences between the eyes of Insects and those of Crustacea they appear to be relatively closely related, when compared with the widely divergent lateral eyes in other Arthropods.

3. Basic plan.

The eyes are built on a common basic plan, very similar in essentials to that in Crustacea. As in Crustacea the number of the cells and their arrangement in each of the several parts of the eye show a relatively narrow range of variation. The only significant departure from this common basic plan is found in those cases in which the retinal cells are disposed in two layers or about a central cell.

4. Stability and evolution of the eye.

From the relative stability in the basic pattern of the eye and its similarity to that in Crustacea and in the absence of any clear indication of the evolution of the compound eye within the limits of these two classes, it seems probable that the true compound eyes in these forms were inherited from a distant common ancestor or that the Insect eyes were derived from those of Crustacea. Moroff's assumption (1913 , p.482) of the convergent evolution of the compound eyes in Insects and Crustacea seems unnecessary.

5. Variation of the eye in relation to phylogeny.

The variation in the eye structure in different orders appears to bear little relation to their phylogenetic position except in the case of the restriction of the double layered retinula to some of the Aptergota and some of the lowest of the Pterygota. Within the Insects the eye appears to have undergone relatively little modification, except in respect of the cone, where the occurrence of the different forms bears no relation to the phylogenetic position of the orders in which they are found.

6. Degeneration of the eye.

In general the mode of degeneration in the eye is similar to that in Crustacea - see p.   Where the units separate in degenerate eyes of reduced dimensions, they generally remain ommatidial except where the degeneration has been carried so far as to produce a mere pigment spot. It is only in Aphaniptera that the degeneration appears to have led to the formation of a single ocellus.

7. Possibility of the origin of the compound eyes from ocelli.

There is little indication in the ontogeny or anatomy of these eyes of their formation from a single ocellus or from a group of ocelli. It seems, however, that the exceptional eyes in Collembola and Lepismata should be considered separately. It is just possible that they represent the retention of a primitive condition (not seen in the eyes of Crustacea or in the rest of the Insects except perhaps in some Insect larvae - see appendix - and in Periplaneta) in which the eye would appear to have been formed from a number of units with a somewhat crowded set of retinal cells. (Analogous conditions appear to exist in the eyes of Scutigeromorpha - see appendix). The relationships of the eyes of Lepismata and Collembola are, however, very doubtful, and, on the whole, it seems probable that they are degenerate rather than primitive. If so they have presumably been re-formed from a degenerate compound eye rudiment - the eye having been

/reduced

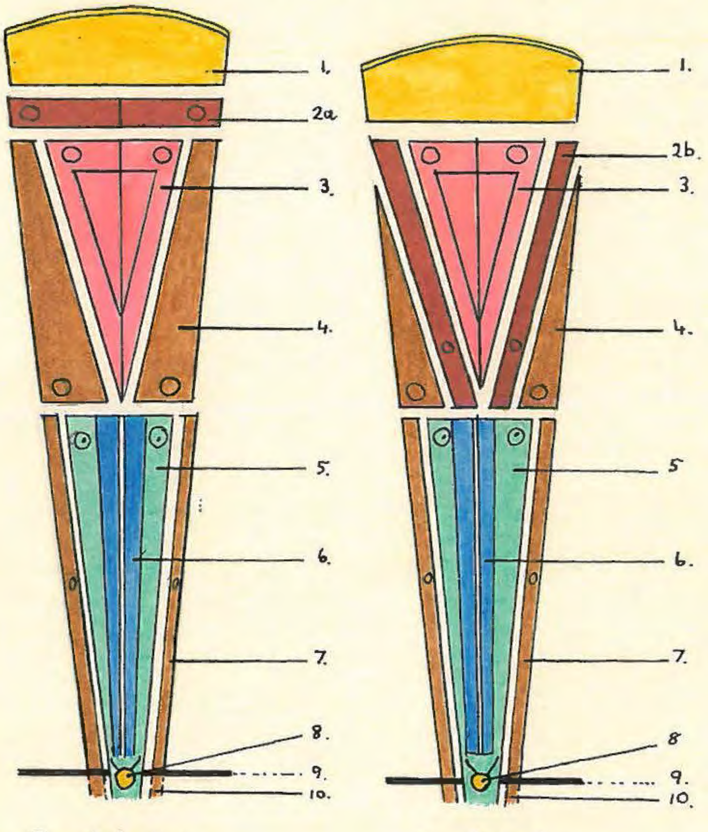
reduced or lost in some of the early Insects (as in the Pauropoda and the majority of the Symphyla).

8. General relationships.

It seems probable that the true, compound, lateral eyes in Insects have been derived directly from a Crustacean or pre-Crustacean type with a well developed compound eye. These eyes are developed on a common basic plan from which there are relatively few departures.

PLATE 11.

DIAGRAMS ILLUSTRATING THE RELATIVE POSITION OF THE CORNEAL HYPODERM CELLS IN A TYPICAL INSECT OMMATIDIUM: IN THE YOUNG AND IN THE ADULT.



Condition in the Young.

Condition in the Adult.

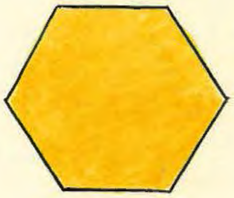
KEY.

1. Corneal lens.
2a. Corneal Hypoderm – not pigmented. Remaining in primitive position
2b. Corneal Hypoderm – converted into "Iris" pigment cells.
3. Cone apparatus.
4. Upper accessory pigment cells.
5. Retinal cells.
6. Rhabdom.
7. Lower accessory pigment cells.
8. Tracheal distributor
9. Basement membrane.
10. Accessory pigment cells associated with the basement membrane and nerve fibre.

PLATE 12.

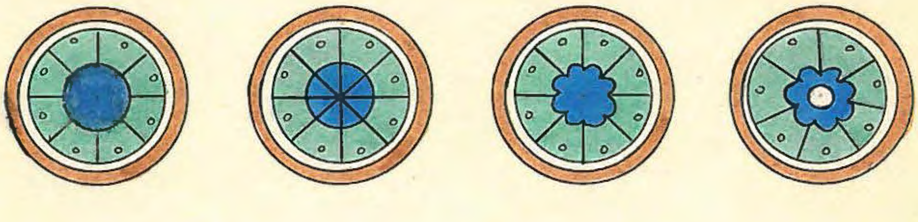
DIAGRAMS ILLUSTRATING AN APPROXIMATION TO A TYPICAL CONDITION IN THE LATERAL COMPOUND EYES OF INSECTA.

TRANSVERSE SECTIONS



T.S. Corneal Lens

T.S. Cone Apparatus and Corneal Hypoderm forming "Iris" pigment cells.

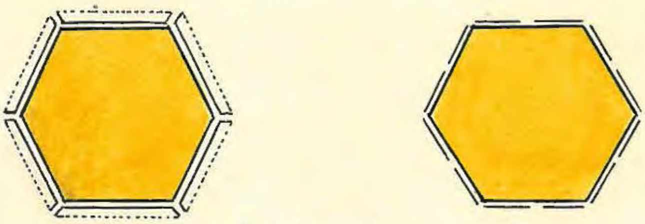


(No one condition of the Rhabdom can be selected as typical of Insects as a whole – Some of the commonest types are shown.)

T.S. Retinal cells, Rhabdom and Accessory pigment cells.

DIAGRAMS ILLUSTRATING THOSE VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYE WHICH OCCUR IN INSECTS, BUT NOT IN CRUSTACEA.

TRANSVERSE SECTIONS



T.S. Corneal Lenses.

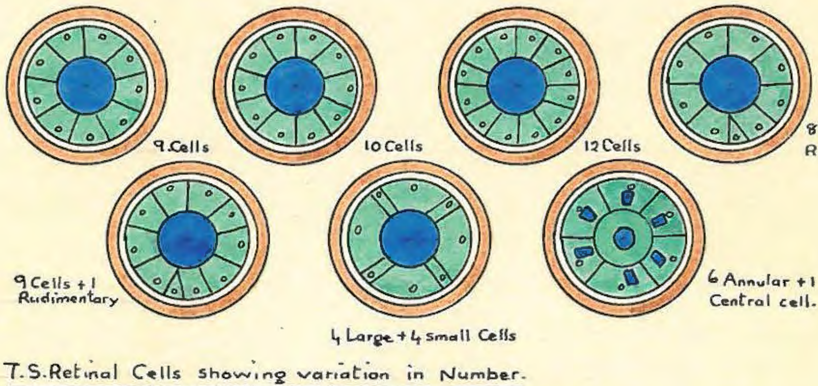
Lenses Separate.

Radial Hairs between Lenses

1. Cell.

4 Cells.

T.S. Corneal Hypoderm Cells
(In undisplaced condition)



9 Cells

10 Cells

12 Cells

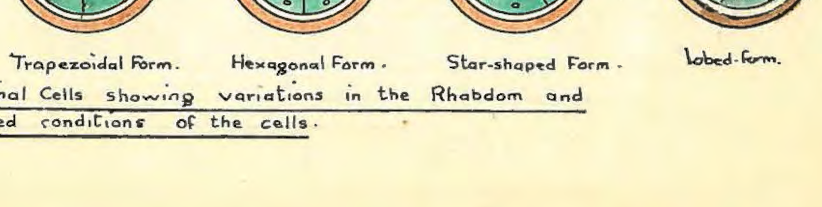
8 Cells + 1 Rudimentary

9 Cells + 1 Rudimentary

4 Large + 4 small Cells

6 Annular + 1 Central cell.

T.S. Retinal Cells showing variation in Number.
(Rhabdom uniformly represented except in last section.)



Trapezoidal Form.

Hexagonal Form.

Star-shaped Form.

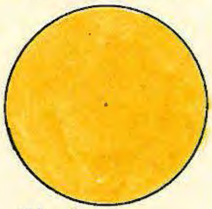
Lobed-form.

T.S Retinal Cells showing variations in the Rhabdom and associated conditions of the cells.

PLATE 14.

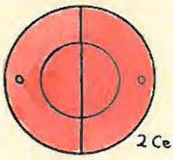
DIAGRAMS ILLUSTRATING THOSE VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYE WHICH OCCUR IN BOTH INSECTS AND CRUSTACEA. TRANSVERSE SECTIONS.

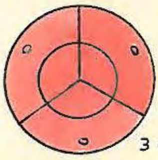
T. S. Corneal Lenses

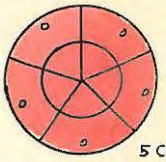

Circular


Unfacetted.

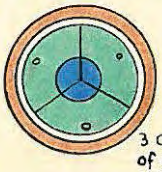
T. S. Cone Apparatus


2 Cells

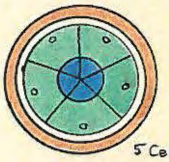

3 Cells

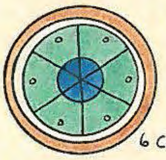

5 Cells

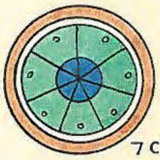
T. S. Retinal Cells showing variation in Number and Arrangement (Rhabdom uniformly shown)

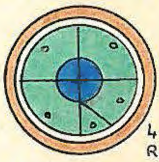

3 Cells (in 1 row of double-layered retinula in Insects)

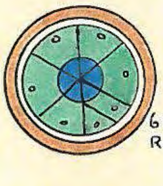

4 Cells

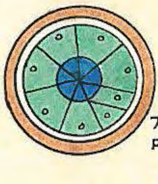

5 Cells

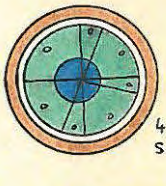

6 Cells

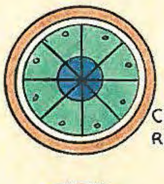

7 Cells

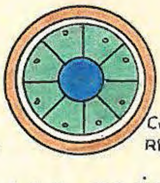

4 Cells + 1 Rudimentary


6 Cells + 1 Rudimentary


7 Cells + 1 Rudimentary


4 Large + 3 Small Cells


Circular divided Rhabdom + 8 cells


Circular undivided Rhabdom + 8 cells


Stellate Rhabdom-rays projecting into cells - + 8 cells

T. S. Retinal Cells showing Variations in the Rhabdom and Associated Conditions of the Cells.


Hollow-lobed Rhabdom + 8 Cells

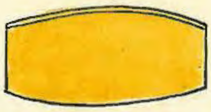

Solid-lobed Rhabdom + 8 Cells.

DIAGRAMS ILLUSTRATING THE COMMONEST VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYE IN INSECTS

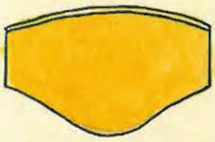
LONGITUDINAL SECTIONS

L.S. Corneal Lenses.

Exocone Condition associated with reduced Cone cells



Slightly Biconvex Form



Highly Biconvex Form.

Epicuticle extends down in pigmented or refractive sheath.

Flattened Form.

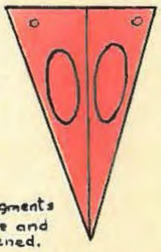
Epicuticle lost.

Unfacetted.

L.S. Cone Apparatus.

Acone condition – cells clear without cone secretion

Pseudocone Condition – Fluid secretion and posterior nuclei.

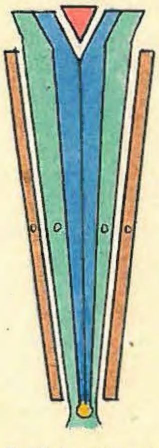


Cone segments separate and unflattened.

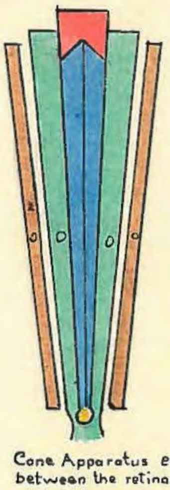
Reduced in association with Exocone arrangement.

Ellipsoidal Cone Apparatus

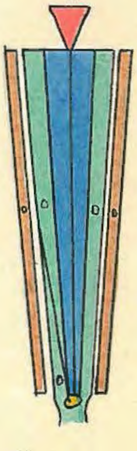
L.S. Retinal Cells and Rhabdom.



Retinal cells and Rhabdom extending round the cone for a short distance



Cone Apparatus extending between the retinal cells and rhabdom for a short distance



Single Basal Cell not participating in Rhabdom formation.

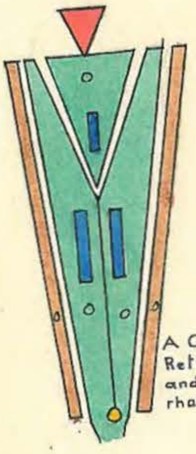
PLATE 16.

DIAGRAMS ILLUSTRATING THE COMMONEST VARIATIONS IN THE STRUCTURE OF THE LATERAL COMPOUND EYES IN INSECTS.

CONTD:–

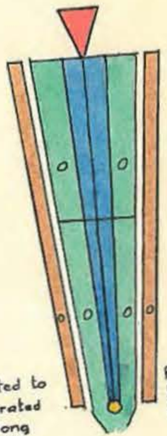
THE RETINAL AND RHABDOM STRUCTURES.

LONGITUDINAL SECTIONS.



A Central distal Retinal cell and separate rhabdomeres

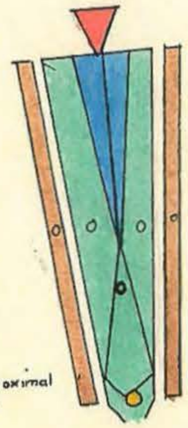
Superposition arrangement. Rhabdom restricted to basal part separated from cone by long clear part of cells. Pigment very sparse



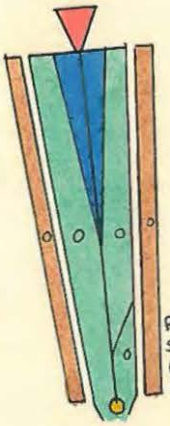
Retinal Cells in two rows as in *Pieris*

NOTE:

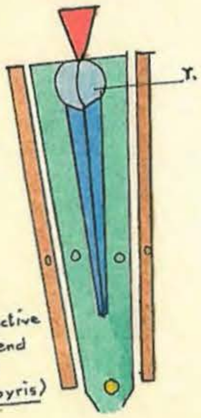
Colours have the same significance as in previous Plates.



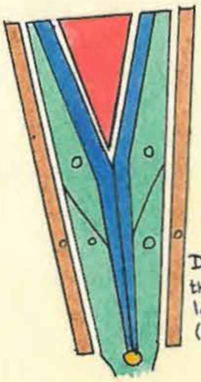
A Central proximal basal cell.



Rhabdom abbreviated. Single cell basally displaced (also associated with other conditions of the retinal cells)



(r) Peculiar refractive body at distal end of abbreviated rhabdom (*Lampyris*)



Double layered arrangement of the Retinal cells, the upper layer surrounding the cone (Collembola, Lepismata)