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

VOLUME II

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Chapter 3.

TRILOBITA AND EURYPTERIDA.

Introduction to the lateral eyes of Trilobita and Eurypterida .

Since Trilobita and Eurypterida are among the oldest known fossil Arthropods, the condition of their eyes is of some interest in indicating the earliest known form of the eye in types nearly related to the ancestral stocks of Crustacea and Arachnida.

In each case and attempt has been made to indicate the primitive and typical conditions and the variation in the structure of the eye , as far as details of its anatomy have been preserved . Some discussion of the relationships of these to the lateral, compound eyes of other Arthropods, together with a summary of the conslusions drawn from the available data ,is attached to each part . The conclusions deal with the comparative anatomy , origin and relationships of the lateral eyes in these forms.

Section A. Trilobita .

Part I. Comparative anatomy of the lateral eyes of Trilobites.

"Compound" Eyes

The Trilobites, together with some Notostraca, are the only Arthropods known from the lower Cambrian beds. Whatever their precise relationships, the Trilobites are clearly an ancient and generalised group. The presence of a "compound" eye in some of the earliest known families - Mesonacidae and Ceratopygidae of the lower Cambrian - (von Zittel, 1937, p.729) points to the Trilobites as a group in which some evidence of the origin of the compound eye, if not the actual stages in its formation, might reasonably be sought.

The lateral eyes in Trilobites are generally described as of two types - "compound" and "simple". The "compound" eyes are absent in Harpedidae and Trinucleidae, families with "simple" lateral eyes, in the blind Conocoryphidae, Schumariidae, Agnostidae, Eodiscidae and Raphiophoridae, as well as in isolated genera of other families. Thus in Beecher's classification as adopted by von Zittel (1937, pp. 720-729) all families of the order Hypoparia are without compound eyes, while these are characteristic of most Opisthoparia and Proparia.

There is no extant evidence that the so-called "compound" eyes corresponded internally to the aggregations ommatidia found in other Arthropods. It is possible that they may have been merely aggregations of ocelli. Since no such groups of ocelli occur in Crustacea, the extant Arthropods most nearly related to the Trilobites - see appendix - it is generally assumed that the external similarity of Trilobite eyes to the compound eyes of other Arthropods justifies the assumption that these were true compound eyes. (In the following remarks the term is used in this sense and the inverted commas omitted.)

The paired compound eyes are symmetrically placed on the dorsal or dorso-lateral surface of the cephalic shield - see [illegible] . On this shield a convex, axial glabella is marked off from the lateral cheeks or genal areas by a longitudinal furrow on either side. Segments corresponding to the five ventral pairs of appendages are marked out on the dorsal surface of the glabella by more or less complete transverse furrows. Each cheek is divided into an inner, fixed and an outer, free portion. The fixed cheek is firmly joined to the glabella. The free cheek, which bears the compound eye, is joined to this along the facial suture, a line to which considerable morphological importance has been attached - see below The facial suture passes from the posterior angle or posterior, lateral margin of the head in round the eye. Anteriorly the two facial sutures may end separately or join in front of the glabella. The course of the sutures determines the position of the eyes and the relative sizes of the two cheek areas. Thus the eye may lie, according to Clarke (1908, p.135) anywhere from

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practically against the glabella to near the lateral margin of the head shield. On the cheek it may lie on a level as far forward as the first or as far back as the fifth glabella segment, although it maintains its relation to the facial suture.

Against the eye the adjacent part of the fixed cheek forms a buttress or palpebral lobe. This with the eye forms a more or less convex, semilunar, ovoid or crescentic elevation varying considerably in size and extent. The eye normally lies with its longitudinal axis parallel to that of the body but may be perpendicular to the latter as in *Encrinurus* - (Woods, 1923, p.227). .

According to Lindstrom (1903) three types of eyes are to be differentiated. Holochroal eyes are provided with approximated, globular, biconvex lenses with the cornea continuous over the entire eye. Such eyes occur in some of the Opisthoparia, for example in *Bronteus* and *Sphaeropthalmus*. Prismatic eyes are provided with plano-convex lenses, with the outer surface of the eye smooth and continuous. The lenses are closely packed, usually hexagonal, occasionally rhombic or square. A parallel condition obtains in certain Crustacea - see p. 104 - where there is a change from the hexagonal to the tetragonal system as a result of the crowding of the eye units. Woods (1923, p. 229) gives as examples of Lindstrom's second type the Opisthoparians *Asaphus*, *Illeenus* and *Nileus*. von Zittel (1937, p. 679) classes these first two eye types together as holochroal. Lindstrom (1903) described a third type - the schizochroal.

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eyes - with globular, biconvex, separate lenses. These are usually circular but by upward and inward migration of the test may appear hexagonal in outline. Woods (1923, p. 229) gives as examples of this type the Phacopidae - Phacops, Dalmanites, etc. (See Figure 38).

Lindstrom considered that the eyes appeared in the chronological succession prismatic, holochroal, schizochroal. Thus in his view the primitive forms generated a compound eye, which later tended to disseminate.

The restriction of the schizochroal eye to the late members of Beecher's order Proparia, which first appeared in the Ordovician - see von Zittel (1937, pp. 723-724) indicates that this eye is probably secondarily evolved from the other types. The separation of the facets and their circular form in the schizochroal eye indicates that a degeneration may have occurred, parallel to that in Isopods and Amphipods in later times.

The lenses, as in the compound eyes of other Arthropods, are usually arranged in regular alternating vertical rows. Delo (1940, pp. 1-32) gives numerous examples of this.

The size of the facets varies from more than .5mm in diametre in some schizochroal eyes to much smaller dimensions in some holochroal eyes, where there may be from six to fourteen facets to the millimetre - von Zittel (1937, p.697).

The eye is largest in Aeglina where it occupies practically the whole area of the free cheeks and extends

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round the entire border of the cephalon according to Woods (1923, p. 227). Otherwise the size varies greatly. There is generally a larger number of lenses in holochroal than in schizochroal eyes. The maximum number for holochroal eyes is found in *Remopleurides radians* with about fifteen thousand lenses (von Zittel, 1937, pp. 697-698). There are about twelve thousand in *Ogygtes nobilis*, four thousand in *Bronteus palpifer* and one thousand in *Bronteus brogniarti* according to Woods (1923, p. 229). Among the schizochroal eyes only five are present, in *Phacops trimerocephalus pentops* (Thomas, 1909, p. 99), eight in *Phacops lotzi* (Thomas, 1909, p. 99) and in *Calyptaulax occidiens* and *Phacops cryptothalmus* (Delo, 1940, pp.106, 135). Eleven or twelve occur in *Acetella rogerensis* (Delo, 1940, p.111), fourteen in *Trimerocephalus volborthi* (Woods, 1923, p. 229), thirty-five in *Phacops lowens* (Delo,1940, p.18), thirty six in *Phacops granulatus* (Woodward, 1905, pp. 152-153), forty-five in *Phacops christata var pipa*, *P. logani var. birdsongensis* and *P. rana* (Delo, 1940, pp. 17, 19. 32), sixty in *Phacops christata*, sixty five in *P. logani*, seventy in *P. raymondi* and one hundred and fourty in *P. reedops* as described by Delo (1940, pp. 14, 19, 24). Two to three hundred occur in some species of *Phacops*, six hundred in *Dalmanites housmani* according to von Zittel (1937, p. 697) and seven hundred and seventy in *Odontochile pratteri* according to Delo (1940, p. 62).

Thus in Schizochroal eyes there is a wide variation in the number of lenses even in different species of the same genus. Moreover in an individual the number varies with

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age. In *Phacops rana* for example according to Clarke (1889, p.153) the number increases up to the adult stage and decreases with old age. This variability is probably an indication of the degenerate nature of the eye which is likely on other grounds - see below.

The eyes vary in convexity from a practically flat form with a few lenses to a highly convex structure with many lenses. Thus in the Phacopidae the eye may lie below the glabella level as in *Phacops gaspens*, *Phacops logani var birdsongensis, Phacops christata var pipa* and *Reedops deckeri*, while in *Acatella caryli*, *Phacops christata*, *Phacops rana*, *Phacopina anceps*, *Eophacops and Greenops* the eye is more or less level with the glabella. It is slightly elevated in *Phacops arkansana* and very convex in *Dalmanitina vidilans*, *Dalmanitina weryhneri*, *Dalmanites platycaudatus*, *Dalmanites vermucosus*, *Dalmanites limulus*, *Odontochile pratteri* and *Odontochile kayserensis* and *Corycephalus dentatus*. It may even be mounted on an unjointed stalk-like structure as in *Coronura aspectans* and *Acetalla achetes.* This range of variability can be demonstrated within the limits of a single genus as in *Calliops*. Thus in *C. fredricki* the eyes are below the glabella surface, in *C. callicephus*, level with it in *C. brevis*, just above it and in *C. armatus* very highly elevated. These examples are drawn from Delo's paper (1940) where they are scattered throughout the text from page 17 to page 96. The variability, especially within the limits of a genus, in schizochroal eyes, argues an instability which would be in accordance with the supposedly degenerate nature of these

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eyes.

A stalked condition is found outside the Phacopidae (Ordovician to Devonian) in *Homalonotus* of the Silurian Calymenidae as described by von Zittel (1937, pp. 723-724), as well as in *Asaphus cornigerus* and *Asaphus kowalewskii* of the middle Cambrian Asaphidae as described by Woods (1923, p.227)

The compound eye in Trilobites appears to have been primitively and typically a convex, sessile structure. In some forms this is reduced and flattened and in others situate on an elevated lobe or stalk-like lateral part of the head, The stalked condition appears to have been evolved at several different times in different families.

The eyes are often placed at the distal end of a raised eyeline extending from the front end of the glabella to near the lateral anterior margin of the eye and palpebral lobe. These are a very archaic feature and characteristic chiefly of Cambrian genera being found according to von Zittel (1937, pp. 705-706) only in the more primitive members of higher and later groups. According to Beecher (1895, p.   ) and Cowper-Reed (1916, p.121) the eyelines probably followed the course of the optic nerves. There is, however, a lack of any constant relationship between the development of the eyes and that of the eyeline. Thus the eyelines may precede the eyes in development as in *Proteus*, *Acidaspis* and *Cerataerges*, or succeed them as in *Ptychoparia*, *Solenopleura*, *Liostracus* and *Triarthrus* according to von Zittel (1937, p. 713), while in the

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development of later forms there is a tachygenetic tendency to the loss of the eyeline in the eyed forms as in Dalmanites (Woods, 1933, p. 231). In other cases, as in Conocoryphidae (von Zittel, 1937, p. 713) the eyeline may persist where no eye is formed. It would be difficult to account for these discrepancies in the development of the eyeline and the eye on the assumption that the eyeline traced out the course of the optic nerve. On the whole it seems more probable that the eyeline is, as suggested by Stubblefield (1936, pp. 421-422), merely an anterior part of a larval ridge, a shell ornament, which runs out from the anterior part of the glabella and which forms at its posterior end the palpebral lobe. The anterior part of the ridge remains as a thin eyeline connecting the end of the lobe - in close proximity to the anterior part of the eye - to the glabella.

Since the condition of the head segmentation in Trilobites is relatively simple and generalised, attempts have been made to define the segmental position of the eye in this group in relation to the cephalic sutures.

From its precise and constant position in relation to the eye and palpebral lobe, the facial suture has been assigned a very considerable morphological significance and has been regarded as a boundary fixing the segmental position of the eye.

The free cheeks are usually taken to represent the pleurae of the ocular segment - see McCoy (1849, p. 396) and von Zittel (1937, p. 707). According to Walcott

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(1918, p. 115) they represent the expanded and flattened ocular peduncles which are assumed to have been present in the primitive forms. This view has not been supported by Stubblefield (1936, pp. 407-414) in his review, in which he deals fairly extensively with the structure of the cheeks.

Most of the earlier authors placed the eye on the second head segment. Although Bernard (1894, p. 414) considered that it was "a lonely wanderer on the face of the Trilobite", he restricted its wanderings by stating that it maintained a general position in relation to the rest of the head morphology in that it never crossed the facial suture, which he regarded as a boundary between the pleurae of the first and second segments.

According to Beecher (1895, pp. 177-178), 1897, pp. 95-96) the first segment was hypostomal and the second ocular. He considered that in the primitive group Hypoparia, the members of which were blind or with simple lateral eyes, the second segment remained below with the hypostome so that no large compound eyes developed on the dorsal surface.

The eyes in later forms, in their movement onto the dorsal surface, carried with them the free cheeks representing the second segment. Thus the compound eyes were always and necessarily enclosed within the facial suture, which had the value of a primary segmental boundary to the ocular segment.

More recent authors, whose opinions are mentioned more specifically below, have abandoned the idea of the immovability of the eye in relation to a supposedly rigid facial suture.

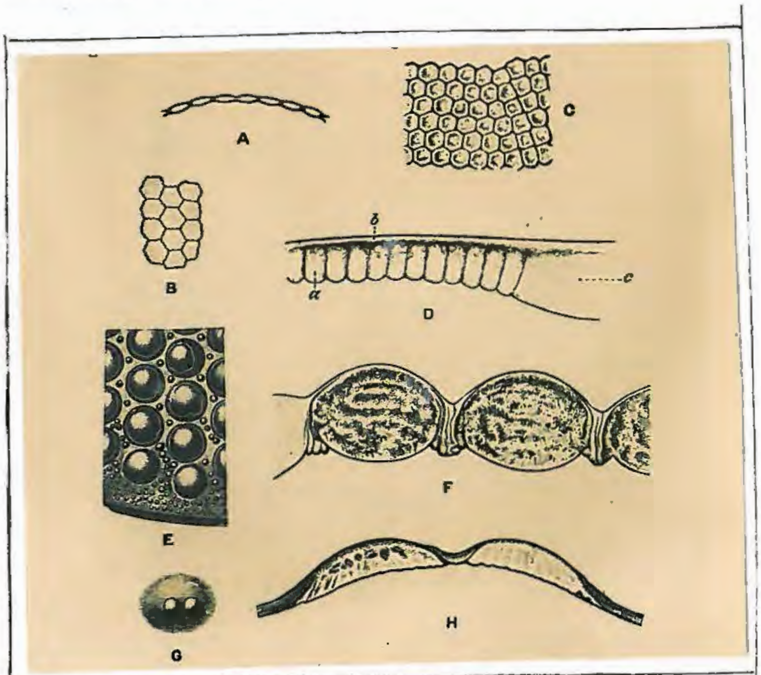
facial suture. In extant Arthropods the head segments are greatly condensed and the limits of the segments no longer clearly apparent. The position of the eye appears to be decided by the relative proportions of the different parts of the head (which vary with the habits of life), rather than by a fixed relation to the rest of the head morphology. If such a relation exists it could only be ascertained by an extensive comparison of the morphology and embryology of the head sclerites and their relation to the nervous system throughout the Arthropoda. Such an investigation is beyond the scope of this thesis. Within the Trilobites themselves the relation of the eye to the cephalic sutures is a matter of great importance in taxonomy and therefore one which has provoked considerable discussion, but although the condition in Trilobites is simpler than in the other Arthropods, it is not sufficiently clear to allow a general deduction to be made on the relation of the eye to the morphology of the head sclerites.

Figure 5

Eyes of Trilobites. (After Lindstrom)
A.B. Sphaerophthalmus alatus, Ang. Upper Cambrian. Vertical and horizontal sections
C. Asaphus fallax, Dalm. Horizontal section
D. Nileus armadillo, Dalm. Vertical section
a. Prismatic lenses
b. Cuticle
c. Part of free cheek
E. Dalmanites vulgaris, Salt. Part of eye
F. Dalmanites imbricatulus, Ang. Vertical section of eye with a part of the free cheek on left.
G.H. Harpes vittatus, Barr.
G. The two lenses of one eye
H. Vertical section of the same.

(Taken from Harmer and Shipley, 1909, p.228, fig.139)

A.B. Holochroal eyes
C.D. Prismatic eyes
E.F. Schizochroal eyes
G.H. "Simple" eyes.



2. The "simple" eyes.

Visual spots, the so-called "simple" lateral eyes, sometimes referred to as "ocelli", are occasionally found. They occur in most members of the Harpedidae as well as in some members of the Trinucleidae namely Tetraspis and the young Cryptolithus (although absent in the adult of this form) as described by von Zittel (1937, p. 711) as well as in some species of the genus Trinucleus - namely T. bucklandi and T. seticornus as described by Cowper-Reed (1916, pp. 118-121) and Richter (1921, p. 194). The Harpedidae were restricted in occurrence to the Ordovician while the Trinucleidae, excluding the peculiar form Orometopus - see below - originated then and persisted to the Devonian, according to von Zittel (1937, p. 729).

These forms with "simple" lateral eyes all fall into Beecher's order Hypoparia, while the remaining members of this order are blind. In all Trilobites, both in the adult and in the development, only one type of lateral eye may occur in the species - either the "compound" or the "simple".

The "simple" eyes are represented by small tubercules on the test. The lenticular structure of these is apparent from Richter's description (1921, pp. 197-198). Their visual function is generally assumed from the fact that they occur only in forms

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which lack compound eyes but in approximately the same position as the latter occupy when present.

Although these small, separate tubercules are probably rightly to be regarded as visual organs of low grade they are not necessarily ocelli, as von Zittel (1937, p. 697) regards them. (He homologises these with "the ocelli of many Crustaceans". There is clearly no extant evidence for any homologies with the median ocelli of Crustacea, while lateral ocelli in the strict sense of the term are not a feature of Crustaceans). Although their biconvex form as described by Richter (1921, p. 195) and their scattered arrangement gives them the appearance of a group of ocelli, similar to those of Chilopods, they might equally well be the separated ommatidial units of a degenerate compound eye, similar to those of Isopods and Amphipods. In the absence of internal evidence their nature can only be indirectly deduced. As the "simple" eyes are here held to be ommatidial, they are considered in connection with the compound eye. (The inverted commas are omitted in the following remarks and the word "simple" used in the restricted sense indicated above).

The number of lenses varies slightly. Richter (1921, p. 196) points out that among the Harpedidae the number is usually two or three, two lenses occurring in *Harpes vittatus* and three in *Harpes ingula*, *Harpes d'Orbigenyanis* and *Harpes kayseri*. He points out that in

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Harpes macrocephalus the eye consists of a large central mound with two smaller mounds, one on either side. Woods (1923, p. 231) described in addition to the three main tubercules other smaller lenses in regular rows. Richter (1921, p. 196) had also found these but had interpreted them, not as lenses, but as mere shell ornaments. It is possible that they represent degenerate lenses and the remains of a larger eye.

In the eyes Trinucleidae there are two lenses on a single elevation according to Richter (1921, p.179) while according to Woods (1923, pp. 230-231) a single tubercule is present. According to von Zittel, (1937, p. 697) one to three lenses occur in Tetraspis.

In this connection the genus Orometopus presents some difficulty. According to Lake (1907,p.45), although this genus possesses a compound eye it is to be placed in the family Trinucleidae. Woods (1923, pp.226, 231, 244, 246) following this places Orometopus, an upper Cambrian form, as the earliest of the Trinucleidae. Under Beecher's classification this genus falls into the Opisthoparia and the rest of the Trinucleidae into the Hypoparia - see von Zittel (1937, pp. 709-710).

If the view of Lake and Woods is accepted in this matter the simple eyes are almost certainly to be derived from the compound eyes through those of forms resembling Orometopus. The condition in Harpes macrocephalus could then be described as the degenerate remnant of a compound condition in Harpedidae. If this

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is not accepted the question of the origin of the simple eyes remain open.

The simple eye lenses are described by Richter (1921, p. 196) as laminated and as resembling the rest of the test. This consists according to von Zittel (1937, p. 691) of carbonaceous and phosphatic compounds of calcium, some of which must originally have been chitinous. In polarised light according to Richter (1921, p. 196) the lenses are clearly distinguishable from the test and shell ornaments.

An eyeline similar in position to that of the compound eyed types, has been described by Richter (1921, p. 195) in *Harpes* and *Trinucleus* species and in particular by Cowper-Reed (1916, pp. 118-119) in *Trinucleus seticornis* and *Trinucleus bucklandi* and by von Zittel (1937, p. 697) in *Harpes* and *Tetraspis* species. Cowper-Reed (1916, pp. 118-119) and Richter (1921, pp. 195-96) consider that this line follows the course of the optic nerve. Cowper-Reed points out that in some blind Trinucleidae the eyeline is replaced by a series of lines radiating out from the point of origin of the eyelines in other forms. He described these (1916, 119-121) in *Trinucleus murchisoni*, *T. gibbsi* and *T. Etheridgei* Although he points out that similar lines are found in some blind Conocoryphyidae (*Dionide*) there is no precedent in other Arthropods for supposing that on degeneration of the eye the optic nerve would be likely to split into a number of surface nervules. The evidence for regarding this line as following the course of the optic nerve seems, as the case of the compound eye, incomplete and unsatisfactory.

The position of the eyes on the surface of the head is approximately the same as that of the compound eyes of other forms. Their precise relation to the cephalic sutures is however somewhat problematical. Instead of a dorsal facial suture a marginal suture is generally assumed to be present and has been described in Trinucleus spp. by Cowper-Reed (1912, p. 341, 1916, p. 119). A marginal suture was clearly defined in Harpes by Richter (1914, p. 146, 1921, p.196). The relation of the facial and marginal sutures to the compound and simple eyes is of some importance in discussing the homology of these visual organs. (In the absence of internal evidence their homology can only be decided by their relation to the rest of head morphology).

That the eyes were of two separate types was the view of Becher (1897, pp. 177-178). He regarded the marginal suture of the simple eyed Hypoparia as homologous with the facial suture found in the compound eyed forms of the Opisthoparia and Proparia. The compound and simple eyes were on different sides of this line and were therefore supposed to have had a separate origin in accordance with the morphological significance attached to the facial suture in its relation to the rest of the head and the position of the eyes.

Thus unless the eyes are diphylectic in origin in a group primitively blind and later developing ventral eyes - all of which conditions are implicit in Beecher's

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classification (1897) - the facial suture cannot be regarded as other than secondary and without strict morphological relation to the position of the eye.

Most subsequent authors, as Rasetti (1945, p.44) emphasises, have denied the rigid morphological relations of the facial and marginal sutures to the eyes. They have therefore been free to regard the compound and simple eyes as of common origin as is suggested by their mutually exclusive occurrence, similarity in position and relation to the eyeline.

That the facial and marginal sutures represent moulting lines without morphological significance was first suggested by Barrande (1853, p. 118). This was upheld by Swinnerton (1919, p.103) who stressed the fact that the assumption of homology between any two moulting lines was likely to be unsound. This view has been expanded by Hendriksen (1938, p.103), who considered that Arthropod moulting was primitively marginal and that the primitive eyed Mesonacid Trilobites and the primitive Trilobites in general, like Eurypterids and early Crustacea underwent a marginal ecdysis. In later groups (Insects and Myriapods), as well as in the more advanced Trilobites, Crustacea and Arachnids this was replaced by longitudinal or transverse sutures or other specialisations. The dorsal facial suture in Trilobites was such a secondary, ecdysial line designed to free the large compound eyes at once in

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and lost or developed as occasion demanded. Cowper-Reed (1916, p.170) considered that the loss of the dorsal facial suture in these simple eyed forms was of positive advantage. In these burrowing forms living under aphotic conditions the loss of the facial suture would render the head a more rigid burrowing tool, while the eyes, reduced under these conditions, no longer require a special moulting line. Stubblefield (1936, p. 410) also regarded the facial suture as of adaptive significance but developed in accordance with the rolling up of the body and the feeding movements.

It seems probable that the primitive condition is that of the Mesonacidae and that a dorsal suture is evolved as an adaptive measure in those with large compound eyes, while it is absent in forms in which the eyes degenerate or fail to develop.

If the compound and simple eyes are homologous,the simple eyes may be either the percursors of the successors of the compound eyes and either ocellar or ommatidial.

There is little or no evidence in favour of the simple eyes being regarded as precursors of compound forms. In geological succession the Harpedidae and the Trinucleidae occur later than the earliest eyed forms. With the exception of <u>Calymene senaria</u>, an Ordovician Proparian, described by Clarke (1889, p. 253), the development of the compound eyes of Trilobites, like that of Crustacea, shows no indication of an origin in the coalescence of separate

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units. In Calymene, the eyes, although schizochroal in the young, are holochroal in the adult. This might appear to indicate the existence of separate units as the condition preceding the compound eye and to point to the Harpedidae and Trinucleidae as forms in which this primitive condition has persisted, although lost both in the adult and in the development of the other earlier types. Calymene is a member of the Proparia, the most lately evolved order, in which the eyes are of a degenerate, Schizochroal type in many cases. It is probable that the development in this case is without relation to the phylogentic sequence in the Trilobites as a whole and merely represents the relatively late development of a complex, aggregated eye from a partially, degenerate type.

The simple eyes are then probably to be regarded as the products of degeneration of a compound eye. Thus evidences of a facial suture and compound eyes in Harpes macrocephalus and Orometopus probably point to the ancestral condition. A parallel case of the degeneration of the eye into a few separated units is known in the Phacopidae (see p.) - where the number of lenses varies from seven hundred and seventy to as few as five- or six- a condition approaching that of the simple eyed Harpedidae and Trinucleidae. Such degenerations are not uncommon in Crustacea - where the products are ommatidia and not ocelli. Whether this is also the case in Trilobites is a matter of conjecture,

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in the absence of internal evidence.

It seems probable that the simple eyes were derived from compound forms, which degenerated into their component units, while the facial suture was lost or failed to develop and a marginal suture was resuscitated or gained.

3. The absence of eyes in Trilobites.

The relationships of the Trilobites are a matter of some uncertainty, since, as Warburg (1925, p. 347) has stressed they were "a short lived group evolving rapidly along different lines, in which the larval forms and environmental adaptations are little understood, so that it is difficult to force them into a satisfactory position in a classification of the Arthropods designed mainly to accommodate modern forms".

It is clear that the differentiation of some at least of the Arthropod classes had advanced to a considerable degree by Cambrian times. The Paleontological evidence, although incomplete, gives as the earliest known Arthropods the Crustacea Notostraca and the Trilobites, without clear indication of forms linking these to the Annelids.

Some authors including Raymond (1920, p. 522) and Hendriksen (1932, p. 103), have regarded the Trilobites as the ultimate ancestors of all the Arthropods. Others have taken a narrower view of their affinities. (Their relationship to the Arachnids is considered in connection with the eyes of Eurypterida). For the most part the Trilobites have been relegated to the Crustacea where they usually occupy the position of a subclass. Among those who have allied them to the Crustacea are the following : Packard (1880, p. 503), Beecher (1897, p. 90 et seq.), Carpenter (1903, pp. 345-346), Walcott

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(1918, p.115), Calman (1919, p. 361), Woods (1923, p.221), Warburg (1925, p. 374) and von Zittel (1937, p. 708).

Their relationship to the separate extant orders of Crustacea is somewhat indefinite. Although Raymond (1920, p. 1) attempted to ally them to the Isopods, Calman (1921, p. 523) pointed out that this was fantastic. Carpenter (1903, p. 332) had placed them with the Leptostraca, but as von Zittel points out (1937, p. 727) they are more generally allied to the Apus-like forms.

Calman (1919, p. 361) pointed out that, while no Trilobite was sufficiently generalised to have given rise to the Crustacea, the earliest forms of both pointed to a common ancestor. Since in the earliest Cambrian times the Trilobites were more widespread and varied than the Crustacea it is probable that the Trilobites were the more primitive group. It remains possible that the Trilobites were derived from Apus-like forms or that Trilobites and Crustacea diverged in preCambrian times from a common Arthropod stem.

The presence of a compound eye in Trilobites must be due to an evolution convergent to that which produced the compound eye in Crustacea or the similarity must be due to the derivation of these forms from a common eyed ancestor. The former case would provide a precedent for Moroff's (1913, p. 482) view of the convergent evolution of the eye in Insects and Crustacea. (The Scutigerid eye might then be regarded as a parallel but more recent evolution).

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On the other hand , since true compound eyes appear to be restricted to the Arthropods,(although less highly differentiated aggregates of eyes are found in some Molluscs (see Patten ,1886) , in some Annelids as in Dasychone (see Austin , 1898, p. 271 et seq.) and in some Echinoderms (Sarasin , 1887,p. 1 et seq.)), it seems probable that all the Arthropod compound eyes are derived from a common, ancestral form.

In this connection , the occurrence among Trilobites of blind forms and their primitive or adaptive significance is of importance. A primitively blind form would imply either that the compound eye had been evolved more than once , or that the compound eye in Crustacea had been evolved from that of a relatively late, eyed Trilobite stock.

The absence of any indication of the evolution of the compound eye within the Trilobites themselves makes it difficult to suppose that the primitive forms were blind, while it is hardly possible to regard the Crustacea as derived from any Trilobite other than an extremely primitive and generalised type. If the eyes were primitively present and the blind forms secondary, the Trilobites could be derived from the early Crustacea or vice versa or both from a common,pre-Crustacean , eyed Arthropod stock.

In spite of the difficulties attaching to the view it has frequently been held that the Trilobites were primitively blind . Although three of the earliest known families were totally blind - namely Agnostidae, Eodiscidae and Conocoryphyidae, which originated in the lower Cambrain and disappeared before the Silurian - the eyed Mesonacidae and Ceratopygidae and some of the eyed genera of Ellipsocephalidae, Olenidae and Paradoxidae fall as early as these in the fossil records according to von Zittel (1937, pp. 709-729). As these records are necessarily incomplete and inconclusive, the primitive condition can only be decided on the grounds of the general comparative anatomy of these forms.

A primitive absence of the eye was maintained by Beecher (1897), Lindstrom (1903), Richter (1921, p.197) and Woods (1923, p. 232). These authors appear to regard Eurycare, an Olenid from the upper Cambrian as the earliest eyed form.

Beecher's insistence (1897, p. 182) on the primitive nature of the blindness of Trilobites is apparent from the position of the blind families in his classification. Thus in the primitive order Hypoparia, Agnostidae, Eodiscidae, Schumariidae and Raphiophoridae are eyeless while Trinucleidae and Harpedidae have only simple eyes. The Conocoryphyidae, at the base of the second order Opisthoparia, are blind, as are most members of the Encrinuridae, the most primitive family of the third order Proparia. The first eyes to appear were ventral according to Beecher (1897, p. 182). Later these moved up onto the dorsal surface carrying with them the facial sutures and the free cheeks.

/There

There are, however, objections to Beecher's views on general, theoretical and on anatomical grounds. The classification rests largely on ontogenetical evidence in itself uncertain and in its relation to phylogeny problematical. Thus as George has emphasised (1933, pp. 115,133) in his paper on Palingenesis and Paleontology "the conditions of preservation, the different bionomic relationships of young and adult forms, the accident of discovery, all militate against a complete series ever being found, so that it is difficult to interpret specimens as the young stages of a species"....while..."in a series with a number of characters the rates of acceleration of the different characters may not be uniform in phylogeny or ontogeny, so that the ontogeny of a late member may contain total stages not represented in any adult member of the series, the stages in the development of one character being advanced on that of another". Although, according to Raymond (1920, pp. 23-24), Beecher did not neglect the study of the larval Mesonacidae, he seems to have based his views, not on this family, now regarded as very primitive - see below- nor on the development of his own primitive order Hypoparia, but on the ontogeny of the late Opisthoparian types.

Beecher's classification is also open to attack on anatomical grounds. Although he considered that the earliest forms must have had ventral free cheeks, he appears to have described these only in the Agnostidae - see Woods, 1923, p. 245. Stubblefield (1936, p. 417)

/points

points out that in no case was he able to describe the ventral eyes which according to his theory should be present in the most primitive types, either in the larva or the adult.

If Beecher was incorrect, as appears likely, the primitive condition probably resembled that of the eyed Cambrian family Mesonacidae. The condition of the eye and facial suture in this family and its taxonomic importance was for some time a matter of dispute. Beecher (1897) described a facial suture in the course of degeneration and this feature, together with the presence of eyes, removed them in his view from the position of primitive Trilobites. Lindström (1901, pp.15, 16) pointed to a raised line running from the eye to the posterior part of the head as being possibly a part of a facial suture. Stubblefield (1936, pp. 423-424) considered that this was merely part of a larval ridge. Walcott (1891, p. 635) had pointed out that the Mesonacidae were without a facial suture and later emphasised this condition in Nevadia (1910, p. 237) probably the most primitive of the Mesonacidae, and Marella (1912, p.192) another primitive form. Swinnerton pointed out (1919, p. 491) that there was no facial suture in Nathorstia transitans, which he regarded as a form linking Trilobites to Merostomata. In the absence of such a suture it resembled both Branchiopods and Merostomata. He therefore formed a primitive order Protoparia in which he placed the Mesonacidae and primitive Trilobite-like forms of

/doubtful

doubtful position (<u>Nathorstia</u>). In this group the absence of a facial suture was regarded as primitive. He derived some of the Opisthoparia from the Mesonacidae and the rest of the Trilobites from the remaining Protoparia. His views are in accordance with those of Hendriksen (1936, p.103) based on the moulting of Arthropods, who considered that a primitive marginal suture was related to the primitive presence of eyes in Trilobites, as in <u>Apus</u> and the Eurypteridae, and not to the absence of eyes as Beecher and other early authors had supposed.

It seems probable that all the eyeless forms are secondary and do not represent the persistence of a primitively blind condition preceding the eyed condition in Mesonacidae.

The facial suture is clearly a structure whose absence or obsolescence is correlated with that of the eyes. If a facial suture is present on the dorsal surface in the absence of eyes, it is clear that these must originally have been present.

Among the totally blind families this is the case in Conocoryphidae of the lower to middle Cambrian and in the Raphiophoridae of the Ordovician to Silurian, according to Swinnerton (1915, p. 452) The remaining totally blind families are the Agnostidae of the lower Cambrian to Ordovician, the Eodiscidae of the lower Cambrian to Carboniferous and the Schumardiidae of the Ordovician.

In the Agnostidae Beecher (1897, p.183), Lindstrom (1903) and Swinnerton (1915, pp. 490-491) found no dorsal facial sutures. Walcott (1913, p. 195) however ranged *Pagetia* with its eyes and facial sutures and *Wallisonia* with its vestiges of these with the Agnostidae. It is probable that other Agnostidae have lost the facial suture and reverted with blindness to the marginal suture. The Eodiscidae are very closely related to these and according to Swinnerton (1936, p. 429) are provided with a facial suture so that their blindness too is presumably secondary. Schumardiidae are without eyes or facial sutures but their late origin in the Ordovician makes it unlikely that their blind nature is primitive - see von Zittel (1937, p. 711).

Eyes are absent in some genera of the following families : Ellipsocephalidae (lower to middle Cambrian), Olenidae (middle Cambrian to Ordovician), Paradoxidae (middle Cambrian), Trinucleidae (Ordovician), Harpedidae, Illaenidae, Encrinuridae (Ordovician to Silurian), Phacopidae, and Cheiruridae (Ordovician to Silurian or Devonian).

Although some of the Olenidae and Paradoxidae are blind as described by Lindström (1903), von Zittel described (1937, p. 714) some of these as having eyelines and a facial suture. In those Illaenidae, where the eye is lost, the loss is accompanied by a straightening of the facial suture and a narrowing of the free cheeks according to Cowper-Reed (1916, p. 171). Among the Phacopidae Schizochroal eyes and a facial suture are normally

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present. The tendency to degneration, which appears to have produced the schizochroal eye, when carried to the extreme, is responsible for the blindness of *Phacops caecus*, *P. laevis*, *P. anopythalmus* and *Dachanalla usgheri* according to Thomas (1909, pp. 99, 200) of *Typhloniscus baini* according to Rennie (1930, pp. 335-336) (where the facial suture is also lost) and of *Ormathops* according to Delo (1940, p.12). In Cheiruridae the eyes are absent in *Placoparia* but present in most cases together with a facial suture, according to Woods (1923, pp. 250-251) and von Zittel (1937, p. 725). Although eyes are absent in some Encrinuridae, (*Areia*, *Dindymene*) eyes and a facial suture are present in related forms according to von Zittel (1937, p. 723) In Ellipsocephalidae the eyes and facial sutures are usually present but for a long time remained so obscure that they were unnoticed as in *Agraulos* and *Ellipsocephalus*, according to von Zittel (1937, p. 717) and Woods (1923, p. 247). In Trinucleidae the simple eyes appear to be derived from the compound eyes of related forms possibly resembling *Orometopus*, which possesses an eye and a facial suture. Cowper-Reed (1916, p.175) points out that the blind forms have probably arisen several times and that the loss is not successional. The development of simple eyed and blind forms in Harpedidae appears to have followed the same course as was taken in Trinucleidae.

Thus it is probable that the primitive Trilobites were eyed and that blind types have been secondarily

/evolved

evolved at several different times. It seems likely that the Crustacea and Trilobites were derived from a common, pre-Cambrian ancestral form possessing an unstalked, convex, compound eye.

SUMMARY

Compound eyes.

Lateral, paired compound eyes, apparently resembling with those of Crustacea, are typically present with their absence or reduction secondary. They lie on the free cheek and rest on the palpebral lobe of the adjoining fixed cheek. They are joined to the glabella by an eye-line, which is probably part of the larval ridge - a cephalic ornamentation. The eyes vary in convexity roughly in proportion to the number of units comprising them. They may be elevated on an unjointed stalk. The stalk appears to have been immovable and evolved at different times in different forms. There is no real evidence of its morphological homology with the stalk of the eyes of some Crustacea. It shows no indications of appendicular origin.

The eye lenses show the same range of variation in their convexity and number as is found in the compound eyes of other Arthropods. Thus they vary in number from fifteen thousand to less than ten, and in convexity from a flat to a very highly biconvex type. As in other Arthropods, the biconvex form is associated with a separation of the eye units accompanying a decrease in the number of component units. Again as in other Arthropods closely approximated lenses are hexagonal and separated lenses more nearly circular in outline. The separated, biconvex, circular lenses of the reduced, schizochroal eyes

/appear

appear to be of later origin than the more flattened, approximated, hexagonal lenses of the holochroal eyes.

The cephalic segmentation is more primitive in Trilobites than in any extant Arthropods. Since traces of this segmentation are apparent in the glabella to which the eye is connected by the eyeline, one might expect to find in Trilobites indications of the original segmental position of the eye. The eyes are placed on free cheeks, which appear to represent the pleurae of an ocular segment. The earlier authors considered that the facial suture defined the limits of this segment, which they regarded as the second in the cephalic series. Later authors have denied the morphological value of the facial suture and have considered the precise position of the eye and the anterior segmentation of the head of Trilobites in general as unsettled.

Simple eyes and their relations to compound eyes.

The so-called "simple" eyes consist of a few small tubercules occurring on the genal areas. Their visual function is assumed from their position and lenticular structure. They are comparatively rare and restricted in time to the Ordovician, Devonian and Silurian periods and in occurrence to some members of the Trinucleidae and to the Harpedidae. The homology of the simple and compound eyes and their separate or common origin, can only be decided on the grounds of their relation to the rest of the

/head

head morphology. On these grounds the older authors considered the simple and compound eyes as of separate origin in spite of the similarities in their position and relation to the eye line and their mutually exclusive occurrence both in ontogeny and in the adult forms. The view is here upheld that the relation of the facial and marginal sutures to the two types of eyes is not such as to exclude the homology of the simple and compound forms. It is suggested that the main cephalic suture is primitively marginal and that its relation to the eye in different forms is incidental to the exigencies of moulting. When the eye is well developed the suture is facial; when the eye degenerates it reverts to a marginal position. Indications of compound eyes and facial sutures in forms nearly related to the simple eyed types, suggests that the simple eyes are the products of the degeneration of compound eyes. In Phacopidae a parallel degeneration has led to the production of schizochroal from holochroal eyes. Similar degenerations are common in Crustacea. Here the degeneration produces not ocelli but ommatidia. Whether this was also the case in Trilobites remains conjectural in the absence of internal evidence. The alternative view, that the simple eyes are in the course of forming a compound eye, is rejected. The simple eyes are of late and isolated occurrence and unlikely to be sole survivors of a pre-compound condition. Indications of forms intermediate between these and compound eyes are

/moreover

moreover absent in the ontogeny of the earliest Trilobites and in Crustacea. The development in Calymene - a late form is probably exceptional and not an indication of the phylogenetic sequence. Thus the simple eyes are regarded as formed by the separation and reduction of the units of a compound eye and not as eyes of a separate type. This brings them into line with the condition in Crustacea so that they do not have to be regarded as a unique formation.

The absence of eyes in Trilobites.

The earliest fossil Arthropods are Trilobites and Crustacea and it is from these and their ancestors that the remaining Arthropods are ultimately derived. Trilobites are more nearly related to Crustacea and especially to the Branchiopods than to any of the later Arthropods and the two appear to have diverged in pre-cambrian times from a common ancestor more primitive than any known Crustacean or Trilobite. Since the compound eyes in these two groups appear to be very similar and since there is no evidence of intermediate stages in their formation in either group it seems probable that the common ancestor was eyed. Of the earliest known Trilobites some were blind, some eyed. Beecher and some of the other earlier authors considered that the primitive condition in Trilobites was that of blindness. This makes it necessary to suppose either that the eyes in Trilobites and Crustacea underwent a convergent evolution or that the Crustacea were derived from a relatively late part of the Trilobite stock after it had

/acquired

acquired eyes. Some theoretical and anatomical difficulties inherent in Beecher's view are pointed out, and the view is here adopted that the primitive Trilobites resembled the Mesonacidae in the possession of a fairly well developed compound eye associated, as in other primitive Arthropods, with a marginal moulting line. All the eyeless forms are probably secondary, degeneration of the eye having occurred more than once, and having led to the production of simple eyes in Harpedidae and Trinucleidae and to the formation of very small, degenerate compound eyes in some Phacopidae, and in some cases to complete blindness. If the primitive Trilobites were eyed, as the primitive Crustacea almost certainly were, it is clear that the compound eye was a feature of the earliest Arthropod stock. There is then no reason to suppose that the evolution of this organ in Trilobites and Crustacea was convergent.

Part II.

Conclusions -Trilobites.

I. Occurrence , type and basic pattern .

Lateral eyes , whether "simple " or " compound " are present. (The view is here adopted that these two types are homologous). "Compound " eyes are typically and primitively found . Absence of the eyes is secondary , whether sporadic or characteristic of an entire family. Reduction to a small number of ommatidia may occur as in the schizochroal eyes. Lateral ocelli do not occur if the view is adopted that the "simple " eyes are the reduced remnants of a "compound " eye and presumably ommatidial. In view of the absence of lateral ocellar aggregations in Crustacea (the Arthropods most nearly related to the Trilobites), the lateral "compound " eyes of Trilobites are generally assumed to have been of the true , compound , ommatidial type.

2. Comparative anatomy .

The internal anatomy has not been preserved so that little is known of the comparative anatomy of these eyes. As far as the lenses are concerned, the range of variation in number and form is similar to that in Crustacea. The typically hexagonal (occasionally square or rhombic) form of the lenses which may be either plano- or slightly bi-convex in form and arranged in regular, alternating , vertical rows

/ the

(the condition in holochroal eyes) is closely paralleled in many Crustacean eyes . The large , separate , circular, highly bi-convex lenses of schizochroal eyes resemble those of the degenerating eyes of Crustacea. Prismatic eyes with their smooth , outer cuticle and inner convex , lenticular prolongations, to some extent resemble the lenses in <u>Limulus</u> , although the lenses are much les distinctly separated and exaggeratedly peg-like than in the latter case.

3. Stability and evolution of the eye .

The relatively stable lens pattern and the well developed form of the eye in some of the earliest known species, together with the absence of any sign of evolution of the eye within the Trilobites, indicate that this was a feature already well- developed in pre-Cambrian forms.

4. Variation of the eye in relation to phylogeny.

Such variation in the eye structure as is known, is related to the general phylogeny of the families. Thus the schizochroal eyes are restricted to the late and in many ways modified Phacopidae, while the "simple " eyes are restricted to a few otherwise nearly related forms.

5. Degeneration of the eye .

"Simple " eyes appear only in Trinucleidae and Harpedidae. The difference in relation of the "compound " and "simple" eyes to the facial suture is not here considered to prejudice the homology of these structures.

/Facial

(Facial and marginal sutures , the latter the more primitive , are here regarded as moulting lines of no great morphological significance and subject to adaptive changes). The "simple " eyes are considered to be produced from a "compound" eye of the type of <u>Harpes macrocephalus</u> and <u>Orometopus</u>, the degeneration taking a course parallel to that producing the schizochroal eyes but carried to greater lengths. There is no extant evidence that the units of degenerate eyes gave rise to ocelli. In the absence of precedent in any known Crustacean form for such a course, it can only be assumed that the "simple " eyes and schizochroal eye units remained ommatidial in form .

6. Possibility of the origin of compound eyes from ocelli

There is no clear indication in anatomy or ontogeny (with the possible but very doubtful exceptional development in <u>Calymene</u>) that the "compound" eyes were formed from a single ocellus or from a group of ocelli.

7. General relationships .

The probable absence of primitively blind forms allows the Crustacean and Trilobitan compound eye to be derived from that of a common pre-Cambrian ancestor. (or to be derived from one another's) without the necessity of supposing the separate and parallel evolution of the compound eye in these forms.

Section B. Eurypterida .

Part I. The comparative anatomy of the lateral eyes of Eurypterida .

Together with some Trilobites and Crustacea ([illegible] p.), the Eurypterida are the only Arthropods known from Cambrian times - (see von Zittel, 1937, pp. 729-732). They appear to have originated in the Middle Cambrian and to have persisted until the Permian age - see Woods (1923, p. 283) and von Zittel (1937, pp. 776, 778, 795).

Although a few of the earlier authors placed the Euryterida with the Crustacea, for example Packard (1880, p. 503), Claus-Sedgewick (1884, p. 479) and Lang (1891, p. 415), they are now by general agreement relegated to the Arachnids in accordance with the evidence brought forward by Laurie (1893, p. 526), Kingsley (1894, p.112), Carpenter (1903, p. 348, 1906, p. 487) and others. The structure of their eyes is therefore of interest in indicating the earliest known form of the eyes in Arachnids.

The sense in which the term Eurypterida is here employed and the systematic position of the animals concerned is as follows. They are placed in the sub-class Merostomata Dana (Syn. Gigantostraca, Haekel; Delobranchiata, Lankester). (Where the Arachnida are divided into the subclasses Eurachnida and Pantapoda, the Merostomata constitute only a division). The Merostomata comprise the orders Xiphosura (the living and fossil species of Limulus) and Eurypterida (fossil forms.) The term Eurypterida is here used in the wider sense as employed by Woods (1923, p. 282). This

/includes

includes von Zittel's orders (1937, pp. 776, 778, 795) Synxiphisura, Eurypterida and Limularva.

The carapace of Eurypterida bears two sets of eyes - the large, lateral "compound" eyes and the median eyes or "ocelli". As in the case of the eyes of the Trilobites only the lenses have remained. The terms "compound" and "ocellar" are therefore used without knowledge of internal structure, but their use appears to be justified by the similarity of the preserved lenses to those of the eyes of related, extant forms with true, lateral, compound and median, ocellar eyes.

The Compound eyes.

Eyes are absent in only a few cases, for example Pseudoniscus - see von Zittel (1937, p. 777). The loss is clearly secondary and sporadic and not a primitive feature.

On the whole the eyes are relatively large and well developed, except in some gigantic forms, for example Stylonurus excelsior - see Clarke and Ruedemann (1912, p. 295) - where, as in many other gigantic forms, the development of the eye did not keep pace with the increase in size of the rest of the body. From the numerous measurements given by Clarke and Ruedemann it would seem that the eye never degenerated in size to any considerable extent, as it has done in some Crustacea, Insecta and Trilobita. Nothing comparable with the schizochroal or the "simple" lateral eyes in Trilobites has been produced in Eurypterida. Where the eye is facetted - see below -

/there

there appears to be no indication of a separation of the facets such as normally accompanies degeneration. Facets, where present, are relatively closely crowded - see Clarke and Ruedemann (1912, p. 37). There is, moreover, no evidence either in the ontogeny or comparative anatomy of the Eurypterid eyes to indicate that the eye is in the course of formation. It seems a stable structure.

Clarke and Ruedemann (1912, pp. 35-37) have pointed out that the lateral paired eyes fall in the main into two classes, differing chiefly in position and in the presence or absence of facets. The first type of eye is crescentic or reniform, appears smooth and unfacetted and is borne on a more or less elevated ocular lobe, of which it normally occupies only the outer portion. The eye is placed on the dorsal surface of the head some distance in from the margin. Such an eye occurs in *Eurypterus*, *Dolichopterus*, *Drepanopterus*, *Stylonurus* and possibly *Strabops*, which is the earliest known form. The eyes in Synxiphosura and Limularva also belong to this first type - see von Zittel (1937, pp. 776, 795). In the second type of eye described by Clarke and Ruedemann (1912, p. 37) the outline is roughly semicircular, the eye occupies the whole of a more or less elevated ocular node, is facetted and placed on the margin of the carapace. *Pterygotus*, *Slimonia* and *Hughmilleria* are examples of this type. In *Pterygotus* and *Slimonia* the eye may be partly pressed over onto the lower side. *Eusarcus* is exceptional in having smooth, reniform eyes as in the first type,

/which

which are, however, marginally placed as in the second type. *Hughmilleria shawangunk* is more or less intermediate between the two types since the eye, although facetted on the inside, is placed some little distance from the margin - (I.c. pp. 35-36).

As is shown by the examples given by Clarke and Ruedemann (1912, pp. 183, 295) the eye varies in convexity from a small, more or less flat structure to a very large, subhemispherical mass. Although the eye is elevated on a lobe there is no indication of the development of an eye stalk. The shape of the eye lobe and the relation of the eye to this varies. As pointed out above the eyes may cover the whole of the node as in *Ptyerygotus* or only its outer surface as in *Eurypterus* - a relation similar to that between the Trilobite eye and its palpebral lobe. In the former case the eye is usually elliptical or circular in shape and in the latter reniform or crescentic. The eye lobe may, however, assume other forms. Thus in *Eurypterus maria* the lobe has the form of a sector rounded outside and angular inside, the eye, at least in the adult, being restricted to a crescent shaped band on the outer side. In *Eusarcus* the eye lobes are pear shaped and the visual surface crescentic. In *Dolichopterus macrochirus* the lobe is oval, in *Dolichopterus testudineus* semicircular with a crescentic eye surface. Occasionally as in *Stylonurus* the mound overtops the visual surface to form a

/bulging

bulging ridge above it. (All of the examples given in this paragraph are drawn from the account of Clarke and Ruedemann (1912, pp. 185, 254, 275))

The authors mentioned above point out (pp.116-117) that the ocular nodes and visual areas are relatively larger in the young than in the adults as is also the case in the eyes and eye ridges in Limulus. This is correlated with a general tendency both in small animals and in some larval stages (for example the zoea larvae and megalops stages in Crustacea) to a relatively large development of the eye.

The relation of the eye to the rest of the head morphology is considerably simpler than in Trilobites, and approximates closely to the conditions obtaining in Limulus. There is nothing corresponding to the Trilobite "eyeline" in Eurypterids, nor has the eye a fixed relation to a facial suture. It has been suggested by Laurie (1893, p. 520) that the free cheeks of the Trilobites correspond to the inturned part of the carapace in Eurypterida and the facial suture of the Trilobites to the margin of the carapace in Eurypterida. If this were the case, the lateral compound eyes in Trilobites and Eurypterida would lie on different parts of the head shield. His view does not seem to have received support. Further, from a consideration of the importance of the facial suture in the head morphology - see p.363 - it would seem that a difference in the position of the eyes in two different forms in relation to such a

/suture

suture, would not preclude their homology. Since the head of Eurypterids is without dorsal traces of segmentation - see Lang (1891, p. 415) - the eye cannot be assigned a segmental position. Clarke and Ruedemann (1912, p. 32-33) have emphasised the similarity between the ridges associated with the eyes in Eurypterida and *Limulus*. Such ocular ridges, although not invariably present in Eurypterida, have been described for example in *Stylonurus* - see von Zittel (1937, 782-783) and *Dolichopterus otisius* - see Clarke and Ruedemann (1912, p..271).

Where the eye is large and convex, it may be supported along its edges by a thickened ring of the test. This is the case in *Pterygotus globicaudatus* ((Clarke and Ruedemann, 1912, p. 378). A similar support is present in *Hughmilleria shawangunk* (Clarke and Ruedemann, 1912, p. 343). Such a ridge is apparently a specialised feature, which is not found in Trilobites or in *Limulus*.

An account of the occurrence and absence of the facets and of the nature of the lenses, has been given by Clarke and Ruedemann (1912, pp. 35-42), the only available account of the Eurypterida which deals with the eyes in any detail. They point out that, in the case of the facetted eyes, it is possible to find five different states of preservation. In view of this the condition of the eye as observed in a single specimen of a species is sometimes misleading as an indication of the presence

/or absence

absence of facets in that species. These conditions are illustrated in the accompanying figure. In Pterygotus, for example, where the outer surface of the eye or a cast of this is presented, as in states 1 and 11, the eye appears smooth and unfacetted. Where the outer test has been removed and the inner surface of the eye lens system is exposed to view, a series of lenticular depressions in a squarish or hexagonal matrix are visible. A section through an eye in such a state of preservation is shown in 111. 1V shows a series of papillae corresponding to the depressions in 111, the whole representing a cast of the condition illustrated in 111. The fifth state of preservation shows a smooth visual surface through which underlying lenticular structures are faintly apparent. From a correlation of the evidence afforded by these five states of preservation it appears that Pterygotus possessed an eye with a smooth, fairly thick, outer cornea, and below this a system of lenses, which were papillary prolongations of its inner side. The third and fourth states of preservation would appear to be best explained by assuming that cornea and underlying lenses were closely attached to one another and had been removed together before fossilisation. These authors explain the fifth state as due to the filling up of the cavities, so formed, with mud before fossilisation occurred. In all the known particulars, then, the structure of the eye of Pterygotus resembles that of Limulus.

/Other

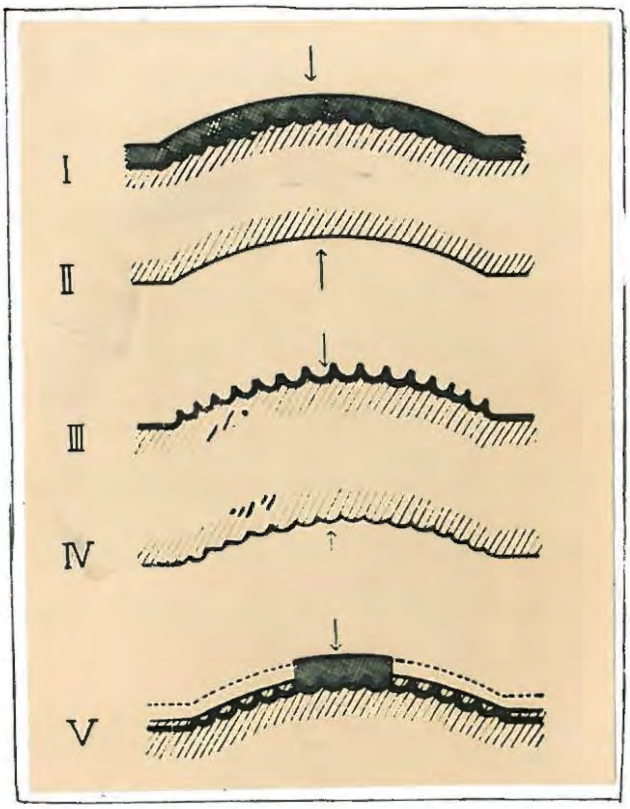


Figure 39

Compound eye of Pterygotus: diagrams of preservation states

(Taken from Clarke and Ruedemann, 1912, p.37, fig.7)

State I.	The visual surface is smooth and seen in exterior view.
State II.	The visual surface is smooth andseen as an intaglio.
State III.	Thevisual surface is seen in an exterior view and shows lenticular depressions in a network of squarish meshes.
State IV.	The visual surface is seen in a cast and provided with a system of low papillae corresponding to the depressions seen in State III.
State V.	This shows the relation between the smooth and papillate conditions. It shows a smooth Visual surface and attached lenses.

Other forms such as *Eurypterus* and *Eusarcus*, although closely related to *Pterygotus* etc. show no facets under any conditions of fossilisation. It is clear that the external surface of these eyes is smooth but Clarke and Ruedemann (1912, pp. 41-42) point out that internally lenses (such as the papillae of the cornea in *Pterygotus*) may have been present but detached from the cornea and lost in fossilisation. Since no such lenses are known either in living or fossil forms related to the Eurypterida, this is unlikely. Alternatively, facets may have been entirely absent or so very feebly developed as to leave no traces in fossilisation. The absence or very feeble development of the facets in some Crustacea - see p.101 - is a condition analogous to this, in which the cornea forms a uniform, unthickened, unfacetted outer layer over the eye. Clarke and Ruedemann (1912, p. 42) suggest that it is possible that *Eurypterus* may have possessed, in addition to this unthickened, smooth cornea, a series of intracellular lenses comparable with the crystalline cone of the compound eye of Insecta and Crustacea.

In cases in which the facets are present, no evidence of their exact size or number is available. From the drawings in von Zittel (1937) and the frequent references of Clarke and Ruedemann (1912, pp. 32-42) to the similarity of these eyes to those of *Limulus*, it is to be supposed that they approximated in these particulars

/to

to the conditions in the eyes of XiphOsura. The pattern of the arrangement of the lenses appears to be as in other compound eyes - in regular, alternating, vertical rows.

Whether the primitive position of the eyes is lateral or marginal is uncertain. Clarke and Ruedemann (1912, p. 120) consider that the ontogentic evidence is in favour of regarding the eyes as primitively lateral. In the young of those forms, which in the adult have dorsal eyes, the eyes are marginal or lie near the margin. This is also the case in the young of Limulus. The eyes of the earliest form - the Cambrian Strabops - lie in a position very near the margin corresponding to that of the larval eyes of other forms. Clarke and Ruedemann suppose that the approximation of the eyes to the margin is a palingenetic feature, which probably points to an ancestor with eyes in this position. The difficulties which are attendant upon the acceptance of evidence of this kind have already been pointed out -

It is probable moreover that the position of the eyes is to be accounted for by its adaptive significance and that the dorsal eyes in Limulus and in those Eurypterida in which they occur, are placed high on the head for the use in burrowing, in which habit marginal eyes would be useless. Clarke and Ruedemann (1912, pp. 76-9) have pointed out that, although none of the Eurypterida are very highly specialised for one particular mode of life to the exclusion of all others, it is

/generally

generally true, that those with eyes on or near the margin were crawlers or swimmers, while those with eyes dorsally placed were burrowers, with the head and eyes as in Limulus.

The details of the Arthropodan affinities of the Eurypterida and the relationships of their eyes to those of the remaining Arthropods have been matters of much dispute. It is obvious from the phylogenetic table of the genera of Eurypterida given by Clarke and Ruedemann (1912, opp. p.124) that they fall into two groups - the Eurypteridae and the Ptyerygotidae, in which differences in the position of the eyes and in the presence or absence of facets [illegible] are correlated with other features. These differences may be due to the derivation of the two groups from separate ancestors or to a divergence which has set in after the definition of the main Eurypterid stock.

Except among those who, like Bernard (1894), are inclined to seek a polyphyletic origin of the Arthropods - an origin which now seems unlikely - the Eurypterida are derived from the Trilobites or the Crustacea or the immediate ancestors of these. Among these possible ancestral forms Trilobites and most of the Crustacea and presumably their immediate ancestors are provided with facetted compound eyes, while among the lower Crustacea there are some which appear to have undergone a secondary loss of facets.

Many authors including Laurie (1893, p. 527),

/Carpenter

Carpenter (1903, p. 348, 1906, p. 480), Ruedemann (1916, p. 234) and Henderson (1932, p. 123) have considered that the Eurypterida sprang from the Trilobite stock. Others, however, such as Spencer (1903, pp. 491, 492), Walcott (1916, p. 732) and von Zittel (1937, p. 772) emphasise that this relationship is a distant pre-cambrian one.

Such a descent from the Trilobites (or from the Crustacea with facetted eyes, or the immediate ancestors of either of these) would account for the presence in Eurypterida of a compound eye. It would not, however, account for the fact that the facetted eyes in Eurypterida differ markedly in structure from those of all possible ancestors. None of these have the rather widely spaced, peglike prolongations characteristic of the cornea of Eurypterida and *Limulus*, although the prismatic eyes of Trilobites are an approach to this form. There is no reason to regard the condition in such eyes as more primitive than, or antecedent to, that in Trilobites or Crustacea, nor to suppose that it represents an aggregation of lateral ocelli unknown in these two groups. Unless the eye is to be regarded as a new and separate development unrelated to that of other Arthropods, it must be derived from a facetted, ancestral type, in which the lenses have enlarged and deepened - an enlargement which in *Limulus* (and probably also in those Eurypterida with well developed lenses) is at the expense of the sense cells.

The relationships of the unfacetted eyes in Eurypterida also present some difficulty. There is no reason to suppose that such an eye, with its unthickened cornea, could have been a single enormous ocellus, or to consider that it represents a precursor of the facetted eyes of related forms. It is possible, as Walcott (1916, p. 732) has pointed out, that such forms are to be derived from a *Protocaris*-like Branchiopod (with unfacetted eyes), invading the land rivers in Pre-cambrian times. Such an origin is supported in some measure by the similarity of Limularva to Crustacea, as pointed out by von Zittel (1937, p.786). The derivation of the facetted-eyed Eurypterida from such a stock (and the consequent necessity of supposing a separate origin of the Eurypterid facetted eye and its evolution parallel to that of Crustacea) has received no support.

If the Eurypterida with unfacetted eyes were not derived from Crustacea with similar eyes, their eyes must be regarded as degenerate derivatives of facetted eyes, in which the individual lenses were lost although the size of the eye as a whole did not decrease.

Whatever the exact relationships of the Eurypterida to their ancestors, it is clear from the similarity in the structure of eyes of *Pterygotus* and its allies and those of *Limulus*, that these are of common origin. Although many authors, including Laurie (1893, p.520), Carpenter (1903, p.348), Clarke and Ruedemann (1912, p.148), Henderson (1932, p.123) and von Zittel (1937, p.772), have considered

/that

that Limulus is not to be directly derived from the Eurypterida, most have admitted that these had a common ancestor either in the Trilobites or Prototrilobites or at the base of the Eurypterid stem. In view of the structure of the eyes the last suggestion seems likely.

Neither the facetted nor the unfacetted eyes in Eurypterida appear to bear any relation to the simple, lateral eyes in Scorpions and other Arachnida. It is possible that such eyes may have been formed by the separation and enlargement of a few of the units of a Eurypterid eye. In the absence of any internal structure in Eurypterida, such suggestions must remain speculative.

Summary.

As the Eurypterida (including Synxiphosura and Limulava) are the earliest known Arachnida, their eyes are of some interest. Paired, lateral, compound eyes are typically present with their absence or reduction secondary. The relation to the head morphology is much simpler than in Trilobita. There is no eyeline and the eye has no fixed relation to facial or marginal sutures. Such ridges as are present appear to correspond to the ocular ridges in Limulus. (A thickened rim surrounding and supporting the eye-cornea is a specialised feature of some forms). There is no indication of the segmental position of the eye and no reason to suppose that it is otherwise than homologous with the lateral compound eyes of other Arthropods. The eyes may be marginal and facetted, in which case they occupy the entire surface of the eye lobe as in Pterygotidae. Alternatively as in Eurypteridae, they may be dorso-lateral, unfacetted and borne on the outer surface of an ocular lobe of the same type as the palpebral lobe in Trilobita. There are exceptional types and some cases intermediate between these two.

/The

The five states of preservation to be observed in the Pterygotid eyes indicate that these resemble Limulus in possessing a smooth, thick cornea with separate, dependant, papillary prolongations, which, when seen from above, through the cornea, lend the appearance of faint facets to the eye surface. In size and number the lenses correspond to those of Limulus and in arrangement they appear to correspond to the regular, alternating rows in the compound eyes of other Arthropods. The eye lobe may be sector-shaped, pear-shaped, oval or semicircular, and the eye may occupy the whole of this or only a crescentic or reniform area of its outer surface, with the mound or lobe occasionally overtopping the surface of the eye. Although there is some variation in the convexity of eye and lobe, the eye is never so exaggeratedly elevated as to be placed on a stalk as in some Trilobites, Crustacea and Insects. Ontogeny points to the possibility that the eyes in all forms were ancestrally marginal and it seems likely that the position is adaptive, dorsal eyes being related to a burrowing habit. In most cases the eyes are well developed and are relatively small only in gigantic forms. The relatively great size observed in the young is common in other small Arthropods. The eye does not tend to degenerate into ocelli or separate ommatidia. There is no evidence in the Eurypterida as to the possible mode of formation of the compound eyes of these or other Arthropods. Unless the Arthropods are treated as polyphylectic, the Eurypterida must be derived from the

/Trilobites

Trilobites or Crustacea or their immediate ancestors. On the whole it seems probable that facetted eyes were primitively present in Eurypterida, and derived from those of Trilobites, Crustacea or their immediate stock. In the course of evolution the lenses increased in size, probably at the expense of the sense cells and an eye resembling that of *Limulus* evolved diverging from the Crustacean type. The rest of the Eurypterida may have been separately derived from an ancestral Crustacean stock with unfacetted eyes, or the eye may have arisen by degeneration of the individual lenses of an ancestral facetted eye. Facetted Eurypterid eyes are clearly related to those of *Limulus*, ~~but~~. The possible origin of the Scorpion eye from these forms is purely speculative.

Part II.

Conclusions - Eurypterida .

1. Occurrence , type and basic pattern.

Lateral compound eyes are typically and primitively present, with their absence rare, sporadic and secondary. The eyes of Pterygotidae, with lenses resembling those of Limulus, are generally assumed to have been internally of the same type as the latter . The eyes of the rest , resembling the unfacetted eyes of some of the lower Crustacea, are assumed to have been of the true, compound , ommatidial type.

Lateral ocelli are absent . There is no tendency to the reduction in the size of the eye and the number of its lenses , (when these are marked out) . There is nothing comparable with the schizochroal or "simple " eyes of Trilobites.

2. Comparative anatomy

As in Trilobites the internal structure has not been preserved , so that little is known of the comparative anatomy of these eyes . The lenses in Pterygotidae resemble those of Limulus in size, number , form and arrangement . They have the same smooth, outer cornea, with separate, dependent, peg-like lenses , imparting a facetted appearance . (The prismatic eyes of Trilobites approach this condition). The smooth , unfacetted cornea over the entire eye in the rest of the Eurypterida resembles that in some lower Crustacea.

3. Stability and evolution of the eye .

The relative stability of the lenticular structures in each of the two eye types indicated above , and the fact that the eye is well developed in the earliest known forms , together with the absence of any evidence for the evolution of these forms within the Eurypterida, indicate that both eye types were well defined in the ancestors.

4. Variation of the eye in relation to phylogeny .

The occurrence of such variation as is known within the eye structure is related to the general phylogeny . Thus the Pterygotidae with their marginal facetted eyes, roughly semicircular and covering the summit of the ocular lobe , differ in these and many other respects from the Eurypteridae, Synxiphosura and Limularva with their dorso-lateral , unfacetted eyes ,crescentic or reniform in outline and covering only the outer surface of the ocular lobe .

5. Degeneration of the eye .

Within the Eurypterida degeneration of the eye into separate units is unknown. If the ocelli of the Arachnida were derived from the separated units of an ancestral eye of the compound type , there is no trace of this within the Eurypterida .

6. Possibility of the origin of the compound eye from ocelli.

6. Possibility of the origin of the compound eye from ocelli.

There is no indication in ontogeny or anatomy that the lateral, compound eyes were formed from a single ocellus or from a group of ocelli.

7. General relationships .

It seems that a tendency to the formation of a lateral, aggregate eye was inherited from the ancestors of the Eurypterida . The lenses in the Pterygotid branch diverged in form from those in the rest of the Eurypterida, increasing in size (presumably , as in *Limulus* , at the expense of the sense cells) and assuming the *Limulus* form . The remaining Eurypterida (without separate corneal lenses) may have been derived from a Crustacean stock with unfacetted eyes ,or their lens structure may have arisen from that of the Pterygotidae by degeneration .

Chapter 4.

ARACHNIDA.

Introduction to the lateral eyes of Arachnida

The Arachnida as a whole are characterised by the possession of lateral ocelli . The occurrence of "compound " or more strictly "pseudocompound " eyes in Xiphosura , resembling the eyes of some of the Eurypterida , is therefore of considerable interest.

The first part of the chapter comprises a description of the eyes of *Limulus polyphemus Latr*. There follows in the second part some discussion of the relationships between these and other Arthropod eyes . The third part consists of the conclusions drawn from these observations as to the comparative anatomy , origin and relationships of the eyes of *Limulus* .

Part I.

The anatomy of the lateral "compound" eyes of Limulus polyphemus Latr.

Grenacher (1879) appears to have been the first to describe the anatomy of the eyes of Limulus. This description is not available but is stated by Lankester and Bourne (1883, p. 201) to be in accordance with their observations. The eyes of Limulus polyphemus Latr. have been described by Packard (1880, pp. 212, 435, 947). He deals especially with the structure of the cornea and the nature of the nerve supply. Lankester and Bourne (1883, pp. 201-205, pls.X, X1,X11) gave a description of the eye of this species, to which Watase's description (1890, pp.300-312) of Limulus sp. has added little detail. (Watase's description is that usually given in summary in the text-books - for example in Sedgewick (1927, p.334, Fig.234). Some developmental details have been worked out by Kishinouye (1891, p. 264-266) and others are given by Korscheldt and Heider (1899, pp. 349-350) but these add nothing new to the previous descriptions with regard to the anatomy.

The material available for sectioning was of Limulus polyphemus Latr - (for synonomy see Pocock, 1903,

/p.260

p.260). This had been preserved for several years in formalin. Although details of the cytoplasmic and nuclear structure were lost, the main form of the cells and especially of the cuticular parts and the pigment granules was clear enough.

External features.

The lateral, paired eyes are usually described as "compound" on account of the similarity between their external features and those of the compound eyes of Insects and Crustacea. In their internal structure they differ very widely from the latter. The term "compound" is used to distinguish these as complex aggregations, whose units are not necessarily homologous with those of the true compound eyes of Insects and Crustacea.

The lateral eyes are dark, conspicuous, convex, reniform structures, placed dorso-laterally on the cephalothoracic shield. They lie immediately below the ridge which divides a flattened, dorsal part from the lateral flange, which is bent down at an angle of about 45° to the main part of the shield. The eyes lie on this lateral portion about two-thirds of the way down the length of the shield.

The eye has an average length of about five millimetres. Although the eye is a prominent feature, its size, relative to that of the head shield, is smaller than in the cases of the best developed eyes of Scorpions and Spiders.

Immediately above the eye the ridge, against which it lies, is produced into a short, blunt spine which over-

/hangs

hangs the eye and presumably affords it some measure of protection. The longitudinal axis of the eye is parallel to that of the body with the convex side of the reniform out-line external.

The cuticle

The cornea consists of a flat, transparent cuticle, evenly laminated throughout and faint chitinbrown in colour, produced on the inner side into a series of separate, elongated lenses, conical in longitudinal section and in transverse section rounded or roughly polygonal (where they are in contact with one another at their extreme upper ends). Each of these lens cones fills the cavity of a cup of sense cells. The outer layer of the cornea is smooth and unfacetted but the lenses can be seen shining through this transparent layer to impart the semblance of facets having the same appearance as the transverse section of the cones at the level of focussing. As Packard (1880, pp. 312, 435, 947) points out, the outer part of the cornea is thinner and more translucent than the cuticle covering the body but otherwise corresponds to it. Hairs and pore canals are absent. The lenses attain a maximum depth of about 25μ and the smooth outer part of the cornea a depth of about 6μ. A transverse section of the cones at their upper ends shows a diametre of about 12μ.

In the structure of the corneal lenses, the eyes resemble those of Eurypterida very closely. They bear a more remote resemblance to the prismatic eyes of Trilobites, in which the lenses are more shallow and more closely

/crowded

crowded together. Their resemblance to the exocone eyes of Insects is clearly convergent and secondary. Otherwise the form of the lens and its great size in relation to the retinal cells (see Figure 41B) is a feature without parallel in the compound eyes of extant Arthropods.

The retinal cells.

Each lens is surrounded by a retinula or group of pigmented retinal sense cells or nerve end cells. These attain a maximum depth of about 50μ and the retinula a maximum diametre of about 100μ

The retinula as a whole is concave anteriorly to fit the lens convexity and convex posteriorly where the nerve enters. As Watase (1890, p. 301) points out, the form and arrangement of the cells resembles that seen in a vertebrate taste bud. At their upper ends the retinal cells embrace the lower part of the cone but are separated from this, at least in sections, by a small space. At their lower ends the cells decrease greatly in diametre to become continuous with the nerve fibres of the optic nerve. Packard (1880, pp. 212, 435, 947) has pointed out that the nerve fibres from each retinula pass back as a single strand into the brain. The intracellular boundaries are fairly complete as seen in Figures 41A, 42 and 43 . In transverse section the retinula has a lobed outline with each lobe corresponding to a single cell. Adjacent retinulae are separated by a small space from one another.

As shown in Figures 42 and 43 the cells vary in

/number

number from seven to fifteen. No relation between the position of the retinula in the eye as a whole and the number of its cells was apparent. Different retinulae, cut at the same level, show different numbers of cells. Grenacher (1879) and Lankester and Bourne (1883, pp. 201-202) have recorded numbers varying from ten to fifteen; Watase (1890, p.303) found some units with eleven, some with nine, and one with as many as fifteen. Lankester and Bourne have suggested that the cells may possibly be arranged in a superior and inferior series interlocking with one another. They did not demonstrate or figure such an arrangement. Watase distinctly showed that only one layer of cells was present. In this case the number of cells in any one retinula was apparently constant throughout its length and no interlocking of the cells could be seen.

The retinal cells contain a considerable amount of pigment, deposited in the cytoplasm in the form of coarse granules. This pigment was especially deposited in a thick layer about the rhabdom and a thin layer about the outer edges of the cells and along their intercellular boundaries. The clear region round the rhabdom described by Watase (1890, p. 303) was not present in this case and has not been described elsewhere. The cytoplasmic structure was poorly preserved and nerve fibrillae could not be traced into the cells. No mention is made of their course in other descriptions.

The nuclei are small, round structures scattered at different levels in different cells. They have a firm

/boundary

boundary with densely granular, deeply staining contents. No nucleolus was apparent. The structure of the nucleus has not elsewhere been described in detail.

The rhabdom.

The rhabdomeres are borne along the inner, longitudinal axial borders of the retinal cells. Each cell bears along its entire length a V-shaped border or rhabdomere, which is a transparent, refractive, homogeneous structure of chitinous material. The contiguous arms of adjacent rhabdomeres have run together so that a star-shaped rhabdom, with an arm projecting between each successive pair of retinal cells, is formed. A fusion of adjacent rhabdomeres, more complete than that normally found, and presumably occasioned by an overcrowding of the retinal cells in the fifteen-celled condition, is occasionally found as illustrated in Figure 42B

Although the rhabdomeres form a single structure, the original components are apparent and the central, axial cavity remains throughout the length of the rhabdom. Lankester and Bourne (1883, p. 204) found the rhabdomeres united only at the anterior end, with a tendency to separate posteriorly. Such a tendency was not observed in this case and has not been described elsewhere.

The ganglion cells.

Watase (1890, p. 303) described one, or sometimes two, ganglion cells, placed at the base of each retinula. He regarded these as bipolar nerve cells, lying in the centre

/of

of the group of retinal cells, and connected by a fibre at one end to the rhabdom and the other end to the brain. These resemble the retinal cells except in the absence of a rhabdomere and the smaller amount of pigment. Such cells were not described by Grenacher (1879) and Lankester and Bourne (1883, p. 201) and could not be made out in the present case. Since no bipolar nerve cells are known to occur in the retinular groupings of other Arthropod compound eyes, it is suggested that this "ganglion" cell is possibly a retinal cell which has lost its rhabdomere (like the retinal cells at the base of the eye in Scolopendromorpha - see appendix) and in consequence of this has been deprived of most of its pigment. It remains in contact with the rhabdom by a thin prolongation of its upper end, although the cell no longer takes part in its formation. Whatever its nature it is clearly one of the many unusual features of the "compound" eye in Limulus.

The pigmented cells (other than the retinal cells).

Pigmented cells occupy the sides of the lenses above the retinal cells and the valleys between the cones. The cells between the cones resemble those of the ordinary hypoderm while those immediately round the retinal cells are somewhat more elongated. Smaller pigmented cells, regarded by Lankester and Bourne (1883, p. 204) as intrusive connective tissue cells, are found at the base of the retinal cells and between the bases of neighbouring eye units. These pass through the basement membrane to clothe

/the

the sides of the nerve fibres. The pigment in all of these is dark brown or practically black and is presumably of the melanin type.

As Watase (1890, p. 305) has pointed out, the pigmented hypoderm cells between the cones secrete the overlying cornea, while those along the sides of the lenses are responsible for the production of the latter.

Basement membrane and nerve fibres.

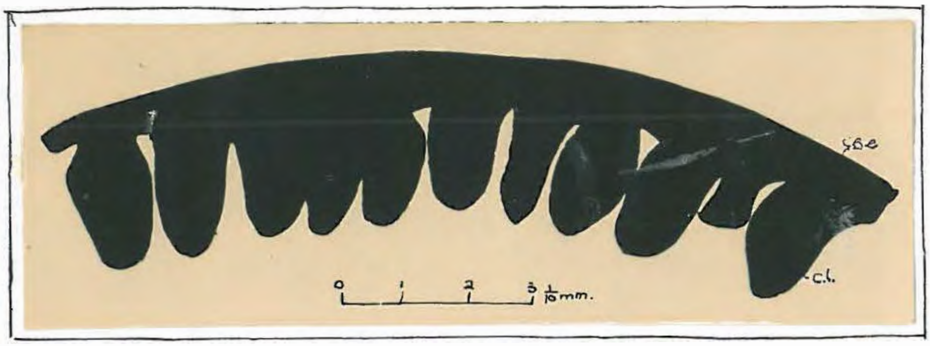
At the base of the eye units is a basement membrane produced by the hypodermal cells, from which the optic cup originates. Through apertures in this the nerve fibres and some of the pigment cells pass into the eye.

Figure 40

o.s.e.	Smooth, unfacetted outer surface of the eye.
c.l.	Inner, conical , dependent, corneal lenses, which shine through the outer layer to lend it a facetted appearance.

Figure 40

Longitudinal section through a potion of the cornea of the eye of Limulus polyphemus.



Microscopy.

8mm Apochromatic eyepiece
X 20 Holoscopic eyepiece
Camera lucida drawing.
4 μ section.

Preparation

Fixation : Neutral Formalin (several years)
Embedding : Double embedding in Ether-Alcohol (75:25) solution of celloidin, through $CHCl_3$ in 60 degrees melting point wax.
Staining : Heidenhain's Iron Alum Haemotoxylon.
Mounting : Through Toluol in toluol-clarite.

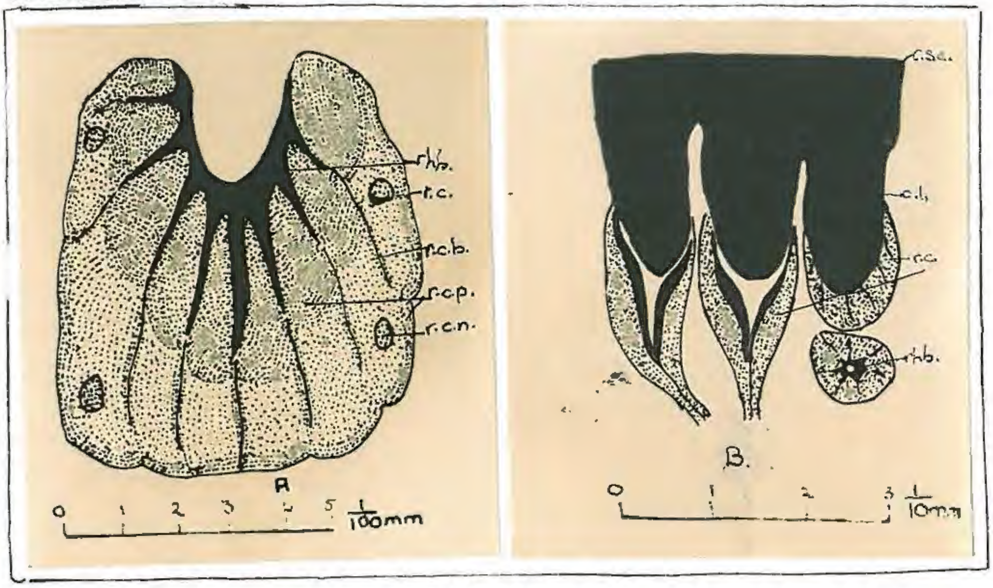
Figure 4I

c.s.e.	Outer smooth surface of the cornea.
c.l.	Elongated inner dependent lenses.
r.c.	Retinal cells- relatively small.
r.c.b.	Retinal cell boundaries.
r.c.p.	Retinal cell pigment granules
r.c.n.	Retinal cell nucleus.
rhb.	Rhabdom structure.

Figure 41

A. Longitudinal oblique section through a single retinula of Limulus polyphemus showing the arrangement of the retinal cells and their pigment and rhabdom structures .

B. Two longitudinal sections through the eyes units and a longitudinal oblique section showing the great size of the corneal lenses in relation to the sense cells.



Microscopy

16 mm Apochromatic objective.
X 8 Holoscopic eyepiece.
Camera lucida drawing.
4 µ section.

Preparation

Fixation : Formalin (several years)
Embedding : Double embedding in Ether-Alcohol solution of celloidin through $CHCl_3$ in 60 degrees melting point wax.

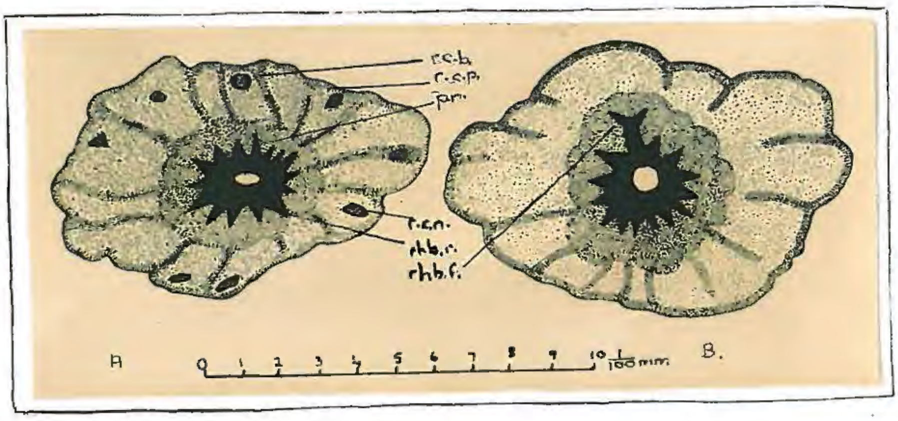
Staining : Partly depigmented in Howland's fluid. Heidenhain's Iron Alum Haemotoxylon. Alcoholic light green.
Mounting : Through Toluol in Toluol-Clarite.

Figure 43

r.c.b.	Retinal cell boundary.
r.c.p.	Large , coarse, numerous retinal cell pigment granules.
p.r.	Pigment granules concentrated especially about the rhabdom
r.c.n.	Retinal cell nucleus.
rhb.r.	Rays of the central , axial rhabdom structure , one projecting between each successive pair of retinal cells.
rhb.f.	Two rhabdom parts partly fused together, in accordance with the crowding of the cells in retinulae with large numbers of retinal cells.

Figure 42

Two transverse sections through the retinula of Limulus polyphemus, showing a fifteen celled condition of the usual type and a fifteen celled condition in which two of the rhabdomere parts have undergone partial fusion presumably in accordance with their crowded arrangement.



Microscopy

8 mm Apochromatic eyepiece
X 8 Holoscopic eyepiece.
Camera lucida drawing.
3 μ section.

Preparation

As for the sections in figure 41.

Figure 43.

r.c.b.	Retinal cell boundaries.
r.c.pg	Retinal cell pigment granules.
rhb cav	Central axial cavity within the rhabdom structure.
rhb .r.	Separate rhabdom ray formed by two cells and lying between these.

In sections A-G the retinal cells and rhabdom rays show a variation from seven to fourteen in number.

Figure 43

Transverse sections through different units in a single eye of Limulus polyphemus showing the variation in the number of retinal cells and their relation to the the rhabdom structures. (The lower row of figures shows the rhabdom structures only).

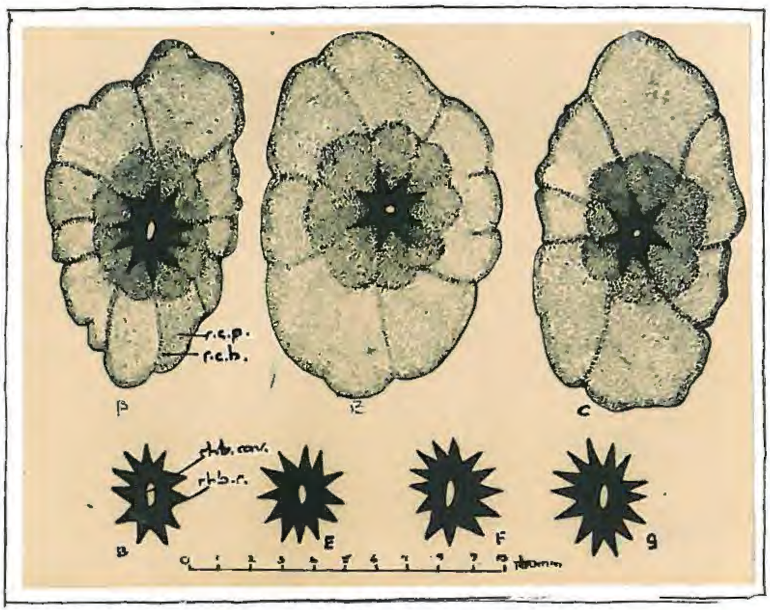
[illegible]

Microscopy

As for the section in Figure 42.

Preparation

As for the section in figure 42.



Part II

The relationships of the eyes of Xiphosura to those of other Arthropods.

The lateral "compound" or "pseudo-compound" eyes of Xiphosura are clearly of a type very different from that found in any other Arthropods, except possibly in some Eurypterida (where the internal structure of the eyes is unknown).

The most notable differences between these and the compound eyes of Insects and Crustacea are the following:-

The peculiar, elongated, conical lenses, large, separated and depending from a smooth cornea; the large and variable number of somewhat irregular hypoderm cells, disposed about the sides of the lens; the absence of a crystalline cone (correlated, as in the Exocone eyes of Insects, with the large development of the corneal lens); the large and variable number of retinal cells; the presence of the peculiar ganglion cells and the simple form and scattered arrangement of the pigment cells. In most of these particulars the eye units approach ocellar conditions. The arrangement of the retinal cells in a single group under each lens, together with the organisation of their rhabdom structures into a central axial rhabdom, are, however, ommatidial features (see pp. 20-23). The eye is therefore of a pseudo-

/compound

compound" type, with the units intermediate in many respects between ommatidia and ocelli.

The ancestry of these eyes cannot be clearly traced further back than the Eurypterida, in which similar eyes were well developed and, at least in their lenticular structure, stable.

It is possible that these eyes and what were presumably the true compound eyes of the earliest Trilobites and Crustacea and their immediate ancestors, were derived from a common ancestral form and subsequently diverged. On the other hand it is possible that these eyes were separate in origin from the true compound eyes. In the latter case they may have been formed anew as a whole, or derived from a single ocellus, or a group of ocelli. Lastly they may be more primitive than any other known Arthropod compound eye. These possibilities are now considered in turn.

If these were derived from the same ancestor as the true compound eyes of Trilobites and Crustacea, it is clear that the two types have diverged very widely from one another. Any intermediate stages in the series of changes, which might once have existed, are of course lost in the fossil record. In the absence of such evidence the case for the common origin of these two eye types is speculative. It remains possible however that from some distant, common ancestor a tendency to the formation of compound eyes was inherited by Trilobites, Crustacea, Eurypterida and Xiphosura and that this has received a modified form of expression in the eyes of Xiphosura, where the lenses have increased in size at the expense of the relative size and the degree of organisation of the rest of the eye, which has in part degenerated, so that the units have approached an ocellar condition.

Alternatively these eyes may be separately derived from those of other Arthropods. That they were formed as a new and entire structure seems unlikely. Although the origin of the compound eyes of the Trilobites and Crustacea from a single ocellus or a group of ocelli cannot be demonstrated, it has been suggested that one of these might be the mode of formation of the <u>Limulus</u> eye. Patten supposed (1886, p.679) that the eye was derived from an aggregation of ocelli, in which the retinal cells were reduced in number, while they increased in size and complexity, and assumed an ommatidial arrangement under each lens. (In contrast to this he derived the compound eye of Crustacea and Insects from a single ocellus, in which the retinal cells increase in number, decrease in size and complexity, and become arranged in retinular groups). Watase, who described (1890, p. 310) the origin of the eye from a series of separate depressions, considered this as

/evidence

evidence of its derivation from a group of ocelli, (the compound eyes of Crustacea and Insects being differentiated within a single mass of hypoderm cells)

Lankester and Bourne (1883, p. 204), on the other hand, have supposed that the Limulus eye represents a stage in the modification of a single ocellus to form a compound eye.

None of these authors however give any reason for supposing that either a single, lateral ocellus, or a group of ocelli actually preceeded the compound eyes in the phylogeny of Xiphosura.

Lastly it is possible that these represent the persistence of a form more primitive than that found in the lateral compound eyes of any other known Arthropod. In view of the absence of any evidence of the internal structure of the related fossil forms this cannot be decided.

As far as their relationships with the eyes of the remaining Arachnids are concerned, attempts have been made to derive the typical Arachnid lateral ocelli from the eyes of the Xiphosura and their ancestors. Lang (1891, p. 420) supposed these ocelli to be derived each from a single eye unit. Lankester and Bourne (1883, p. 204) regarded the eyes of Xiphosura and the other Arachnida as diverging from a common ancestral type and considered one scorpion ocellus as corresponding to several eye units in Limulus. The differences

/between

between these forms are however very wide and there is no indication of intermediate types so that the postulation of such an origin must remain speculative. It is possible that the eyes of the remaining Arachnida are of a separate origin from those of Xiphosura. The latter eyes are not very highly developed and may well have been restricted to the Xiphosura while the terrestrial Arachnida evolved a new eye type.
(see appendix)

The lateral "compound" eyes of Xiphosura are thus without clear relationship to those of other Arthropods. They represent a form so unique and isolated that a case could be made out for any of the views of their affinities stated above. It cannot be definitely claimed that they arise from or degenerate into one or more ocelli, but these remain possibilities. Their chief interest is perhaps in indicating that a tendency to the formation of a compound eye was present at the base of the Arachnid stem, although all trace of it has been lost in more recently evolved forms.
Otherwise their anatomy is of isolated interest and the course of their evolution so doubtful as to shed little or no light on that of the compound eyes in other Arthropod classes.

Part III.

Conclusions - Arachnida.

I. Occurrence and type.

The "pseudocompound " eyes are restricted to the Xiphosura, the remaining Arachnida being provided with a variable number of ocelli. Eyes are primitively and typically present and their absence or reduction is secondary.

2. Comparative anatomy and basic pattern of the"pseudocompound " eyes.

It is clear that these eyes , whatever their ancestry, are not constructed on the same plan as the lateral compound eyes of other Arthropods. except possibly those of some Eurypterida. , of which the internal structure has not been preserved. Their units are intermediate between ocelli and ommatidia.

3. Stability and evolution of the "pseudocompound " eye .

The "pseudocompound " eye was presumably inherited from a similar type in the Eurypterida but beyond this its ancestry cannot be traced with any reasonable certainty. The instability in the internal structure , which varies from one unit to the next in the same eye , may be degenerate . It is suggested that the increase in the size of the lenses has been at the expense of the degree of organisation of the internal structure and that this has accordingly become somewhat irregular.

/ 4.Condition

4. Condition of the eye in relation to phylogeny.

The presence of such an unusual eye in Xiphosura is not out of keeping with their general phylogenetic relationships with the remaining Arthropods. They are clearly a very primitive group in some ways specialised, particularly in their nervous system . It would seem that the tendency to the formation of a lateral, aggregate eye is a primitive feature of the base of the Arachnid and Eurypterid stem, which has here achieved a modified expression differing from that in all other Arthropods .

5. Degeneration of the eye .

The eyes of Xiphosura are not known to give rise to ocelli. It is possible that the remaining, Arachnid, lateral ocelli have arisen in this way but there is no real evidence of this having occurred.

6. Possibility of the formation of the "pseudocompound" eye from ocelli .

The eyes of Xiphosura may have arisen from an aggregation of lateral ocelli, as Watase supposes, but if so there is no evidence that such ocelli existed in any of the possible ancestors.

7. General relationships .

In view of their unique structure and isolated occurrence (the fossil forms which might possibly have bridged the gap separating these from other Arthropod eyes having none of

/the

internal structure preserved) the relationships of these eyes is very obscure . It seems probable that they are the representative of a primitive tendency to the formation of a lateral , aggregate eye . In Xiphosura this tendency has been expressed in a modified way, differing from that of any other Arthropods, and lost in all other Arachnida.

Chapter 5.

DIPLOPODA with a note on PAUROPODA and SYMPHYLA.

Introduction to the conditions of the lateral visual organs in Diplopods with a note on the condition in Pauropoda and Symphyla

The condition of the visual orgnas in Pauropòda , Symphyla and Diplopoda is of interest for comparison with that of Chilopoda . Eyes of any kind are absent in Pauropoda and are either absent or represented by a single pair of ocelli in Symphyla (see Sedgewick, I927, p. 605) . Lateral eyes are , however , primitively present in Diplopoda . In living forms these are ocelli very similar in structure to the ocelli of Chilopoda. In fossil forms there is some suggestion that compound eyes were present . In the first part of this chapter the condition of the lateral eyes of fossil Diplopods is mentioned and in the second part conclusions drawn from this are tabulated ,as in the other chapters, with regard to the comparative anatomy , origin and relationships of these eyes.

Part I.

The lateral eyes of fossil Diplopoda.

In living Diplopods the lateral eyes are ocellar and never compound in type. A large number of ocelli may be present so that the eye assumes a convexity of form and the lenses a degree of crowding approaching that of the true compound eyes of Insects and Crustacea and the peculiar eyes of the Scutigeridae. Thus in *Julus* and *Glomeris* species, which were examined, although the eyes appeared externally at first sight to resemble small compound eyes, several differences between these and true compound eyes were apparent when these were examined with a lens. There are relatively few lenses, not more than forty, each abnormally large when compared with average ommatidial lenses. These are rather loosely grouped and each retains its round and convex form and is clearly separated from its neighbours. Although the central lenses tend, to some extent, to be flattened against one another, they never assume the regular pattern of alternating, vertical rows of hexagons, seen in most true compound eyes, and to some extent in the eyes of Scutigeridae. Internally it is quite clear in all the eyes, which have been examined, that there is no approach to a compound condition. The eyes are composed of a number of ocelli resembling those

/of

of *Julus*.

It has sometimes been stated as for example by Snodgrass (1935, p. 542) that the fossil Diplopods were in some cases provided with compound eyes. This is clearly an attempt to bring the Diplopods into line with the other Arthropods and to provide in particular an analogous case in Diplopods to that of *Scutigera* in Chilopods. Verhoeff (1925, pp. 332,357) in his work on the Diplopods points out that there is no legitimate ground for considering the large eyes of some of the fossil Diplopods as compound eyes. The largest of these occur in *Glomeropsis ovalis*, where six hundred lenses are present. Each lens, however, remains round and clearly separated from its neighbours, an arrangement similar to that in living Diplopods. He stressed the fact that, as nothing approaching the compound condition has yet been found in living Diplopods, it cannot at present be assumed that the fossil eyes are other than very large groups of ocelli.

Part II.
Conclusions - Diplopods

I. Occurence and type

In living and fossil forms lateral eyes are typically and primitively present and their absence or reduction is secondary and sporadic. The known eyes of all living Diplopods comprise ocelli or groups of ocelli, aggregated to form "ocellar compound" eyes. It has been suggested that the fossil forms possessed true compound eyes. In the absence of internal evidence and in view of the lack of any precedent to the contrary, it must be assumed that the fossil eyes were also of the type of ocellar aggregations.

2. Comparative anatomy, basic plan, evolution and variation in relation to phylogeny.

Of the comparative anatomy of these supposed compound eyes in the fossils little is known, Their lenses do not differ from those of the "ocellar compound" eyes of modern Diplopods. The eyes were presumably constructed on the same plan and appear to have been a stable structure showing no evolution within the class, or any variation in relation to phylogeny of the orders.

3. Degeneration of the eye

If the ocelli are the products of degeneration of an ancestral true compound eye, there remains in the Diplopods no clear trace of the eye from which they

/arose

arose.

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

There is no clear evidence that the lateral aggregations of ocelli at any time evolved into a true compound eye.

5. General Relationships.

The origin of the supposed compound eyes in fossils and the lateral groups of ocelli in living forms may be due to the operation of a tendency to formation of a lateral aggregate eye analogous to that, which operating in a different way, produced the compound eyes of other Arthropods. There is no internal morphological similarity between these ocellar aggregations and the compound eyes of Insects and Crustacea or the eyes of Xiphosura.

Chapter 6.

CHILOPODA .

Introduction to the lateral "compound"eyes of Chilopoda.

Among the Chilopoda "compound " (or , more strictly , "pseudocompound " eyes) are restricted to the Scutigeromorpha , the remaining forms being blind or provided with lateral ocelli. The isolated occurrence and peculiar form of the eyes of Scutigeromorpha , makes them of considerable interest.

The first part of this chapter comprises a descriptions with figures of the eyes of Scutigerina weberi . The second is a discussion of the relationships existing between these and the lateral compound eyes of other Arthropods . The third part comprises the conclusions drawn from the first and second parts as to the comparative anatomy , origin and relationships of the eyes of Scutigeromorpha.

Part I.

(Original description.)

The structure of the lateral "compound" eyes in *Scutigerina weberi* Silvestri. 1903.

The so-called lateral "compound" eyes of Chilopods are confined to the Scutigeromorpha (Scutigeridae of some classifications). Grenacher's original description (1879) could not be seen. Ademsamer's description (1893, pp . 573-578) of the eye in *Scutigera coleoptrata* apparently agreed with that of Grenacher except in the presence of corneal hypoderm cells , cone cells and cone cell nuclei which Grenacher had not found. Rosenstadt (1896,pp.369-375) mentioned having investigated the eyes of *Julus*,*Glomeris* , *Lithobius*, *Scolopendra* and *Scutigera*. His observations are confined to a few theoretical speculations and the figures which he gives are clearly taken from Ademsamer and Grenacher. Hemenway (1900, pp. 205-213) described the eye in *Scutigera forceps*. His paper is not available . Verhoeff (1925, pp. 41 42) mentions it in his bibliography but quotes Ademsamer's description almost verbatim and does not mention any differences between this and that of Hemenway. Hanstrom's description of the eye in *Thereuonema* and *Thereuopoda* (1934, pp. 1-14) is not available. The only available abstract gives a brief list of the number of each type of cell in the eye unit . The only other description of the eye of a member of the Scutigeromorpha (or Scutigeridae)

/ appears

appears to be that of Packard (1880, pp.683-684) dealing with the eye of *Cermatia forceps* (= *Scutigera forceps*). He describes the eye as an aggregate of ocelli and finds no cones, only a single rhabdom to each lens (a condition most unusual in an ocellus), and a vitreous corneagen layer. The description is summary and inaccurate. Thus of the literature on the eyes of Scutigeridae the only useful and available, original description is Ademsamer's work on the eyes of *Scutigera coleoptrata*.

The work was here confined to the two South African species (*Scutigera coleoptrata* and *Scutigerina weberi*.) In the case of *Scutigera coleoptrata* observations merely confirmed Ademsamer's description. A description of the eye of *Scutigerina weberi* is given, and the conditions in *Scutigera coleoptrata* mentioned in connection with this. Where Ademsamer's description of the adult eye is quoted, it has been confirmed by observation unless otherwise indicated.

The eye of *Scutigerina weberi* Silvestri 1903. External features.

The paired eyes are sessile and immovable, and appear externally as more or less equilateral, black triangles. They occur on either side of the head, about half way down its length. They are mainly dorsal in position but extend downwards slightly on the sides of the head. The most anterior of the three angles of the eye is laterally placed, the remaining two being dorsal. Although the eyes are conspicuous in view of their colour and from the fact that they have a convexity greater than that of the surrounding parts of the head, they do not occupy relatively a very

/large

large area of its surface. The external layer consists of transparent facets through which the inner, pigmented parts are visible. The convexity of the eye and the presence of large number of units is presumably due to the fact that these animals, though they tend to hide in crevices in wait for their prey, are active, predacious forms, and, according to d'Herculais (1911, p.399), are sometimes found running about in the bright sunlight.

The external cuticle.

The cuticular lens system of the eye consists of a transparent, colourless or slightly yellowish secretion, chitinous and continuous with that which covers the general surface of the body but, unlike it, in being without external decoration. The maximum depth of the cornea of the eye does not greatly exceed that of the cuticle of the body. The cornea is broken up into facets, arranged in regular, alternating, vertical rows. The facets are hexagonal but not as exactly symmetrical as in the compound eyes of Isects and Crustacea. An unthickened part of the cuticle bounds each facet so that in surface view they do not appear entirely contiguous. In Scutigera coleoptrata Grenacher (1879) described five or six sides to each lens. Ademsamer (1893, p.573) described six sides of somewhat irregular length. Verhoeff repeated this (1925, pp.41-42). Each facet is a single entity and without divisions to correspond to the separate underlying cells responsible for its secretion.

/Each

Each facet consists of two parts - ~~an outer -~~ an outer, thin, deeply-staining, thickly-chitinised layer, homogenous and about 3μ thick, and an inner, thicker layer staining more faintly and made up of superimposed layers laid down in growth of the lens. This structure does not differ essentially from that of the rest of the body. There are about fifteen lenses across the eye in a transverse section passing longitudinally through the eye units across the maximum width of the eye. Sections in the plane perpendicular to this show about ten to twelve lenses. In all there are about one hundred and seventy to each eye. The lenses are plano-convex, or slightly concavo-convex with the convexity external - see figures 44.46.52 . No bi-convex lenses were seen. According to Grenacher, (1879) in <u>Scutigera coleoptrata</u> plano- , concavo-, and bi-convex lenses could all be seen in different specimens, while according to Ademsamer (1893, p.574) all these types occurred in the same individual as developmental stages, the bi-convex lenses being confined to the older forms. Only plano- and concavo-convex lenses were here observed. Verhoeff (1925, pp. 41-42) considers that the convexity varies in different lenses as an adaptation to different types of sight. In these cases the lenses measure peripherally about 15μ and centrally about 22μ as compared with a thickness of about 20μ for the body cuticle. Each lens has a diametre of about $45-50\mu$ They are more or less uniform in thickness, size and area with no perceptible changes at the eye margin.

/The corneal

The corneal Hypoderm.

This is the uppermost layer of cells, which escaped Grenacher's attention. The cells are thin and seen with difficulty, since they are readily squashed in sectioning, so that the base of the cone appears to be in contact with the under surface of the cornea along the greater part of its length. They must, in the young animal, presumably have covered the entire area corresponding to the under surface of the facets but have probably shrunken as their function decreased and that of the cones increased, as in some Insects and Crustacea - see pp. 108, 267 They do not form pigmented iris cells as in some Insects - see pp. 267 . The cytoplasm is thin and stains poorly, the nuclei are small and the cell boundaries indistinct. There appear to be only two cells to each eye unit, see Figure 52 . In Scutigera coleoptrata, there appears to be a larger number of cells, although these are difficult to count in view of their small size and indistinct boundaries. Ademsamer (1893, p. 574) described from eight to twelve cells in each unit lying round the base of the cones and covering the latter except for a small central part. Hanstrom (1934) described eleven to thirteen cells in Thereuonema with fourteen to fifteen in Thereuopeda.

The nuclei are small and centrally placed within the cells, with a thin membrane, finely and sparsely granular contents and with no nucleolus apparent. The cell boundaries are indistinct, the lateral boundaries

/between

cells of adjacent units having disappeared. The cells form a ring round the upper regions of the cone, from which they usually appear to be separated by a small space. They abut below on the underlying pigment cells surrounding the cone. The boundaries between these and the hypoderm cells are sometimes seen as in Figure 52 but are frequently indistinct.

The cone and the cone cells.

In the living eye the cone is as usual a conspicuous, transparent, colourless, refracting apparatus, lying immediately below the cornea. Its material is as a rule difficult to fix satisfactorily, being in a semi-liquid state and not in the form of a hard, solid body, as in most Insects and Crustacea - see pp. 126, 278. Adensamer (1893, p.574) described the cone in Scutigera coleoptrata as composed of a granular material, which readily cracked and which he described as containing ground, yellow fat droplets. Such structures were not observed in either of the species investigated. The cone appeared in both cases homogeneous.

The limits of the cone segments are indicated by walls passing between them. These are apparent in Figures 46-48, 50, 52. . Although the cones are conspicuous structures, they do not form such a uniform, solid regular layer as in the eyes of Insects and Crustaceans. They are more or less conical in shape, with the base towards the cornea, and the apex of the cone some distance from

/the

basement membrane. The cone apparatus is about 45-50µ in length, while the entire unit is about 100µ in length. The width of the cone at its base is about 30-35µ from which measurement it tapers to a fine point at the apex. The segments, which are more or less wedge shaped, are separated from one another by double contoured membranes of an undulating course. They are unequal and assymetrical and may be arranged about a central segment or this may be absent. The arrangement, although irregular, is roughly radial. Some of the segments are shorter than others and wedged out apically. Each unit possesses at its base a maximum number of segments. This varies in the different units and may be five, six or seven as shown in Figure 46-48 Within each unit this number decreases along the length of the cone until only one segment remains at the apex - see Figures 47-49.50 In *Scutigera coleoptrata* Grenacher (1879) found eight or nine as the maximum number. Ademsamer (1893, p.574) found five or six the usual maximum number with seven segments occurring in a few units. Verhoeff (1925, p.42) described the numbers as varying from five to nine. Hanström (1934) described seven or eight in *Thereuonema* and six or seven in *Thereuopoda*.

There is in the adult no vestige of the cone cell cytoplasm or nucleus in either of the species examined. Grenacher (1879) considered on these grounds that this was not to be regarded as a true intracellular

/crystalline

cone, comparable with that of the compound eyes of other Arthropods. He therefore termed it a "crystalline body". The difficulty was overcome by Adomsamer (1893, pp. 574-575). He showed the nuclei and cone cell cytoplasm in very young individuals in Scutigera coleoptrata. He found that a secretion appeared in the young cells and accumulated round the nuclei, which were eventually transformed into the material of the cone secretion, while the secretion filled the whole cells, of which only the cell boundary remained. Verhoeff (1925, p. 42) repeated this. The young and adult conditions are illustrated in the attached plate.

The relationships of the upper surface of the cone to the cornea and hypoderm have already been described. Laterally at their upper ends the cone segments are surrounded first by a ring or corneal hypoderm cells and then by a deeper ring of pigment cells shared between adjacent units and isolating them in this region one from another. This is shown in Figure 52 in longitudinal section, in Figure 50 in transverse, and Figure 46 in oblique section. For the remaining (and major) portion of their length the cone segments are surrounded by the upper row of retinal cells, from the rhabdomeres of which they are separated by a short distance in sections, although the two may be in contact in life, see Figures 47-50.

The retinal cells.

The retinal cells of the eye are arranged

/in two

two superimposed layers and in this respect are unlike the lateral compound eyes of any Crustacean and of the great majority of adult insects - see pp. 153,300 The number of cells in the upper row varies considerably. The variability in their number is similar to that of the cone segments since, within the same eye, the number is not the same for different eye units. As far as could be judged from a large number of serial sections, the number of cells, unlike the number of cone segments, was constant throughout the length of a single unit. This number varied in different units from eight to eleven. In the lower row of retinal cells there are five cells at the upper end and four at the lower. The variation in the number of cells in the upper row is shown in Figure 47-49 and the lower row in Figure 51 . In *Scutigera coleoptrata* Grenacher (1879) described nine to twelve cells in the upper row, Ademsamer (1893, p. 575) nine to thirteen (nine to eleven were seen in the sections), while Verhoeff (1925, p. 4) repeated Grenacher's numbers. All of these authors described a lower row of four retinal cells decreasing to three in each unit.

Hanström (1934) described ten to twelve cells in the upper row of retinal cells in *Thereuonema* and *Thereuopoda* with three to four cells in the lower row in *Thereuonema* and two to four in *Thereuopoda*. Packard's description (1880, p.784) of a single "rhabdom structure" corresponding to each lens is incomprehensible, while he

/makes

makes no mention of a double layer of retinal cells.

The arrangement of the retinal cells throughout the eye and their size at corresponding levels in different eye units is more or less constant so that the sections show a definite pattern of arrangement. This, in general impression, is not as regular as that to be observed in the compound eyes of Insects and Crustacea. The arrangement is also more loose and open than in eyes of approximately corresponding size in Insects and Crustacea.

The retinal cells are approximately cylindrical in shape, but in accordance with the outer convexity of the eye and the internal convergence of the eye units, the cells decrease in size in each unit towards the base of the eye. This tendency to compression is more noticeable in the lower than the upper row. In the lower row, which is naturally more crowded than the upper, an entire cell is squashed out apically. In general shape, pattern and arrangement, these do not differ from the retinal cells of <u>Scutigera coleoptrata</u>.

The cells of the upper row have a maximum diametre of 9μ at the top, decreasing to about 6μ at the base, with a length of 40-45μ, while the cells of the lower row have a length of about 30μ with an upper diametre of 7 - 10μ and a lower of 3-5μ. At any one level in the unit the cells are of more or less equal size and symmetrically disposed. The upper row of retinal cells lies round the cone, just below the pigment cells - see Figure 52. The upper row ends at the

/cone

cone apex so that the latter is surrounded by the rhabdomeres of the upper retinal cells only. Scutigera coleoptrata did not appear to differ in this respect. In this species Ademsamer (1893, p. 575) found that the upper retinal cells ended above the level of the cone apex, which is therefore surrounded by the rhabdomeres of the lower row of retinal cells.

The lower row of retinal cells extends from just below the cone apex to the basement membrane. Through this membrane the retinal cells are, as in the compound eyes of other Arthropods, continuous with the nerve fibres of the optic nerve - [illegible])

The retinal cells are filled with a fairly dense cytoplasm, staining deeply but unevenly. The peripheral part,together with a small region round the rhabdomeres, in each cell stains more deeply than the rest. In undepigmented sections this area is seen to be occupied by large pigment granules, densely and evenly packed. This arrangement is seen in Figure 50 . The pigment is deep brown in colour, and its distribution resembles that of the retinal cells of the compound eyes of other Arthropods, living under the same conditions and killed in daylight - [illegible]. The pigment is presumably a melanin.

Between the pigmented parts is a region of finely granular, lightly staining cytoplasm, which shows in all sections a striated appearance, fine striae

/running

running out from the rhabdomere area in each cell. This appears to correspond to Hesse's "schaltzone" (1901, p. 347 et. seq.) - see p. 13 - which he regarded as cytoplasm devoid of pigment, through which the passage of the neurofibrillae on their way into the rhabdomeres could readily be traced. These striations cannot, however, be traced into the rhabdomeres, but appear to end blindly in their neighbourhood. This is in accordance with the views of Nowikoff (1931, p. 19) and others on the nature of the termination of the optic nerve fibrillae in the compound eyes of other Arthropods - see p. 14

The nuclei stain deeply and are oval in shape, with a distinct boundary. They contain throughout a finely and densely granular material with one or two small nucleoli. The nuclei lie partly or wholly within the outer pigmented area of the retinal cell cytoplasm. They may occur at any level in either of the layers of retinal cells.

The individual retinal cells of each layer are contiguous and their mutual lateral boundaries are frequently obliterated to a greater or lesser extent. The distinction between the cells remains apparent in the external lobations - see Figure 48-50 and internally is apparent in lines running out from the rhabdomeres. The latter are especially clear in the lower layer of retinal cells - see Figure 51 .

/The boundary

The boundary between the two layers of cells is not always clear and their components tend to run into one another in some cases. The separation is obvious in the arrangement of the rhabdomeres and retinal cell nuclei and is shown for example in Fig. 52

The rhabdomeres.

Rhabdomeres are present in the retinal cells of both rows. They are axial and borne along the inner, longitudinal borders of the cells, as in the compound eyes of other Arthropods. Each rhabdomere is coextensive with the cell responsible for its production. In the upper row the rhabdomeres as a rule remain separate but occasionally run together to some extent to form a more or less continuous ring, in which the boundaries of the original rhabdomeres are fairly readily traced - see Figures 47-50. Centrally they are separated by the cone, round which they form a loose funnel. In the lower row of retinal cells the rhabdomeres are laterally and centrally contiguous and they tend to unite to a greater or lesser extent to form a rhabdom. Very varying degrees in the extent to which the lower rhabdomeres have united are to be found within a single eye. Figure 51 shows transverse sections through the lower row of retinal cells at different levels in different units of the same eye. Figure 51 A shows a complete fusion of

/the

the rhabdomeres to form a solid rhabdom in the upper five-celled part of the lower layer of retinal cells, while figure C shows a similar condition in the lower region - the four-celled part of the lower retinal layer. Figures B and D show five and four celled conditions in which the rhabdomeres are incompletely fused to form a ring. Towards the base of the lower layer, in the four-celled region, the rhabdomeres may remain unfused - see figures E and F.

The rhabdomeres in the upper row measure about 4 - 5 μ in thickness at the upper end, where they are largest. Like the cells, they decrease slightly in diametre towards the base of the eye. Oblique sections such as that in Figure 48 of course give the impression of a larger size. Where the rhabdomeres run together to form a ring, they are slightly reduced in thickness - see Figure 43. In the lower row the thickness of the rhabdom structure does not exceed 3.5μ at the top, and 2.5μ at the base. The rhabdomeres and rhabdoms (where present), stain deeply and homogeneously with nuclear stains in both species. The striations sometimes described in the compound eyes of other Arthropods are not apparent.

The pigment cells.

As mentioned above, pigment is deposited in granules in the retinal cells of both layers, as well as

/along

along both sides of the basement membrane, and along the nerve fibres of the optic nerve stem. Pigment occurs also in special accessory cells, which isolate the eye units from one another. In Scutigerina weberi there are two types of such accessory cells. The first of these comprises a row of cells surrounding the upper part of the cones below the hypoderm cells and above the upper layer of retinal cells. These are shown in transverse section in Figure 46, which passes through the upper ends of the cones. They contain pigment granules resembling those of the retinal cells but more densely packed, and evenly distributed - see Figure 46. The cells do not abut on the cornea as appears to be the case in Figure 46. The deceptive appearance is due to the obliquity of the section, which passes through the lenses of one row of eye units and the pigment cells of the next. The true relative position of the cells and cornea is seen in the longitudinal section shown in Figure 52. Since the pigment cells merely serve to fill the space between the upper ends of the eye units, they are somewhat irregular in shape. They achieve a maximum depth of about 10μ and width of about 4μ. They may be contiguous with the cone along their inner surfaces as in Figure 46 or slightly seperated from it as in Figure 48.

Their nuclei are larger than those of the hypoderm cells and smaller than those of the retinal cells. They may be oval or somewhat irregular in shape.

/They

They have a distinct outer membrane and coarsely staining, densely granular contents. Like the accessory pigment cells of other Arthropods, and unlike their retinal cells , they are without a nucleolus. They are generally centrally placed within the cells, although they vary slightly in level. The boundaries between adjacent cells have practically disappeared, so that it is very difficult to count the number to be assigned to each separate eye unit, especially as they are shared between two adjacent eye units. The number is of the order of six but appears to vary slightly.

Lower down between the upper retinal cell groups of adjacent eye units there is a second set of accessory pigment cells. These are few in number and scattered in disposition. They are spindle shaped and similar in their cytoplasmic and nuclear structure to the main,accessory pigment cells round the upper part of the cone. Whether the pigment cells are of mesodermal or ectodermal origin cannot be judged from their appearance and could only be decided on an embryological study. The pigment cells in <u>Scutigera coleoptrata</u> appeared very similar to those described above. In this species Grenacher (1879) and Ademsamer (1893, p. 576) however, described three types of accessory pigment cells. The first and second of these corresponded to the main, accessory pigment cells described above. In each unit,

/in

each unit, in addition to these, four cells of a third type occurred at the upper ends of the proximal retinal cells. These are not represented in <u>Scutigerina weberi</u>. Verhoeff (1925, p. 32) described an arrangement similar to that of Ademsamer, while Hanström (1934) found a similar arrangement of three sets of pigment cells with a large but indefinite number of cells in <u>Thereuonema</u> and <u>Thereuopoda</u>. It is probable that as in the compound eyes of other Arthropods - [illegible] there is not a fixed pattern of arrangement of the pigment cells characteristic of the Scutigeridae but that their number and arrangement is determined by the closeness of packing of the eye units.

The basement membrane.

A thin, continuous, cuticular basement membrane is secreted at the base of the eye roughly parallel to its surface. Through it the retinal cells are continuous with the nerve fibres. As in the compound eyes of other Arthropods, the retinal cells appear to be the generating cytons of the optic nerve fibres. Pigment granules are scattered in small cells along both sides of the membrane and it was presumably their nuclei which Packard (1880, p. 784) regarded as the nuclei of the connective tissue, of which he considered the membrane to be formed.

Nerve fibres.

As seen in figure 52 the lower layer of

/retinal

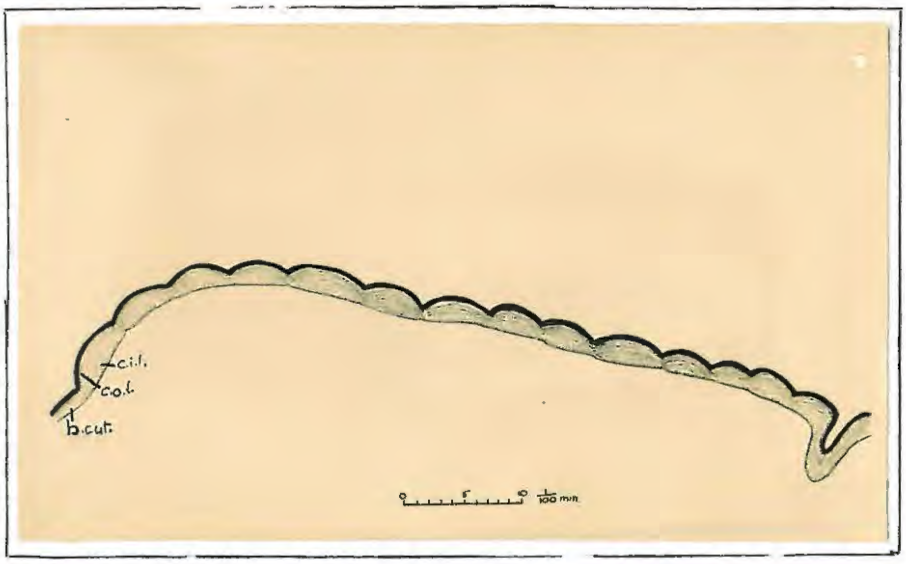
cells is clearly continued through the basement membrane into the nerve fibres of the optic nerve. In *Scutigerina* the passage of nerve fibres into the upper layer of retinal cells could not be traced in transverse or longitudinal section. In *Scutigera coleoptrata* a similar difficulty occurred. In connection with this species Ademsamer (1893, p. 575), however, remarked that he had been more fortunate than Grenacher in tracing the nerve fibres into the upper layer of retinal cells. These fibres ran along the outside of the lower layer of cells and entered the upper cells at their lower margins. Although these fibres could not be traced in the sections it is clear that they must follow a course similar to that described by Ademsamer. Proximally to the basement membrane the fibres of a single unit unite, and run, through the short course of the optic nerve, into the optic ganglion.

Figure 44.

b.cut.	Body cuticle
c.o.l.	Outer homogeneous layer of the cornea
c.i.l.	Inner laminated layer of the cornea.

Figure 44.

A transverse section through the head of Scutigerina weberi, passing longitudinally through the separate eye units. Showing the corneal facets across the eye (at its widest point) and a portion of the body cuticle.



Microscopy

8mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
2.5-3 μ section
(Drawing re-enlarged before photography.)

Preparation : Fixation Carnoy's fluid
Embedding Double
Staining Delafield's Haematoxylon
Aqueous Eosin
Mounting Through Toluol in Tol-Clarite

Figure 45.

c.f.	Irregularly hexagonal corneal facet
i.c.	Thin cuticle separating facets

Figure 45.

A section of the outer surface of the eye cornea seen from above.

Microscopy

8mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
2.5-3 µ section

Preparation

Fixation Carnoy's fluid
Embedding Through Xylol in58 degrees M.P. wax
Staining Iron Alum Haematoxylon
Mounting Through Toluol in Toluol-Clarite

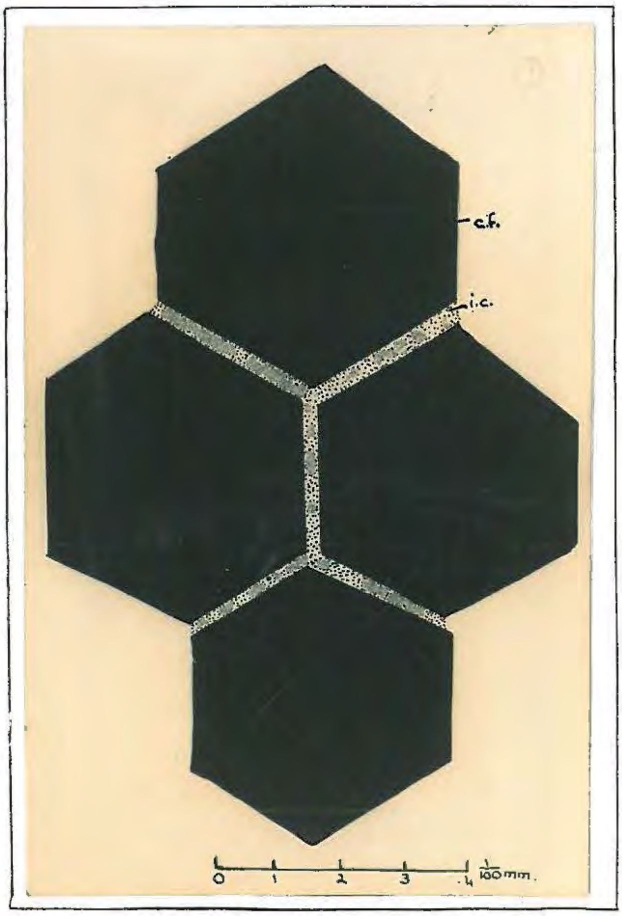


Figure 46.

c.o.l.	Thin outer corneal layer
c.i.l.	Laminated inner layers of cornea
c.c.s.	Segments of the cone (varying in number in different ommatidia)
p.c.c.	Granular cytoplasm of the pigment cells surrounding and in contact with the cones
c.c.w.	Membranes separating the segments of the cone
p.c.n.	Nucleus of the accessory pigment cell.

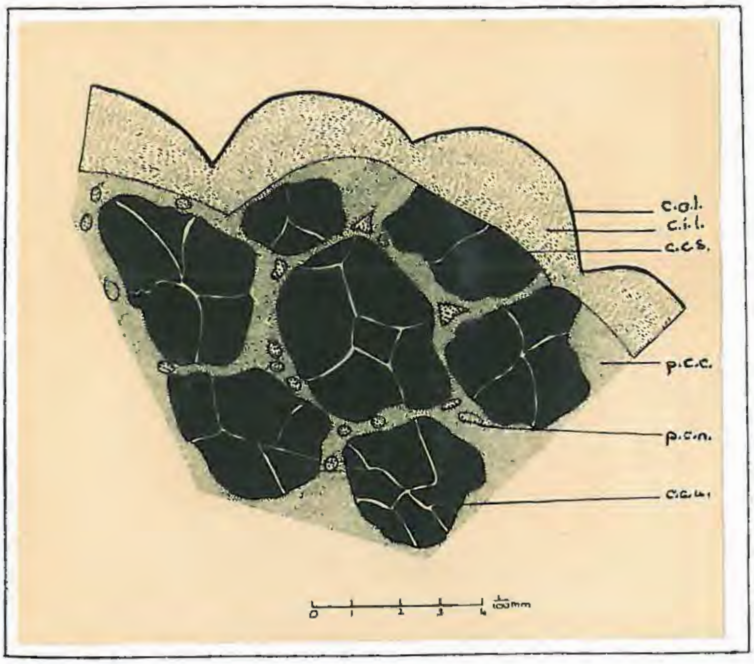


Figure 46.

An oblique section through the cornea of one row of units and the upper regions of the cones and their surrounding pigment cells of succeeding rows of units

Microscopy

4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
2.5-3μ section
(Drawing re-enlarged before photography)

Preparation

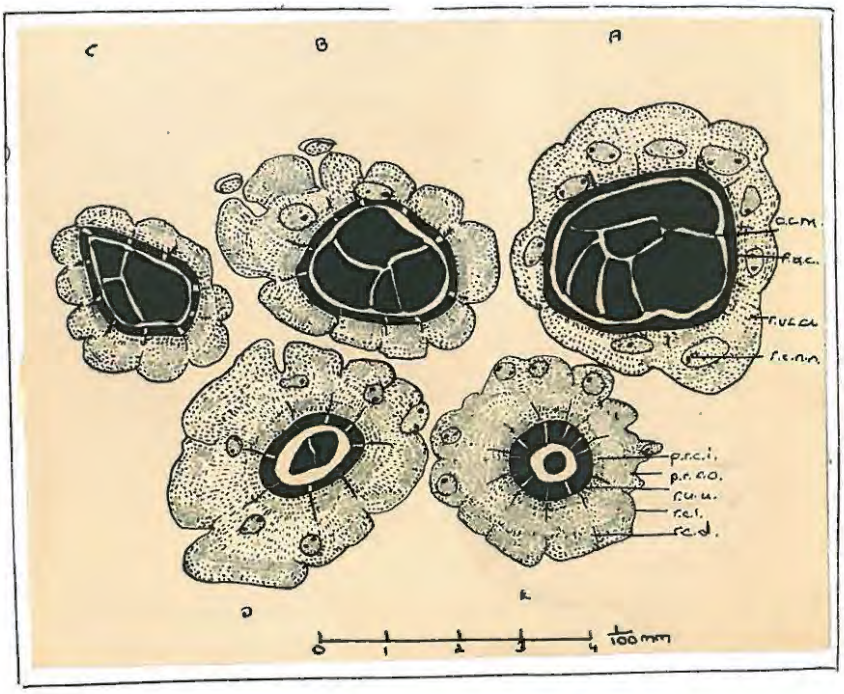
Fixation	Susa's fluid(24 hours)
Embedding	Through white Cedarwood oil in 58 degrees M.pt. wax
Staining	Heidenhain's haematoxylon in Light Green
Mounting	Through Toluol in Tol-Clarite

Figure 47.

A–E	Sections through the cone showing respectively 6,5,3,2 and I segments
c.c.m.	Membrane dividing the cone cells one from another
r.u.c.	Rhabdomeres of the upper layer reduced to form a thin continuous layer separated from the com cone by a small apace.
r.u.u.	Rhabdomeres of the upper layer only partly compounded to form a thin layer round the cone
r.vc.u.	Retinal cells of the upper row numbering 9.IO, IO, 9, II in A to E respectively
r.c.n.n.	Retinal cell nucleus with nucleolus
p.r.c.i.	Inner pigmented region of the retinal cells
p.r.c.o.	Outer pigmented region of the retinal cells
r.c.l.	External lobation of the retinal cells
r.c.d.	Internal divisions between the retinal cells

Figure 47

A transverse section through the eye of Scutigerina weberi, cut through the cones of different ommatidia below the accessory pigment cells, showing the variation in the number of cone segments along the length of the eye unitx and the variation in the number of cells in the upper layer of retinal cells



Microscopy
4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
2.5-3μ section

Preparation

Fixation	Alcoholic Corrosive sublimate
Embedding	Double embedding in an Ether-Alcohol (75:25) solution of celloidin, through $CHCl_3$ in 50 degree's M.pt. wax
Staining	Heidenhain's Iron Alum haematoxylon Light Green
Mounting	Through Toluol in Tol-Clarite

Figure 48.

r.c.u.	Retinal cell of the upper layer
p.c.m.a.	Main accessory pigment cell round upper part of cone
p.c.n.	Pigment cell nucleus without nucleolus
r.c.n.n.	Retinal cell nucleus with nucleolus
r.c.p.i.	Inner pigmented part of the retinal cell
r.c.p.o.	Outer pigmented region of the retinalcell
s.z.	Clear middle region of the retinal cells - faintly radially striated
rh.o.s.	Separate rhabdomeres cut obliquely
rh.o.c.	Rhabdomeres more or less coalesced with the divisions still visible internally
c.c.s.	Cone sgments
r.co.	Region in which the pigment and upper retinal cells pass into one another. In some cases the boundaries are distinguishable - see figure 52.

Figure 48

Two oblique sections passing through the upper ends of the cones. Proximally these pass below the pigment cells and through the upper retinal cells, while distally through the accessory pigment cells. These sections show the variation in the degree of approximation of the rhabdomeres of the upper retinal cell layer.

Microscopy

4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
2.5–3 μ section

Preparation

Fixation : Carnoy's fluid

Embedding : Through Xylol in 58 degree's m.p. wax

Depigmented: in Grenacher's fluid
Staining : Heidenhain's Iron Alum haematoxylon
Bordeaux Red

Mounting : Through Toluol in Tol-Clarite

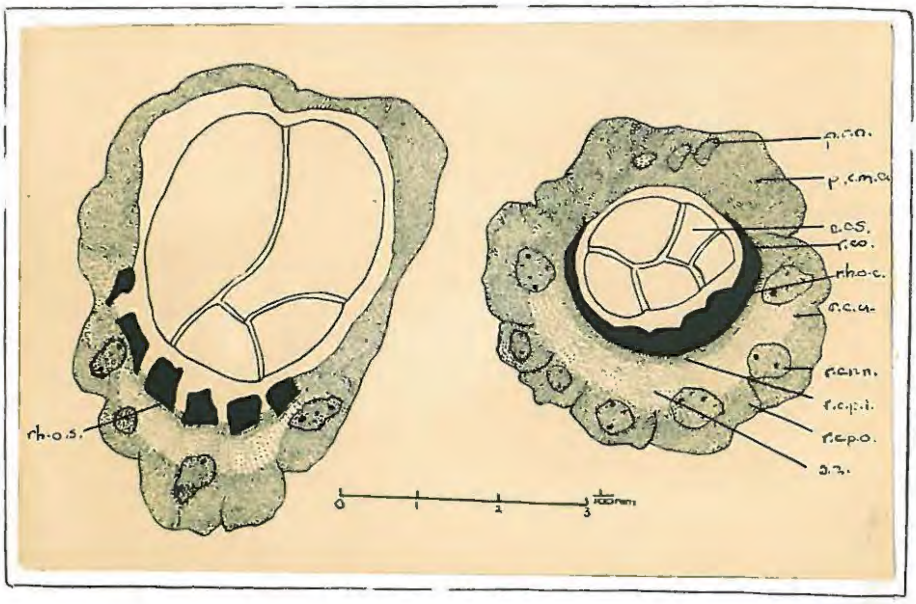


Figure 49.

r.c.u.	Retinal cells of the upper layer
r.c.n.	Retinal cell nucleus
r.c.p.ii.	Inner pigmented part of the retinal cell
r.c.p.o.	Outer " " " "
s.z.	Middle region faintly striated
c.s.	Single cone segment at the base of the cone
r.hg.s.	Separate rhabdomeres of the retinal cells numbering 9 and IO in figs A and B respectively.

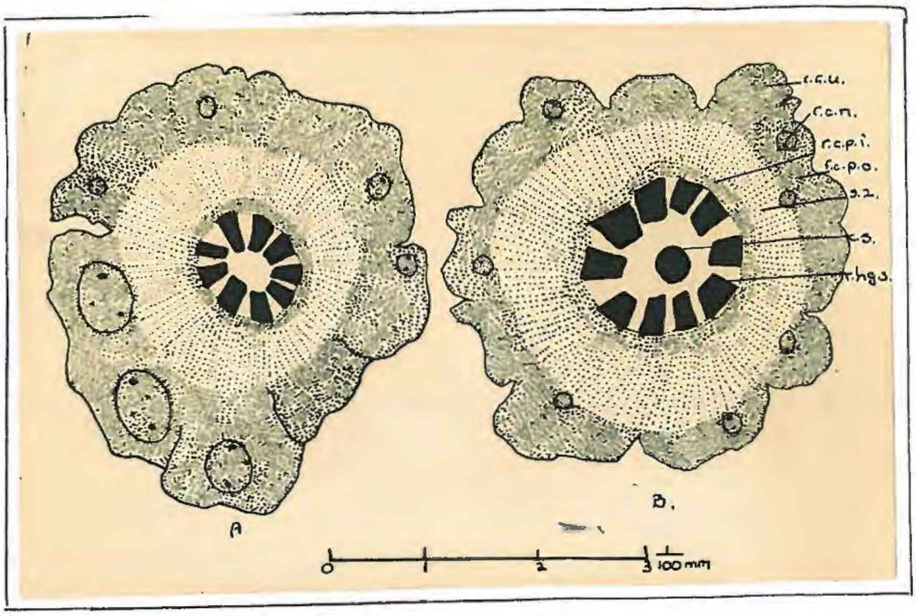


Figure 49

Transverse sections through the eye units of Scutigerina weberi
A. Through the upper layer of retinal cells just below the end of the cone
B. Through the upper layer of retinal cells just above the end of the cone

Microscopy
4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
Drawing re-enlarged
3 μ section

Preparation

Fixation	: Carnoy's fluid
Embedding	: Through Xylol in 58 degree's wax
Staining	: Depigmented in Grenacher's solution Heidenhain's Iron Alum haematoxylon Bordeaux Red
Mounting	: Through Toluol in Tol-Clarite

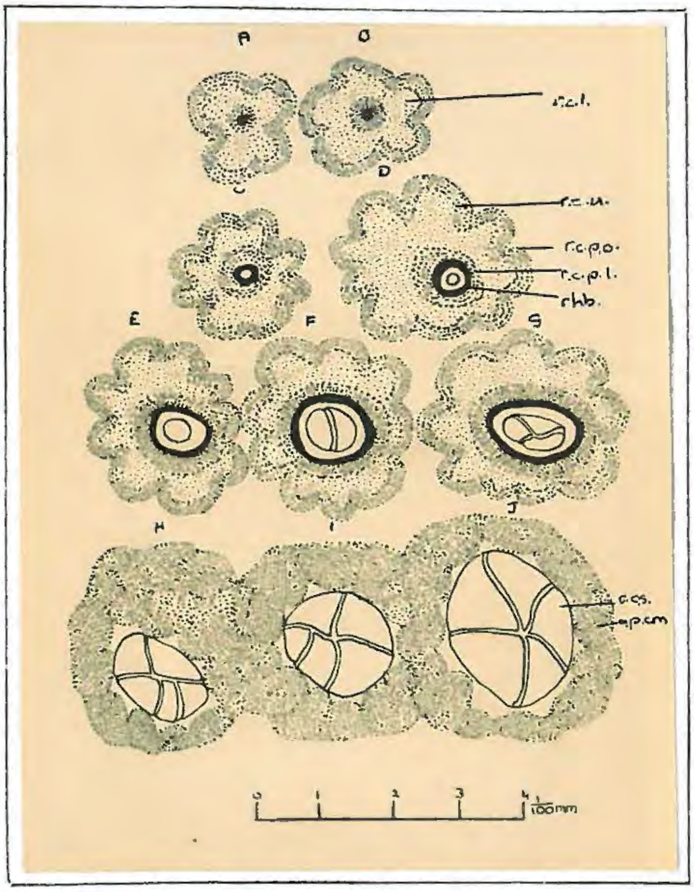
Figure 50.

r.c.u.	Retinal cells of the upper layers
r.c.l.	" " lower "
r.c.p.o.	Outer pigment of the retinal cell
r.c.p.i.	Inner " " "
rhb.	Rhabdomeres apparently continuous
c.c.s.	Cone segments
a.p.c.m.	Main accessory pigment cells.

Figure 50

An undepigmented section (transverse) of the eye with different units cut at different levels

a. Through the base of the lower row of retinal cells
b. Through the five celled part of the lower retinal layer
c. Through the upper retinal layer just below the cone
d. Through the upper retinal layer just above the base of the cone
e.f.g. At successively higher levels through the cone
h.i.j. Through the cone and upper accessory pigment cells.



Microscopy

4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida draing
2.5-3 μ section

Preparation

Fixation : Susa's solution
Embedding : Through white Cedarwood oil in 58 degree's m.p. wax
Staining : Light green (MOUNTING as for previous figure.)

Figure 51.

A. Through the five celled upper region of the lower layer of retinal cells showing the rhabdom as a pentagonal, solid structure.
B. Through the same region or slightly lower down showing the rhabdomeres as contiguous but arranged about a central lumen
C. Lower down through the four celled regionof the lower row of retinal cells showing the rhabdom as a solid, square structure
D. Through the same region showing the rhabdomeres as contiguous but arranged about a central lumen
E.F. Successively lower sections near the base of the retinal cells of the lower layer showing the rhabdomeres as separate structures

rhb.	Rhabdom
rh.	Rhabdomere
r.c.n.	Retinal cell nucleus
r.c.u.	Upper retinal cells
r.c.l.	External lobations showing the divisions between the lower retinal cells
r.c.d.	Internal divisions between the retinal cells
r.c.p.i.	Inner pigmented part of the retinal cells
r.c.p.ol.	Outer pigmented part of the retinal cells
s.z.	Middle clear zone of radially striated cytoplasm

Figure 51

Transverse sections at successively lower regions of the lower layer of retinal cells to show the different arrangements of the retinal cells at various levels

Microscopy

4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing - Re-enlarged
3 μ section

Preparation

Fixation	: Susa
Embedding	: Celloidin in Ether alcohol Through Celloidin in CHCl3 in 60 degree's m.p. wax
Staining	: Depigmented in Grenacher fluid Azo carmine with aniline blue and orange blue after phosphotungstic acid mordant
Mounting	: Through Toluol in Toluol-Clarite

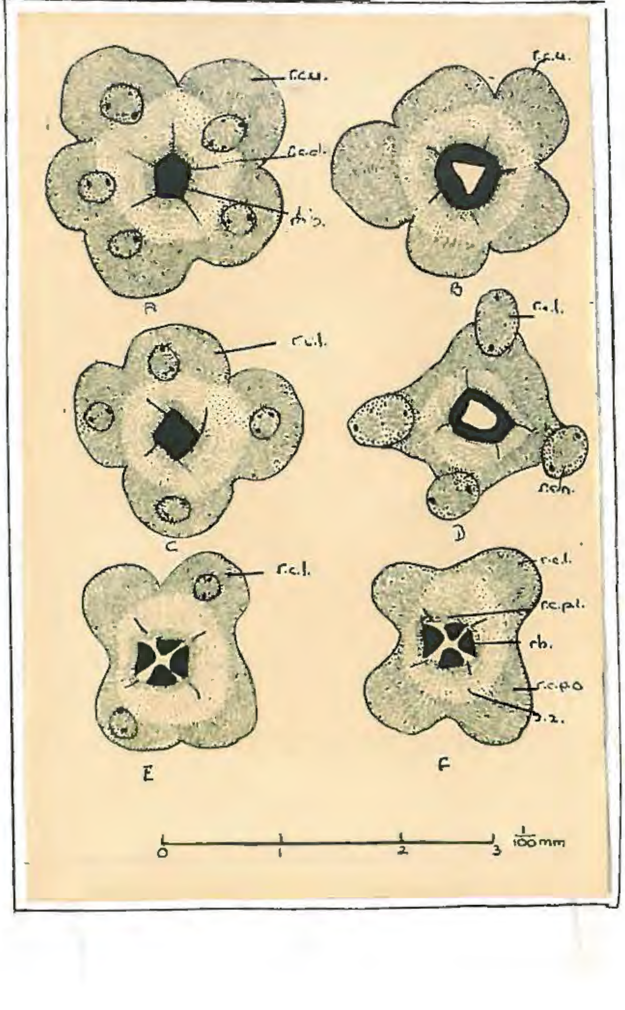


Figure 53.

c.f.	Corneal facet
c.hyp.	Corneal hypoderm
p.m.a.	Main accessory pigment cell
c.c.	Cone segments
r.u.	Retinal cells of the upper layer
r.l.	Retinal cells of the lower layer
r.c.n.n.	Retinal cell with nucleolus of nucleus
b.	Boundary between the two rows of retinal cells
rhb.u.	Rhabdom of the upper row of retinal cells
rhb.l.	" lower " " "
b.mp.	Basement membrane covered with upper and lower pigment layers
n.f.	Nerve fibre continuous through the basement membrane with the retinal cells

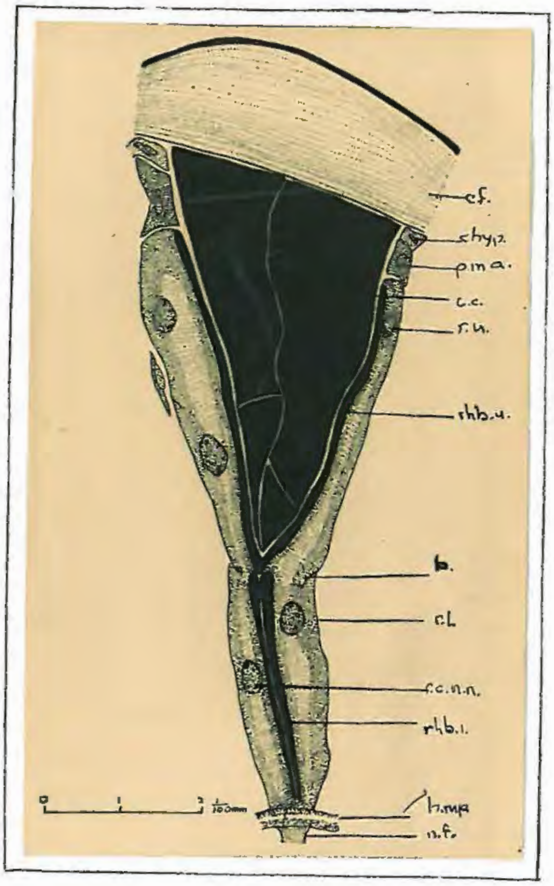


Figure 52

Longitudinal section of a single eye unit from the eye of Scutigerina weberi

Microscopy

4mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
3 µ section.

Preparation

As for the section in Figure 5I.

Part II

The relationships of the eyes of Scutigeromorpha to those of other Arthropods.

A comparison of the eyes of Scutigeromorpha (the only Chilopods possessed of "compound" or rather "pseudocompound" eyes) with the true compound eyes of Insects and Crustacea and the eye of Xiphosura, shows that the eyes of Scutigeromorpha are of a type very different from that found in any other Arthropod. They are anatomically and phylogenetically remote from the eyes of Xiphosura. In the grade of their organisation they approach the true compound eyes but in the details of their construction differ significantly from these.

In their general form, structure and configuration the corneal lenses are similar to those of true compound eyes but show a variability in different units of the same eye, which is rare in the latter. Where there are typically two corneal hypoderm cells associated with each facet in true compound eyes, the number in Scutigeromorpha may be two or more than this and is variable.

The cone in true compound eyes is formed as an intracellular secretion (primitively solid) of a small number of cells, constant in number throughout the length of the unit and the eye as a whole. At least some vestiges of the cells remain round the secretion in most cases, and the nuclei are clearly apparent in the fully formed apparatus. In Scutigeromorpha the cone arises as an intracellular, fluid secretion of a large number of cells, decreasing in number towards the inner end of the unit, and varying from one unit to the next. The entire cells and their nuclei are converted into the substance of the cone in the adult. The component parts of the cone apparatus are, moreover, not symmetrically arranged throughout the eye, or even within their own unit, so that sections present a more ragged and irregular appearance than seen in the eyes of Insects and Crustacea.

Perhaps the most striking differences are in the retinal cells. In both cases these are pigmented nerve end cells, arranged in a retinular group, about the axis of the eye unit, and bearing rhabdom structures along their inner, longitudinal, axial borders. In Insects and Crustacea there is typically a single row of sense cells, extending from the apex of the cone apparatus to the basement membrane and comprising a small fixed number of cells, (eight or less with few exceptional cases), constant in number throughout the eye , and throughout the major part of the length of each unit, although one or two of the cells are sometimes reduced towards the base. (This of course excludes the peculiar double layered arrangements found in some Insects - see appendix). In contrast to this the retinal cells in Scutigeromorpha are arranged in two superimposed rows, the lower occupying approximately the position of the retinal cells in true compound eyes, and the upper surrounding the cone throughout its length. The upper row comprises a large and variable number of cells (eight to thirteen) constant in number in any one unit but varying throughout the eye, while the lower row comprises four or five cells, reduced to two or three at the base of each unit.

The rhabdomeres in true compound eyes show a very variable degree of concretion, but whatever the form of the rhabdom to which they give rise this is constant throughout the eye, concerned. In Scutigeromorpha the degree of concretion of the rhabdomeres, in both the upper and lower layer of retinal cells, varies considerably within a single eye.

The pigment cells, always a variable feature of the eye, do not differ significantly from those of Insects and Crustacea.

From this comparison it is apparent that the eye in Scutigeromorpha differs greatly from that in Insects and Crustacea.

If the ancestors of the Chilopods inherited a general tendency to the formation of a lateral aggregate eye, which tendency appears to have been present at the base of all other main Arthropod stems, it is clear that this has achieved an expression very different from that in any other extant Arthropod.

The salient characteristics of the eye in Scutigeromorpha are the large and variable number of the cells comprising each part of the eye and their subjection, at least in the case of the cone and retinal cells, to a severe overcrowding, accompanied by a tendency to elimination of cells at the base of the eye. The instability of the structure of all parts of the eye seems to indicate that this is of relatively recent evolution or of degenerate origin.

It is possible that the differences between these and true compound eyes may be secondary and due either to the degeneration of specialisation of the eye in Scutigeromorpha. Alternatively the eye in Scutigera may be of an entirely new type and formed either as a single, complete, new structure or by a coalescence of units possibly resembling the ocelli of Chilopods. These suggestions are discussed in turn.

There is no precedent case in other

Arthropods for supposing that a compound eye of the type in Insects and Crustacea on degeneration (or by any known process of specialisation) could have given rise to a structure resembling that in Scutigeromorpha. Degeneration of a compound eye is known to produce one or more ommatidia of simplified structure but there is no indication that this process has ever produced an increased number of cone cells or a retinula group at once so large and so elaborate.

The eye, since it is apparently not derived by degeneration of the compound eyes of other Arthropods, must presumably have arisen either as a separate, entire, new structure or by an aggregation of separate units.

In view of the dissimilarities between adjacent eye units and the distinct indications of unequal reduction of their cells (due to severe overcrowding), it seems probable that the eye units were at one time separate and larger than at present and that the eye has arisen relatively recently by their aggregation.

It is at least possible that the units from which the Scutigerid eyes were formed were of the type of Chilopod ocelli. The changes involved in such a transformation are dealt with more fully in the Appendix after a description of the anatomy of these ocelli.

In this connection the eyes of other Arthropods give little guidance as to the probable course of evolution. Among the remaining Arthropods (as is pointed out more clearly in the appendix) there is no case known in which it can definitely be claimed that the eye has arisen relatively recently by a coalescence of well developed ocellar units. It is possible (as Watase (1890) holds) that the eye of *Limulus* was developed by a coalescence of units but the evidence for this is not very satisfactory and the resulting eye is totally unlike that of Scutigeromorpha. Any such coalescence which might be postulated as preceding the formation of the compound eye in Insects or Crustacea must clearly have taken place in a very distant ancestor, the product having become a stable and well established unit in the vast majority of cases.

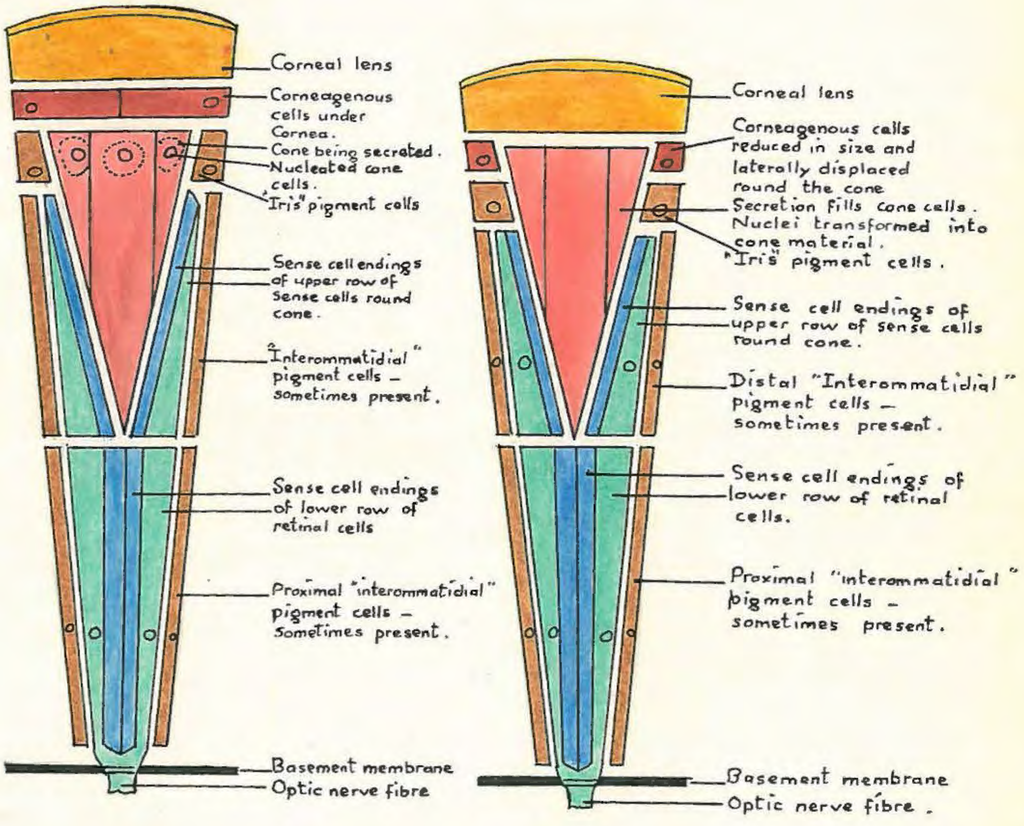
It has been suggested as possible that the eyes of Collembola and Lepismata, however, may retain the impression of a primitive formation by an aggregation of separate units. The eyes are similar to those of *Scutigera* in possessing a well defined upper row of retinal cells, surrounding the cone throughout its extent. The cells in the Insects differ from those in *Scutigera* in their much smaller number and in the fact that the upper row is not coextensive with the cone but continued for some distance below this. (In the remainder of their structure the Insect eyes are of the true compound type and differ widely from those of Scutigeromorpha). If the possibility, that the retinal conditions in these Insect eyes are primitive, be accepted, the double nature of the retinula would be a formation parallel to that in Scutigeromorpha and the two cases would presumably have been produced in an analogous fashion - namely by the aggregation and appression of separate units.

It is much more probable however - see p. 304 - that the retinal conditions in these Insect eyes are degenerate. Although the main line of the derivation of these Insect eyes is directby from a Crustacean form, it seems probable that the eyes were secondarily lost or severely reduced in some of the earliest Insects. In Collembola and Lepismata, which appear to have been derived from these latter forms, the eyes were presumably re-developed from the remaining rudiments, with their structure modified in accordance with their degenerate origin.

The eyes of Collembola and Lepismata cannot, therefore, be regarded as having been formed by a coalescence of separate units. The similarity between their retinal cells and those of Scutigeromorpha is probably superficial and without relation to a common mode of formation in these eyes.

In conclusion it seems likely that the eye in Scutigeromorpha is a secondary formation without near relationship to the lateral eyes of other Arthropods, probably formed relatively recently by a coalescence of units, in the course of which there was a severe and unequal reduction in the number of their cells. It is possible that these units may have resembled the ocelli of Chilopods - this is discussed in the appendix after the ocelli have been described. This coalescence is probably the expression of the general tendency to the formation of aggregate eyes such as is present at the base of all the other main Arthropod stems. Its morphological expression is very various and, in Scutigeromorpha, distinct from that in any other Arthropod.

The Structure of the Eye in Scutigeridae illustrated by Longitudinal Sections.



In the Young.

In the Adult.

A. T.S. CORNEA.

1. Hexagonal Form.
2. Pentagonal "
3. Irregular "

B. T.S. HYPODERM CELLS.

1. Two celled
2. Eight celled to
3. Fifteen celled.

C. T.S. UPPER END OF YOUNG CONES

1. Five celled.
2. Six "
3. Seven "
4. Eight "
5. Nine "

N.B. In Section C and in succeeding sections the separate pigment cells are not defined since their number when they are present is variable

D. T.S. UPPER ROW OF SENSE CELLS THROUGH THE CONE BASE.

1. Seven Celled.
2. Eight "
3. Nine "
4. Ten "
5. Eleven "
6. Twelve "
7. Thirteen "

N.B. All of these have the rhabdomeres only loosely fused or separate.

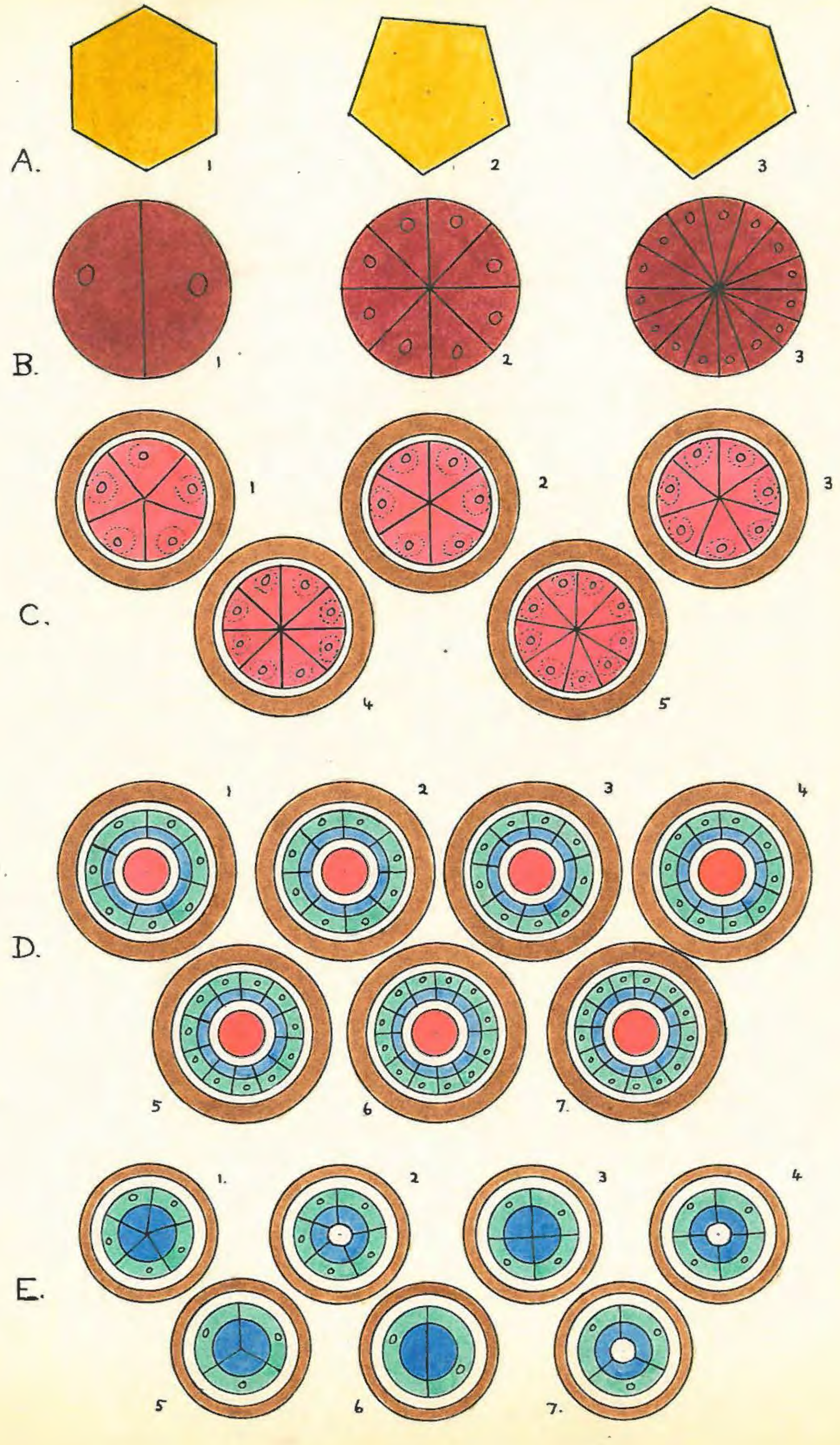
E. T.S. UPPER ROW OF SENSE CELLS THROUGH THE CONE BASE.

1. Five Cells with fused solid Rhabdom.
2. " " " separate rhabdomeres and central cavity.
3. Four " " fused solid Rhabdom.
4. " " " separate rhabdomeres and central cavity.
5. Three " " fused solid Rhabdom.
6. Two " " " " "
7. Three " " separate rhabdomeres and central cavity.

Most of these Variations are to be found within an eye in Scutigerina but the illustrations show the entire range of variation in the eyes of Scutigeromorpha.

PLATE 18.

VARIABILITY OF THE EYES OF SCUTIGEROMORPHA ILLUSTRATED IN DIAGRAMMATIC TRANSVERSE. SECTIONS — See legend opposite.



Conclusions-Chilopoda .

I. Occurrence and type

Lateral "pseudocompound " eyes are present only in Scutigeromorpha. Scolopendromorpha and Lithobiomorpha are provided with lateral ocelli in small groups, while Geophilomorpha are blind . Except in Geophilomorpha Blindness is rare and secondary.

2. Comparative anatomy and basic plan

The eyes of Scutigeromorpha are clearly very remote anatomically and phylogenetically from those of Xiphosura. Although their component units are of the ommatidial grade of development , these are very variable and differ significantly from those of the true compound eyes of Insects and Crustacea. There is no reason to suppose that a true compound eye would , on degeneration , have given rise to an eye of the type of Scutigeromorpha.

3. Variability and evolution of the eye .

The variability of the eye units and their unequal reduction and severe overcrowding seem to indicate that these were at one time separate and larger than at present and that the eye has arisen relatively recently by their approximation.

4./ Degeneration.

4. Degeneration of theeye .

The origin of the Chilopod ocelli by degeneration of the "pseudocompound eye " is unlikely. The ocelli , together with those of Diplopods , which they resemble closely, are stable and uniform and appear to be a primitive acquisition of the two classes. while the "pseudocompound"eyes appear a relattively recent evolution. This is discussed further in the appendix dealing with the lateral ocelli.

5. The possibility of the origin of the "pseudocompound" eyes from aggregated units.

It seems probable that the"pseudocompound " eyes arose by an aggregation of units. That these may have resembled Chilopod ocelli is discussed further in the appendix. In the remaining Arthropods there is no case in which the relatively recent origin of any form of compound eye from such an aggregation can definitely be claimed. It is possible that the eyes in Xiphosura have been formed by an aggregation of separate units but the evidence for this is not very satisfactory. It has been suggested that the eyes in Collembola and Lepismata retain the impression of such an origin and that the double retinula has been formed along lines parallel to those operating in the evolution of the eye in Scutigeromorpha. It seems more probable , however , that in these Insects the eyes were re-developed from a true compound eye rudiment inherited from an early Insect ancestor

/in which.

in which the eyes were secondarily and severely reduced. The similarity between these eyes and those of Scutigeromorpha is thus probably superficial and without relation to a common mode of formation.

6. General relationships.

A tendency to the formation of lateral , aggregate eyes appears to have been present at the base of all the other main Arthropod stems . It seems that such a general tendency may have been inherited from an early ancestor in which it was present . Its expression in the eyes of Scutigeromorpha is one morphologically remote from that in any other Arthropod.

General conclusions on the Comparative Anatomy , Origin and Relationships of the different types of lateral Compound Eyes in Arthropods.

I. The different types of lateral compound eyes and their distribution .

There is a general tendency for the end organs of the optic nerve to take the form of lateral, aggregate eyes, which, although homologous in origin , are diverse in structure. This tendency achieves its highest expression in the true, lateral, compound eyes which are typically and primitively present in Insects and Crustacea.

The eyes of the majority of the Trilobites were presumably of the same type. Among the Eurypterida some of the eyes were probably of this type , while others (those of Pterygotidae) approached the condition of the "pseudo-compound "eyes of Xiphosura, in which the units are intermediate between ocelli and ommatidia. The aggregated eyes of fossil Diplopods, like those of the modern forms, were presumably of the ocellar type. The "pseudo-compound" eyes of Scutigeromorphs are ommatidial but differ in their anatomy from the lateral eyes of other Arthropods. In Arachnida and Chilopoda , other than those mentioned above, lateral eyes are of the ocellar type. (These are considered, together with other lateral ocelli, in the appendix).

Sporadic absence of the eye in a few forms or its loss throughout an entire order or family is not uncommon. The latter condition obtains in some Trilobites, in

/some

some Apterygote Insects, in Pauropoda and in some Symphyla and in Geophilomorphous Chilopoda and several Diplopod families. The presence of a lateral eye is clearly a widespread and primitive feature in Arthropods and it is probable that the absence of the eye is universally secondary, the eyeless forms being ultimately derived from eyed ancestors. This is certainly the case in those Insects and Trilobites concerned and is very probably the case in the remainder of the blind groups.

2. Comparative anatomy, basic plans and range of variation of these eyes.

In the case of each class an attempt has been made to indicate the primitive and typical form of the eye and the main variations to which it is subject. The coloured plates illustrating the most important of these conditions indicate the approximate form, number and relative position of the cells involved but do not show details of the cytoplasmic or nuclear structure of the cells or the finer structure of their secretions. .

The eyes of Insects and Crustacea, although they differ in some respects, and have a different range of variation, are clearly formed on a common basic plan which remains relatively stable through an enormous number of forms. Departures from this pattern, such as are represented by the hyaline cells in Crustacea and by the form of the cone and retinal cells in some Insects are comparatively rare. There is no necessity to suppose a convergent evolution of the eye in these two classes and their similarity is presumably due to a common origin.

The eyes in the majority of Trilobites and in many of the Eurypterida (in Eurypteridae) presumably agreed in structure with the true compound eyes and like these were stable and well developed, there being no indication of the evolution of the eye within the limits of the classes concerned. The eye in these classes would appear to have been inherited from a distant, common ancestor, in which it was already well developed and fixed in inheritance. The lateral eyes of Xiphosura are without near anatomical relationships to those of any extant Afthropods. It is probable ,however, that the eyes of Pterygotidae were of this type , while the prismatic eyes of some Trilobites may internally have approached the same condition. The variability in the eye units in Xiphosura, the cone loss and the increase in the number of the retinal cells, (when compared with the conditions of the ommatidia of true compound eyes), are presumably degenerate features, the increase in the size of the lenses being correlated with a reduction in the organisation of the under-lying structures.

The lateral eyes of Chilopoda Scutigeromorpha differ from those of all other Arthropods both in the pattern of their formation and in their extreme variability, which is apparently due to a recent origin rather than a degenerate formation.

3. Variation of the eye within the classes in relation to the phylogeny of the forms in which these variations occur.

Within a class variations in the eye structure are often correlated with other structural differences. As is indicated above (see p.206) this is particularly apparent in Crustacea. It is not however at all marked in Insects , where the variations in the cone and retinal cells are scattered through the different orders, without apparent reference to their phylogeny. . In Trilobites the degenerate, schizochroal eyes are restricted to late and otherwise modified forms, while the "simple " eyes are restricted to a small group of genera, which are otherwise nearly related. Each of the two forms assumed by the eye in Eurypterida occurs in association with other structural features, whose combination separates these forms into two distinct groups, whose affinities , like those of their eyes , lie on the one hand with the Xiphosura, and on the other hand with the Trilobites and the lower Crustacea. The peculiarities of the eye in

/Xiphosura

Xiphosura are in accordance with the somewhat isolated and specialised position of these forms. Among the Chilopoda the "pseudo-compound" eyes are restricted to an order, which on other grounds is well defined and separated from the remaining forms. Thus, although the lateral eyes are subject to adaptive modification in many cases, and are therefore not a reliable index of the phylogenetic position in any one form, the variation in their structure within the different classes shows a general relation to the main phylogentic trends within those classes.

4. Degeneration of the lateral compound eyes.

In Crustacea degeneration of the compound eye may result in the formation of a very small number of separated ommatidia but the changes are not sufficient to convert the units into ocelli. In Insects degeneration of the eye is along lines parallel to those followed in Crustacea but in Aphaniptera this appears to have led to the formation of a single ocellus. In no case does the eye degenerate into a group of ocelli . In Trilobites degeneration in schizochroal and "single" eyes is along lines parallel to those followed in Crustacea and it is therefore to be assumed that the produds were ommatidia and not ocelli. Degeneration into separate units is not known in Eurypterida . There is in Arachnida no clear indication of the formation of

/the typically

the typically ocellar eyes from a Xiphosuran or some other compound form. Among the Diplopods the lateral ocelli are not known to have arisen from anything other than an ocellar aggregation. It seems unlikely that the eyes of Scutigeromorpha gave rise to the ocelli of other Chilopoda, the latter being apparently the more stable , widespread and ancient type.

Thus in no case is a compound eye of any kind definitely known to degenerate into a group of ocelli.

5. The possibility of the formation of the compound eye from one or more ocelli.

There is no clear indication in the ontogeny or anatomy of any part of the lateral compound eye in Insects, Crustacea , Trilobites , Eurypterida or Xiphosura of its formation from one or more ocelli .

Among the Insects the eyes of Collembola and Lepismata are sometimes supposed as intermediate between a group of ocelli and compound eyes but their peculiarities are more probably to be regarded as partly degenerate, while the lateral ocellar groups of Insect larvae are probably without phylogenetic importance - see appendix. If the eye of *Limulus* arose in this way, as Watase supposed, there is no extant evidence of the existance of separate units in any of the possible

/ ancestors

ancestors and convincing evidence for such an origin is lacking. . In Diplopods there is no indication that the ocellar units at any time produced an eye other than an ocellar aggregation. (Whether the ocelli were primitively separated or aggregated in this class is unknown) . In spite of the absence of any precedent for such an origin for a lateral compound eye of any kind in other Arthropods, it seems probable that the eye in Scutigeromorpha has arisen from an aggregation of large, separate units. The eye appears to have had a relatively recent origin, completely separate from that of the lateral, compound eyes in other Arthropods.

6. The general relationships and the course of the evolution of these eyes .

The true compound eyes of Insects and Crustacea and (probably) of Trilobites are built on a common basic pattern, presumably inherited from a common ancestral stock ,in which it was already well developed and stabilised. In some of the earliest Insects the lateral eye rudiment appears to have undergone a very severe reduction and its subsequent redevelopement in Collembola and Lepismata bears the marks of its degeneration. At the base of the Arachnid stem the tendency to formation of an aggregate eye is preserved but modified (in Pterygotidae and Xiphosura) by an increase in the size of the lenses at the expense of the underlying parts . In the remaining Eurypteridae the

/flattened

flattened cornea may have been derived by degeneration of the condition in Pterygotidae (although there are no intermediata stages to imdicate this) ot may have been inherited from a lower Crustacean stock in which the lenses have this form. In Xiphosura the peculiar expression of the tendency to formation of a lateral aggregate eye is probably due to its degeneration. (In the remaining Arachnida this eye is lost and replaced by ocelli) . The Diplopod eyes are relatively poorly developed and have probably arisen from a stock in which the lateral eye rudiment has undergone very severe reduction. These units are sometimes aggregated but show no tendency to formation of an ommatidial compound eye. In Chilopods it would appear that there was a severe reduction of the lateral eye rudiment in the ancestral stock (as in some of the earliest Insects - to which this stock was probably related) . This reduction was so severe that the eyes when formed anew have in most cases taken the form of ocelli. The"compound"eyes of Scutigeromorpha appear to be a more recent and secondary formation arising from the aggregation of large separate units, exemplifying in Chilopods the general tendency to formation of an aggregate eye, but without near anatomical or phylogenetic relationship to the lateral eyes of other Arthropods.

Appendix .

The lateral ocelli of Arthropods.

Introduction A study of the comparative anatomy of the lateral compound eyes or Arthropods necessarily includes some mention of the lateral ocelli. Some information on the origin and relationships of the lateral ocelli is therefore to be found scattered through the various chapters in the main section of the thesis. It seems desirable to collect this material and to correlate it somewhat more fully.

It is not possible to make a detailed study of the comparative anatomy of the lateral ocelli and they are therefore considered only from such aspects as appear to have some bearing on the questions raised in connection with the comparative anatomy and relationships of the lateral compound eyes and especially of the eyes of Scutigeromorpha.

In this part an attempt is made to indicate whether, in each of the classes of Arthropods, the lateral ocelli have arisen by degeneration of a compound eye, or whether there are any indications in phylogeny or ontogeny of the primitive or secondary formation of any type of compound eye by the aggregation of numerous ocelli or the elaboration of one of these.

This information is of particular interest in connection with the origin and relationships of Chilopod eyes.

1. Lateral ocelli in Crustacea.

True lateral ocelli are absent in Crustacea. The compound eyes never degenerate into ocelli but only into scattered ommatidia. The common use of the term "ocelli" to describe the reduced compound eyes of some Crustacea is unfortunate since they fall within the morphological limits of the ommatidium. In some degenerate eyes the retinal cells may increase beyond the number normally found in an ommatidium (see p.148) and approximate in this particular to the ocellar condition but in these cases the presence of a typical cone and of axial groups of rhabdomeres are clearly ommatidial features.

There seems to be no clear indication in the anatomy or ontogeny of the lateral compound eyes of Crustacea that these were formed from a modified ocellus or an aggregation of ocelli. Each part of the eye seems to be a structure of ancient and well established standing, and subject to a somewhat restricted range of variation. It is possible that the common tendency to reduction of one of the retinal cells at the base of the ommatidium is the remnant of an archaic tendency to reduction in the large number of sense cells in an aggregation of units. It seems much more likely that the reduction is due to a series of/

of convergent evolutions, necessitated by lengthening of the ommatidia and the approximation of their inner ends in relation to an increase in the external convexity of the eye as a whole. Patten's view (1886) of the compound eye as formed by the elaboration of a single ocellus is not supported by any later authors. His argument is unconvincing. Watase's view (1890) of the eye as formed by a recent coalescence of ocelli is based mainly on the eyes of <u>Limulus</u>. There is little or nothing to support this view in the anatomy or development of the compound eyes of Crustacea.

The so called simple lateral eyes of some Copepods are specialised and aberrant. They are probably to be regarded as displaced median ocelli - see Calman (1909, pp. 84, 86) and (I9II, p. 21).

Thus there is little or no evidence within the Crustacea for supposing that the compound eye on degeneration gave rise to ocelli or that it arose from a single ocellus or an aggregation of ocelli,. In a few cases, in which lateral compound eyes are absent, the dorsal ocelli may undertake a lateral migration, but no true lateral ocelli are known in Crustacea.

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2. Lateral ocelli in Insects.

a. In Adult Insects

It has already been pointed out that there are several cases in which the lateral compound eyes (typically and primitively present in Insects) are absent or reduced. Reduction to a very small number of units has been described in some cases in Isoptera, Coccidae, Psocidae and Coleoptera. Reduction to a single unit is characteristic of the orders Mallophaga and Anopleura. In these forms the products of reduction are clearly ommatidia and not ocelli, except in those cases in which the degeneration has been carried so far that the resulting eyes are pigment spots with practically no organised structure at all. In Aphaniptera it appears that the single eye unit is an ocellus, presumably produced by the degeneration of the compound eye, carried further than in other forms. The "pseudo-ocelli"of Myrientomata are not simple lateral eyes but post-antennal sense organs. The numerous lateral ocelli forming an "ocellar compound" eye in Strepsiptera are unique in Insects and are probably formed by a retention and multiplication of the lateral, larval ocelli of these forms. (The eyes are well developed with closely packed units and are clearly not degenerate.)

Thus extreme reduction of the compound eye

in/

in adult Insects may result in the production of a single ommatidium or very rarely of a single ocellus (in Aphaniptera).
In no case is the degeneration of the compound eye known to produce a group of separated ocelli.

In the vast majority of adult Insects there are no indications in the anatomy or ontogeny of the formation of the compound eyes from a single ocellus or from a group of ocelli.

The eyes of Collembola and Lepismata constitute the only possible exception to this. It has been suggested that these eyes may retain the impression of a primitive formation by an aggregation of units. This possibility has been discusses elsewhere (see p. 304) and on the whole it appears more probable that these eyes are degenerate and that they do not indicate a formation of the eye from separate units either in their immediate ancestors or in the Insect stock in general

2. Lateral eyes in Insects.

b. In the larvae.

Among Insects with a complete metamorphosis the larvae are typically provided with a small group of lateral ocelli. Such functional precursors of the compound eyes(which are in these cases first differentiated in the pupae) are of course not represented in the development of hemimetabolous forms, where the compound eyes are first differentiated at a fairly early stage in the nymphs. In a few cases in Diptera, Mecoptera and Lepidoptera compound eyes are precociously differentiated in the larvae but this is exceptional.

The number of ocelli in the group is small, usually not exceeding seven or eight on each side of the head. The number is not fixed for the species but varies within fairly narrow limits.

Although these ocelli are all developed as end organs of the optic nerve, they are morphologically very diverse. The different types are distributed without references to the phylogenetic relationships of the forms which they occur.

These eyes vary very considerably from simple pigment spots to structures resembling the ommatidia of compound eyes. Simple pigment spots -(presumably

/merely

merely capable of distinguishing light from dark) are found in Ceratopogon (Diptera) according to Berlese (1909, P. 636) and Imms (1934, p.79, Fig. 78A). The eyes are reduced to a pair of visual cells with two surrounding pigment cells. Similar eyes have been described in Gastropacha and Arctia (Lepidoptera) by Comstock (1933, p. 136 - 137).

Very simple ocelli, with a small number of sense cells provided with simple, unassociated, apical rhabdomeres -- (the whole presumably capable of distinguishing light intensities) -- are found in some cases, as in Tipulidae - see Constantineanu (1930) and Snodgrass (1935, p. 537, Fig 280A).

Usually, however, the eyes are somewhat better developed. In some cases the retinal cells are disposed in the form of a pigment beaker, so that the ocellus is selective, in that the sense cells receive light from certain directions only. The retinal cells in Dytiscus are arranged in this fashion (see Korscheldt,1924,p.393)

In many cases the dioptric apparatus has been elaborated and the retinal cells have increased in their depth and degree of organisation, so that the ocelli are presumably suitable for the perception of movement or possibly the formation of crude images.

The elaboration of the dioptric system consists in the formation of a "vitreous body" to supplement the

/corneal

corneal lens. This "vitreous body" may comprise a small number of transparent, scattered hypodermal cells lying below a poorly developed lens, as in Culex -- as described by Constantineanu (1930) - see Snodgrass (1935, p.538 Fig. 280). In other cases the hypoderm cells form a continuous, thickened, transparent layer, either poorly developed as in Melusina (Simulium) or well formed as in Allantus (Tenthredinidae) -- as described by Constantineanu (1930) and Corneli (1924). In the more highly developed forms some of the hypodermal cells may give rise to a solid or fluid secretion, resembling the crystalline cone of Insects compound eyes, but differing from this in the rounded form and (generally variable) number of the cells from which it arises. In Chironomidae such a "vitreous body" is present and is formed from four or five cells. (A degenerate ocellus without the vitreous body often accompanies and is attached to the fully developed structure).
Snodgrass (1935, p. 538) includes a figure of this eye in his survey of the larval ocelli. A very similar "vitreous body" comprising three segments has been described in Myrmelion (see Berlese [1909, pp.653-654, Fig. 807]) and in some Tricopterous, Lepidopterous and Coleopterous forms (mentioned in connection with the compound eye --- see p. 303).
A more elaborate vitreous secretion made up of eight

/parts

parts is found in *Sialis* as described by Hesse (1901) and in *Dytiscus* as described by Korschel~~d~~t (1924, p. 391).

Thus the supplementary, dioptric structures of the eyes of Insects vary from a very simple, ocellar type to one in some respects resembling the condition in ommatidia of the adult compound eyes, although the arrangement and number of its parts never exactly corresponds to that of the typical condition of the ommatidia.

The retinal cells also show a tendency to elaboration. In some cases, as in *Sialis*, this results in a very specialised arrangement. As has been described by Hesse (1901) and figured by Berlese (1909, Fig. 806) the retinal cells in this case are arranged in two concentric strata in which the rhabdomeres, although remaining apical, are partly coalesced with those of neighbouring cells. The condition of the retinal cells is however generally less elaborate than this.

In the simplest forms the retinal cells are arranged in a continuous layer below the lens. The cells are not associated into groups and bear small, separate, apical rhabdomeres. Reduction in the number of the retinal cells and their convergence to, or arrangement about, a single axis (with adjacent rhabdomeres associated together in an axial rhabdom) are not uncommon features.

In the ocelli of Dytiscidae as described by

/Korschel~~d~~t

Korshel~~y~~t (1924, p. 393) it is apparent that the retinal cells have been pushed inwards to form a cup below the lens and vitreous body. The rhabdomeres, while remaining morphologically apical and separate, as in a typical ocellus, (Fig. p.) are so arranged that they lie along the sides of a narrow, central cavity. In this arrangement of the cells about a single, central, longitudinal axis they resemble the ommatidial condition, although the eyes are morphologically distinct from compound eye units.

A more advanced condition obtains in the larval eyes of Tricoptera, Lepidoptera and some Coleoptera (Bru~~g~~chidae). These resemble very closely the eye of Collembola and Lepismata, differing from them only in the number of the cells involved in the formation of the "vitreous body" and in the number of the retinal cells. (The retinal cells as in Lepismata and Collembola are in two layers but differ from these in that the upper row is composed of three and the lower of four cells) - (See Berlese, 1909, pp. 653-654). These eyes, although usually spoken of as ocelli, are therefore all but ommatidial in form and combine the best developed type of vitreous body with the most highly organised rhabdom arrangement found in the larval eyes in Insects.

In connection with the relationships of the lateral larval ocelli in Insects there are two main possibilities.

/Firstly

Firstly these eyes may represent the retention of a primitive condition, indicating the phylogenetic origin of the compound eye from separate, ocellar units. Alternatively the eyes may be adaptive and secondary, without phylogenetic importance, and offering no indication of the mode of formation of the compound eye in Insects.

These possibilities are considered in turn.

From an anatomical aspect it is rather tempting to adopt the first view. In the larval eyes there are indications of numerous stages in anatomical transition between a simple pigment spot, a pigment beaker ocellus, (like that of Dytiscus), and an ocellus differing very little from an ommatidial condition. It is fairly easy, in theory, to derive lateral eyes of the Dytiscus type from simpler forms by a deepening of the retina and consequent depression of the cells to form a cup, accompanied by such elaborations of the accessory dioptric and retinal structures as are common in well developed ocelli. By another step eyes of the type of Lepidopterous larvae are fairly readily derived from those of the Dytiscus type. Aggregation and elongation of the latter would lead to a reduction in the number of sense cells. Elongation of the cells might well result in those at the base of the cup becoming nearly vertical and forming a lower layer, separate from the upper layer

/formed

formed by the cells along the walls of the cup. In such a transformation the rhabdomeres would be drawn out to lie in the axis of the eye. Further elongation and approximation of the rhabdomeres, together with a reduction in the number of cells comprising the vitreous body would complete the changes necessary to convert a Dytiscus ocellus into an eye of the type of the Lepidopterous larvae. (See Plate I9.)

The comparative anatomy of the larval eyes is therefore not incompatible with a view of these as representing an early phylogenetic stage in the formation of the compound eye from separate units. The fact that possible traces of such a stage have been preserved in the development of the holometabolous insects, while these are absent in other Insects, as well as in Crustacea and Trilobites, might be explained by the peculiarly lengthened duration of the early stages in the development of these Insect forms. It is possible that the phylogenetic stage (supposed on this view to be represented by the larval ocelli) is passed through very rapidly or is completely omitted in other forms, in which the early stages in development are abbreviated and do not achieve the independent and active existence of Insect larvae.

Such a view of the larval eyes as indicating the mode of formation of the compound eye takes no account of

/the

the fact that they might well have been modified by their early development as functional elements so that their condition may no longer be any guide to the course of evolution of the compound eyes in Insects.

In considering the primitive or secondary significance of the larval ocelli it must be emphasised that larvae are absent in the most primitive Insects. The Larval form itself is often considered as secondary and is certainly adaptive in many of its features, especially those which, like the eyes, are related to the active collection of food. Avebury (1902, pp. 80 - 81) emphasised the adaptive and secondary nature of the larval morphology - "It is evident that while the embryonic development of an animal in the egg may be the epitome of its specific history, this is by no means the case in types in which the young forms have a separate and independent existence, where the form of the young depends largely on conditions, which are generally different from those in the mature forms, with the changes undergone in the young due to its immediate wants rather than its final form"

Whatever their phylogenetic relationship to the compound eye, it is a remarkable feature of their ontogeny that the larval eyes, even when they approximate to the conditions of an ommatidium, do not become elements of the adult compound eye. The compound eye is

/independently

independently formed from the epidermis and shows no traces of a stage in ontogeny resembling the larval ocelli. In a few cases the larval ocelli are said to be retained in the adult along with the compound eye but they are never transformed into ommatidia. They are sometimes withdrawn into the head, where they are found as rudiments attached to the optic nerve as in Dytiscus (see Snodgrass, 1935, p. 536) and sometimes regress completely. Thus, at least in ontogeny, the ocelli do not give rise to ommatidia.

In the remaining Insects (without larvae) as well as in Trilobites and Crustacea, the compound eye, (which throughout these classes is formed on a remarkably stable pattern) shows little or no indication in its anatomy or development of formation from separate units. It would therefore be remarkable to find such indications in the eyes of Insect larvae.

The similarity between the larval eyes of the Lepidoptera, Trichoptera and Bruchidae and the adult eyes of Collembola and Lepismata seems to call for some comment.
The condition in these eyes is also interesting in having some resemblance to that in Scutigeromorpha - see p. 447 . Since the larval eyes are probably to be regarded as secondary and adaptive, these similarities are presumably due to parallel evolution.

It has already been pointed out that the condition in Lepismata and Collembola is probably degenerate

/rather

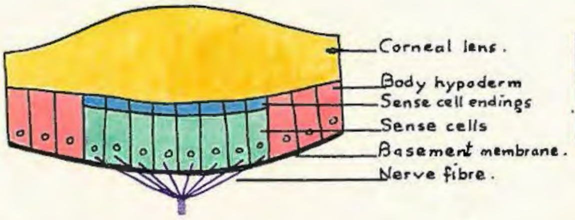
rather than primitive. It appears probable that these eyes have arisen from a partially degenerate compound eye rudiment, remaining in forms in whose ancestors the eyes had become very much reduced. In Collembola and Lepismata the re-formation of the eye has followed the main lines of development of the true compound eye, with the structure modified by degeneration. It seems probable that the ommatidia — like larval eyes — are to be accounted for in a similar way. The larval eyes are in all cases formed from an early, lateral eye rudiment. In some cases this is poorly developed and the resulting eyes are ocellar in type. In some cases however this eye rudiment has achieved a higher grade of organisation. In a few cases this may even result in the compound eye itself achieving a precocious differentiation in the larva. In others the rudiment is slightly less highly developed but is sufficiently well organised to retain the main form of the adult ommatidium, although this is modified, as in Collembola and Lepismata, in this case by the early stage of its formation and in the latter by partial degeneration of the eye, to achieve a morphologically similar expression.

Thus while the anatomy of the larval eyes is not incompatible with the view that they represent the retention of primitive ocellar precursors from which the compound eye arose, it seems on the whole more probable that the larval ocelli are secondary structures.

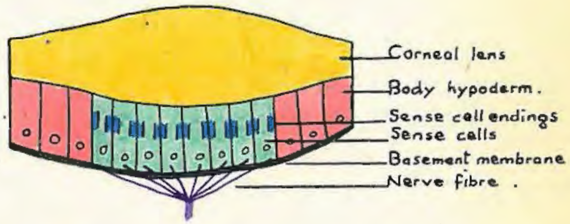
/Although

Although they all arise from early, lateral eye rudiments and are developed as the end organs of the optic nerve they are morphologically diverse, their variation being without apparent relation to the phylogenetic position of the forms in which they occur. Like many other larval features they are variously developed in accordance with the immediate wants rather than the final forms of the animals. It is probable the eyes in phylogeny, as in ontogeny, do not give rise to ommatidia and that they are merely secondary and temporary adaptations to an active larval life and without real phylogenetic significance.

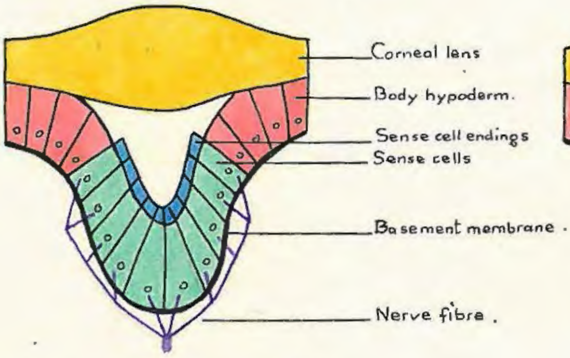
Some Common Variations in the Form of the Lateral Ocelli of Insect Larvae.



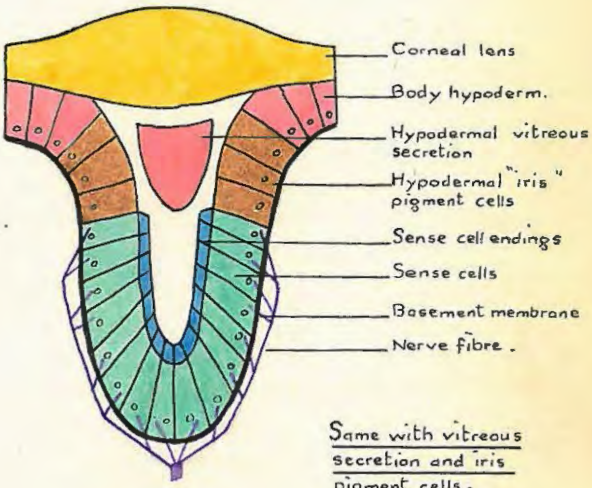
Simple Flat ocellus with unassociated retinal cells with apical end organs.



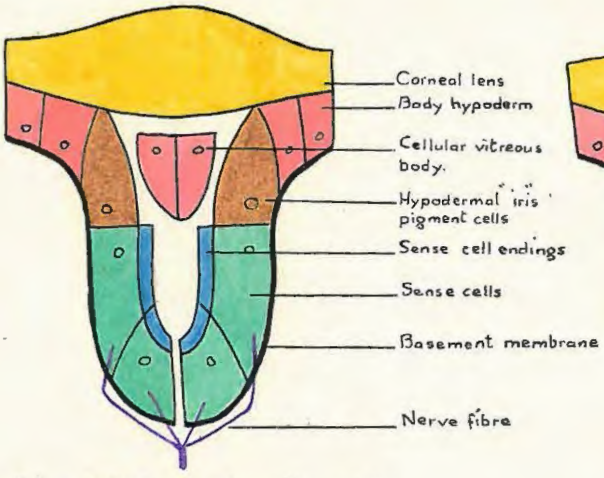
Simple flat ocellus - The retinal cells associated in small groups round short axial end organs.



Pigment Beaker Ocellus. Retinal cells about a single axis with apical rhabdomes.

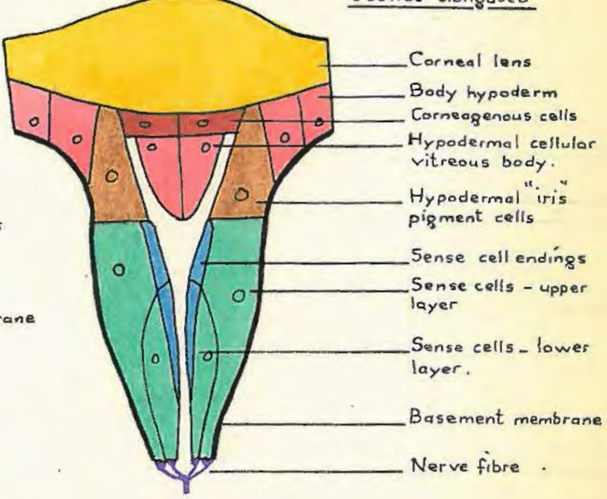


Same with vitreous secretion and iris pigment cells. Ocellus elongated



Pigment Beaker Ocellus. with cellular vitreous body*. Retinal cells about a single axis, reduced in number and enlarged, lying longitudinally with axial end organs.

*and "iris" pigment cells (omitted.)



Pigment Beaker Ocellus with cellular vitreous body, separate reduced corneagen cells, retinal cells in two superimposed layers with axial end organs.

3. Lateral ocelli in Trilobites .

So called "simple" lateral eyes are present in some Trilobites, in which compound, lateral eyes are absent. As these are here regarded as the products of degeneration of a primitive compound eye, they have been considered in connection with the latter. -

In some cases the compound eyes have degenerated to produce a schizochroal compound eye in which the lenses are separated and enlarged, circular and biconvex. As far as the preserved details show, the course of degeneration has followed the same lines as in Crustacea. Whether these and the so-called "simple" lateral eyes are of ommatidial or ocellar structure must remain unknown. In view of the fact that degeneration of the compound eyes in Crustacea is never known to produce ocelli, it is to be assumed that these simple eyes were probably ommatidial.

As in Crustacea there is no clear indication in the anatomy or development of the lateral compound eyes that these were formed from a single ocellus or an aggregation of ocelli. The only possible evidence which might be claimed as indicating such an origin is the development of <u>Calymene</u>, where the eye units

proceed/

proceed from a separate, or schizochroal, condition to a closely approximated, or holochroal, condition. This is, however, a late form, and the mode of development unusual, so that the development of the eye is probably without relation to the main, phylogenetic sequence.

For various reasons given above (see p. 369) it is suggested that the blind forms are secondary and have arisen sporadically, that the compound eye was not evolved within the Trilobites, but was a common ancestral heritage, shared with the primitive Crustacea.

4 Lateral ocelli in Eurypterida

There is nothing in Eurypterida comparable with the simple, lateral or schizochroal eyes of Trilobites and no evidence in anatomy or ontogeny that the compound eyes are in the course of formation. They appear to a stable and well established structures.

The smooth, unthickened corneae of some forms point to a secondary loss of facets, similar to that which appears to have occurred in some of the lower Crustacea. The Cornea is uniform and unthickened and clearly not of an ocellar type.

The occasional absence or reduction

in sixe of the eye is clearly secondary. There is no evidemce of the formation of the eyes from separate units.

5. Lateral ocelli in Arachnida .

In Arachnida other than Xiphosura the lateral eyes, where present, are universally ocellar in type. Lateral eyes are absent in Palpigrada, Podogona, Phalangida and Pentastomida. Purcell (1892, p.461) has described the structure and emphasised the median origin of the ocelli in Phalangida, while Sokolow (1912,pp.183-184) and Hanstrom (1927, p.247) have dealt similarly with the eyes of Pentastomida. The eyes in Palpigrada are replaced by hair-like sense organs (see Hansen, 1917, p.66). For the rest the eyes have been described among the Scorpiones in *Scorpio* (Graber, 1879), in *Androctonus funestus* and *Euscorpius italicus* (Lankester and Bourne, 1883, pp.182,186), in *Scorpius europaeus*, *Buthus afer*, *Ischnurus caudicula*, *Lychas americanus*, *Androctonus funestus*, *Euscorpius italicus*, *Euscorpius carpathicus*, *Androctonus ornatus* and *Centurus* sp. (Parker 1887, pp. 196 & 201). Among Araneida the eyes have been described in Epeiridae, Lycosidae and Salticidae (Grenacher, 1879, pp.39 - 59), in *Stalita taenaria* and *Hadites tegenaroides* (Simon 1878, pp. 8 - 23), in *Agelina naevia* (Locy 1886, pp. 89 - 94) (Mark 1887, p.49 et seq.), *in Theridium tepidatorium* (Mark 1887, p.49 et seq.), in Areneina in general (Kishinouye, 1891, p.353), in *Attus sp*, *Lycosa meridiana*,

Tarentula /

Tarantula aculeata, Tarantula sp, Lycosa hortensis, Lycosa sp, (Hentschel, 1899, p.533 et seq.) in Epiera, Zilla, Meta, Tegenaria, Theridium, Amaurobius and Lycosa (Widmann, 1907, p.755 et seq.) in Megadictyna (Dahl, 1907 pp. 60 - 64) in Salticidae, Epieridae and Dysderidae (Hanstrom, 1921 p. 15 et seq.) Among the Pseudoscorpiones the eyes have been described in Chelifer (Carriere, 1886, p.6). Among the Acarini lateral ocelli have been described in Ixodidae by Bonnet (1906, p.509 - 511) and Gossel (1935, p.177) and in Hydrachidae by Lang (1906, p.453) (No detailed description of the eyes in Pedipala and Solifuga is available.)

In all of the descriptions which have been consulted as well as in the eyes of Epiera diadema which have been examined, there is no suggestion that the eyes are other than ocellar. They are invariably provided with a well developed, biconvex lens. The retinal cells are not organised into retinular groups and, although the rhabdomeres of adjacent cells may sometimes combine to form a rhabdom of a very low grade of organisation, the number of cells combining does not exceed three and the arrangement is irregular and not on a definite pattern throughout the eye. The

rhabdomeres/

rhabdomeres are apical or where axial are very short and lie just below the apex and have presumably been secondarily transferred from the apical to the axial face of the cell.

There is no indication in the structure of these lateral eyes that they are tending to the formation of a compound eye by aggregation of many, or differentiation of one, of their numbers. If the Arachnids were primitively provided with a compound lateral eye, resembling that of *Limulus*, it is possible that these eyes may have been derived from it by separation and loss of some of its units and their subsequent modification. The differences between the unit of a *Limulus* eye and the ocellus of a spider are so profound that, in the absence of any evidence of transitional stages, this is difficult to credit. It seems more reasonable to suppose that the compound eye was lost and that lateral ocelli were developed in its place to supplement the median eyes, which have achieved a greater development here than in other Arthropods. It seems probable therefore that the lateral ocelli of Arachnids are a secondary development and without relation to the ocellar or compound, lateral eyes of other Arthropods.

6. Lateral ocelli of Diplopoda .

A survey of all the available literature on the ocelli of Diplopods has been made by Verhoeff (1932, pp. 238, 332, 335, 340, 343, 353, 356,- 359, 1164 - 1172, 1158 - 1164, 1100 - 1102). From his work as well as from the examination of the eyes of *Julus sp.* it is clear that these eyes do not differ in essentials from those of Scolopendromopha. (For this reason no detailed description is given here).

It is clear that, even where large numbers of units are present, and where these are so closely approximated as to assume the external semblance of a compound eye, they remain ocelli. Crystalline cones are never present, the retinal cells are grouped in very large numbers about a central axis and the rhabdomeres are perpendicular to this.

There is no reliable evidence that a compound eye was present in the ancestors of these forms (see p.423 .) nor any indication of a tendency for the eye units to assume the ommatidial form. The ocelli are not known to have been formed from, and (within the Diplopods) do not give rise to any eye other than an ocellar aggregation.

They are all of a distinct type and bear a very close resemblance to Chilopod ocelli.

7. The Lateral ocelli in Chilopoda with a note on Pauropoda and Symphyla .

Among the Chilopoda lateral ocelli are present in Scolopendromorpha and Lithobiomorpha. Since these are of particular interest in connection with the origin of the eye in Scutigeromorpha they are described in detail below.

a. The anatomy of the lateral simple eyes of Scolopendromorpha

Descriptions of the eyes of forms designated Scolopendra sp. have been given by Sograff (I879, pp. I6-I8) , Grenacher (I879), Graber (I879 , p. 58) , Mark (I887, pp. 60-63) , Heymons (I90I , p. I et seq), Hesse (I90I , p. I0) and Verhoeff (I925, pp. 40, 4I, I02). Sograff , who described the eyes as"resembling those of Coleopterous larvae and those of spiders ", gave a short and incomplete account which does not accord with later work. Grenacher's description seems to have been more accurrate but differs in some respects from that given below . It is available only in abstract in the work of later authors. Graber's description has been severely critisised by later authors as very inaccurrate, especially with regard to the retinal cells, which he apparently examined only in thick sections. Mark was concerned mainly with theoretical aspects of the origin of the eye and the question of whether it was formed by involution of the hypoderm or simple infolding. His account of the anatomy is slight and adds no new material to the earlier work. Heymons demonstrated the origin of the eye in a hypodermal depression but did not describe the adult structure in detail. Hesse was concerned mainly with the rhabdom. Verhoeff has pieced some of this earlier work together but added nothing to it. Thus, apart from the summary of Grenacher's work, no detailed account of the anatomy of any one species is available. (Verhoeff's composite account is gathered from authors holding different views and probably working on different species).

The eyes of Ethmostigmus trigonopodus Leach and two local Scolopendra spp. were sectioned. These differed from one another only in the dimensions of their parts. The description is therefore confined to the first of these species.

The lateral simple eyes of Ethmostigmus trigonopodus Leach 1903

External features.

A group of four ocelli is placed laterally and marginally on either side of the flattened head. They lie near the front end and are small, inconspicuous structures, presumably not of great importance in the life of the animal. The individual lenses of each group lie at the corners of a rhombus and appear as clear, colourless patches, considerably more convex than the surrounding head surface. Through these the inner pigmented parts of the eye are visible. Heymons (1901, p.1) observed, in the species which he investigated, that the most posterior of the lenses was more elongated and convex than the rest, and Verhoeff (1925, p. 41) considered that the two ocellar types differed in function. In this case the lenses appeared uniform.

The cuticle.

The lenses (c. cut .) are shown in Figures 53 and 54, 55. Like the body cuticle they have, along their outer edge, a thin, homogeneous deeply staining layer, not more than .5μ in thickness. This is succeeded by a series of thick, clearly laminated, chitinous, cuticular layers, differing from one another in the density of their laminations, and their staining reactions. (They are well differentiated by the azocarmine -aniline blue- orange G stain). The body cuticle is composed of three such layers, of which the innermost is the most dense. In the eye lenses only two such layers, both greatly thickened, are represented. These appear to correspond in structure to the first and third layers of the body cuticle. The cuticle over the general surface of the body is about 35μ in thickness, the separate layers being about .5μ, 25μ, 5μ and 5μ respectively. The thickness of the layers in the lenses is about .5μ, 65μ and 15μ through the maximum depth of the lens, where this is rather more than twice the depth of the ordinary body cuticle. This arrangement is indicated in Figure 55 and shown more diagrammatically (under lower power and with less differentiation in the staining) in Figures 53 and 54. Pore canals and hairs are frequently found in the cuticle covering the general surface of the body, but are absent from the lenses. Pore canals were described in the lenses of Scolopendra sp. by Graber (1879, p. 58) but do

/not

not seem to have been observed by other authors. The lenses are colourless or very pale yellow, in contrast to the highly pigmented cuticle of the body. At the point where they join the body cuticle there is a considerable constriction. This, together with the degree of approximation of the lenses, is indicated in Figure 53 . The lenses are all highly biconvex with the radius of curvature of external and internal surfaces approximately equal.

The corneagenous cells.

Under the ordinary body cuticle the hypodermal or corneagenous cells form a conspicuous and continuous layer - see Figures 53 and 55 (b. hyp.) These cells are regularly arranged with large, distinct, central, granular nuclei, with their boundaries fairly distinct and their cytoplasm staining readily. A thin, continuous basement membrane is apparent at the base of the layer. In this form the corneagenous cells responsible for the secretion of the lens are similar to the cells of the body hypoderm but are somewhat reduced and are clearly apparent only at the edge of the lenses, where they are continuous with the cells of the body hypoderm, as shown in Figure. 56 . Since the lenses have clearly been laid down in a series of even laminations, the corneagenous layer must presumably, in the young animals, have formed a continuous layer across the eye. This has apparently been pushed out to the periphery of the lens and reduced in size as the central part of the lens increased in thickness. This accords with the observations of Grenacher (1879) and

and Heymons (1901, p.240). Grenacher found a corneagenous layer in the young of *Rhysida*, which was complete and continuous across the eye, or interrupted only for a very small distance in the centre of the lens. This was temporarily reformed from the reduced layer of the fully developed ocellus, when the lens was regenerated in moulting. Heymons described the reduction and lateral displacement of a continuous, corneagenous layer in the development of *Scolopendra* sp. Graber (1879, p. 58) however, described in *Scolopendra* sp. a continuous series of corneagenous cells made up of elongated, transparent cells forming a distinct vitreous layer, enclosed in a basement membrane corresponding to that at the base of the body hypoderm cells. Mark (1887, p. 60) accepted this description (apparently without confirming it, and although he rejected Graber's views on the retinal cells,) since he was anxious to show that the ocelli of Chilopods had been formed on the same plan as that described by Locy (1886, p. 56) in Spiders, i.e. as a three-layered involution with pre-retinal, retinal and post-retinal layers. It is probable that in this, as in other respects, Graber's description was inaccurate. The condition here described accords with that given by Grenacher, Heymons and Verhoeff and not with that given by Graber and accepted by Mark.

The retinal cells.

The main part of the eye is composed of a collection of retinal, ~~or~~ pigmented sense cells arranged

/round

round the sides of an open beaker or cup below the lens. All the cells about the sides of the cup are arranged with their axes perpendicular to the axis of the lens and the direction of the incident light as condensed by the lens. These cells are radially arranged in superimposed layers about a slender, longitudinal, axial cavity, below the central part of the lens. Towards the base of the eye the cells are slightly inclined towards the axis of the ocellus, while a few cells at the base of the cup are parallel to this. The cells at the upper edge reach a length of up to 80μ, the inclined cells towards the base of the eye decrease in length to 30μ, while those at the base of the eye and parallel to its axis are only about 15μ in length. All the cells are conical in form, wedge shaped in longitudinal section, and taper towards their inner ends in the axis of the eye. Their arrangement is remarkably symmetrical.

The nuclei are always near the outside of the cells. They are relatively large, stain deeply, have a conspicuous, outer wall and dense, granular contents including one or two nucleoli.

In animals killed in the light the outer ends of the cells, containing the nuclei, are filled with densely packed, dark brown pigment granules. Below the nucle nuclear region, and between this and the rhabdom, the pigment granules are regularly arranged in a layer along the sides of the cells. The rest of the cell is filled with a finely granular, faintly staining cytoplasm. The

/distinct

distinct boundaries of the cells, which are slightly flattened against one another, impart to transverse or oblique sections the appearance of a slightly irregular pattern of polygons - see Figure 57.

The rhabdom.

At their inner ends, in the axis of the eye, the retinal cells bear sense rods or rhabdoms. Their arrangement is shown in longitudinal section in Figures 53, 54, 56 and 58 and in transverse section in Figure 57. These cells vary in length throughout the eye but not strictly in proportion to the length of the cells bearing them. At the top of the eye they are about 35μ in length and at the base of the eye about 12μ.

Each retinal cell is encased in its lower part by a thickened wall - the rhabdom. This is contiguous on all sides with the hollow rhabdomes of the surrounding cells so that the sense rods of the entire eye form a loose mesh, when viewed in transverse section, as seen in Figure 57. In longitudinal section the contiguous walls of adjacent cells form a single continuous structure as seen in Figure 58.

A continuation of the cytoplasm of the retinal cells (c. r. c.) fills the axial hollow of the rhabdom rods as seen in Figures 54 and 58. This is so thin and stains so poorly that it sometimes appears practically absent as in Figure 57.

The rhabdoms themselves seem at first sight uniform, deeply staining masses. When carefully observed

/under

under higher powers, they appear striated perpendicularly to their length as shown in Figure 58.

The description of the retinal cells and rhabdoms given above accords with that given by Heymons (1901, p. 140), Hesse (1901, p.10) and Verhoeff (1925, pp. 40-41), all of whom describe the rhabdom as a hollow rod filled with protoplasm. The earlier authors gave no very precise description of the retinal cells and rhabdom.

Nerve fibrils could not be traced into the rhabdoms, nor have they been described in related forms. The rhabdoms appear to be chitinous secretions of the retinal cells, probably refractive in function. This is in accordance with Nowikoff's view of the rhabdom, see p. 14

The retinal cells at the base of the eye, which run parallel to its axis, differ from the remaining retinal cells in being uniformly pigmented throughout their length and in being devoid of rhabdoms. Like the rest of the retinal cells, they are supplied with nerve fibres as seen in Figures 54. 56. 57 and are probably derived from retinal cells which, being unfavourably orientated, have lost their sensory function. The peculiar orientation of the retinal cells which possess rhabdoms, that is, their arrangement perpendicular to the main incident light rays, appears designed to expose the rhabdom to the maximum possible illumination.

<u>Basement membrane and associated structures.</u>

The entire eye is surrounded by a thin, structureless membrane, which is a continuation of the

/basement

basement membrane of the hypoderm of the body wall. The retinal cells are presumably responsible for its formation. No post_retinal cells are apparent. Grenacher (1879) although not entirely convinced, had conditionally assented to their presence and this was acceptable to Mark (1887,p.62) since it was favourable to his view of Myriapod ocelli as fo formed by a three layered involution. No post-retinal cells have been described by other authors working on Scolopendromorphs.

The optic lobes are small and the ocelli supplied by branches of a single optic nerve. These branches consist of numerous fibres contained within an outer sheath. In the neighbourhood of the eye the fibres spread out and each one enters one of the retinal cells as shown in Figures 56 and 57.

Small pigment cells of irregular form and disposition lie about the nerves and below the basement membrane. These are presumably of mesodermal origin. The nuclei of some of these are apparent in Figure 56 (pig.c.n.)

No tracheal branches could be traced in the immediate neighbourhood of the eye.

Figure 53.

c.cut.	Corneal lens.
b.cut.	Body cuticle.
b.hyp.	Body hypoderm.
c.cut.	
I.	Thin,homogeneous,outer layer of lens
C. cut.	
2.	Inner thick,laminated,cuticular layers of lens- here not further differentiated.
p.b.c.	Longitudinal section showing the open pigment beaker formation of the eye .
r.c.	Retinal cells.
b.r.c.	Basal retinal cells.
r.c.n.	Retinal cell nucleus.
r.c.p.	Retinal cell pigment.
rhb.	Oblique section of several superimposed layers of rhabdom structures.
b.m.	Besement membrane.
n.f.	Nerve fibres.

Figure 53

Section passing through three of the ocelli of the group of four.

A. Longitudinal section
B. Oblique section
C. Superficial oblique section through the upper ends of the retinal cells

Microscopy

8mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
4 μ section

Preparation

Fixation :	Alcoholic Bouin
Embedding :	Double embedding in Ether-Alcohol (75:25) solution of celloidin, through $CHCl_3$ in 60 degree's m.p. wax
Staining :	Heidenhain's Iron Alum haematoxylon Aqueous Eosin
Mounting :	Through Toluol in Toluol-Clarite

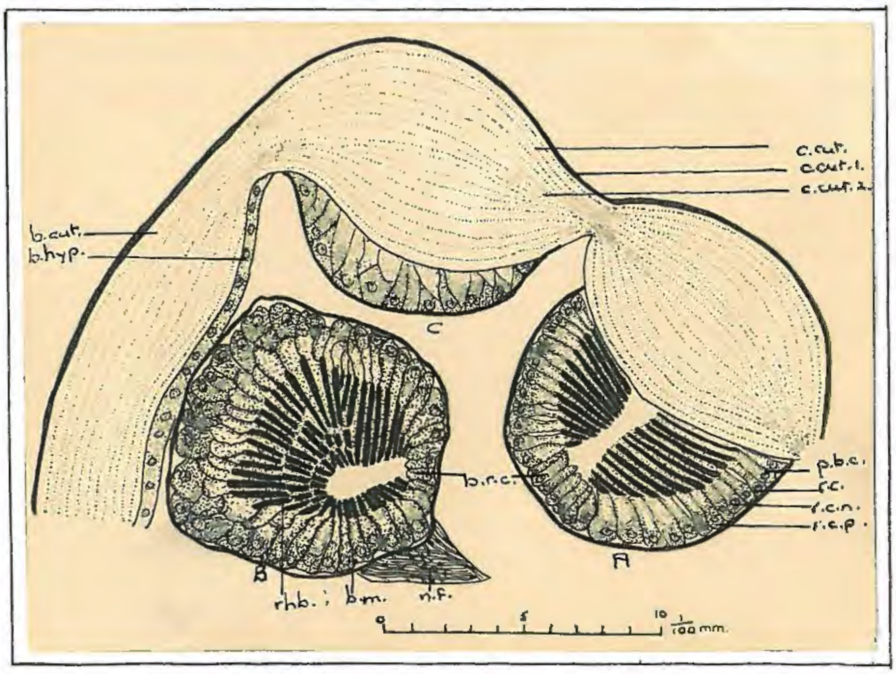


Figure 54.

c. cut .	Corneal lens.
b.cut.I.	Thin, homogeneous, outer layer of lens.
c.cut.2.	Inner, thicker, laminated, cuticular layers- here not further differentiated.
c.l.c.	Central, longitudinal cleft between the two parts of the ocellus- possibly at least in part an artefact.
r.c.	Retinal cells, perpendicular to the eye axis.
b.r.c.	Basal retinal cells deeply and uniformly pigmented without rhabdom structures.
r.c.n.n.	Retinal cell nucleus with nucleolus.
r.c.p.	Retinal cell pigment granules.
r.c.cy.	Clear, axial cytoplasm of the retinal cells
rhb.	Rhabdom structures.
b.m.	Basement membranes .
n.f.	Nerve fibres.

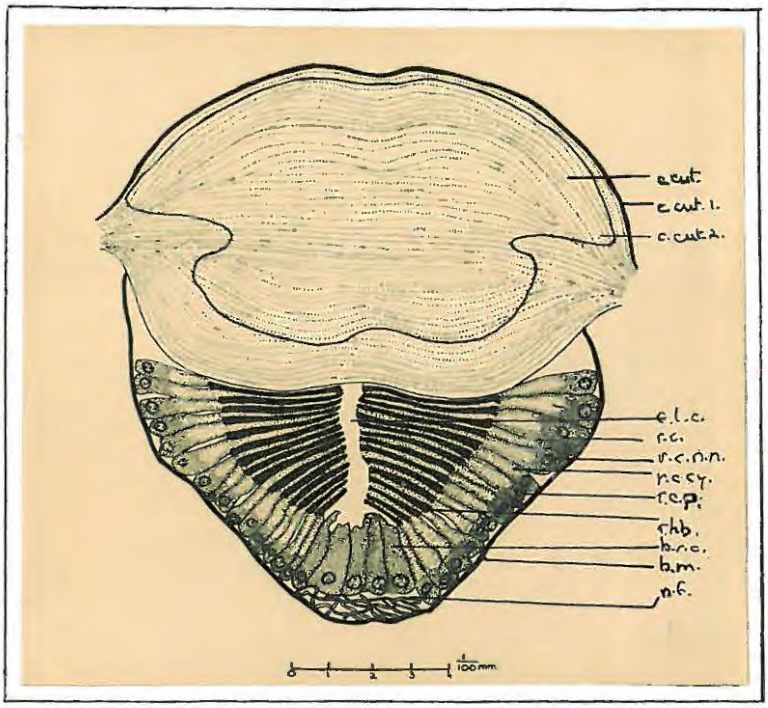


Figure 54

Longitudinal section through one ocellus

Microscopy
8mm Apochromatic objective
X20 Holoscopic eyepiece
Camera Lucida drawing
2.5–3 μ section

Preparation

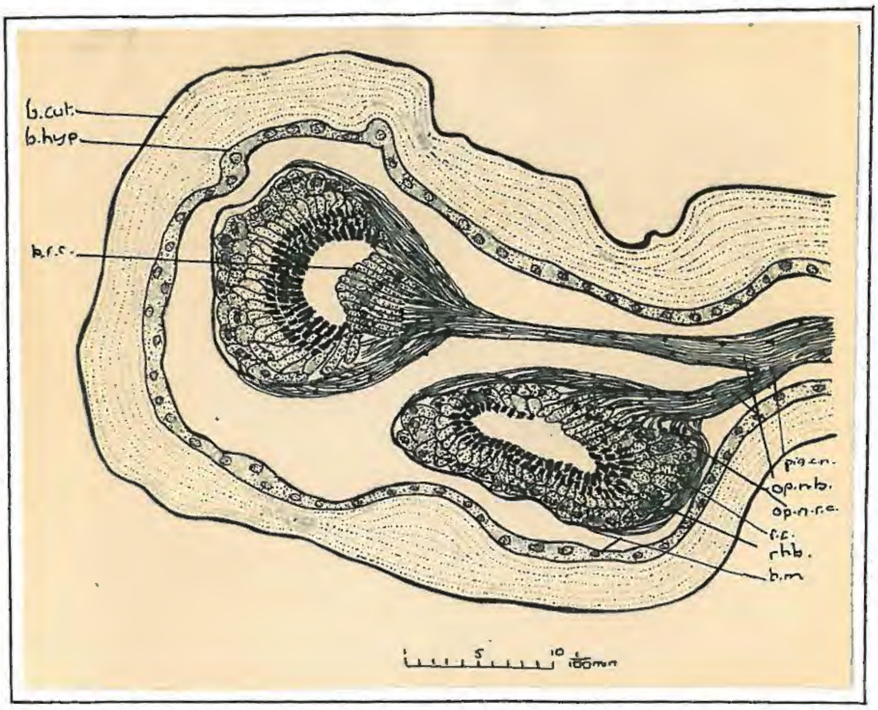
Fixation	: Alcoholic Bouin
Embedding	: Double embedding in Ether-Alcohol (75:25) solution of celloidin, though $CHCl_3$ in 60 degrees m.p. wax
Staining	: Depigmented in Grenacher's fluid Azo-carmine Aniline blue Orange G.
Mounting	: Through Toluol in Toluol-Clarite

Figure 56.

b.cut.	Body cuticle.
b.hyp.	Body hypoderm.
op.n.b.	Optic nerve branching.
op.n.r.c.	Optic nerve entering the retinal cells.
r.c.	Retinal cells.
b.r.c.	Basal retinal cells.
rhb.	Rhabdom structure.
b.m.	Basement mebrane.

Figure 5a.

Longitudinal section through two of the ocelli showing their connections with the optic nerve fibres.



Microscopy
8mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
3 μ section

Preparation

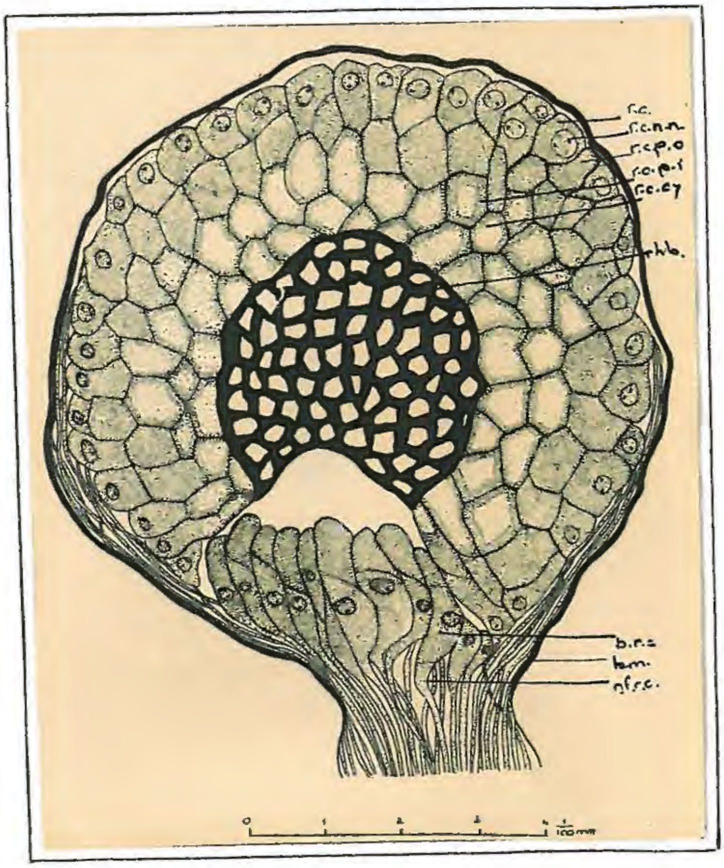
Fixation : Alcoholic Bouin
Embedding : Double embedding in Ether-Alcohol (75:25) solution of celloidin, through Chloroform in 60 degrees m.p. wax
Staining : Depigmented in Grenacher's fluid
Methylene blue
Mounting : Through Toluol in Toluol-Clarite

Figure 57.

r.c.	Retinal cells seen in transverse to oblique sections, appressed to assume a somewhat irregular, polygonal form.
r.c.n.n.	Nucleus of retinal cell with nucleolus.
r.c.p.o.	Large, outer pigment granules .
r.c.p.i.	Pigment granules clothing the sides of the inner parts of the retinal cells.
r.c.cy.	Inner, finely granular cytoplasm of the retinal cells . (This actually extends into the rod region - see Figure 58 but stains so faintly in this region that it is hardly apparent).
rhb.	Rhabdom structures of the whole ocellus forming a loose mass.
b.r.c.	Basal retinal cells - two sets cut obliquely- deeply and uniformly pigmented and continuous with nerve fibres.
n.f.r.c.	Nerve fibre passing into retinal cell.
b.m.	Basement membrane deficient where the optic nerve passes into the eye .

Figure 57.

Longitudinal abaxial section of one of the ocellus to show the rhabdom structure and the disposition of the pigment, in the retinal cells.



Microscopy
8mm Apochromatic objective
X 20 Holoscopic eyepiece
Camera Lucida drawing
(Drawing re-enlarged before filling in details)
3 μ section

Preparation

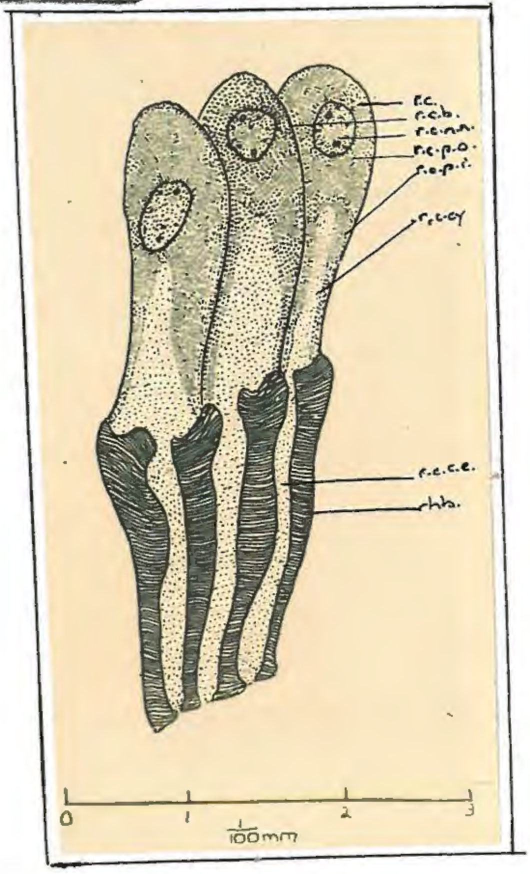
Fixation : Alcoholic Bouin
Embedding : Double embedding in Ether-Alcohol (75:25) solution of celloidin, through CHCl3 in 60 degrees m.p. wax
Staining : Depigmented in Grenacher's fluid
Azo-carmine, Aniline blue, Orange G.
Mounting : Through Toluol in Toluol-Clarite.

Figure 58 .

r.c	Retinal cell.
r.c.b.	Boundary of retinal cells.
r.c.n.n.	Nucleus with nucleolus.
r.c.p.o.	Outer, dark, dense mass of pigment surrounding the nucleus.
r.c.p.i.	Continuation of the retinal cell pigment along the sides of the cell.
r.c.cy.	Clear retinal cell cytoplasm .
r.c.cy.e.	Extension of the retinal cell cytoplasm into the cavity of the rod. This staims very faintly.
rhb.	Rhabdom structure - very faintly transversely striated. The walls of the retinal cells are their lower ends are thickened to form these rods which are shared between adjacent cells.

Figure 58 .

Enlarged detail of three of the retinal cells in longitudinal section.



Microscopy .
3 mm Apochromatic objective.
X 20 Holoscopic eyepiece.
Camera Lucida drawing-outline.
(Re-enlarged before details were drawn in).
3 μ section.

Preparation.

As for figure 57 .

b. The anatomy of the lateral ocelli of Lithobiomorpha.

The eyes of the only common local Lithobius species proved on examination to be very degenerate and to constitute little more than a pigment spot below a small lens. Better developed eyes have been described in Lithobius spp. by Graber (I979,p.58), Grenacher (I879), Sograff (I979, pp. I6-I8), Willem (I89I, p. 482), Hesse (I90I) and Verhoeff (I925, pp. 40, 4I, I02 et seq). The work of Graber and Sograff is rather summary and has been condemned as inaccurate by the other authors concerned. Graber and Sograff were apparently working with thick sections.

In its essential structure the eye of Lithobiomorpha resembles that of Scolopendromorpha. The number of retinal cells is reduced. These are larger and shorter and are differentiated into two types. The lower cells resemble those of Scolopendromorpha very closely while the rods of the upper cells are reduced in thickness to form slender hair-like structures, which are highly refractive. These cells, like the lower retinal cells, are pigmented, have a nerve supply and are disposed in a layer with the rods perpendicular to the axis of the eye. Together with the lower retinal cells they form a continuous cup and it is to be presumed that they are modified retinal cells.

/This

This view is taken by Hesse and Verhoeff. A continuous, corneagenous layer, such as that described in some phases of development in Scolopendromorpha has not been found in Lithobiomorpha, the corneagenous cells being restricted to the sides of the lens as in the usual arrangement in Scolopendromorpha. (Willem (1891, p. 482) had described scattered remnants of the corneagenous cells below the lens in Lithobius but this has not been confirmed). Apart from these minor differences the lateral ocelli are remarkably uniform in structure, and are all clearly ocellar with a well developed, biconvex lens, with nothing resembling a cone or additional refractive secretion, with unorganised retinal cells, not associated into retinula groupings and with separate rhabdom structures, morphologically apical and arranged perpendicularly to the incident light. In none of these particulars do they approximate to the compound eye conditions.

c. The relationships of the lateral simple eyes of Chilopods.

The following are the main possibilities with regard to the origin and relationships of the lateral ocelli in Chilopods. Firstly they may be the products of degeneration of the eyes of the Scutigeromorpha type. Alternatively they may be primitive precursors of these. Thirdly they may have been separately evolved (in forms in which the compound eye has been lost or has failed to develop) and unrelated to the lateral eyes of other Arthropods

/-pods

pods other than those of Diplopods. These possibilities are considered in turn.

Rosenstadt (1896, p. 374) has upheld the first suggestion - namely that the ocelli are derived from the "pseudocompound" eyes by degeneration. There is an entire lack of precedent for supposing such a course in the evolution of the eye. In no other cases is a compound eye of any kind definitely known to degenerate into a group of separate and well formed ocelli. These ocelli are of a distinct type, resembling closely the ocelli of Diplopods. Within the Chilopods and Diplopods they are widely distributed, well established structures in contrast to the "pseudocompound" eyes, which are restricted in distribution and highly variable with every appearance of a recent origin. It seems probable therefore that the ocelli were not derived from the "pseudocompound" eyes by their degeneration.

It has been pointed out, in the section dealing with the compound eyes, that these have probably been formed by a relatively recent aggregation of separate units. It is possible that these units may have been of the type of the lateral ocelli of Chilopods.

A formation of the eye of Scutigeromorpha by a coalescence of ocelli, resembling those of Scolopendromorpha and Lithobiomorpha would involve the changes indicated in outline on pp. 24,25 . If such a transformation occurred its course would probably have been as follows. An increase in the number and approximation of the units would lead to their narrowing and elongation, accompanied by crowding out of the cells at the base of the eye and a reduction in the number of the retinal cells. In accordance with the elongation of the unit these cells would be drawn out in a direction perpendicular to that in which their main axis had been disposed in the ocellar units. This might well be accompanied by a transference of the rhabdom structures to the axial faces of the cells and their approximation to form a central rhabdom. In accordance with the new conditions of illumination and functioning the crowded condition at the outer surface of the eye (resulting from the aggregation of ocellar lenses) would have led to the flattening and approximation of these lenses. This reduction might well have led to the development of supplementary dioptric structures - the cones - arranged below the surface of the eye. The cones so formed would have been placed between the upper ends of the existing retinal cells, some of which in the course of further approximation and elongation of the ommatidia would probably have been drawn down to form a lower layer.

Thus, while it is probable that the eye in Scutigeromorpha has been formed relatively recently by an aggregation of separate and many celled units, it is by no means certain that these units were of the type of Chilopod ocelli. There are no forms, intermediate in internal structure, linking these eyes and the gap remains a condiderable one, although the absence of any other type of eye unit, (from which the pseudocompound eyes might have been formed), suggests that this gap may have been bridged.

On the whole the following is suggested as the most probable course for the evolution of the eyes in Chilopods and Diplopods. Chilopods and Diplopods were presumably derived from ancestors resembling the Pauropoda and Symphyla. These forms are blind or provided with only very poorly developed lateral ocelli (a single pair).

They were probably nearly related to some of the early Insects, which were secondarily blind or with very reduced eyes. These Insectan types appear to have given rise to the Collembola and Lepismata, in which the eyes have been re - developed from a lateral eye rudiment along lines corresponding to those of the true compound eyes (presumably present in their distant ancestors) but modified by intermediate degeneration.

The degeneration of the eye rudiment in Pauropods and Symphyla appears to have been carried further that that in the forms giving rise to the Collembola and Lepismata.

Thus when eyes were re-formed, presumably in response to an increased exposure to illumination, in the ancestors of the Chilopods and Diplopods, they bore no resemblance to the compound eyes of the distant, supposed ancestors but were simple ocelli (an ocellar evolution parallel to this appears to have taken place in Insect larvae - see p. 478) The "pseudocompound" eyes of some Chilopods are apparently of more recent origin and formed anew from aggregated units.

These "pseudocompound" eyes together with the lateral ocellar eyes of Diplopods are presumably the expression of a very widespread and general tendency to the formation of lateral, aggregate eyes - a tendency present in all the main Arthropod classes, although expressed in morphologically diverse fashion. It is possible that the "pseudocompound" eyes were formed from the ocelli of other Chilopods or that they arose from an eye rudiment more generalised than these and of which no trace is preserved in the living forms.

Thus the eyes of Collembola, Lepismata and Scutigeromorpha are all apparently formed from ancestral types in which the eyes were lost or severely reduced). The pattern of the true compound eye has been preserved in the Insect types, while the "pseudocompound" eye in the Chilopods is formed in a new way by aggregation of separate units, possibly resembling Chilopod ocelli possibly more generalised than these.

Conclusions - The lateral ocelli.

I. Occurrence .

Lateral ocelli are absent in Crustacea and probably in Trilobites and in Eurypterida . They are present in all the remaining Arthropod classes. They never exist simultaneously with compound eyes , although they may preceed the latter in development as functional end organs of the same nerve.

It is possible that these eyes may be the phylogenetic successors or precursors of the different types of lateral, compound eyes or that they may be without relation to the latter. An attempt has been made to decide this for each class of Arthropods.

2. Comparative anatomy .

There is no common anatomical pattern such as is traceable in many of the lateral, compound eyes. Lateral ocelli vary from pigment spots to ommatidia-like structures. Among Insects lateral ocelli are rare in adults and when present are poorly developed. In the larvae they show the full range of variation in structure. (The "ocellar compound " eyes of adult Strepsiptera are probably the result of retention and multiplication of lateral, larval ocelli)

The ocelli in Arachnida are characteristic of the class as a whole, are well developed, and show relatively little variation in structure. The ocelli characteristic of Diplopods and of Chilopods, other than Scutigeromorpha, are very similar and of a distinct and constant form . They do not resemble in detail the lateral ocelli of any other Arthropods , although a similar type of eye is known in the pigment beaker ocellus of some Insect larvae.

3. Indications of the formation of ocelli from compound eyes.

Such indications are few and uncertain . The conditions are as follows :- .

(i) In Crustacea .

Compound eyes on degeneration give rise to units , which , although modified , are clearly ommatidia and not ocelli. (The so-called lateral ocelli of Copepods are displaced median, dorsal eyes).

(ii) In Insect adults .

The compound eyes , on degeneration , normally give rise to one or more ommatidia , unless the degeneration is so complete that only a pigment spot remains . Degeneration appears to have produced a single ocellus in Aphaniptera but in no case does the compound eye degenerate into a well developed group of ocelli.

(iii) In Insect larvae .

The larval ocelli preceed the compound eyes in ontogeny and are not the products of its degeneration

(iv) In Trilobites .

The "Schizochroal " eyes resembling those of some Crustacea (where the comopound eye has degenerated) and the so-called simple lateral eyes , are both apparently derived from lateral, compound eyes. In the absence of internal evidence it must be presumed that these eyes , like the products of degeneration of the compound eyes in Crustacea, were ommatidial rather than ocellar in form.

(v) In Eurypterida .

The lateral eyes do not degenerate into separate units and there is no indication that they are ever other than compound in type.

(vi) The Arachnida .

It is possible that the lateral, simple eyes in Arachnida have been formed by the degeneration of a *Limulus*-like eye . There remains however a wide gap between these eyes and it seems more likely that the compound eyes were lost and the ocelli formed anew so that they are secondary and without near relation to the lateral eyes of other Arthropods.

(vii) In Diplopods .

The lateral ocelli characteristic of living Diplopods are not known to have been formed from anything other than ocellar aggregations.

(viii) In Chilopods .

The ocelli of Chilopods do not appear to have been formed by the degeneration of a lateral compound eye. There is no precedent for such an origin for a group of lateral ocelli, which can be claimed with certainty.

4. The possibility of the formation of compound eyes from ocelli .

There is no clear evidence that a compound eye was formed, either primitively or secondarily, from a single ocellus or from a group of ocelli in Crustacea , Trilobites , Eurypterida or Diplopods. It is possible that the eyes of Xiphosura may have arisen from a coalescence of separate units but the evidence for this is very incomplete - see p. 4I7 . It is probable that the larval ocelli are secondary and adaptive features and do not indicate the formation of the compound eye from separate units. They are formed from a lateral eye rudiment whose general state of organisation determines the degree of their approach to the adult ommatidial condition . The similarity of some of these eyes to the eyes of Collembola and Lepismata is probably convergent . The peculiarities of the latter are due to their re-formation from a partially degenerate compound eye rudiment and of the former are due to the early stage of development, at which the eye rudiment becomes functional. In the remaining Insects there is no indication in ontogeny or anatomy of the formation of the compound eye from separate units. It seems probable that in the ancestors of the Chilopods eyes were lost or very severely reduced. When end organs of the optic nerve were reformed , these were of the ocellar type and very similar to those of Diplopods. The "compound" eye in Scutigeromorpha appears to have been formed relatively recently by an aggregation of separate units, possibly resembling those of other Chilopods , possibly of a more generalised type. The eye of Scutigeromorpha is therefore a new and separate formation , of more recent origin than the compound eyes of other Arthropods, in which an origin from an aggregation of separate units cannot be claimed with certainty.

NOTE ON TECHNIQUE.

Collection of material.

Most of the material which was used was collected in the neighbourhood of Grahamstown, or at Port Alfred. The specimens of Philoscia and Scutigera were obtained at Durban, while the Limulus material was American.

Direct examination of material.

External examination of the eye as a whole shows only the form of the lenses. This is more clearly made out after removal of the underlying, pigmented tissues with KOH.

Attempts were made to examine the internal structure by dissection after maceration in Bela Haler's mixture (see Lee, 1921, p. 347, No. 532). The form of the corneal lenses could be seen and the number of the cone cells counted but the method was otherwise unsatisfactory and sectioning was necessary.

Microscopic examination of material.

Killing and fixation.

For general information on histological technique the text-books of Mell (1902), Lee (1921), Geyer (1927) and Eltringham (1931) and Carleton and Leach (1938) were consulted.

In all cases spec~~c~~imens were killed in the

/fixative

fixative to be employed. The head was separated from the body and in larger forms the eyes were dissected out immediately after the animal had died. This was done with fine needles except where the fixative contained corrossive sublimate. In the latter case finely pointed glass tubing was used.

Fixatives containing corrossive sublimate or picric acid appear to be those most generally suited to work on Arthropods. As Eltringham has pointed out (I93I , p. 48) osmic acid is generally to be avoided where pigmented structures are present, as in the eye . The following fixatives were used : a saturated solution of corrossive sublimate in distilled water , in sea water or in alcohol; Corrossive sublimate in water with acetic acid or with formol (Eltringham , I93I,pp. 44,46); Bouin's fixative made up with distilled water, with sea water or in alcohol(Eltringham , I93I, p. 47); Picro-Chloro-Acetic acid (Eltringham , I93I,p. 48); Picric acid in 96 % alcohol (Lee , I92I , p.56); Susa's fixative (Carleton and Leach , I938,p. 30); Petrunkevitch's fixative (Lee , I92I,p. 49); Carnoy's fluid (Eltringham , I93I,p.47); Zenker's fluid (Carleton and Leach , I938 ,p.3I) and Perenyi's fluid (Lee , I92I, p. 38).

Alcoholic corrossive sublimate and alcoholic Bouin gave good results with the smaller forms with a thinner cuticle. Where the cuticle was thick

/the more

the more penetrating fluids of Petrunkevitch and Carnoy gave better results. , although Carnoy's fluid tended to dissolve the cone secretion in Scutigeromorpha. Most of these fixatives were best employed from about ten to twenty hour hours , according the the size and permeability of the tissue being fixed. Slight heating of the fixatives produced no appreciable difference.

Dehydration and washing out of fixatives.

Excess fixative material was washed out in the usual way - picric acid fixatives in watrr or in 70% alcohol, and sublimate fixatives in I_2 in 70% alcohol. Dehydration was carried out in the usual way, prolonged exposure to alcohol being avoided as far as possible to minimise hardening of the tissues. Complete dehydration is however very essential to celloidin embedding.

Softening .

The use of phenol or diaphenol baths in the course of dehydration is often recommended for the softening of Arthropod material. Sections of the eyes prepared in this way were not very satisfactory and the treatment was omitted in most cases . Sectioning of the eyes alone minimises the difficulty of cutting the chitinous parts. In the examination of Dilopod eyes it was possible to obtain newly moulted specimens so that it was not necessary to decalcify the exoskeleton

exoskeleton in acid baths.

Bulk staining and depigmentation .

It is convenient not to remove the pigment until after the sections have been cut. Its presence allows small eyes to be readily seen and orientated in embedding and cutting. On the slides it is more readily removed than in bulk and the degree of its solution can be easily controlled. Bulk staining is therefore impracticable.

Clearing .

At first ordinary wax embedding was attempted. The following clearing agents were used : Toluol, Benzol, Xylol, Carbon tetrachloride, Chloroform , Terpentine, Terpineol, Clove oil and Cedar wood oil of varying grades. Clove oil had an escessively hardening effect . Penetration of the wax after Benzene , Carbon tetrachloride , Chloroform , and Terpentine was poor in most cases . Toluol, Xylol and Cedar wood oil were the most satisfactory and of these the last was the best although clearing was rather a lengthyprocess

Embedding.

Plain paraffin wax was the first embedding medium used . Waxes with melting points of from 48-62 degrees were tried . Most of the sectioning work was done in summer and waxes with melting points

/between

55 and 60 degrees were found to be the most satisfactory These wax sections were however readily torn especially in their outer parts.

A preliminary passage of the tissues through a Methyl Benzoate solution of Celloidin and a subsequent passage through Benzol into wax was then attempted. A preliminary infilatation of Celloidin was used by Imms (1939, p. 275) for the sectioning of Myriapods. It involves the following baths;

I. Methyl Bezoate solution of Celloidin (1%) for twenty hour hours after complete dehydration of the tissues.

2. Benzol for one hour and thmn for three hours above the oven.

3. Embedding in wax for twelve hours..

The sections were mot appreciably better than those obtained by the first method.

Eltingham's double embedding method (1931, p. 62) was much more successful and was used the the majority of the preparations described here. The dehydrated tissues are immersed in a dehydrat 2% solution of Celloidin in a mixutre of seventy five parts of ether with twenty five parts of absolute Alcohol This is allowed to evaporate gradually to the consistency of treatle more solution being added when nemessary. Gurr's Celloidin wool (mixed with alcohol) and

and solid Scheuring -Kahlbaum Celloidin were used - the former with greater success . After infiltration of Celloidin (usually over a period of not less than ten days) the tissues were embedded in small blocks- in water colour paint pans . These were cut to the required shape and size after hardening in Chloroform vapour. The blocks are then placed in a saturated solution of wax in Chloroform and remain there for some hours until they sink to the bottom after which they are embedded through four wax baths of a total duration of about an hour , the wax remaining round the Celloidin as a border in the final block. This facilitates the formation of a ribbon in cutting. The method gives an even penetration of the embedding medium without the necessity for prolonged heating and consequent hardening of the tissues. It also eliminates the use of clearing agents which have a hardening affect on the tissues.

Cutting

A Cambridge Rocking Microtome was used. Sections thicker than 3μ to 4μ are of little use for the demonstration of the neurofibrillae, the structure of the rhabdom or any of the finer points in the anatomy of the eye . Sections between 2μ and 3μ in thickness are necessary to make out these structures .

Mounting

Mayer's albumen was used as an adhesive material. The sections were mounted in the usual way. Great difficulty was experienced in obtaining thin,flat sections of Celloidin , this substance showing a strong tendency to wrinkle. Sections had to be left for at least a week before staining was attempted. If stained after a shorter time they floated off the slide very readily.

Solution of wax and Celloidin before staining .

Before staining the wax was removed in Toluol and the Celloidin in a bath of ether (seventy five parts) and Alcohol (twenty five parts) .

Degigmentation.

The pigment is removed by Grenacher's fluid (see Eltringham , I93I , p. 92) or Howland's fluid (see Howland , I9II, p. I45) . The length of time does not exceed five or six hours and depends on the thickness of the sections . Depigmentation can be stopped at any point . Washing out of the depigmentaing fluids must be carried out before staining is begun.

Staining .

The following nuclear stains were used :- Haematoxylon of Delafield , Regaud , Kleinenberg, Weigert and Heidenhain , Haemalum with and without acetic acid, Borax carmine, Acetocarmine, Azocarmine, Carmalum, Paracarmin, Babe's safranin, Carbol Fuschin, Bismark Brown, Methylene Blue, Formalin Methylene Blue, aqueous Thionin, Methyl Violet and Methyl Green.

/The

The following cytoplasmic stains were used in various combinations with the nuclear stains:- van Gieson , Erythrosin (aqueous and alcoholic), Ornage IIβ Naphthol, Orange G (aqueous and alcoholic), Eosin (aqueous and alcoholic), Congo Red, Bordeaux Red, Acid Fuschin, Rose Bengal, Biebrich Scarlet , Neutral Red, Metanyl Yellow, Water Blue Orcein, Aniline Blue, Alcoholic light green, Fast Green in alcohol and clove oil,and Picronigrosin. These stains were all made up and used in accordance with the instructions given in Lee and Carleton and Leach. The adherence of the celloidin to the slide was weak so that it was found best to stain the slides individually and in a horizontal position instead of in a staining trough.

Heidenhain's Iron Alum Haematoxylon was the best of the nuclear stains. This differentiated the cone and cornea the rhabdom and the neurofibrillae in varying shades of black and purple. This could be successfully counter-stained with almost any red or green plasma atain and was most generally used. The Azo Carmine- Aniline Blue- Orange G stain recommended by Gurr in his pamphlet (, p. IO) gives a brilliant effect in some cases - e.g. in Myriapod ocelli, but for general use the time taken and the difficulty of transferring celloidin sections through the large number of baths involved , was not really justified. The differentiation with

/Haematoxylon

Haematoxylon was sufficiently and involved only two baths as opposed to the following baths involved in the Azan stain:-

(1) A .25% aqueous solution of Azo Carmine with 1 m.l. of glacial acetic acid used to stain the sections at 50° C for one hour.

(2) A .01% solution of Aniline Oil in 90% Alcohol used to differentiate the stain until only the nuclei are of a red colour.

(3) 1 m.l. of Glacial Acetic acid in 100 m.l. 96% Alcohol used to stop the differentiation.

(4) A 5% solution in distilled water of Phosphotungstic acid used for one to three hours as a mordant.

(5) A solution made up as follows :-

Water soluble aniline blue	.5 gm.
Orange G	2.0 gm
Glacial Acetic Acid	8.0 ml
Water	100 ml

Warm and filter when cold and for use dilute one in three in water

and used as a stain for one to three hours.

Methylene Blue was useful in some cases in showing up the nerve fibres - see fig.56. Other Haematoxylons, i.e. other than Heidenhain's, gave fair results but the differentiation was not as good as in the case of Iron Alum Haematoxylon.

The results obtained with Carmines were on the whole poor, though Acetocarmine was useful as a temporary stain

- where -

where it was desired to retain the pigment and stain the nuclei a contrasting colour. Bismark Brown and the remaining nuclear stains were more diffuse and did not give as fine a differentiation or as permanent a colour as those mentioned above.

Most of the cytoplasmic stains were of more or less equal merit. Light Green and Fast Green were quick, useful stains giving a good contrast to the pigment granules where it was desired to retain these. Light Green kept its colour satisfactorily for at least two years. Eosin and Erythrosin were the most commonly used stains as they gave a rapid and permanent colour and a good contrast to the Iron Alum Haemotoxylon.

Final Mounting.

The slides were cleared in Xylol or Toluol and mounted in Clarite or Balsam.

Microscopy and Drawing.

These particulars are indicated on the sheet attached to each of the figures. The drawings were made with a camera lucida in nearly all cases. Where the outlines were small, even under high powers, they were enlarged by projection through a camera before the details were filled in.

NOTE ON LIST OF REFERENCES.

Where references have been quoted from an abstracting journal , the sourceof the abstract is indicated together with the original source.

Where references are quoted from the work of another author (in cases in which the original papers are not available) , they are marked in the list with an asterisk.

LIST OF REFERENCES.

Abramowitz,A.A. I937.

The comparative physiology of the pigmentary responses in Crustacea.
J. Exp. Zool., Philadelphia, Vol. 76 (3) , pp. 407-422.
Abstracted in Biol. Abs.,Vol. I2,I938, p. 40 , No. 660.

Ademsamer ,T. I893.

Zur Kenntnis der Anatomie und Histologie von *Scutigera coleoptrata* - Das Auge.
Verh. k-k zool-bot. Ges. Wein, Bd. XLIII, pp. 573-578, Taf. VII.

Altemberg,E. I927.

A working model demonstrating the mosaic theory of the compound eye .
Br. J. Exp. Biol. , Edinb., Vol.IV, pp. 8-45.

* Andrews, E.A. I898.

Compound eyes in Annelida.
J. Morph., Philad.,Vol. V , pp. 27I-299, 2 pls.

* Ariola , V. I904.

Rigenerazione naturale eteromorphica del opthalopodite in *Palinurus vulgaris.*
Arch. Entw. Mech. Org., Berlin., Vol.XVIII, pp. 248-252, pl. XIX.

* Ast,F. I920.

Über der feineren Bau der Komplexaugen bei Neuropteren .
Zool. Jahrb., Abt. Anat., Bd. 4I. pp. 4II-458, pls. XXVI-XXXIII.

Attems, C. I926 .

The Myriapoda of South Africa .
Annals of the South African Museum ,
Vol. 26.,pp. I-43I, Figures, I-566,
plates I-XXVI.

Avebury, The Rt. Hon. Lord. I902.

The Origin and Metamorphoses of Insects.
Macmillan ,London, pp. i-x,I-I08,
text-figures I-60.

* Baldwin ,E, and Beatty , R.A. I94I.

The pigmentation of cavernicolous animals.
I. The Pigments of some Isopod
Crustacea.
J. exp. Zool.,Philadelphia, Vol. I8,
No. 2, pp. I36-I43.

Balfour, F.M. I880.

A treatise on comparative Embryology.
Macmillan .,London, Vol. I. pp.
I-492, i-xvi , figures . I-275.

Barbieri , N.A. I933.

Les Arthropodes ne possedent pas d'yeux
composes.
Ve. Congres international d'entomologie,
Paris, Juillet, I932.
Pub. L. Berland et R. Jeannel.
Deuxieme Section . Morphologie , Physiologie, Developpement .
pp. 267-269, text-fgiures I-9 ,pls. IX-
XI.

Barnard , K.H. I93I.

Contributions to the Crustacean Fauna of South Africa. No. IO. Revision of the Branchiopoda. Annals of the South African Museum , Vol.XXIX, pp. I8I-277, figures I-33.

Barnard,K.H. I934.

Contributions to the Crustacean Fauna of South Africa, No. II. Terrestrial Isopoda. Annals of the South African Museum, Vol.XXX , pp. I79-388, figures I-807.

* Barrande ,J. I852.

Systeme Silurien de centre de le Boheme. Ire partie . Recherches paleontologiques. (Continuation editee par le Musee Boheme). Paris. Tom . I. Trilobites. pp. i-XXX, I-935, pls. I_53.

Bassindale, R. Ig33.

Abnormal eyes in wild *Gammarus chevreuxi* . J. Mar. Biol. Ass.,Plymouth, Vol. XIX,No.I, pp.297-298, figures I-2.

Bateson,W. I894.

Materials for the study of variation treated with special regard to discontinuity in the origin of species. Macmillan , London and New York, pp. I-598, i-xv, figures I-208.

Beadle ,G.W. Ig37.

The development of eye colours in *Drosophila* as studied by transplantation. Amer. Nat , New York, Vol. LXXI, pp. I20-I26

Becker, E. 1939 .

Über die Natur des Augenpigments von *Ephestia kuhniella* und seinen Vergleich mit den Augenpigments anderen Insekten.
Biol. Zbl. Leipzig. Bd. 59 (II/I2), pp. 597-627, Taf . I-4.
Abstracted in Biol. Abs. , Vol. I4, I940, No . I2928.

* Bedau, K. I9II.

Das Facettenauge der Wasserwanzen.
Z. wiss. Zool. Leipzig. Bd. 97, I9II, pp. 4I7-456, Taf. I-2.

Beddard, F.E. I884.

Preliminary notice of the Isopods collected on the Voyage of H.M.S. Challenger during the years I873-I876. Part I. The Genus *Serolis*.
Challenger Reports, Vol. II (IX), pp. 20-23, pl. IX.

Beddard, F.E. I884.

Report on the Isopods collected by H.M.S. Challenger , I873-I876.
Proc. zool. Soc. London , Vol. 54, pp. 330-34I.

Beddard, F.E. I887.

On the minute structure of the eye in certain Cymothoidae.
Trans. roy. Soc. Edinb., Vol. XXXIII, Pt. II, pp. 443-452, Pl. XXX.

Beddard, F.E. I887.

Note on a nww type of compound eye .
Ann. mag. Nat. Hist. London, Vol. 20, 5th Ser., pp. 233-236, pl. XXV.

Beddard, F.E. I890.

On the minute structure of the eye in some shallow and deep water species of the *Arcturus* genus

Beddard,F.E. I890. contd.

Proc. zool. Soc. London. Vol. for I890, Part XII,
pp. 365-375, pl. XXXI.

*Beecher,C.E. I895.

The larval stages of Trilobites.
Amer. Geol. , Vol. I6, pp. I86-I97. (Minneapolis).

*Beecher,C.E. I897.

Outline of a natural classification of the
Trilobites.
Amer. J. Sci. New Haven. , Vol. 4 , Pt. 3,
pp. 90-Io6, I8I-207.

Bélehrǎdek, J and Huxley,J.S. 1930

The facet eye growth and its variation in
Gammarus chevreuxi .
J. exp. Biol. Cambridge, Vol. VII, No.I. ,
pp. 37-40.

*Bellonci,G. I88I.

Systema nervoso ed organi del sensi dello
Sphaeroma serratum.
Atti R. Acad. Lincei. Memorie. Ser 3, Vol. X,
pp. 9I-Io8,figs . 1-II3.

Berlese, A. I909.

Gli Insetti, loro organizzazione , sviluppo,
abitudini e rapporti coll'uomo.
Vol.Primo . Embryologica e Morphologia.
Societa Editrice Libraria Milano,I909.
Chapter XI. Systema nervoso ed Organi del senso.
pp. 559-799, figs. 663-866.

*Bernard,T. I894.

The systematic position of the Trilobites
Q.J. Geog. Sci. Vol . 50, p. 4II.

* Blanc, H. 1883.

Observations faites sur la Tanais Oerstedtii Krayer. Leipzig
Zool. Anz., Jhrg. XI. No. 154, pp. 634-637.

Blanc, M. 1879.

Compound eyes and cervical organ of the Phyllopoda.
Arb. zool. Inst. Warburg, Vol. II.
Abstracted in J. R. micr. Soc. London.
Vol III, No. I, pp. 79-80.

Bodenstein, D. 1941.

Investigations on the problems of metamorphosis. VII. Further studies on the determination of the facet number.
J. exp. Zool. Philadelphia, Vol. 86 (I), pp. 87-111, 3 figures.
Abstracted in Biol. Abs: 1941.

Bonnet, A. 1906.

Sur l'anatomie et l'histologie des Ixodes.
C.R. Acad. Sci. Paris, No. 142, pp. 296-298.
Translation in Ann. Mag. nat. Hist. London, Ser. 7, Vol. 17, pp. 509-511.

Bridges, C.B. 1919.

Purple eyes in Drosophila.
J. exp. Zool. Philadelphia, Vol. 28, pp. 265-305.
Abstracted in J. R. micr. Soc. London, 1919, p. 250.

Bridges, C.B. 1919.

Eye colour in Drosophila melanogaster.
J. exp. Zool. Philadelphia, Vol. 28, pp. 337-384.
Abstracted in J. R. micr. Soc. London, 1919, p. 348.

Brown, F.A. I939.

Pigment changes in Crustacea. Humoral control
of Crustacean chromatophores.
Amer. Nat. N.Y., Vol. LXXIII, pp. 247-255.

Buddenbrock, W. von. I935.

Die Physiologie des Facettenauges.
Biol. Rev. Cambridge, Vol. X, No. 3, pp. 283-3I6.

* Bullar , J.F. I879.

On the development of parasitic Isopoda.
Philos . Trans . London , Vol. I69, pp. 505-82I , pls. 45-47.

* Burmeister, H. I835.

Ueber den Bau der Augen bei *Branchipus paludosus*
(Chirocephalus Ben Prevost).
Arch.f. Anat. Phys. wiss. Med., Jahrg. I835,
pp. 529-534, Taf XIII, figs. I-4.(Berlin)

* Burmeister, J. I883.

Beitrage zur Anatomie und Histologie von *Cuma rathkii* .
Inaugural dissertation, Kiel, H.F.A. Lütjie,
pp. I-44, 2 Taf.

Butler, C.G. I938.

On the oecology of *Aleurodes brassicae* Walk.
Trans, Ent. Soc. London, Vol 87, Part I3,
pp. 29I-3II, 5 text-figures.

Calman , W.T. I909.

A Treatise on Zoology. Part VII Appendiculata
3rd Fascicle - Crustacea.
Ed. E. Ray Lankester.
Adam and Charles Black, London, pp. i-viii,
I-345, figs. I-I94.

Calman, W.T. I9II.

The life of Crustacea.
Metheun, London, pp. I-289, figs. I-85.

Calman, W.T. I9I9.

Dr. Walcott's researches on the appendages of Trilobites.
Geol. Mag. N.S. Decade VI, Vol. VI, pp. 359-363. (London).

Calman, W.T. I92I

A review of Percy E. Raymond's paper on The anatomy and relationships of the Trilobites (published in Memoirs of the Connecticut academy of Arts and Sciences , Vol. VII, I920, pp. I-169, pls.I-II , Portrait and text figures).
Geol. Mag. Vol. LVIII, pp. 52I-523. (London) .

Carpenter ,G.H. I903.

On the relationships between the classes of Arthropods.
Proc. R. Irish Acad. Dublin, Vol. XXIV, Section B, Part 4, pp. 320-360, pl.VI.

Carpenter ,G.H. I905.

Segmentation and Phylogeny of the Arthropods.
Quart.J. micr . Sci. London, Vol. XLIX, 469-49I pp., I pl.
Abstracted in J.R. micr. Soc. London, I906, p.664).

Carleton,H.M. and Leach,E.H. I938.

Histological technique.
Oxford University Press, London, New York and Toronto, pp. I-383 .

* Carriere,J. 1885.

Die Sehorgane der Thiere, vergleichend-anatomisch dargestellt.
Munchen u.Leipzig, R.Oldenbourg,
pp. I-6 , I-205, Abb. I-147, Taf .I.

*Carriere,J. 1886.

Die Entwicklung und verscheidenen Arten der Ocellen.
Zool. Anz., Leipzig, Bd. IX, pp.496-500.

Carriere, J. 1886.

Kurze Mittheilungen aus fortgesetzten Untersuchungen der Sehorgane - *Gyrinus natator*, *Bibio*, *Chloeon dipterum* .
Zool. Anz.,Leipzig, Bd. IX , pp. 143-142,
479-481.

Cavillee,E . 1942.

The phenomenon of Homeosis.
Amer. Nat. New York, Vol.LXXVI, No 766,
pp. 494-506

* Chatin,J. 1877. 1878.

Recherches pour servir a l'historie du battonet optique chez les Crustacees et les vers.
Ann. sci. nat. Paris , Ser. 6, Zool., Tom. V,
Art . 9, pp. I-45. (1877)
Tom.VII, Art. I, pp. I-36, pls. I-3. (1878).

*Chun , C. 1896.

Atlantis. Biologische Studien über pelagische Organismen . 6. Leuchtorgane und Facettenaugen.
Bibl. Zool. Leipzig, Bd. VII, Ht. 19, pp. 191-263, pls. XVI-XX.

* Claparede, E. I860 .

Zur Morphologie der Zusammengesetzten-Augen bei den Arthropoden.
Z. wiss. Zool., Leipsig, Bd. X, pp. I9I-2I4, Taf. XII-XIV.

* Clarke ,J .M. I889.

The structure and development of the visual area in the Trilobite *Phacops rana* Green .
J. Morph., Philadelphia, Vol.II, pp. 253-270. pl. 2I.

Clarke, J.M. I908.

Early Devonic History of New York and Eastern North America.
New York State Museum Memoir No. 9. Vol,II, pp. I-366.

Clarke ,J.M. and Ruedemann,R. I912.

The Eurypterida of New York.
New York State Museum , Memoir , No.I4,VolI, pp. I-439, figs. I-I2I.

* Claus,C. I87I.

Untersuchungen über die Bau und die Verwandschaft der Hyperiiden.
Gottingen, Nachrichten , pp. I49-I57.

* Claus,C. I875.

Ueber die Entwicklung, Organisation und Systematischen Stellung der Arguliden.
Z. wiss . Zool., Leipzig, Bd. XXV,pp. 2I7-284, Taf. XIV-XVIII.

* Claus,C. I876.

Zur Kenntnis der Organisation der Daphniden und verwandten Cladoceren.
Z. wiss. Zool. ,Leipzig, Bd. XXXII,pp. 362-402, Taf. XXV-XXXIII.

* Claus,C. I877.

Zur Kenntnis des Baues und der Organisation der Polyphemiden.
Denkschr. Acad. wiss.,Wein , Bd. XXXVII, pp. I37-160, Taf. I-VIII.

* Claus,C. I879.

Die Organisation der Phronimiden.
Arb. Zool. Inst. , Wein , Tom. II, Ht. I, pp. 59-I46, Taf. I-VIII.

Claus, C. I884.

Elementary text-book of Zoology.
Translated by A. Sedgewick and F.G. Heathecoate.
Swan Sonnenschein,London, pp. I-6I5, figs. I-49I .

* Claus , C. I886.

Untersuchungen ueber die Organisation und Entwicklung von *Branchipus* und *Artemia* nebst vergleichenden Bemerkungen an anderen Phyllopoden.
Arb. Zool. Inst. Wein, Tom. XI, Heft III, pp. 267-370, Taf. I-XII.

Claus,C. I886.

On the development and minute structure of the pedunculated eyes of *Branchipus* .
Ann. Mag . nat hist. London, Vol XVIII, ser. 5, pp. 78-80.

* Claus,C. I888.

Ueber die Organisation der Nebaliden und die systematischen Stellung der Leptostraken.
Arb. Zool. Inst.,Wein, Tom. VIII, Ht. I, pp. I-I48, Taf. I-I5.

Cockayne,E.A. I926.

Homeosis and Heteromorphosis in Insects.
Trans. ent. Soc.,London, Vol. LXXIV, Part II, pp. 203-228, pls. LXI-LXIV.

Cockayne, E.A. I930.

Insect Teratology. Part I. Homeosis and Heteromorphosis.
Trans. ent Soc., London, Vol. LXXVIII, Part II, pp. 309-326, pls XI-XIII.

Cole , J. I944.

A History of comparative anatomy from Aristotle to the eighteenth century.
Macmillan , London , pp. I- 440.

* Corneli, W. I924.

Von dem Aufbau des Sehorganen der Blattwespen Larven und der Entwicklung des Netzauges.
Zool. Jahrb, Jena. Abt. Anat., Vol.46, pp. 573-608, figs . I-5.

Collinge , W.E. I94I.

Notes on the terrestrial Isopoda (Woodlice)
The North-Western Naturalist, I94I, pp. 247-256.

Comstock, J.H. I933.

An Introduction to Entomology.
Revised Edition.
The Comstock Publishing Company, Ithaca, New York, pp. i-xix, I-I044, figs. I-I228.

Congdon, E.D. I907.

The effect of temperature on the migration of the retihal pigment in Decapod Crustaceans.
J. exp. Zool. , Philadelphia, Vol. IV , pp. 539-548.

* Constantineanu,M.J. I930.

Die Aufbau der Sehorganen im Susswassenlebenden Dipterenlarven und bei Puppen und Imagines von *Culex.*
Zool. Jahrb., Jena, Abt. Anat., Bd. 52 (2), pp. 253-346, pls. I-I2, figs I-35.

Cowper-Reed, F.R. I9I2.

Sedgwick Museum Notes. Notes on the genus *Trinucleus* -Part I.
Geol . Mag. N.S. Decade V. Vol. IX,pp. 346-353.(London).

Cowper-Reed, F.R. I9I6.

Sedgwick Museum Notes. Notes on the genus *Trinucleus* - Part VIand Part VI.
Geol. Mag., N.S. , Decade VI , Vol. III,pp.II8-I23, pp. I69-I76.(London).

Cussans,M. I904.

Gammarus - Liverpool Marine Biological Committee Memoirs. No XII.
Williams and Norgate , London, pp. i-viii, I-47, pls I-IV.

* David, L.T. I938.

The effect of temperature on the eye colour of *Habrobracon juglandis* Ashmead.
Amer . Nat. ,New. York, No. 738, pp. 573-577.

Dahl, A. I907.

Die gestreckte Körperform bei Spinnen und das System der Araneen.
Zool. Anz.,Leipzig, Bd. XXXI, pp. 60-69.

Day,E.C. I9I2.

Pigment migration in the eye of the Crayfish.
Bull. Mus. Comp. Zool. Harvard,Vol LIII,Part II, pp. 305-343, 5 pls.
Abstracted in J R. micr Soc .,London,I9I2,Part II, p. I84.

* Della Valle, A. I888.

Sopra le glandole glutinifere e sopra gli occhi
degli Ampeliscidi del golfo di Napoli.
Atti. Soc. Nat. Modena , Memorie , Ser.3.
Vol VII , pp.90-96.

Delo, D.M. I940.

Phacopid Trilobites of North America.
Geol. Soc. I940, Sc. Papers, No. 29,
pp. I-I35, pls. i-xiii.

Dembowski, J. I9I4.

The eyes of _Ocypoda ceratopthalma_ .
Zool.Jahrb., Jena, Abt. Anat., Vol. XXXVI,
pp.5I3-524, pl.I.
Abstracted in J. R. micr. Soc., London, I9I4,
Part I, p.43 .

Demoll, R. I9II

Migration of Iris pigment in the compound eye .
Zool. Jahrb., Jena, Abt. Anat., Vol.XXX, pp. I68-I80, figs I-2.
Abstracted in J. R. micr . Soc., London, I9II,
p. 6I6.

Dickler, H. I934.

White eye mutation in _Phronima regina_ Leingen.
Amer. Nat., New York, Vol. LXXVII, pp. 287-288.

* Dietrich , W. I908.

Doppelaugen bei Dipteren .
Zool. Anz., Jena, Abt. Anat. Bd.XXXII, pp. 470-472.

* Dietrich, W. I909.

Die Facettenaugen der Dipteren.
Z. wiss . Zool., Leipzig, Bd. 92 , pp. 465-539,
Taf. I-4.

Dobkiewicz,L. I912.

Eyes of depp sea Galatheidae.
Z. wiss. Zool.,Leipzig, Bd. XCIX, pp . 588-6I7,
pl. I, figs I-I2.
Abstracted in J. R. micr Soc,,London , I9I2,
pp. 307-308.

* Dor , H. I86I.

De la Vision chez les Arthropodes.
Arch. Sci. phys. nat.,Geneve, Tom.XII, p.22,
pl I.

Driver,E.C. I926.

The temperature effective period- the key to the facet number in *Drosophila.*
J. exp. Zool,, Philadelphia, Vol 46 (3) , pp.
3I7-328, figs I-4.
Abstracted in Biol. Abs.p. I7I, No. I9282,
I926.

Eggert ,B. I927.

Beitrage zur Rückbildung der Augen bei
Isopodenfamilie *Cymothoidae.*
Zool. Anz.,Leipzig, I927, Bd. 73,pp. 33-4I.

Eltringham ,H. I9I9.

Butterfly vision .
Trans. ent. Soc.,London, I9I9, Part I, pp. I-49
pls I-V.

Eltringham,H. I930.

Histological and illustrative methods for
entomologists.
Clarendon Press Oxford,I930,pp. i-ix,I-I39.

Eltringham, H. I93I.

On the structure of the compound eye of *Aleurodes
brassicae* .
Trans. ent. Soc. London.,Vol. LXXIX, Part III,
pp. 43I-434, pl. XXV.

Eltringham , H. I933.

Presedential address on the Insect eye .
Proc. ent . Soc.,Londnn, Vol. VII,pp. I22-
I28 .

Eltringham,H. I933.

The senses of Insects.
Metheun, London (Monographs on Biological
subjects) , pp . i-vii, I-I26 ,figs. I-25.

Eltringham,H. I936.

The Insect eye .
Proc. ent . Soc. ,London, Ser. A. General
Entomology, Vol. II Parts 6-I3, p. II5.

Ephrussi,B. I942.

Analysis of the eye colour differences in
Drosophila.
Cold Spring Harbour Symposia on Quantitative
Biology, Johns Hopkins University Circular
No. I0, I942, pp. 40-48.
Abstracted in Biol. Abs. Vol. I7, I943, ie.
No. I9490.

*Exner,S, I89I.

Die Physiologie der Facettierten Augen von
Krebsen und Insekten. Eine Studie.
Deutikke, Leipzig u. Vienna, pp. I-206,
pls. I-7.

*Fauvel,P. I899.

Sur les pigments des Arenicoles .
C.R. Acad. Sci.,Paris. Vol. CXXIX , pp. I273-
I275.

Fischer- see Korschelt,I933

*Frey,H. and Leuckart,R. I847.

Lehrbuch der Anatomie der wirbellosen Thieren.
Voss, Leipzig, pp. I-8, I-626, numerous
text-figures.

Ford, E.B. and Huxley, J.S. I929 .

Genetic rate factors in *Gammarus*.
Z. wiss. Biol., Abt ,D. Arch.Entw. Mech. Org.,
Berlin, I929, pp. 67-79.
Abstracted Biol Abs. I932, No. 6I83.

Frisch, K. I908.

Studien uber Pigmentverscheibung in
Facettenaugen.
Biol. Centralbl, Leipzig, Bd. XXVIII, No. 20-2I,
pp. 462-47I, 698-704.

Gardiner, M.S. I935.

The origin and nature of the nucleolus.
Quart. J. Micr. Sci., London, Vol 77, N.S.,
pp. 523-547.

* Geisbrecht, W. I9IO.

Fauna und Flora du Golfs von Neapel -
Stomatopoda.
Stat. Neap. Monog., Freidlander, Berlin,
I910, No. VII, pp. I-239, Taf. I.

George , T.N. I933.

Palingenesis and Paleontology.
Biol. Rev. , Cambridge, Vol. VIII, No. 2,
pp. I07-I35.

Geyer, K. I9I2.

Beitrage zur kenntnis der Facettenaugen der
Hymenopteren .
Zool. Anz., Leipzig., Bd. XXXIX, pp. 374-386 ,
figures I-6.

Gillman,H. Ed. I944.

Organic Chemistry an Advanced Treatise.
Willey, New York, Second printing, Vol. II,pp.
Io79 -I983 plus i-lxvii.

* Girschner, E. I888.

Einiges uber die Farbung der Dipterenaugen.
Berlin. Ent. Zeitschr.,Bd. XXXI, pp. I55-I62,
Taf. I.

* Gossel,P. I935.

Beiträge zur Kenntnis der Hautsinnesorgane
und Hautdrüsen der Cheliceraten und der Augen
der Isodiden.
Z. wiss. Zool .,Abt. A,Morphol. u. Oekol.,Leipzig.
Bd. I7, Part 3093, pp. I77-205, figs.I-39.

Graber,V. I879.

Unicorneal eyes in Tracheata.
Arch. mikr. Anat. Bonn, Bd. VXII, pp. 58-93,
Taf . I-3
Abstracted in J.R. micr. Soc.,London, Vol.III,
pp. 6I-63.

*Grenacher,H. I874.

Zur morphologie und Physiologie der Facettierten
Arthropoden Auges .
Gottingen, Nachrichten, pp. 645-656.

*Grenacher,H. I877.

Die Augen der Arthropoden.
Klinische Monattsblätter für Augenheitkunde,
Bd. XV, pp. I-42 , with woodcuts.

* Grenacher,H. I879.

Untersuchungen über das Sehorgane der Arthropoden
im besonderen der Spinnen, Insekten und
Crustaceen.
Göttingen, 4to, pp. i-vii, I-I88, pls.I-XI.

* Grimm,O. I880.

Blind Amphipods of the Caspian Sea.
Arch. Naturgesch.,Berlin, Bd. XLVI , ppI17-II3
Translated in Ann. Mag . Nat. Hist. ,London,
Vol. XVI Ser. 3, p. 85.

* Grobben,C. I88I.

Die Entwickelungsgeschichte der Cetochilus
septentrionalis .
Arb. Zool. Inst . ,Wein, Bd. II, pp. 243-283,
pls. I-4.

* Gruber,E. I865.

Ueber die Gattungen Estheria und Limnadia und
einen neuen Apus .
Arch. Narurgesch. Berlin, Jahrg.XXXI ,
Bd. I. pp. 203-282.

* Günther ,K. I9I2.

The eyes of Dytiscus.
Z. wiss. Zool.,Leipzig, I9I2, pp. 60-II5, figs.
I-36.
Abstracted in J.R. Micr. Soc.,London, I9I2,
Part 4. p. 40I.

Gurr,G.T.

Biological Staining Methods .
Compiled and published by G.T. Gurr.
Pegg,London, pp. I-I6.
(An undated pamphlet).

Guyer, M.F. I927.

Animal Micrology. Practical exercises in Zoological micro-technique.
University Press, Chicago. 9th impression,
pp. i-xi , I-289, figs. I-62.

Hansen, H.J. I9I7.

On the trichobothria ("auditory hairs") in
Arachnida, Myriapoda and Insects with a summary
of the external sensory organs in Arachnida.
Ent. Tidskr. Stockholm, I9I7, pp. 240-259.

Hanström, B. I927.

Neue Beobachtungen uber Augen und Sehsentren von
Entomostraca, Schizopoda und Pantopoda.
Zool. Anz., Leipzig, Bd. 70 , pp. 236-25I, pls I-5.

Hanström ,B. I927.

Uber die frage ob functionelle verscheidene
Zapfen- und Stabchenartigen Sehzellen im
Komplexaugen der Arthropoden vorkommen.
Z. wiss. Biol.,Abt. C, Z. vergl. Physiol.,
Berlin, Bd.6 , (3/4) , pp. 566-597.
Abstracted in Biol.Abs., I930, No. 4388.

Hanström,B. I933.

Neue Untersuchungen uber Sinnesorgane und
Nervensystem der Crustaceen - II und III.
Zool. Jahrb., Abt. Anat . u. Ontog. der Thiere.,
Jena, Bd. 56 (3/4) , pp. 387-520, figs I-68,
Bd.58, pp. IoI-I44), figs . I-3I.
Abstracted in Biol. Abs. I936, p. 774, No. 7I68.

Hanström, B. I934.

Neue Untersuchungen uber Sinnesorgane und
Nervensystem der Crustaceen - IV.
Arch. Zool. Stockholm , Bd. 26 A , No 23.
pp. I-66, figs I-38.
Abstracted in Biol Abstracts , I936. No.7I67.

Hanström ,B. I92I.

Uber die Histologie u. vergleichende Anatomie
der Sehganglien und globuli der Araneen.
Kungl. Svenska . VetenskAkad. Handl.,Uppsala
und Stockholm, Bd. 6I , No. I2, pp.3-39.
(with plates).

Hanström ,B. I934.

Bemerkungen ubder das Komplexauge der Scutigeriden.
Lunds Univ. Arsskr. No. 30, Paper 6,pp.I-I4
figs I-II.
Abstracted in Biological Abstracts, I937, Vol. II,
p.I604. No. I5028.

Hatch , M.H. 1926.

On the morphology of the eyes of Coleoptera.
J.N.Y. ent .Soc, Vol. XXXIV, I926, pp.343-348,
pl. XXVI.

X Hemenway , R. I900.

The structure of the eyes of *Scutigera forceps.*
Biol. Bull. ,Boston , Vol. I, pp. 205-2I3, pls.
I-2.

Hendriksen , K. I932.

The manner of moulting in Arthropods.
Notul. ent., Helsingfors, Bd.XI, I. IV.,
pp. Io3-I27, figures I-I4.

Hentschel,E. I899.

Beiträge zur Kenntnis der Spinnen Augen .
Zool. Jahrb.,Abt. f. Anat. u. Ontog. der Thiere.Jena .
Bd.I2, pp. 509-534 , pls 26-27.

Herbst,C. I895.

Uber die regeneration von Antennähnlichen
Organen an Stelle von Augen.
Arch. Entw. Mech. Org.,Berlin, Bd. II, pp. 544-
558, pl. XXXI.

d'Herculais,J.K. I9II.

Habits of Scutigera coleoptrata.
C.R. Acad. Sci.,Paris, Tom. CLIII, pp. 399-
40I.
Abstracted in J.R. micr. Soc.,I9II, p. 752.
(London).

* Herrick, F.H. I886.

Notes on the development of Alpheus and other
Crustacea and on the development of the
compound eye.
Johns Hopkins Univ. Circ , No. VI, pp.42-44,
I woodcut. (Baltimore).

* Herter ,R. I928.

Ueber die Komplexaugen der Korpfenaus
Argulus foliaceus L..
Zool. Jahrb., Abt. Allg. Zool . u. Physiol.,
Jena, Bd. 45 , pp. I59-I76,pl. I&2 , figs, I-I3.

* Hesse,R. I90I.

Untersuchungen uber die Lichtempfindung bei
neideren Thieren .
VIII. Vom den Arthropoden -Augen.
Z. wiss. Zool,Leipzig., Bd. 70, pp. 347-473,
figs . I-2, Taf. I-6.

Hewitt,C.G. I907.

Ligia . Liverpool Marine Biological Committee Memoirs. No. XIV
Williams and Norgate , London, pp. i-viii, I-37, pls. I-4.

*Heymons,R. I90I.

Die Entwickelungsgeschichte der *Scolopendra.*
Zoologica, Stuttgart. Bd. I3. (33), pp. I-244, I90I, Tef. 2I4.

*Hickson,S.J. I885.

The eye and optic tract of Insects .
Quart, J. Micr. Sci. London, Vol. XXV, pp. 2I5-25I, pls. XV-XVII.
Abstracted in. J.R. Micr. Soc.,London, Vol. V,(2), p. 633.

Hickson,S.J. I885.

The retina of Insecta.
Nature, London, Vol. XXXI, pp. 34I-, 342, 433. (These are replies to letters by Lowne in nature on " The compound vision and morphology of the eyes in Arthropods ").

Hickson, S J. I894.

The fauna of the deep sea.
Kegan , Paul, Trench and Trübner, I894, pp. i-xvi, I-I69, figs. I-23. (London).

Horstman,E. I935.

Die tages periodische Pigment Verwanderung im Facettenauge von Nachschmetterlings.
Biol. Zentralbl. , Leipzig, Bd. 55 , pp. 93-97, figs. I-3.
Abstracted in Biol. Abs., I937, Vol. II (2), p. 96, No. 935.

Howes , G.B. I887.

An abnormal *Palinurus*

Howes, G.B. 1887.

An abnormal *Palinurus* .
Proc. zool. Soc. London, 1887, pp. 468-470.
I woodcut.

Howland,R.B. 1911.

Migration of the retinal pigment in the eyes
of *Branchipus gelidus* .
J. exp. Zool,,Philadelphia, Vol. II, No. 2,
pp. 143-158, figs. 1-4.

Hutchinson, G.E. 1930.

A Re-study of some Burgess Shale Fossils.
Proceedings of the Unites States National
Museum, Vol. 78, Art. II , pp. 1-24, pl. I.
(Washington).

Huxley , J.S. and Wolsky, A. 1933.

The structure and development of the normal
and mutant eyes of *Gammarus chevreuxi*.
Proc. roy. Soc.,London, Ser. B, Vol. 114,
pp. 364-392.

Huxley,J.S. and Wolsky,A. 1936.

The structure of the non facetted region in
in the bar eyed mutant of *Drosohpila*
and its bearing on the analysis of genic
action on Arthropod eyes.
Proc. zool. Soc.,London, 1936, Pt. 2,
pp. 485-489, 2 text-figures.

Huxley,T.H. 1896.

The Crayfish , and introduction to the
study of Zoology.
Kegan Paul, Trench and Trübner,London,
6th Ed., 1896, pp. i-xiv, 1-371, text-figures
1-82.

Imms, A.D. I906.

Anurida .
Liverpool Marine Biological Committee
Memoirs.
Williams and Norgate , London, pp. i-viii,
I-99, pls. I-7.

Imms, A.D. I93I.
Recent Advances in Entomology.
Churchill, London, pp. i-viii, I-374,
84 text-figures.

Imms, A.D. I938, I942.

A general text book of Entomology
including the anatomy, physiology, development
and classification of Insects.
Metheun, London , 4th Edition , I938 and
5th Ed . I942.
pp. i-xii, I-727 , text figures I-82I.

Jackson , H.G. I9I3 .
Eupagurus.
Liverpool Marine Biological Committee Memoirs
No. XXI , pp. 1-72 , pls. I-6 , text figures
I-3.

Jackson, H.G. I926.

The morphology of theIsopod head .
Proc. zool. Soc., London, I926. Pt. III,
pp. 885-99I . (Part I. The head of *Ligia
oceanica*) . pls. I-IV, text figures I-II.

*Johannsen , H. I892.
Über die Entwacklung des Imagoauges von
Vanessa.
Zool. Anz.,Leipzig, Bd. XV, pp.353-355.

Johannsen , O.A. and Butt, F.H. I94I.

Embryology of Insects and Myriapods. The developmental history of Insects , Centipedes and Millipedes from egg deposition to hatching McGraw Hill Publs. in Zoo. Sciences - New York and London, Ist Edition , pp. i-xi, I-462 , figures I-370 .

*Johnas , W. I9II.

Die Facettenaugen der Lepidopteren . Z. wiss . Zool, Leipzig, Bd. 67,pp. 2I8-26I , Taf I-3.

Jordan , H.J. I929.

Allgemeine Vergleichende Physiologie der Tiere.
Gruyter, Leipzig, pp. i-xxvii, I_ 76I, text-figures I-279.

*Jorschke , H. I9I4.

Die Facettenaugen der Orthopteren und Termiten .
Z. wiss . Zool . , Leipzig, Vol. III, pp. I53-280 , pl. IV.

Kalmus , H and Mayer , A.E. I94I .

The shape and distribution of thefacets in an Arthropods eye as systems of points on a sphere.
Proc. ent. Soc,, London, Ser. A. General Entomology , Vol. I6, Parts I-3, pp. I-32 I5-32, figs I-7.

Kingsley , J.S. I886.

The developmet of thecompound eyes of <u>Crangon</u> .
Zool. Anz., Leipzig, Bd. IX, No 334, pp. 597-600.

* Kirchoffer , O. I908.

Untersuchungen über die Augen Pentamerer Käfer
Arch. Biontol, Berlin , Bd. 2, pp 237-277,
7 pls.

* Kirchoffer,O. I9I0.

The eyes of *Dermestes*
Arch. Naturgesch. Bd. LXXVI , pp. I-36 , 2 pls,
7 figures. (Berlin).

Kirkpatrick, T.W. I937.

Colour vision in the Triungulin larva of
a Strepsipteron - *Corioxenos [illegible] antestii*
Blair.
Proc. Ent. Soc., London , Ser. A , General
Entomology, Vol. I2, Part 3 , pp. 40-44.

Kishinouye , K. I89I.

A preliminary note on the development of
Limulus longispinus.
Zool. Anz., Leipzig, I89I, pp. 264-266.

Kishinouye , K. I89I.

The lateral eyes of Spiders .
Zool. Anz., Leipzig, I89I , pp. 353-38I.

Korschelt, E. I924.

Bearbeitung Einheimischer Tiere-
Erste Monographie : Der Gelbrand
Dytiscus marginalis L.
Engelmann, Leipzig, pp. I- 863,
47I text figures.

Korechelt, E. 1933.

Part Author in
Handworterbuch der Wissenschaften, Zweite
Auflage . (Insekten). Separat.
Author for the Zoological section .
Fischer, Jena , pp. 597-648, 50 figures.

Korschelt, E. and Heider ,K. 1899.

Textbook of the Embryology of Invertebrates.
Translated by Bernard M. and Woodward , M.F.
Swan Schonnenschein , London , Macmillan,
New York. Vol . II.
pp. i-xv , I-305 , figures I-165.

*Kuhn , O. 1926.

Die Facettenaugen der Landwanzen und Zicaden.
Z . Morph. Ökol . Tiere, Berlin , Bd. 5
(3) , pp. 489-558 , 50 figures .
Abstracted in Biol. Abs. , 1928 , No. 19653.

*Lake , E. 1907.

A Momograph of the British Cambrian Trilobites.
Part II.
Paleontological Society Monographs .
1907, No. 61 , pp. 28-48 , pls. III-IV.
(London).

*Landois , H. 1866.

Die Raupenaugen der Lepidopteren
(ocelli compositi mihi).
Z. wiss . Zool., Leipzig, 1866, pp. 27-44,
Taf . I-3.

Lang , A. 1891.

Text Book of Comparative anatomy. Vol.I
Translated by Bernard , H.M. and M .
Macmillan , London and New York.
pp. i-xviii, I-562, figures I- 383.

Lang , P. I905.

The Structure of Hydrachnid eyes.
Zool. Jahrb. Abt. Anat . , Jena , I905 , pp. 453-494 , pls . I-2.
Abstracted in J.R.micr. Soc., London, I906,p.25.

Lankester , E. and Bourne ,A.G. I883.

The minute structure of the lateral and central eyes of <u>Scorpio</u> and <u>Limulus</u>.
Quart . J. micr. Sci.,London , Vol. XXIII, N.S. pp. I77-2I2 , pls. X,XI,XII.

Lankester , E. Ray. I885.

Letter to Nature concerning Lowne's views of the morphology of the compound eyes of Insects.
Nature , Vol. XXXI , p. 504.

Lattin , G. de. I938.

Untersuchungen an Isopoden augen (unter besonderer Berucksächtigung der Blinden Arten)
Zool. Jahrb. Abt Anat . u. Ontog. Tiere, Jena , Bd . 65 (3) , pp. 4I7-468 , pls . I-2, 27 figures .
Abstracted in Biol. Abstracts. , I939, Vol. I3, No. 5I26.

Laurie , M. I893.

Anatomy and relations of the Eurypteridae.
Trans. roy. soc . Edinburgh, Vol. XXXVII, Part II, pp. 509-528.

Lea , A.M. I905.

Blind Coleoptera of Australia and Tasmania.
Trans. ent . Soc . London , I905, Part. Iv, pp. 365-368.

Lee , A.B. I928.

Bolles Lee 's Microtomist's Vade Mecum .
A Handbook of the methods of microscopic anatomy.
9th Edition .
Ed. by J. Bronte Gatenby and E.V. Cowdry.
Churchill, London. pp. i-x, I-8I4

Lederer, E. 1940.
Les pigments des Invertebres (a l' exception des pigments respiratoires).
Biological reviews, Cambridge, Vol. I5 . No. 3, pp. 276-306.

Leinemann , K. I904.

The number of facets in beetles' eyes.
Zool. Zentralbl, Jena, Bd. XIII, pp. I9I-I93.
Abstracted in J.R. Micr. Soc., London, I906, pp. 30I-303.

* Lenz ,H. I877.
Estheria californica Pack. , notes on.
Arch . Naturgesch. Jahrg.XLIII, Bd I.
pp. 234 -40 , Taf . III-IV .

* Leydig, F. I855.

Zum feineren Bau der Arthropoden .

Arch,Anat . Phys. u. wiss. Med .,
Jahrg. I855, pp. 376-480 , Taf. XV-XVIII.

* Leydig, F. I857.

Lehrbuch der histologie des Menschen und der Thiere.
Meidinger , Frankfurt, pp. I-I2, I-55I,
Many text figures.

* Leydig, F. 1864.

Das Auge der Gleiderthiere.
Laupp und Siebeck, Tübingen , pp. I-50.

Lister J.J. 1927

See Sedgewick.

* Lindstrom , A. 1903.

Researches on the visual organs of Trilobites
K. svenska . Vetensk-Akad. Handl. ,
Stockholm ., Bd. 34 , No. 8, pp. I-8[illegible].

Locy, W.A. 1886.

Observations on the development of
Agelina naevia.
Bull. Mus . Comp. Zool. Harvard, Vol. XXI,
pp. 63-103 , pls. 1-4.

Lönnberg , E. 1934.

On the occurrence of carotinoid pigments
in the eyes of certain animals.
Arch. Zool, , Stockholm , Vol 28 A , pp. I-I4.
Abstracted in Biol. Abstracts , Vol. 7, I937,
p. 370 , No . 3493.

Lowne , B.T. 1875.

On the modification of the simple and
compound eyes in Insects.
Philos. Trans ., London, Vol. CLXIX, pp.
577-602 , pls. LII-LIV.

Lowne , B.T. 1878.

On the modifications in the structure of the simple and compound eyes of Insects , Philos. Trans ., London , Vol. CLXIX pp. 577-603 , pls. LII-LIV , I wood cut.

Lowne , B.T. 1884.

On the compound vision and morphology of the eye in Insects . Trans. Linn. Soc . (Zool) , London., Ser. 2. Vol. II, pp. 389-420 , pls. XL-XLIII.

Lowne , B.T. 1885.

Letter to Nature on the compound vision and morphology of the eye in Insects. Nature, London , Vol. XXXI, p. 433.

Lowne , B.T. 1890.
On the structure of the retina of the Blowfly *Calliphora erythrocephala* . Proc. Linn. Soc. (Zool). London., Vol. XX, pp. 406-417, pl. XXVII.

Lubbock , J. 1889.

On the senses , instincts and intelligence of animals with special reference to Insects. Kegan Paul, Trench , London , pp -i-xxix, 1-292, figures 1-118.

* Lucas , R. I868 .

Quelques mots sur un cas de cyclops
observie chez une Insecte Hymenoptere de
la tribu des apiens (*Apis mellifica*)
An . Soc. Ent. Fr.,Paris, 4e Serie , Tom.
VIII , pp. 737-740, pl. XII, figures I-3.

Ludtke ,H. I94I .

Die embryonale und postembryonale Entwicklung
des Auges bei *Notonecta glauca* (Hemiptera
Heteroptera). Zugleich ein Beitrag zum
Wachstums und Hautungsproblem.
Z . Morph. Okol. Thiere, Bd. 37 (I), pp.
I-37 , figures I-28 . (Berlin).
Abstracted in Biol. Abs ., No. I598I, I94I.

Machatschke , J.W. I936.

Die cuticulare Aufbau des Rhabdoms im
Arthropodenauge.
Vestnik Ceskoslovenske Zoologicke
Spolecnosti V Praze, (Memoires de
la Séciete Zoologique Techcoslavaque
de Prague) , I936, Iv, pp. 90- 27.
Taf I-II.

Mainx , F. I937.

Analyse der Gehirnwirkung durch Faktor-
combination. Die Augen von *Drosophila
melanogaster* .
Z. indukt . Abstamm .- u. VererbLehre,
Berlin , Bd. 73 (3I4) , pp. 470-47I .
Abstracted in Biol. Abs . I938,Vol.I2, p.
824, No. 9I59 .

Mallock, A. I922.

Divided composite eyes.
Nature, London, Vol. II0 ,pp. 770-77I ,
2 figures.

Mark , E.L. I887.

Simple eyes in Arthropods.
Bull. Mus. Comp. Zool., Harvard, Vol. XIII,
No 3 , pp. 49-I05 , pls. I-5.

Marshall, W.S. I937.

The development of the compound eye of the
confused flour beetle - <u>Tribolium confusum</u>
Jacq.
Trans. Wisc . Acad. Sci . Arts Lett .,
Maddison , Vol. XXIII, pp. 6II-630, pls.
I6-I9.

Mayer , F. I943.

The Chemistry of natural colouring matters.
Reinhold Pub. Comp. , New York.
pp. I-354.

*McCoy, F. I849.

On the classification of some British
fossil Crustacea with notes on some new
forms .
Ann. Mag . Nat . Hist .,London, Series 5,
(2) , p. 396.

Méhely , L.V. . I927 .

Gibt es zweiauige Trichonisciden .
Zool. Anz., Leipzig.,Bd. 72 , pp. 8I-83.

Mell, F.H. I902.

Biological Laboratory methods .
Macmillan , New York, pp. i-xii & I-32I.

*Milne -Edwards , H. 1834.

Histoire naturelle des Crustacea .
Comprenant l'Anatomie la Physiologie et la
Classification de ces animals.
Rovet, Paris , Tom I. pp. 469, figures I-35.

*Milne-Edwards , A. 1864.

Sur une cas de Transformation de pedoncle
oculaire et antenne observe chez une Langouste
Tom. LIX, p. 7IO. Compt.,Rend.,Paris.

*Moroff , T. I9II.

Über die Entwicklung der Facettenauges bei
Crustaceen .
Biol. Zentralbl., Leipzig, Bd. XXXI, No.5,
pp. I44-I45 , text figures I-3.

Moroff, T.H. I9I3.

Developement of the compound eye in
Crustaceans.
Zool. Jahrb., Jena , I9I3, pp. 482-558,
pls. I-IO , figures I-7.
Abstracted in J. R. Micr. Soc.,London,
I9I3, p. 483.

Morgan ,T.H.I90I
Regeneration.
Macmillan , London and New York ,
Columbia University Biological Series , VII,
pp. i-xii, I-3I6, figures I-66.

Morgulis, S. I9IO.

Is regeneration a repetition af the
ontogenetic and phylogenetic processes ?
Amer. Nat ., New York or Lankester,
Vol. XLIV , pp. 92-IO7.

* Muller, J. 1826.

Zur vergleichnnden Physiologie des Gesicht
sinnes des Menschen und der Thiere nebst
einer Versuch über Bewegungen des Auges
und über den Menschlichen Blick.
Cudlock , Leipzig, pp. I-32 , I-462,
Taf . I-8

* Müller , J. 1829.

Fortgesetzte anatomische Untersuchungen
über den Bau der Augen bei den Insekten und
Crustaceen
Arch.Anat.Physiol. (Meckel's) , Jahrg.1829,
pp. 38-64, Taf . I-III, figures I-17.
(Berlin).

* Müller, F. 1864.

Ueber den Bau der Schurenasseln
(Asellotes heteropodes)M.Edw.
Arch.Naturgesch.,Berlin, Bd. XXX,
pp. I-6.

Needham , J.G., Traver , J.R. and Tsu , Y.
assisted by specialists in certain subjects. 1935.

The Biology of the May Flies, with a
systematic account of the North American
species.
Comstock Publ. Comp., Ithaca, New York,
1935 ,pp. i-xiv , I-759, figures I-168, pls.
I-XL.

* Newton , E.J. 1873.

The structure of the eye of the Lobster.
Quart, Jour. Micr. Sci., London, N.S.
Vol. XIII , pp. 325-343, pls. XVI-XVII

Nopsca ,F. 1926.

Heredity and Evolution .
Proc. zool. Soc. London, 1926, Part II,
pp. 633-665 , figures I-9.

Nowikoff, M. I905.

Ueber die augen und Frontalorgane der Branchiopoden .
Z, wiss . Zool. Leipzig., Bd. LXXIX, pp. 433-464
pls. XXII, XXIII , pls I-9.
Abstracted in Zool Zentralbl,,Jena, Bd. XIII,
pp. I74-I75.

Nowikoff, M. I93I

Untersuchungen über die Komplexaugen von
Lepidopteren nebst einiger Bemerkungen über
die rhabdomeder der Arthropoden im allgemein.
Z. wiss. Zool., Leipzig, Bd. I38, No. 69,
pp. I-67, text figures I-3 , pls. I-IV.

Nowikoff, M. I93I.

Das Modell des Rhabdoms von Komplexaugen .
Biol. Zentralbl.,Leipzig, Bd. 5I (6) , pp.
325-329, I figure.

* Nusbaum , J. I887.

L'embryologie de Mysis chameleo (Thomson)
Arch. Zool. exp. gen. Paris, Ser. 2 Tom. V,
pp. I23-202 , pls V-VII, I887,

* Oudemans , J.T. I887.

Beiträge zur Kenntnis der Thysanura und
Collembola .
Bijdr. Dierk ., Amsterdam , Bd. XVI , pps.
I47-227, pls . i-iii.

Packard , A.S. I880.

The structure of the eye of Limulus .
Amer , Nat. New York, Lankester, Vol. XIV,
pp. 2I2 , 2I3, 500, 588.
Repeated in Ann. Mag , Nat. Hist .London,
Ser. 5, I880, p. 435.
Abstracted in JoR. Micr. Soc.,London ,
I880, pp. 947-948.

Packard — , A.S. , I880.

On the eyes and btain of Cermatia forceps
Amer. Nat. New York , Lankester, Vol. XIV,
p. 602-604.
Abstracted in J.R. Micr.Soc. London,
Vol. III, I880, pp. 783-784.

Packard , A.S., I903.

A text book of Entomology including anatomy,
physiology, embryology and metamorphoses of
Insects.
Macmillan , New York and London ,
First published I898 , reprinted I903 ,
pp. i-vii, I-I729 , figs. I-654.

Pankrath,O. I890.

Das Auge der Raupen und Phyrganiden larven.
Z. wiss . Zool.,Leipzig, Bd . XLIX, pp.
690-708, pls. XXXIV-XXXV.
Abstracted in J.R. Micr. Soc.,London,
I890, p. 450.

Parker, G.H. I89I.

The Compound eyes in Crustaceans.
Bull. Mus . Comp. Zool . Harvard,
Vol. XXI , No. 2 , pp. 45-I40, pls. I-X.

Parker, G.H. I890.

The Histology and development of the eye in
the Lobster.
Bull. Mus. Comp. Zool. Harvard, Vol. XX,No.
I, pp. I-60., pls. I-4.

(The numbers 555, 556 have been acidentally omitted
in numbering the pages).

Parker, G.H. I896.
Pigment migration in the eye of *Paleomonetes*
Zool. Anz.,Leipzig, I896, pp. 493-520
and in
Deuts. Zool. Gesell, I896., pp. 28I-284
(Leipzig).

Patten , W. I886.

The eyes of Molluscs and Arthropods.
Mitt. Zool. Stat . Neap. ,Berlin,
Bd . 6, Ht.IV, pp. 542-756, Taf. 28-32.

Phillips,E.F. I905.

The Structure and development of the
compound eye of the Honey Bee .
Proc. acad. nat . Sci. Philad.,Vol. LVII,
pp. I23-157, text figures I-7.

Peabody,E.B. I939.

Pigmentary responses in the Isopod *Idothea*
J. exp. Zool, Philadelphia, Vol. 82 (I),
pp 47-83 , figures I-9.

Peabody , E.B. I939.
Development of the Isopod *Idothea* .
J. Morph, Philadelphia, , I939, No. 64,
pp. 5I9-553.

Pearson, J. 1908 .

Cancer .
Liverpool Marine Biologisal Committee
Memoirs, No. XVI ,
Williams and Norgate ,London.
pp. i-viii, I-309 , pls. I-I3.

Pocock, R. I902.

The Taxonomy of recent species of *Limulus* .
Ann. Mag. Nat. Hist.,London,
I902, 7 , IX, pp. 256-266, pls.xii,xiv.

*Purcell, F, I892.

Bau und Entwicklung der Phalangiden.
Zool. Anz.,Leipzig,Bd,XX, No. 408,
pp. 461-465, figures I-3.

Raffray , A. I895.

The occurrence of blind Insects in
South Africa.
Transactions of the South African
Philosophical Society, Cape Town, Vol. IX,
Part I, pp. 20-22.

Rasetti, F. I945.

The evolution of the facial suture in Trilobites (*Loganopeltoides* and *Logenpeltis*)
Amer. J. Sci.,New Haven.
No. 243 (I), pp. 44-50, Ipl.
Abstracted in Biol. Abstr., I945, Vol.I9,
p. I050, No. 9688.

Raymond, P.E. I920.

The Pygidium of Trilobites.
Geol. Mag.,N.S., Vol. LVII, No.I.
pp.22-25. (London).

* Reichenbach, H. 1886.

Studien zur Entwicklungeschichte der Flus-
krebbes.
Abh. senckenb, naturf , Ges., Frankfurt.
Bd. XIV , Ht. I, pp. I-137 , Taf. I-XIV.

Rennie , J.V.L. 1930.

Some Phacopidae of the Bokkeveld series.
Trans . R. Soc . S. Afr. Cape Town,
Vol. XVIII, Part IV,pp. 327-360, pls. IX-X.

Richter ,R. 1911.

The structure of the Trilobite Harpes.
Zool. Anz., Leipzig, Vol. XLV , pp. 146-152.
Reviewed in Geol. Mag . N.S. , Decade VI.,Vol
III, 1916 , (London), p. 36

Richter ,R. 1921.

Beiträge zur Kenntnis Devonischer Trilobiten-
uber die Organisation von Harpes einen
sonderfall unter Crustaceen .
Abh. senckenb. naturf. Ges.,Frankfurt,
Bd. 37 , pp. 177-222, figures I-2.

Rosenstadt , B. 1896.
Zur Morphologische Beurtheilungen der
Augen von Scutigera .
Zool. Anz.,Leipzig. Bd. XIX , pp. 493-520

Ruedemann, R. 1916.

On the presence of a median eye in Trilobites,
Proc. Nat. Acad. Sci. Washington, Vol 2, pp.
234-237.

* Sanchez, D. I9I6.

Development of the retinal elements of *Ganoris brassicae* .
Trab . del. Lab. de Ivest. Biol.de Madrid, I9I6.

* Sanchez, D, I926.

Relactions entre los orugas y los de las mariposas .
Eos, Madrid. Vol 2I , pp. 53-II3, figures I-I6.
Abstracted in Biol. Abs . ,I928, No.788

* Sarsarin , P.B. and C.F. I887.

Die Augen das Integument der Diadematiden
Ergebn, NaturForsch.,Ceylon, Vol. I,Ht.I, pp. I-I8 , pls . i-iii.

* Sars ,G.O. I867.

Histoire naturelle des Crustacea d'eau douche de Norvege . Les Malacostraca Christiana.
Johnsen , Christiana , pp. I-I55,pls. I-I0.

* Schatz, E. I939.

Bau und Entwicklung des Auges von *Gammarus*.
Z. wiss . Zool.,Leipzig.,Bd. I35, pp. 539-573, figures I-37 .

* Schmidt , I879.

Die Form der Krystallkegel im Arthropoden Augen.
Z. wiss. Zool.,Leipzig.,Bd.XXX, Suppl. pp. I-I2, pl.I.

(The number 56I was accidentally omitted from the page numbering).

x Schultze , M. I868.

Untersuchungen über die Gesichtorgane bei den
Crustaceen und Insekten.
Cohen , Bonn, 4to. ,pp. I-32 , Taf. I-2.

Scourfield ,D.J. I939.

The oldest known fossil insect - *Rhyniella*
precursor Hirst and Maulik.
Proc. Linn. Soc.,London, Vol. I52, Part 2,
pp. II3-I3I.

x Seaton , F. I903.

The compound eyes of *Machilus*.
Amer . Nat., New York and Lankester,
Vol. XXXVII , pp. 3I9-329.

Sedgwick , A. I927.

A Student's text-book of Zoology.
Vol. III. Co [illegible]
(The Introduction to the Arthropods , the Crustacea and Xiphosura by J.J. Lister and
The Insecta and Arachnida by A.E. Shipley,
In the text these references are quoted as
from Sedgwick.
George Allen and Unwin , London.
First published I909 , Reprinted , I927.
pp. i-xi, I-975, figures I-570.

Sexton ,E.W. I932.

Degeneration and loss of the eye in the
Amphipod *Gammarus chevreuxi* Sexton
Part I.
J. Mar. Biol. Ass., Plymouth,
Vol. I8 (I , pp. 355-394, pl. I-4 , figures
I-7.

Sexton , E.W. and Clarke,K. I936.

Variations in the white pigment in the eye of
Gammarus chevreuxi with a description of a
new genetic type,the clotted eye.
J. Mar. Biol. Ass.,Plymouth, Vol. 20 (3),
pp. 691-699, I figure.
Abstracted in Biol. Rev. Vol. I0 (8), I936,
p. I856, No. I7769,

Sexton, E.W. , Clarke ,K., and Spooner,G.M.,1930.

Some new eye colour changes in *Gammarus
chevreuxi*,Part I.
J. mar. Biol. Ass. Plymouth, Vol. XVII,
No.I., pp. 204-236.

Sexton,E.W. , Clarke,K.,and Spooner , G.M. I932.

Some new eye colour changes in *Gammarus
chevreuxi* - Part II.
l.c. Vol. XVIII, No.I, pp. 307-336

Sexton,E.W., and Fantin , C.F. I927.

Inheritance in *Gammarus chevreuxi* Sexton.
Nature ,London.
Vol. II9, I927, pp. II9-I20.

Sharp,D. I922.

Insects , Peripatus Myriapods.
Vol. VI. Cambridge Natural History.
Editdd by S.F. Harmer and A.E. Shipley.
Macmillan ,London, pp. i-xii, I-626
figures I-293.

Shipley A.E. I927.

See Sedgwick. I927.

* Simon, E. I879.

Arachnides nouveaux de France , d'Espagne et
d'Algerie . Premier memoire.
Bull. Soc. Zool. France, Paris, IV, I879,
pp. 251-263.

Sexton , E.W. and Wing .,M.B. I916.

Inheritance of eye colour in *Gammarus chevreuxi*.
J. Mar. Biol. Ass.,Plymouth, Vol. XI, p. I8-50 , I pl.

* Smith , S.F. I880.

On some points in the structure of a species of the Willemoisia group of Crustacea.
Ann. Mag.Nat,Hist. ,London, Ser.5 , Vol.V, pp. 269-273.

Snodgrass , R.E. I926.

The morphology of Insect sense organs and Nervous system.
Smithsonian Miscellaneous Collections, Washington, Vol. 77, No. 8, Pub. 283I, pp. I-80 , figures I-32.

Snodgrass, R.E. I925.

The anatomy and physiology of theHoney Bee.
MacGraw Hill , New York , Ist Ed. I925, pp. i-xv , I-327, figures I-II8

Snodgrass ,R.E., I935.

Principles of Insect Morphology.
Ist Ed. , 2nd Impression.
MacGraw Hill, New York, pp. i-ix, I-667, figures I-633.

Sograff,N. I879.

Vorlaufige Mittheilungen über die Organisation der Myriapoden.
Zool. Anz.,Leipzig, Jahrg I879, No. I9. pp. I6-I8

Sokolow, I. 1911.

The eyes of Pantopoda.
Z.Wiss.Zool.,Leipzig,Vol. XCVIII, pp. 339-380,
pls. I-2, figure I.
Abstracted in J. R. Micr. Soc London,
1912, Part II, pp. 183-184.

* Spengenberg, F. 1875.

Zur Kenntnis von *Branchipus stagnalis* .
Z. Wiss. Zool.,Leipzig, Bd .XXV, Suppl.,
pp. I-64, Taf. I-III.

Spurgeon , C.H. 1915.

The eyes of *Cambarus setosus* and *C. pellucidas*.
Biol. Bull, Woods Hole, Vol. XXVIII,
pp. 385-396, Taf . 1-9.

Steele , M.I. 1907.

Regeneration of the compound eye in Crustacea.
J. Exp. Zool.,Philadelphia, Vol.V, No.2,
1907, Pls. I-16, text-figures I-2, pp. 163-244.

* Steinlin, W. 1868.

Ueber Zapfen und Stabchen der Retina .
Arch. Mirk. Anat.,Bonn, Bd. IV, pp. 10-21,
Taf . II.

Stubblefield , C.J. 1938.

Cephalic sutures and their bearing on the current
classification of the Trilobites ,
Biol. Rev., Cambridge, Vol. II , No. 4,
pp. 407-440 , figures I-9.

* Strohm , K. 1910

Die Zusammengesetztenaugen bei Mannchen von
Xenos rossii.
Zool. Anz.,Leipzig.,Bd.36, pp. I55-I59.

Swinnerton , H.H. I915.

Suggestions for a revised classification of
the Trilobites.
Geol. Mag . N.S. Decade VI, Vol.XI, pp. 487-496,
538-545.(London).

Swinnerton , H.H. I919 .

The facial suture of the Trilobites.
Geol. Mag., Vol. LVI, N.S. Decade . VI, pp.
I03-II0.(London).

Swinnerton ,H.H. I932.

Unit characters in fossils
Biol. Rev. Cambridge, Vol. VII, No. 4 , pp.
32I-336

Svensson ,E. 1933 .

Ueber die Augen und das Gehirn *Haploops tibicola* Lilj.
Abstracted in Biol. Abs , Vol. I0 (3)
p.763, No. 70I6. from
Arch. Zool. Stockholm, 25A (4 . No.I8),
pp. I-I6 , figure 7 . I933.

Tatersall, M. I927.

Report on Crustacea Mysidacea.
Trans. Zool. Soc.,London, Vol 22 (3) , pp. I85-
I99, figures I-3 .

Tillyard, R. I926.

Insects of Australia and New Zealand ,
Angus and Robertson, Sydney, pp. i-xi, I-560
figures I-2B4

Thomas , T . I909.

A new Devonian Trilobite and Lamellibranch
from Cornwall.
Geol Mag.,N S. Decade V. ,Vol.VI, No.III,
pp. 97-I02.. (London).
Notes on the Trilobite fauna of Devon and
Cornwall.
l.c. pp. I93-204.

Tiegs , O.W. I940.

The embryology and affinities of the Symphyla
based on a study of *Hansiella agilis* .
Quart. Jour. Micr. Sci.,London, Vol . 82,
Part I, N.S. , pp. I-234.

Tschugunoff,N. I913.

Über die Veranderung des Auges bei
Leptodora Kindtii (Focke) unter dem
einfluss von Nahrungs entziehung.
Biol. Zentralbl.,Leipzig.,pp350-36I,
Jahrg. I9I3.

Uchida , H. I924.

Colour changes in the eyes of the longicorn
Grasshopper *Homocoryphus lineosus*
in relation to light.
J. Fac . Sci . Univ. Tokyo,(Zool),Vol. 3,
Part 3 , pp. 5I7-525 , text figures I-7.

Umbach,W. I934.

Entwicklung und Bau des Komplexauges der
Mehlmotte Ephestia kuhniella Keller
nebst einigen Bemerkungen über Entstehung der
optischen ganglien .
Z . wiss. Zool., Abt, Anat. Morph.Okol .Tiere
Bd. 28 (5), pp. 56I-594, figures I-26.
Abstracted in Biol. Abs. Vol. 8 ,1934, No,
I7056.

Verhoeff , K.W. 1925.

In Bronn's Klassen und Ordungen das Tier-
reichs. Chilopoda. Bd.II.
pp. 40-44, Io2, 665-666, 669-67I , figs
II7I-II72.
Chilopoda,Bd.II , pp, I173-I178
Diplopoda , pp. 283-332, 359, , II58-II64,
II00-II02 , II64-II73.
figures . 659-664.

Vejdovsky,F. I905.

Reduction in the eyes of Gammarids.
S.B. k. .Bohm . Ges. Wiss .,Bd. XXVIII,I905,
pp. I-40 , 2 pls, II figures.
Abstracted in J.R. Micr. Soc.,London, I906,p.308.

Verrier, M.L. I940

Reductions culaires par degenerescence e
chez les Crustaces.
C.R. Acad. Sci.,Paris, No. 2II , pp. I48-I50.
Abstracted in Biol. Abstracts , Vol . I7,
I943, No. 2278I.

* Vigier, P. I904.

Sur la presence d'un apparat d' accomodation
les yeux composes des certains Insectes.
C .R. Acad. Sci.,Paris, Tom.CXXX(XVIII)
pp. 7I5-777

* Vigier,P. I907.

The structure of the compound eye in Muscidae.

* Vigier , P. I907.

The structure of the compound eye in
Muscidae.
C.R. Acad. Sci., Paris , Tom. CXLV,
pp. 533-536, I fig.
Abstracted in J.R. Micr. Soc.,London,
pp. 675-676.

von Rosen , T . I9I3.

The eyes of Termites.
Zool. Jahrb.Abt. Anat.,Jena, Bd. XXXV,pp.
625-664, pls. I-3 figures I-I0.
Abstracted in J.R. Micr . Soc.,I9I3,
Part II, p. I67. (London).

von Zittel, K.A. I937.

Text Book of Paleontology, Vol. I .
Invertebrates.
Edited by Eastman, C.R. adapted from the
German of von Zittel, K.A.
Macmillan , London , pp. I-X, I-839,
figures I-I594.

Walcott,C.D. I89I.

I0th annual report of the United States
Geological Survey. I89I, p. 635.

* Walcott C.D. I9I0.

Cambrian Geology and Paleontology -
<u>Olenellus</u> and other genera of the
Mesonacidae.
Smithsonian Miscellaneous Collections,
Washington, No. 53 , pp. 23I-423.

*
Walcott , C.D. I9I2.

Cambrian Geology and Paleontology -
Middle Cambrian Branchiopoda, Malacostraca
Trilobita and Merostomata.
Smithsonian Miscellaneous Collections,W
Washington, No 57 , pp. I45-228 and
I5 pp. not numbered. pls. XXIV-XXXIV.

*Walcott, C.D., 1918.

Researches on the appendages of the Trilobites.
Smithsonian Miscellaneous Collections, Washington ,D.C. , LXVIII, No 4 , pp. 115-316 plus index , pls. XIV-XLII , Taf . 1-3.

Watase , S.H. 1890.

On the morphology of the compound eyes of Arthropods.
Johns Hopkins University Bulletin , Baltimore , Vol. IV , pp. 287-334, pls. XXI-XXXV.

Watase , S.H. 1890.

On the compound eyes of Arthropods.
Ann. Mag. Nat. hist. 6th Series , Vol. 6, p. 123.

Waterhouse, C.O. 1889.

Notice of an Entomological Exhibit for the Entomological Society of London.
Proc. R. Ent.Soc.,London, 1889, pp. xxiv-xxv

* Wagner , R. 1835.

Einige Bemerkungen über die Bau der Zusammengesetzten Augen.
Arch. Naturgesch.,Berlin, Bd. I.,p. 372 et. seq.

Weber, E. 1925.

The Trilobites of Lepteana Limestone in Dalarne .
Bulletin of the Geological Institute of Uppsala, Vol. XVII, pp. i-viii,1-466, pls. I-X , figures 1-23, and pp. 374-376.
Abstracted in Geol. Mag .,Vol. LXII, 1925 , pp. 374-376. (London).

Weber , H. I937.

Morphologie und Entwicklungschichte
der Arthropoden.
Fischer , Jena, pp.28-86.

* Weismann , A. . I874.

Über die Bau und Lebenserscheinungen von
Leptodora hyalina Lilleborg.
Z. wiss. Zool. Bd. XXIV ,Abt. Anat ,
pp. 349-4I8 , Taf. XXXIII-XXXVIII.
(Leipzig)

Welsh , J.H. I930.

The mechanism of migration of the distal
pigment cells in *Paleomonetes* .
J. exp. Zool. Philadelphia , Vol. 56 (4)
pp. 459-494 , pls. I-4 , figures .I-4,
Abstracted in Biol. Rev.,I932, p.430
No . 3945.

Welsh , J. . I930.

Diurnal rythm in the distal pigment cells
of certain Crustacea.
Proc. Nat. Acad. Sci., Washington, Vol.
I6 (6) pp. 386-395 , figures I-3.
Abstracted in Biol. Abs .,I93I, No.
23270.

Welsh J.H. and Chase ,A. Jnr. I938.

Eyes of deep sea Crustaceans and Sergestidae.
Biol. Bull. Woods Hole , Mass., Vol .
74 (3) , pp. 364-375.
Abstracted in Biol. Abs. Vol. I2, p. I156,
No. I2450.

Welsh , J.H. and Chase , A. Jnr. I938

Eyes of Acanthephyridae.
Biol. Bull. Woods. Hole . Mass.,Vol. 72,
(I), pp. 57-74 , figures I-I7.

*Wenke , W. I909.

The eyes of Apus.
Z. wiss. Zool., [illegible], Bd. XCI, pp. 236-265
I pl. , I3 figures. Leipzig.

Werringloer, A. I932.

Die Sehorgane und Sehzentren der Dorylinden
nebst Untersuchungen über die Facettenaugen
der Formiciden.
Z. wiss. Zool. , Leipzig., Bd. I4I (3)
.pp. 432-524 , figures I-49,
Abstracted in Biol. Abs . Vol. I0(I).
p. 226 , No. 2002, I936.

Wesche , W. I909.

The eyes of Diptera.
Journal of the Queckett Microscopical
Club , London , I909, pp. 367-384,
I pl.
Abstracted in J.R. Micr . Soc., London,
I909, Part 4 , p. 468.

*Will, E. I840.

Beiträge zur Anatomie der Zusammengetzetsten Augen mit Facettierte Hornhaut.
Voss, Leipzig. pp. I-32, I Taf.

Widman ,E..I907.

The structure of Spider's eyes .
Zool.Anz., Leipzig, Bd. XXXI , pp. 755-
762 , figures I-7.
Abstracted in J.R. Micr Soc. ,London,
I907, p. 434.

Wigglesworth, V.B. I933 .

The physiology of the cuticle and of
ecdysis in Rhodnius prolixus (Triatomida
- Hemiptera) with special reference
to the function of the oenocytes and the
dermal glands.
Quart , Jour. Micr. Sci.,London, No. 302,
N.S. ,pp.269-318 , text figures
I-I5.

Wigglesworth ,V.B. I934. I938.

Insect Physiology.
Metheun's Monographs on Biological
subjects , [illegible] EditionsIst. and 2nd .
Metheun , London, pp. i-x , I-I34 , figures
I-I3 .

Wigglesworth , V.B. I939.

The principles of Insect Physiology .
Metheumn , London, Ist Edition .
pp. i-viii, I- 434 , figures I-3I6.

Willem , M.V. I89I.

On the struc-ture of the ocelli of
Lithobius .
Ann. Mag. Nat . Hist., London , Ser. 6,
Vol. VIII, pp. 482-483.

Willem , M.V. I897.

Le yeux et organes postantennaires
des Collemboles.
Ann. Soc. ent. Belg.,Brussels, Vol VI ,
(vii) , pp. 225-226.

Williams , C.B. I930.

Unusual formation of the eyes in certain
Aleurodidae.
Proc. ent. Soc.,London, Vol.V.aPart II,
p. 56. Note on an exhibition made
on Wednesday , I8th June , I930.

Wolsky , A. I93I
Naturliche fälle heteromorpher regener-
ation am Auge des Sumpfkrebes.
Zool. Anz.,Leipzig, Bd. 96, (I-2)
,pp. I8-22 , figs. I-2 .
Abstracted in Biol. Abs. Vol. 6 , I932,
p. 2III , No. 20503.

Wolsky, S. I934.

Phylogenetische und Mutative Degeneratin der Gammaridenauges.
Ungarische Acad. wiss , Bd. 5I , pp. 645-670 , fig. I.
Absracted in Biol. Abs . I937, p. 2I23, No. I9668.

Woods,H. I909.

Trilobites in Crustacea and Arachnida . Cambridge Natural History . ~~Vol. IV.~~
Ed. Harmer ,S.F. and Shipley ,E.A.
Vol. IV.
Macmillan , London , pp. 22I-254 , figs .I36-I5I.

Woodward,H. I905.

Notes on a series of Trilobites obtained by Mr. Howard Fox from the Devonian of Gant Hill, St, Minver , Cornwall.
Geol. Mag. N.S. Decade V, Vol. II, NO. IV, pp. I5I-I54. (London).

Yonge , C.M. I932.

On the nature and permeability of chitin I. The chitin lining of the fore gut of Decapods Crustacea and the function of the tegumental glands.
Proc. Roy. Soc.,London , Ser. B.
Vol. CXI , pp. 298-329 , pl. I4.

Yossi , N. I93I.

Note on a Japanese spiny Lobster with an antenna in place of an eye .
J. Fac. Sci. Imp. Univ . Tokyo,
Sect. Zoo. Vol. II , Part 4 , pp. 445-447,
3 text figures.

* Zaddach, E.G. I84I.

De Apodid cancriformis.
Bonnae Typis Carolis Georgii .

pp. I-72 , pls. I-4.

Zavrel, J. I907.

Die Augen einiger Diperen larven und Puppen.
Zool. Anz., Leipzig. Bd. XXXI , I907, pp
247-255 , figures I-I3.
Abstracted in J. R. Micr. Soc., London,
I907, p. 546.

Zawarin , A. I9I4.

Histologische Studien Über Insekten .
IV Die optische Ganglien der Aeschna
larven .
Z. wiss. Zool., Leipzig, Bd. I80 , Ht. 2,
pp. 175-25I(pp. I85-I87 - eyes) .
Figure 4.

* Zeleny ,C. and Matoon E.W. I9I5.

The bar eye mutant of Drosophila .
J.R. Micr. Soc., I9I6 , pp. 293-294.
Abstract of paper in J. exp. Zool., Philadelphia , Vol. XXX , I9I5 , pp.
5I5-530 , figures I-5.

Zeleny , C. I906 .

The regeneration of an antenna like
organ in place of [illegible] the vestigeal
eye of a blind Crayfish .
Science, New York, Vol. 23, p. 527.

Zimmerman , K. I9I3.

The facetted eyes of Libellulidae ,
Phasmidae and Mantidae.
Zool. Jahrb ., Abt. Anat., Jena , Bd. XXXVI(E)
pp. I-36 , pls. I-2 , figs. I-3.
Abstracted in J.R. Micr. Soc. , I9I3,
Part 2 , p. 539 .
