

The Structure of the Double-Eyes of *Baetis* and the Uniform Eyes of *Ecdyonurus* (Ephemeroptera)

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Summary. The lateral eyes of *Baetis vernus* are structured similarly in both sexes. They are eucone apposition eyes with a closed rhabdom formed by eight retinula cells. The accessory pigment cells surround the ommatidia over their entire length. The morphological adaptation to different illuminations consists of a radial displacement of mitochondria and endoplasmic vacuoles. The dorsal eyes of the male *Baetis*, often called turban eyes, differ remarkably in structure and size from the lateral organs by a large clear zone which is only crossed by thread-like elongations of the retinula cells; the rhabdom is divided in a distal part next to the cone and a large basal part. Each of the seven retinula cells contributes microvilli to both parts of the rhabdom. The pigment cells only surround the cone and the distal part of the rhabdom, whereas the basal rhabdoms are optically isolated from each other by a ring of trachea. No morphological adaptation to different illumination is detectable in the dorsal eyes. The relation of the two different eyes of the male, being optically isolated but forming a morphologically connected complex, are discussed. With the description of the dorsal eyes of the subimago the formation of the dorsal eyes is investigated. A possible mode of function is considered. The male of *Ecdyonurus venosus* has larger eyes than the female, but they are structured after the same scheme. The eyes are similar to the lateral eyes of *Baetis*.

A. Introduction

The best known fact about the optic system of Ephemeroptera is the presence of large dorsal eyes, called turban eyes, in the male of some families. In addition, these animals also have lateral eyes just as the females do. Most works published on the ephemeropteran optical system deal predominantly or entirely with the dorsal eyes. The early and most cited author Zimmer (1898) gave a broad spectrum of the morphology of different ephemeroptera, especially of the turban eyes. Unfortunately the nomenclature used by him differs largely from the

one used now (Ulmer 1934), which results in some confusion. Whereas Shafer (1907) and Priesner (1916) completed our knowledge at the light microscope level, there are some electron microscope investigations of the dorsal eyes of *Cloeon* by Horridge (1976) and Wohlburg-Buchholz (1976). Because the works of the latter authors have been entirely restricted to the male dorsal eyes, there are no publications about the lateral eyes or the photoreceptors of the female and subimaginal animals. The present work should fill this gap and analyze the structure of the eyes of two other ephemeropteran species. The investigation of *Ecdyonurus* should answer the question whether the considerably larger eye of the male includes only one type of ommatidia as compared with that of the female or whether there are several different parts in the sense organ. The two superficially divided eyes of the male *Baetis* are compared with each other and with the eyes of the female and subimagines to show the relation of the two differently structured photoreceptors.

B. Materials and Methods

The two species *Baetis vernus* (Fabricius) and *Ecdyonurus venosus* (Curtis) were caught as subimagines near the river Wutach in the Black Forest. They were kept in a dark room at 10° C; after 1 week most of the animals had moulted into imagines. The isolated eyes were fixed in 3% glutaraldehyde for 2 h, then rinsed in phosphate buffer and finally treated with 2% osmium tetroxide for 3 h. After washing in buffer again and dehydrating with ethanol and propylene oxide, the organs were embedded in Araldite resin, sectioned with an ultramicrotome Om U2 (Reichert) and stained with uranyl acetate and lead citrate. Dark-adapted animals were dissected in a dark room with red light ($\lambda > 700$ nm) and kept in a dark box during the whole fixation. Light adaptation was performed under sunlight for at least 4 h. A staining procedure after Richardson et al. (1960) has been used for semithin sections.

C. Results

1. The Compound Eyes of *Baetis*

Apart from the lateral eyes the male of *Baetis* has a pair of large dorsal eyes, called turban eyes, which are absent in the female (Fig. 1 c and d). Although there is no difference in the structure of the lateral eyes of the subimago and imago of both sexes, there is a remarkable development of the dorsal eyes in between these two stages, leading to different structures in the adult insect.

a) *The Lateral Eyes.* The diameter of the hemispheric cornea covering the whole organ ranges from 0.30 to 0.35 mm and in females it is a little larger than in males. The ommatidia can reach a length of 140 μ m, their facettes are about 16 μ m wide (Fig. 2 e). The biconvex cornea lens is 6 μ m thick. The conus beneath the cornea has a maximal length of 30 μ m and near its distal end it is about 11 μ m thick. The nuclei of the four cone cells form a distal cover over the cone. Each cone cell extends like a long thread along the rhabdom towards the basement membrane. The rhabdom is in tight contact with the tip of the cone, but the rhabdomeres do not surround it. In all ommatidia

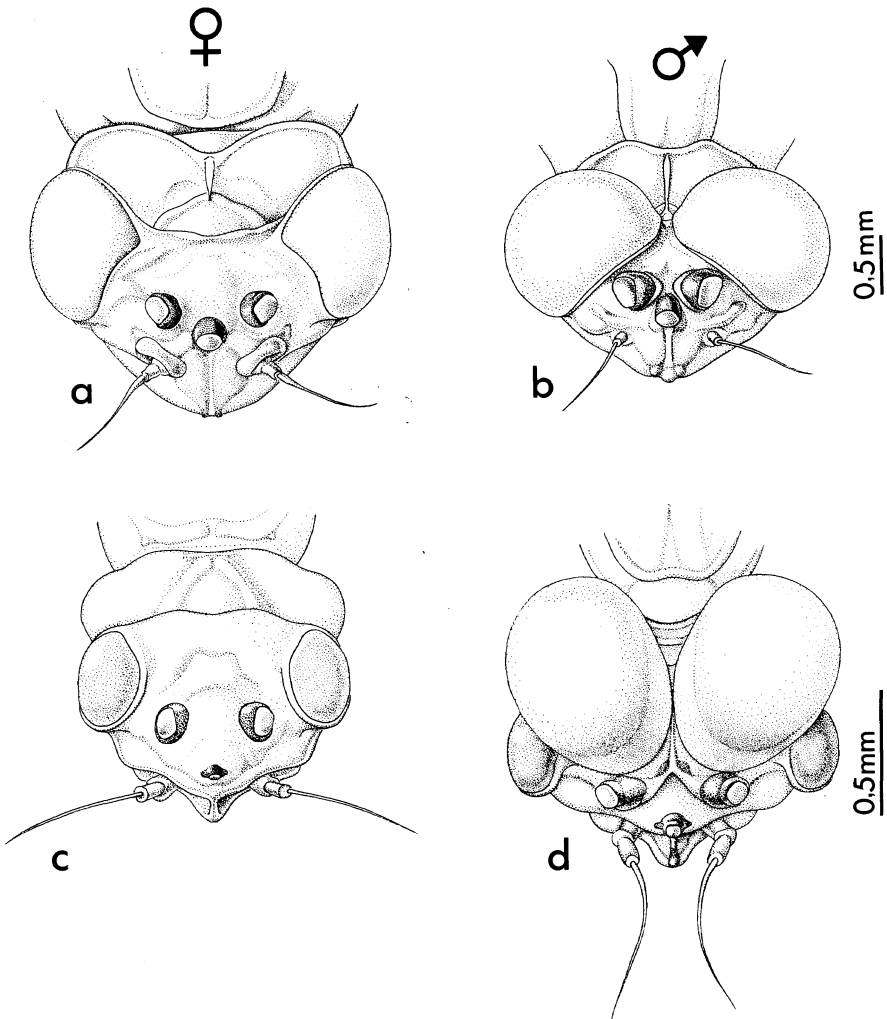
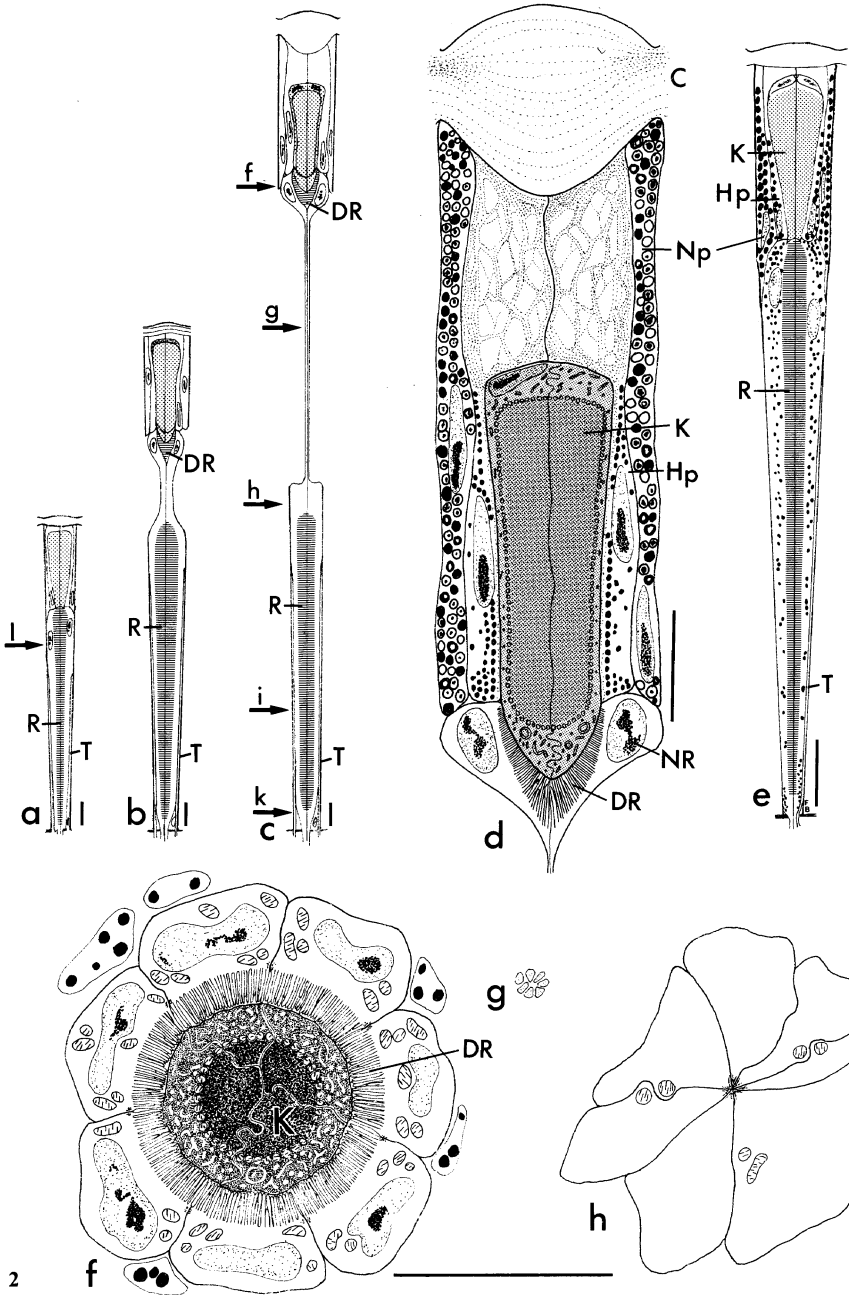


Fig. 1a–d. External view of the heads of two ephemeropteran species: *Baetis vernus* (c, d) and *Ecdyonurus venosus* (a, b). In both species a sexual dimorphism is eminent, for the eyes of the males are larger. In *Baetis* they are not only larger but divided in lateral eyes, similar to the female ones, and a huge dorsal optic organ

there are eight retinula cells (Figs. 21 and 3c). Their rhabdomeres form a closed rhabdom of about 90 μm length. There is no structural difference between these cells. The directions of their microvilli can differ from cell to cell; two or even three neighbouring ones can show parallel directions (Fig. 3a and b). The nuclei of the retinula cells are situated at their distal ends. There are many pigment grains, some mitochondria, and a well developed system of endoplasmic reticulum in these cells. In the dark-adapted eye the endoplasmic reticulum forms large cisternae around the rhabdom which are often called palisades,



while the rest of the organelles is found in the periphery of the retinula cells (Fig. 3b). During adaptation to bright light the mitochondria and the pigment grains move towards the rhabdom (Fig. 3a). The endoplasmic cisternae disintegrate into many smaller vesicles lying in the outer regions of the retinula cells. This mode of adaptation is characteristic for the apposition type of com-

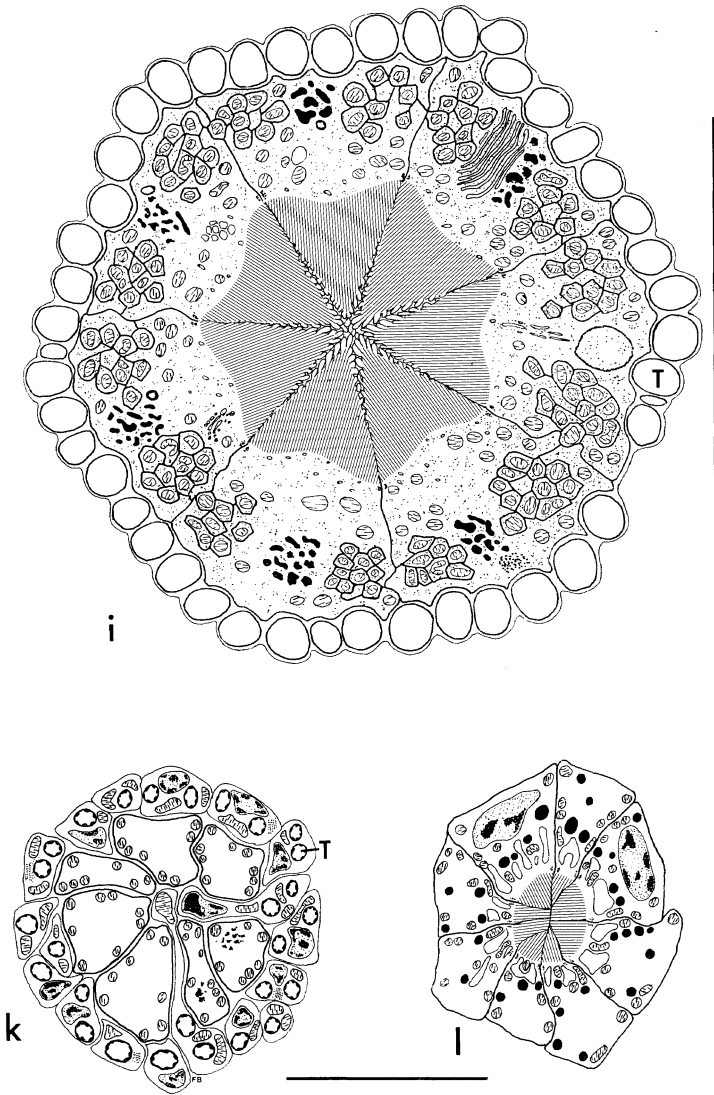


Fig. 2a-l. The ommatidia of *Baetis vernus*. Longitudinal section of a lateral eye (a, e) at different magnifications, and of a dorsal eye of a subimaginal (b) and an adult male (c). Longitudinal section of the distal part of the dorsal eye, with the distal rhabdom, the cone and the cornea at higher magnification (d). Cross sections at the levels indicated at figures a and c. Section through the distal rhabdom (f), the thread-like connecting part (g), the area closely proximal to the clear zone (h), the large proximal rhabdom (i) and the region just above the basement membrane (k). Cross-section of an ommatidium of a lateral eye adapted to darkness (l). Scale = 10 μ m

pound eyes. There are two primary pigment cells surrounding the cone and various numbers of accessory pigment cells. Whereas the electron dense grains in the primary pigment cells are very similar, only a little larger than in the retinula cells, in the accessory cells they are different, i.e. less electron dense and often washed out during the embedding procedure.

b) *The Dorsal Eyes.* The huge dorsal compound eyes are only partly integrated in the head of *Baetis*, the predominant part being on the top. They are contained in a cuticular cylinder 0.25 mm high covered with a slightly convex cornea. At the top the cylinder is 0.9 mm long and 0.7 mm wide (Fig. 1 d).

The most remarkable fact about these eyes is the wide clear zone between the distal part of the ommatidia and the proximal part with large rhabdoms. Figure 4a gives a good view of a section through the whole eye on a microscopic scale, while the sections in Fig. 2 are the result of electron micrographs.

The biconvex cornea lens of a typical ommatidium has a diameter of 26 μm ; at the periphery it is 6 μm and in the centre 25 μm high. Below the cornea there is a space of about 20 μm width which has a spongy structure formed by the endoplasmic reticulum of the primary pigment cells (Fig. 2d). Only small cytoplasmic threads and lamellae are present here. The cone is formed by four cells. Together they make up a cylindrical shape rounded at the distal ends and slightly pointed at the proximal ends next to the small rhabdom (Figs. 4c and 5a). The cone is heterogenous. A central, granulated, electron dense part is covered by a layer of tightly packed, globular mitochondria (Figs. 2d and 5a). Cytoplasm with a system of many endoplasmic tubules and with the nuclei at their distal end is surrounding the central cone.

The cone cells are enclosed by two primary pigment cells, which also fill the space between cornea and cone as mentioned above. Numerous pigment grains with a maximal diameter of 0.6 μm are located around the cone. The flattened and bent nuclei of the primary pigment cells are surrounded by the grains. The accessory pigment cells are arranged around the cone, and the other pigment cells form a circle of about 25 cells. These pigment cells do not extend to the basement membrane as in most compound eyes of other insects, instead they are only about 50 μm long, ending at the distal ends of the retinula cells (Fig. 2d). Thus both types of pigment cells have the same length. The grains of the accessory pigment cells have a maximal diameter of 0.83 μm , therefore they are considerably larger than those of the primary cells. They especially show pigment grains which are mostly not as compact and electron dense as described for other insects. Quite often they are heterogenous, frequently they are stained only slightly and sometimes the material even seems to be washed out by the embedding procedure. Only the accessory pigment cells show grana of the typical structure.

The rhabdom in the dorsal eye is separated by the larger clear zone into a huge basal part and a small distal one, surrounding the tip of the cone like a cap. In each ommatidium there are seven retinula cells which each have a distal rhabdomere of 10 μm length and a second one in the proximal part extending to about 150–200 μm . Like the rhabdom the retinula cells also have a distal part (Figs. 5a, 2c and d;) containing the nuclei and a large proximal part. They are separated by the clear zone. Across this zone the two parts are connected by a thread-like cell extension of 0.3 μm diameter (Fig. 5b). These filiform cell parts of each ommatidium are loosely bundled together and are surrounded by a homogenous intercellular liquor. In the distal rhabdomeres the microvilli are arranged radially to the cone. The proximal part of the rhabdom has a rosette-like cross section (Fig. 6a), which becomes almost

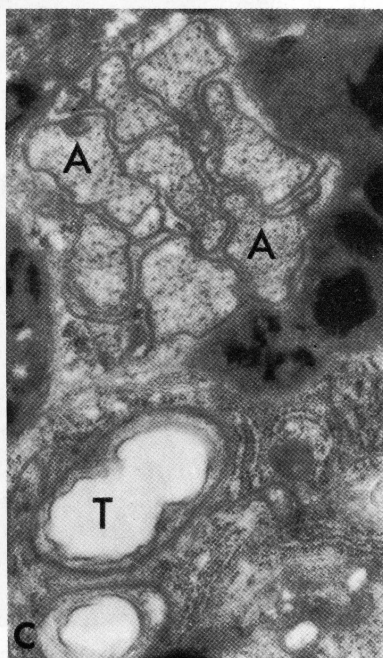
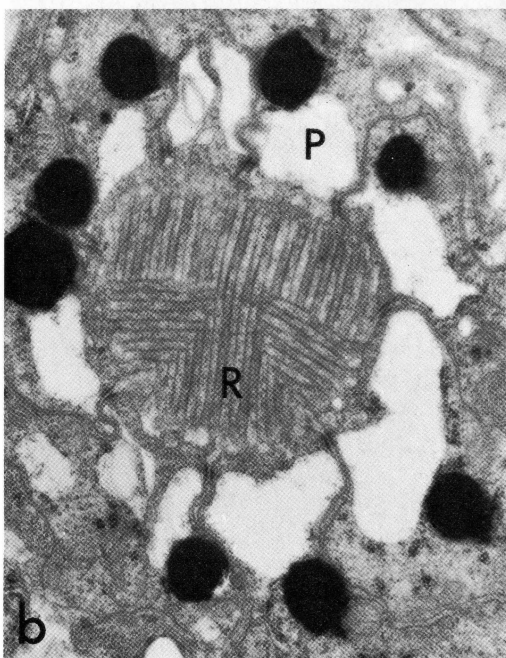
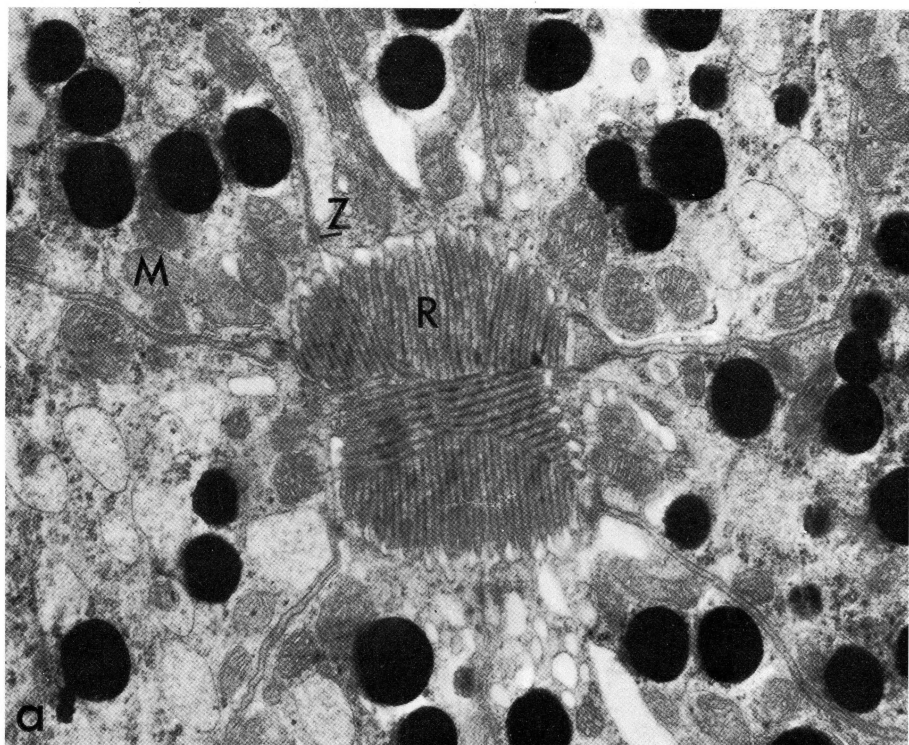


Fig. 3a-c. Cross section through a rhabdom of a lateral eye, with 8 retinula cells from a light-adapted *Baetis* (a) and a dark-adapted animal (b). A section next to the basement membrane, showing 8 axons belonging to one ommatidium (c). ($\times 19,000$)

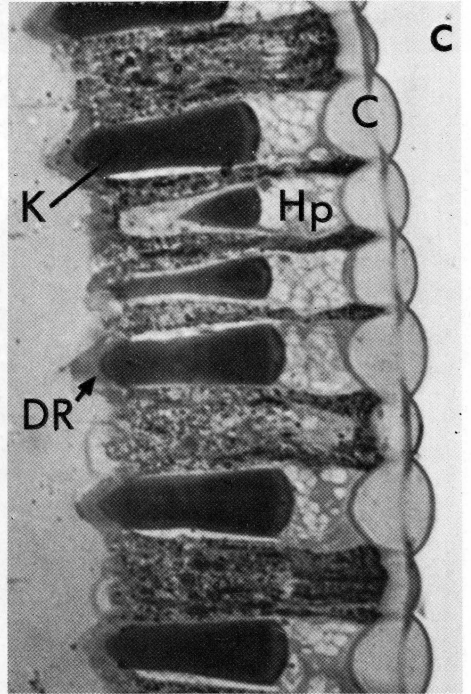
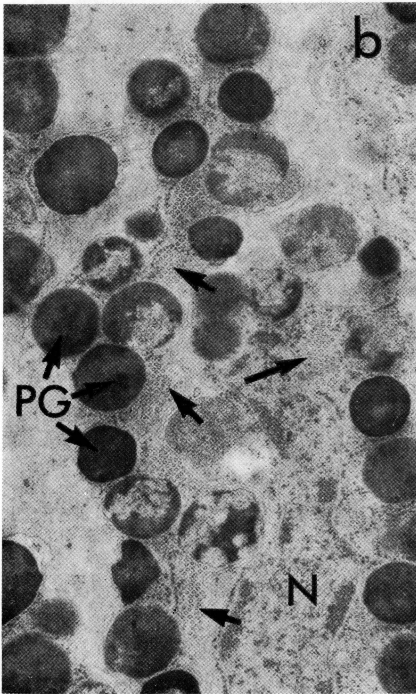
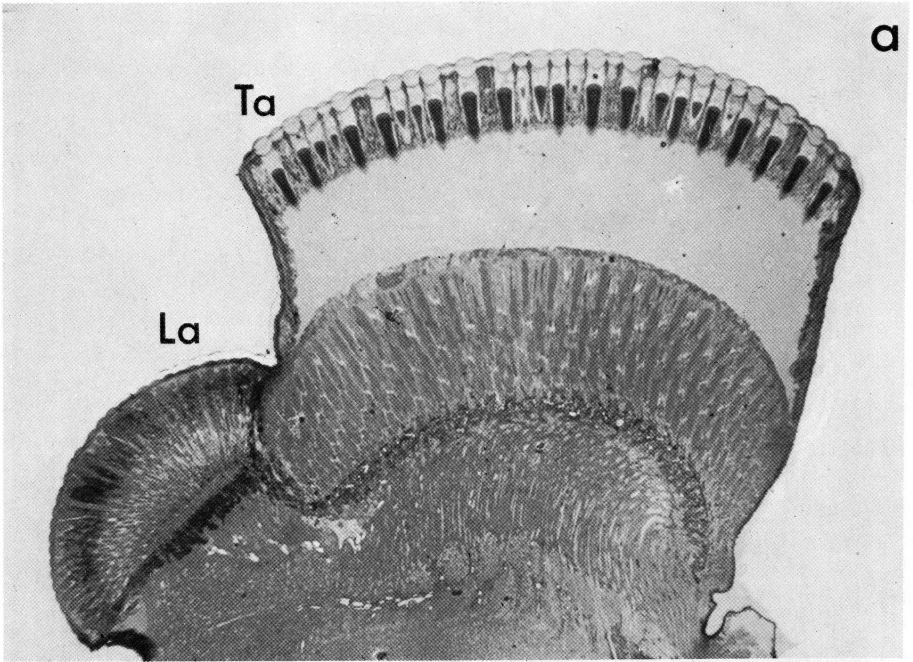


Fig. 4a-c. Light-microscope section showing dorsal and lateral eye of *Baetis* (a) and through the distal part of the dorsal eye at higher magnification, with cones, cornea, pigment cells and distal rhabdom (c). Electron microscope cross-section through the pigment cells at the area where both eyes are connected (b), where large bundles of microtubuli (arrows) are seen next to the pigment grains. Magnification: a $\times 120$; b $\times 19,000$; c $\times 500$.

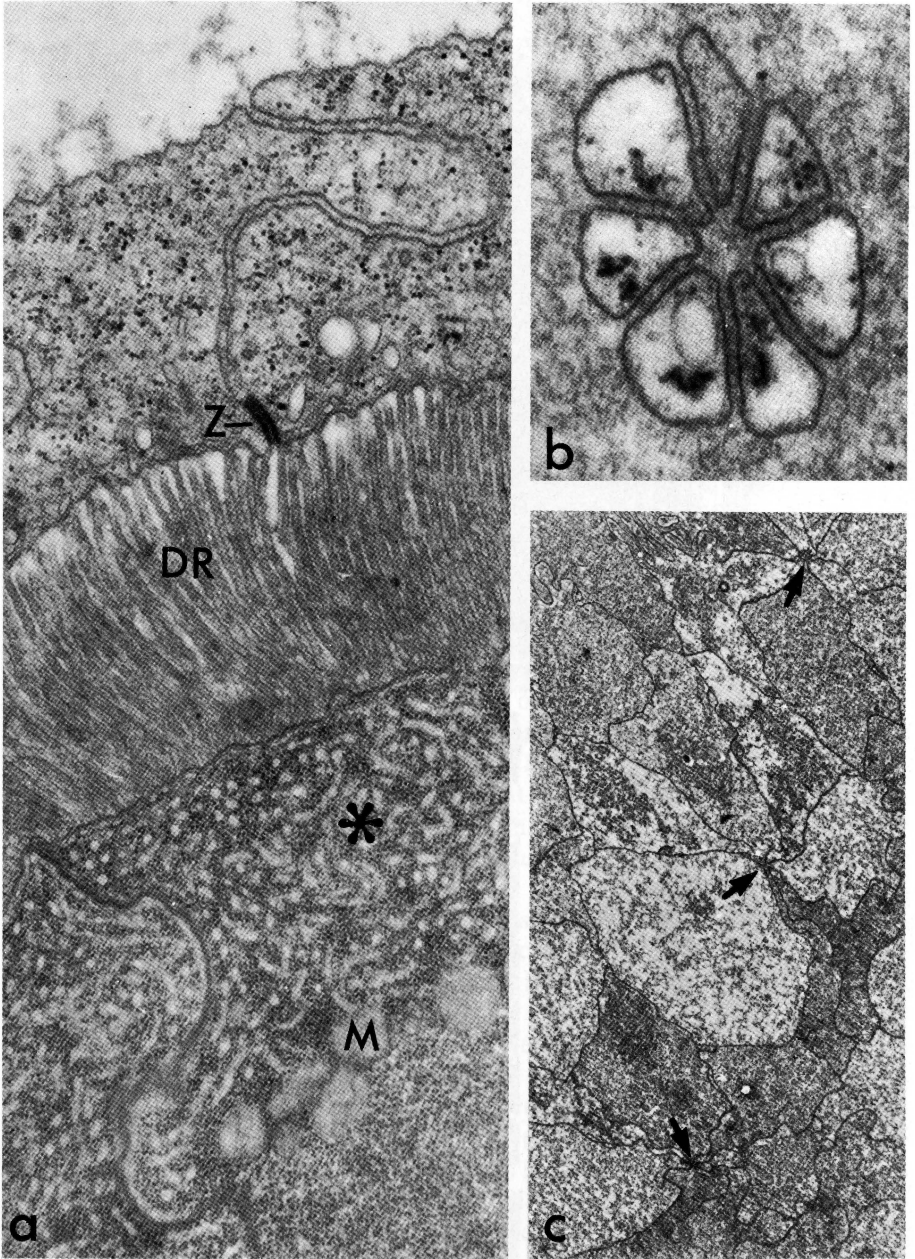


Fig. 5a-c. The ommatidia of the dorsal eye of *Baetis*. Cross-section through the distal rhabdom, the cone tip (*) and the distal part of two retinula cells (a). Section of the thread like part of the retinula cells in the clear zone (b). Just distal to the clear zone is a region where the retinula cells of an ommatidium do not generate a rhabdomere but only contact structures (arrow) (c). Magnification: a $\times 9,200$; b $\times 35,000$; c $\times 3,600$

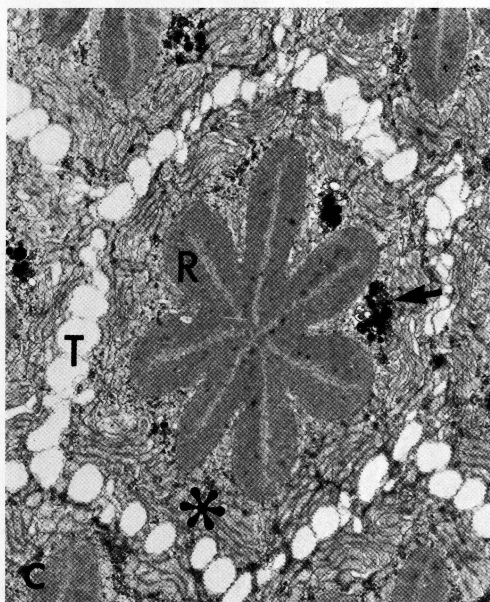
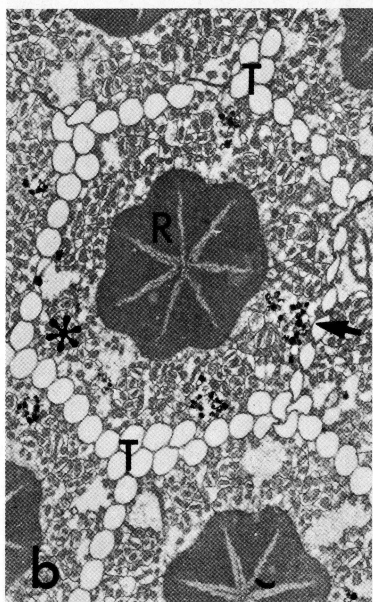
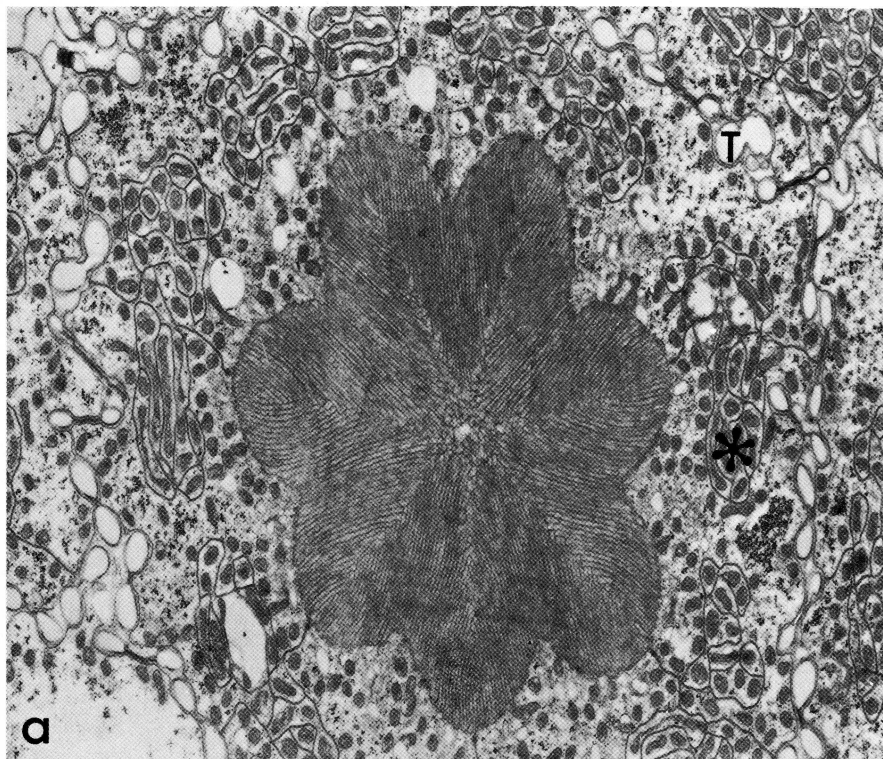


Fig. 6a-c. Cross-sections through the large proximal rhabdom of *Baetis*. In the distal region the rosette-like rhabdom (a) is surrounded by many mitochondria often enveloped by intruding membranes (*). At the middle and basal parts (b) the tracheoles surrounding the ommatidia become more prominent. Between the enclosed mitochondria (*) there are many irregular electron dense granules (arrow). An ommatidium of an animal with star-shaped rhabdoms (c). Magnification: a $\times 19,000$; b $\times 3,600$; c $\times 5,400$

circular towards the basement membrane. The diameter varies from 6 to 8 μm . In some animals transverse sections of all the ommatidia were obtained in the form of an asterisk (Fig. 6c), but no relation to a light- or dark-adapted state could be found. The microvilli in the proximal part of one cell are parallel, but their direction varies in the neighbouring cells (Fig. 6a). Distally to the large rhabdom, at the base of the clear zone, there is a region about 20 μm wide where the retinula cells have regained their normal thickness and where zonulae adhaerentes are present, but no microvilli or other organelles can be seen (Fig. 5c). In a basal region of about 10 μm thickness the microvilli are missing, too. Often the tips of the microvilli are slightly enlarged so that a star-shaped region with a lower concentration of light sensitive membranes appears in the centre of the transversal sections of the rhabdoms (Figs. 2i and 6b). It could not be demonstrated that this was an artifact caused by the fixation.

Beside the proximal rhabdom two invaginations of the outer cell membrane form numerous long tubes which are in contact with each other (Figs. 2i and 6a). They are oriented parallel to the axis of the ommatidia and each contains a row of rod-shaped mitochondria which amount to about half of the total mitochondria. These voluminous invaginations, filling most of the proximal part of the retinula cell, are always in contact with the lateral outer cell membrane through a ridge formed by two membranes. Between the tubular invaginations in the basal part of the retinula cells, groups of irregularly shaped osmiophil material (Fig. 6b and c) are found. Quite often next to the grains stalks of membranes are seen (Fig. 2i), but as they are without smaller vesicles at the periphery they do not look like the typical dictyosomes. Occasionally lipid droplets or proper dictyosomes are present in the retinula cells. A ring of about 20–30 tracheoles surrounds each ommatidium in its basal part (Fig. 6). The nuclei of the tracheoblasts are situated just above the basement membrane. The tracheoles do not reach the distal ends of the large proximal rhabdoms. Besides the retinula cells and the tracheoblasts there are no other cells in the proximal part of the retinula, because the accessory pigment cells do not cross the clear zone and the cone cells have no filiform projections in the dorsal eye.

In the eyes of scorpions a circadian movement of pigment grains has been demonstrated by Fleissner (1974); Nässel and Waterman (1979) showed changes in the rhabdomere of crabs in a daily rhythm. The eyes of the tipulid fly show diurnal changes, too (Williams and Blest 1980). To observe such circadian changes subimagines and adults of both sexes have been fixed at noon, midnight, 6 A.M., and 6 P.M. in light-adapted as well as dark-adapted state. But even an intensive search has not produced differences which gave any hint for morphological adaptation in the dorsal eyes. The lateral eyes showed the typical adaptation to light and dark, described above, but no influence of the time of fixation.

A large number of ommatidia which consist of the proximal part only is found at the periphery of the turban eye. The distal part containing cornea lens, cone pigment cells, and distal rhabdom is missing. Here the nuclei are situated above the distal end of the large basal rhabdom.

c) *The Relative Position of the Two Eyes.* The dorsal as well as the lateral eyes are separated from the inner head by the basement membrane which is missing at the area where both eyes are in contact with each other. Because of the different size of the eyes the basement membrane of each is at a different level (Fig. 4a). The membrane is discontinuous but in the cells between the two parts a remarkable number of microtubuli are found. In the area where both eyes are in contact with each other lies a belt of long cylindrical cells containing large bundles of microtubuli and many grana of shielding pigment (Fig. 4b). These long cylindrical cells separating both eyes are very similar to the accessory pigment cells of the lateral eyes since they contain microtubuli and pigment grains of the same dimensions. In the lateral ommatidia the bundles only consist of a few tubuli.

d) *The Dorsal Eyes of the Subimagines.* While the lateral eye of the subimagines shows no distinct difference to the adult one, in the dorsal eye marginal changes occur during the last moulting, predominantly concerning the clear zone. Although the rhabdom is already separated into two parts (Fig. 7c), in this stage the gap is only about $30\ \mu\text{m}$ wide and the connecting part of the retinula cells shows a diameter of $3\ \mu\text{m}$, compared to $0.3\ \mu\text{m}$ in the imago. During the development of the adult stage the clear zone can grow up to $120\ \mu\text{m}$. The connecting part of the subimaginal retinula cells contains a considerable number of organelles like mitochondria, osmiophil grana and ER vesicles (Fig. 7b) which are missing in the adult animal (Fig. 5b). Inside each of the tracheoles surrounding the proximal part of the ommatidia is a tubular structure (Fig. 7a), which I can not interpret yet. In the subimago the spongy part of the primary pigment cell between cone and cornea is missing.

2. *The Undivided Compound Eyes of Ecdynurus venosus*

The eyes of *Ecdynurus* display typical euconic apposition ommatidia with a closed rhabdom. A superficial view shows that the eyes of the male are much larger than those of the female (Fig. 1a and b). A section through both eyes shows that the difference is not caused by the number of ommatidia, but by their length (Fig. 8b and c). The male ommatidia can be up to $560\ \mu\text{m}$ long while the female ones only measure up to $250\ \mu\text{m}$. Especially the rhabdom of the male ($460\ \mu\text{m}$) is longer than it is in female animals ($180\ \mu\text{m}$). The difference in the cone is not so conspicuous, it is $85\ \mu\text{m}$ long and $25\ \mu\text{m}$ in diameter compared to $60\ \mu\text{m}$ and $18\ \mu\text{m}$ in the female. Except for the dimensions, the eyes of both sexes are alike. There is a thin biconvex cornea lens and a cone, formed by four cells, each with a thin projection to the basement membrane. Two primary pigment cells surround the cone. The eight retinula cells form a closed apposition rhabdom with a diameter of $2.3\ \mu\text{m}$ in the female and $3.5\ \mu\text{m}$ in the male. The ommatidia are surrounded by varying numbers of accessory pigment cells. Only a few tracheoles are found in the basal part of the retinula. The structure of the lateral ommatidia was compared with

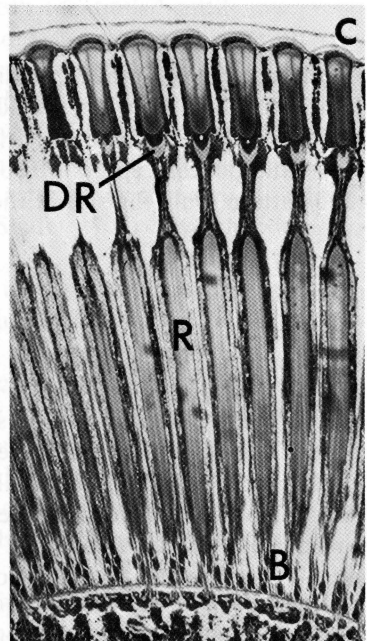
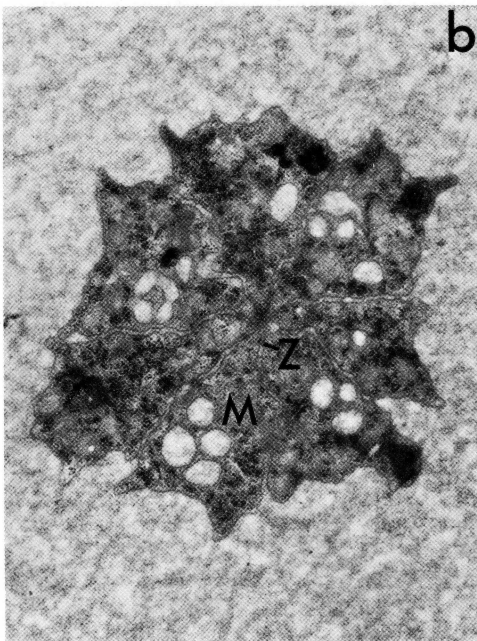
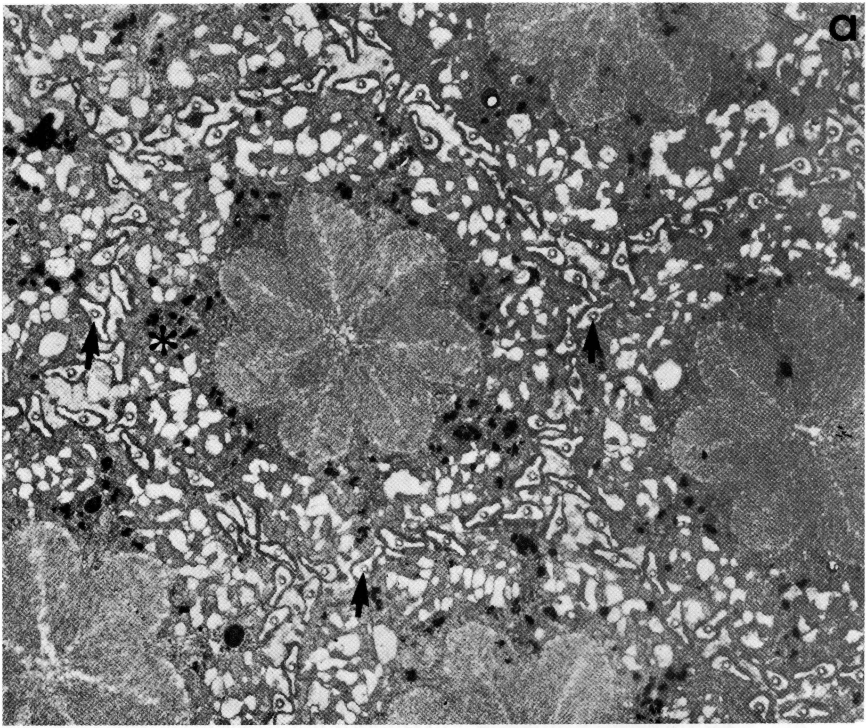


Fig. 7a-c. The eyes of a subimaginal *Baetis*. Section through the large proximal rhabdoms (a). The arrows mark a small tube inside the compressed tracheoles. Section through the clear zone where it is crossing the clear zone (b), in comparison to a section through the eye of an imago (Fig. 5b). Longitudinal section through several ommatidia of the dorsal eye (b). Magnification: a $\times 3,600$; b $\times 9,200$; c $\times 340$

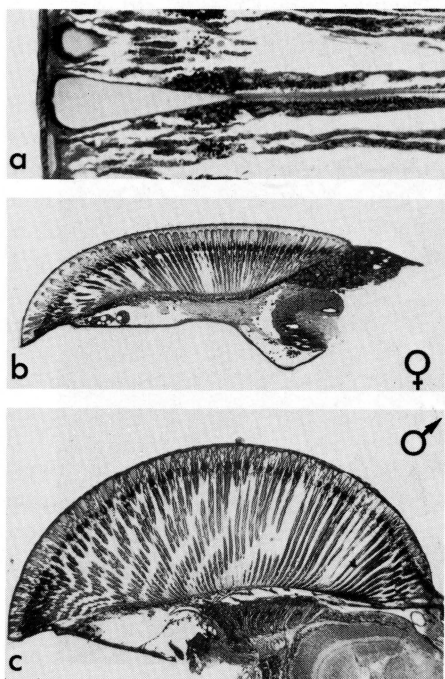


Fig. 8a-c. The eye of *Ecdyonurus vernus*. Longitudinal section through the dioptic structures and the distal part of the rhabdom of a female imago (a). View of the female (b) and male (c) eye for comparison at the same magnification and at corresponding directions. Magnification: a $\times 339,6$; b $\times 42$; c $\times 42$

that of the central receptors. No difference could be detected, neither in the female nor in the male, which could give support to the idea of two different kinds of ommatidia representing a lateral and a dorsal part of the compound eye. Thus, the photoreceptors of both sexes of *Ecdyonurus* are fashioned after the same pattern, only the size of the eyes is rather different.

D. Discussion

1. The Double Eyes of *Baetis*

The dorsal eyes of *Baetis* have a similar structure to those of *Cloeon*, also a Baetidae. The eyes of the latter were described by Wohlburg-Buchholz (1976, 1977) and Horridge (1976). Naturally the absolute sizes of the eyes differ as do their components. There are some structural variations, too, i.e. the accessory pigment cells of *Baetis* are not flat and overlapping like in *Cloeon*, but cylindrical. The proximal constriction of the cone of *Cloeon* is missing in the animals investigated here. While in *Cloeon* the proximal parts of the retinula cells inside a single ommatidium are highly convoluted towards each other the cell membrane in *Baetis* is invaginated into its own plasma. The tubular membrane structures containing the mitochondria described here are not found by Horridge (1976). This accumulation of cell and mitochondrial membranes in *Baetis* has been seen by Zimmer (1898) with the light microscope, who

interpreted it as 'accessory rods' (Nebenstäbchen). The shape of the rhabdom cross-sections demonstrated by Horridge for *Cloeon* is about circular, whereas *Baetis* has sections similar to rosettes or even asterisks. Priesner (1916) found lobulated rhabdoms in the retinula of *Cloeon* which had moulted shortly before. It is dubious whether the appearance of the asterisk-like cross-sections could have the same reason in *Baetis*, because the subimaginal rhabdoms sectioned showed rosettes. The small distal rhabdom first mentioned by Shafer (1907) for *Callibaetis hageni* and anticipated by Horridge for all Baetidae is present in *Baetis* too. The functional aspects of this structure will be discussed later.

An extensive description of the double eyes of *Callibaetis hageni* was published by Shafer (1907). He also investigated the development of these organs in nymphal and subimaginal stages and demonstrated that both eyes differentiate out of a common anlage. The definitive shape of the dorsal eye, especially the large clear zone is preformed in the subimago and finished during moulting into the imaginal stage. The intermediate part of the retinula cells stretches out into long thread-like connections. All these observations on a light microscope level could be confirmed with the ultrastructural investigations published here. With this technique the uncertainty about the area between cone and cornea could be ended. The 'hypodermal space' characterized by Shafer as 'cell analogues' and by Zimmer as the site of the nuclei of the pigment cells are filled by spongy structures of the primary pigment cells.

Because the modern authors do not describe the lateral eyes, a remarkable difference to the dorsal organs has not been mentioned until now. While the ommatidia of the turban eyes of *Baetis* contain seven retinula cells (Figs. 2k and 5b), the lateral rhabdom is composed of eight cells (Fig. 3a). Thus, at the level of the basement membrane eight axons leave the compound eye (Fig. 3c). Zimmer wrote that the 'normal eyes' of Ephemeroptera contain seven retinula cells and Streble drew seven nuclei in his work, this remarkable divergence may thus be restricted to *Baetis*. It is astonishing that two eyes developing out of a common anlage (Carrière 1886; Shafer 1907) have rhabdoms formed by a different number of cells.

Reflecting on the double eyes in insects one can see that there is no uniform scheme describing all of them. There are insects like the beetle *Gyrinus*, which have two totally divided eyes with slightly different ommatidia and then there are those that have eyes with large structural divergence under a common cornea, i.e. *Gerris* (Schneider and Langer 1969), *Ascalaphus* (Ast 1920) and *Gryllus* (Burhause 1979). Viewed from the outside, the double eyes of *Baetis* are totally separated by the cuticular cylinder enclosing the dorsal organs. But underneath, both eyes have contact with each other. As in other compound eyes, in *Baetis* the organ is separated from the interior of the head by a basement membrane. This membrane is situated at a different level in the dorsal and in the lateral eye, it is therefore not continuous throughout. But at the area where both eyes are in contact, the basement membrane has no contact with the epidermis. Thus the eyes are not divided by this membrane. The optical isolation of the two different eyes and their morphological stability is achieved by a great number of long cylindrical cells containing great bundles of microtubuli and many pigment grains. Cells like these also connect the basement membrane

of the lateral and dorsal eyes. These cells are similar to the accessory pigment cells in the lateral eyes. The structure and size of the pigment grains are alike and both contain bundles of microtubuli, although they are larger and more numerous as in the ommatidia of the lateral eye. Thus the cells between the two parts of the optical organ are structures normally occurring inside the lateral eyes. Even though they are isolated optically and at the surface are separated by a stripe of cuticula, there are no structures beneath, separating the two, that are foreign to complex eyes.

Looking at the eyes of other Ephemeroptera with turban eyes Streble (1960) and Zimmer (1898) showed (for *Cloeon dipterum* and *Cloeon fusca*, respectively) structures like the one described above. In a species which Zimmer calls *Baetis crenata* (probably *Heptagenia crenata*) because the size of the two parts are not as different as in *Baetis*, both eyes have a continuous basement membrane. Even though the eyes of different groups of Ephemeroptera are organized differently, the family of Baetidae shows a common structure.

Comparing the eyes of *Baetis* with those of *Ecdyonurus* it is obvious that the latter are organized more simply. Because the male organ is far larger than the female one, there is a sexual dimorphism. This difference is of minor importance, since the structures of the eyes are alike and only the ommatidia of the male are longer. The slight increase of the number of ommatidia in the larger eye is negligible. There is no part in the male eye which shows a divergent structure. Not the slightest trace of a double eye is found in *Ecdyonurus*.

2. Functional Considerations

The lateral eyes, belonging to the apposition type, therefore show radial movements of pigment grains as well as the formation of palisades during adaptation to different intensities of illumination. The optical properties and their function have been described as light guides or wave guides by numerous authors, summarized by Snyder (1975).

But the situation in the turban eyes is not as simple. While most of the authors (Zimmer 1898; Priesner 1916; Streble 1960; Wohlburg-Buchholz 1976) consider these eyes as a well functioning superposition system, Horridge 1976; Horridge and McLean 1978) has developed a sophisticated model for the eyes of *Cloeon*. Based on modern theories of wave guide optics (Snyder 1975) and regeneration of the photopigment (Hamdorf and Schwemmer 1975), Horridge denies the possibility of superposition. This is supported by the lack of adaptation movements and by the refractive index of the cone. The missing adaptation may be interpreted also as a result of the exclusive perception of UV light by the dorsal eye. Such a situation is known in *Ascalaphus* (Schneider et al. 1978), too. Horridge stated that the light which is important to perception is focussed slightly onto the distal end of the connecting parts of the retinula. They represent ideal wave guides leading the light to the proximal rhabdoms. This obviously is a very sensible way of functioning. The light which is not caught by the wave guides is assumed to pass through a filter, formed by the distal rhabdom. It will then be scattered through the clear zone and finally

be perceived by the photopigment for reisoimerisation. This certainly is a tempting model. But several assumptions are required to ensure that this model will work. Thus the photopigment in both parts of the rhabdom must be different. Otherwise functioning of the filter is not possible. It is not clear why the basal parts of the ommatidia are isolated optically by a tight ring of tracheoles which undoubtedly will hinder the spreading of the scattered light for isomerisation. Because the light necessary for reisoimerisation is distributed over the whole sky and therefore available to all ommatidia of the dorsal eye, the reason for the development of this huge clear zone is inexplicable.

Yet there is also a point in favour of the light guide theory: Since the male *Baetis* has to recognize the female against the dim sky, a superposition eye would have to be focused to the point. This will be unlikely in an eye like that of *Baetis*. So the model of Horridge will need further investigation, especially on the question of the perception of the distal rhabdom. Also, the spectral sensitivity and the absorption peak of the photopigment in both the distal and proximal part of the retinula cells has to be investigated.

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Abbreviations (used in figures)

<i>A</i>	axon of the retinula cell	<i>Np</i>	accessory pigment cell
<i>B</i>	basement membrane	<i>NR</i>	nucleus of a retinula cell
<i>C</i>	cornea	<i>P</i>	palisade
<i>DR</i>	distal rhabdom	<i>PG</i>	pigment grains
<i>Hp</i>	primary pigment cells	<i>R</i>	rhabdom
<i>K</i>	cone	<i>T</i>	tracheole
<i>La</i>	lateral eye	<i>Ta</i>	turban eye
<i>M</i>	mitochondrion	<i>Z</i>	zonula adhaerens
<i>N</i>	nucleus		

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