Recent Research in Neuropterology. – Gepp J., H. Aspöck & H. Hölzel ed., 1986, Graz.

Comparative Morphology of the Larval Eyes of Neuropteroidea

By Hannes F. PAULUS, Freiburg
Institut für Biologie I (Zoologie) der Universität Freiburg

Larvae of holometabolan insects have lateral lenses called lateral ocelli or stemmata. This eye type is constructed in very different ways, some of them resemble in their morphology the lateral eyes of the Myriapoda, especially those of the beetles (PAULUS 1979). Because of this similarity most of the earlier authors (HESSE 1901, DEMOLL 1917, WEBER 1933) considered the stemmata as derived from the lateral eyes of the myriapodan ancestors of insects. But PAULUS (1979) could demonstrate that these stemmata are modified ommatidia of a formerly large facetted eye found today in the adult stage. Such an insect ommatidium as a part of a facetted eye can be found in all hemimetabolan insects and even in the Entognatha (Collembola) (PAULUS 1975). It consists of a cuticular lens, the cornea, a eucon crystalline cone consisting of four parts (semper cells), two primary pigment cells, and eight retinula cells forming a monaxonal unilayered rhabdom. This type of ommatidium is an old derivation of the precursors of the Mandibulata because it is found even in primitive Crustacea and has there identical cell numbers.

In the following chapter I want first to give a comparative consideration of the known larval eyes of Holometabola to give a better understanding of the neuropteroidean larval eyes. Moreover I want to demonstrate that the hypothesis is suitable which says that the stemmata have derived from the typical insect ommatidia. Besides this I want to ask: can the morpology of these stemmata have consequences for the phylogenetical and systematical position of the orders?

1. THE STEMMATA (LATERAL OCELLI) AS MODIFIED OMMATIDIA

The simplest way to demonstrate that stemmata come from a degenerated facetted eye is to find a recent representative possessing facetted eyes in the larval stage. In fact most Mecoptera have small facetted larval eyes which are constructed in a similar way to those of the adults. In **Panorpa** we find a small facetted eye composed of 30 - 35 typical ommatidia (PAULUS 1979) (Fig. 1 d). There is no doubt that the possession of this small facetted eye represents the basic situation for the holometabolan larva. Like the hemimetabolan larvae **Panorpa** larva hatches out of the egg with a small facetted eye. But the hemimetabolan eye is enlarged during larval development by adding new ommatidia rows (MEINERTZHAGEN 1973). In **Panorpa** the small facetted larval eye persists during the whole larval period, disappears in the pupa, and is replaced by the facetted imaginal eye. This type of development and replacement ist typical for the Holometabola and is a synapomorphic character.

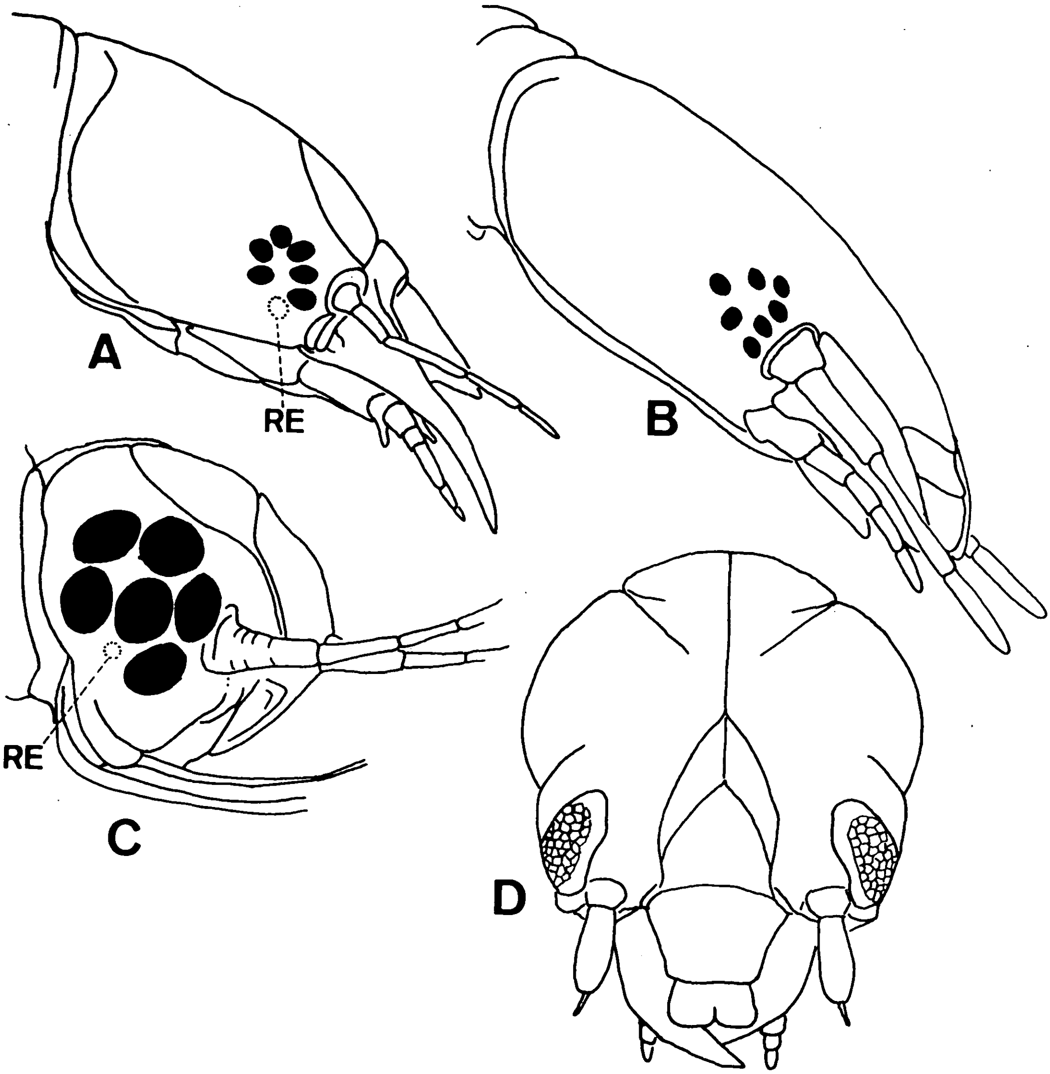

Fig. 1: Heads of neuropteroid larvae to show the position of stemmata. A. **Sialis lutaria** (Megaloptera), lateral. B. **Raphidia** sp. (Raphidioptera), lateral. C. **Sisyra fuscata** (Planipennia), frontolateral. D. **Panorpa communis** (Mecoptera) with facetted larval eyes, frontal.
RE = rudimentary eye.

The further evolution leading to typical larval eyes, that means leading to isolated lateral ocelli, has occurred independently in most orders and in different ways. From a large comparative morphological research of many larvae (PAULUS & WORTMANN 1986, PAULUS & SCHMIDT 1978, PAULUS & BAUER 1986, PAULUS & LEHN 1986) I can summarize some principles of the modifications of this basic small facetted eye leading to stemmata:

- Larvae of Hymenoptera have on each side of the head one large black spotted lens. Under this lens we find rudiments of the old small facetted eye, mainly the old retinulae, each consisting of 8 retinula cells. I assume that here all the previously

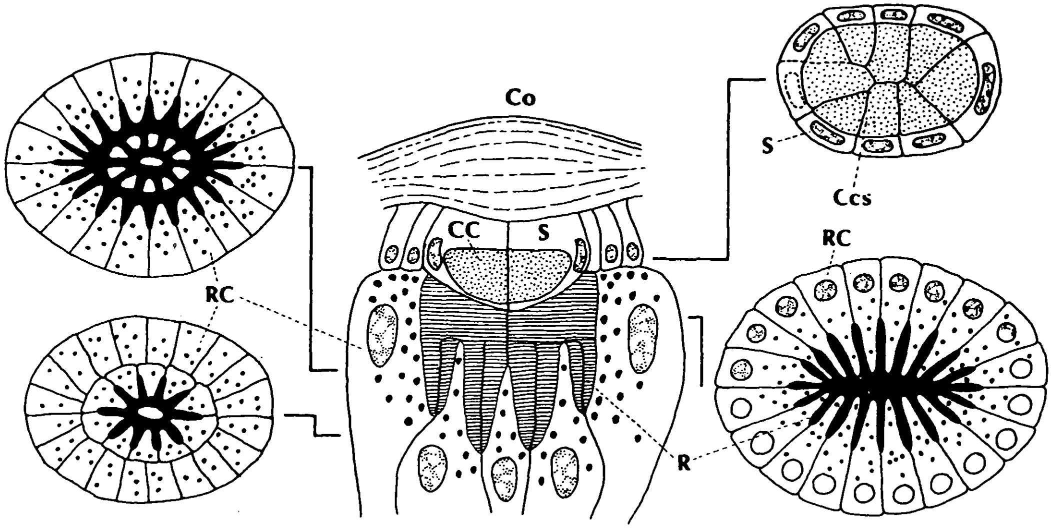

Fig. 2: Schematic reconstruction of the stemma of **Sialis lutaria.** Longitudinal section (middle) and transverse section at levels indicated. In transverse sections rhabdomeres not separated. About 40 retinula cells are arranged in two layers. The crystalline cone is composed of 8, in some cases of 9 sectors.

Abbreviations for all following figs.:
Ax = axon, CC = crystalline cone, Ccs = crystalline cone sector (within a Semper cell), Cg = corneageaneous cell, Co = cornea, eC = enveloping cell, PP = primary pigment cell, R = rhabdom (composed of rhabdomeres), RC = retinula cell, S = Semper cell (crystalline cone cell), SP = secondary pigment cell.

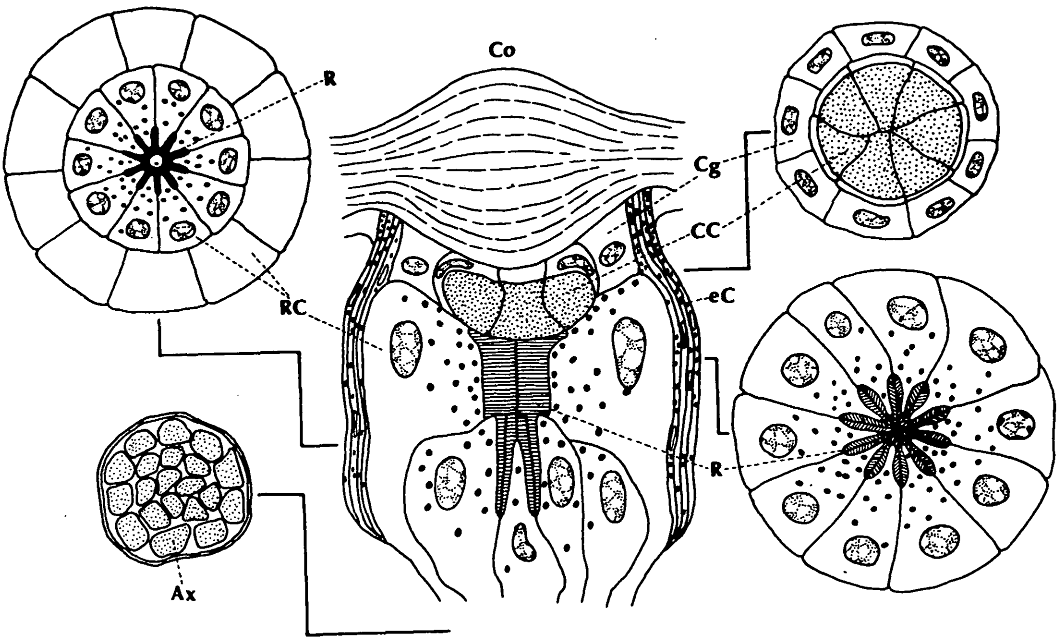

Fig. 3: Stemma of **Raphidia** (from investigations of **R. flavipes** and **xanthostigma**). 20 - 25 retinula cells form a starlike rhabdom at two levels.

separated corneae have fused to one single large lens. I therefore called this eye type the "unicorneal composite eye" (PAULUS 1979).

- Another way of eye modification is desintegration of facets to single lenses (ommatidia). Today we find up to seven of such larval ommatidia in Trichoptera, Lepidoptera (PAULUS & SCHMIDT 1978), some primitive Coleoptera, and Diptera.
- Such isolated larval ommatidia are further modified. One type of modification results in larger numbers of cell elements than in the basic ommatidium. This developed by fusion of two or more larval ommatidia to a double stemma or by secondary growth and multiplication of the cells during larval development.

Double stemmata can be found in Trichoptera (PAULUS & SCHMID 1978), in Diptera and Coleoptera. Secondary multiplication of the numbers either has occurred already in the course of evolution (as in Coleoptera: Adephaga and Neuropteroidea) or in the course of individual development (Planipennia). It is evident from this short overview that each insect order has evolved larval eyes in different ways from the common ancestor.

2 LARVAL EYES OF NEUROPTEROIDEA

The larval eyes of these orders have hardly been investigated. There are only histological studies on **Myrmeleon** (HESSE 1901, JOKUSCH 1967), **Protohermes** (YAMA-

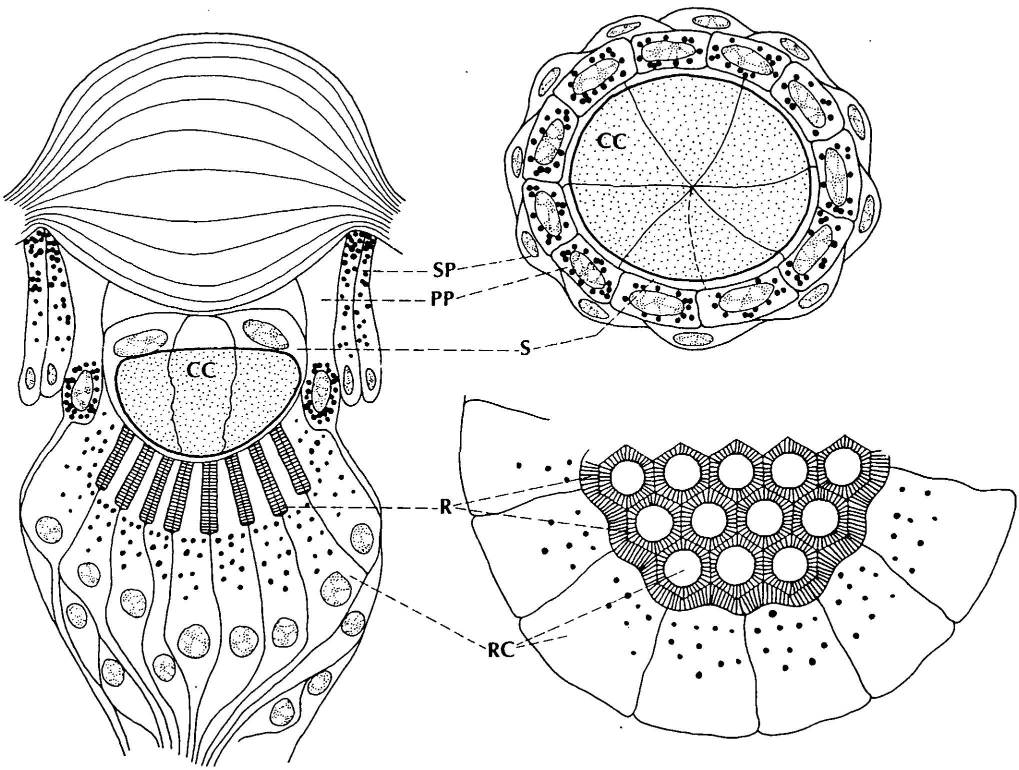

Fig. 4: Stemma of **Euroleon nostras.** The eucon crystalline cone (B) is normally composed of 6 - 7 Semper cells and surrounded by 11 - 12 primary pigment cells. The number of the one-layered retinula cells is depending on larval stage (e. g. L3: ca. 70). Rhabdom is netlike (C).

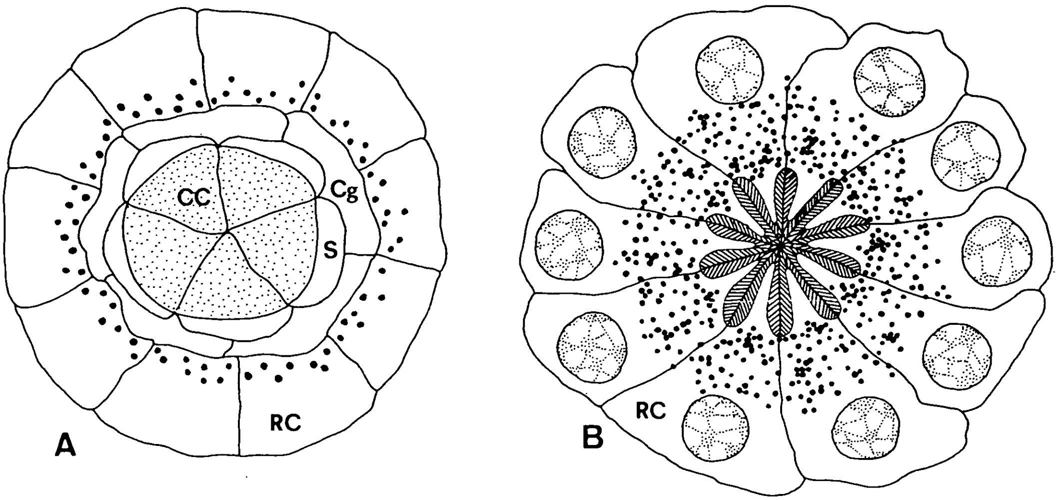

Fig. 5: Stemma of **Sisyra fuscata.** Cross section at the crystalline cone level (A) and the distal retinula cell level (B).

MOTO and TOH 1975) and **Sialis** (GRENACHER 1879, HESSE 1901). We have made electromicroscopic studies on **Raphidia** (**flavipes** and **xanthostigma**) (Raphidioptera), **Sialis lutaria** (Megaloptera), **Euroleon nostras, Sisyra fuscata** and **Hemerobius** spec. (Planipennia). A crystalline cone of the eucon type is common to all forms. The number of cone cells is in **Sialis** 8 (rarely 9) (Fig. 2), in **Raphidia** 7 - 8 (Fig. 3), in **Euroleon** 5 - 6 (Fig. 4), in **Sisyra** 5 (Fig. 5), and in **Hemerobius** 6 (Fig. 6) (see Table 1). Primary pigment cells are not present in the typical form. They are ususally simple epidermis cells which function as cornegeanous cells. The retinulae are of diverse shapes. The number of retinula cells differs from one species to another (Table 1). The shape of the rhabdom is either monaxonal (**Raphidia, Sialis, Sisyra, Hemerobius**) or netlike and polyaxonal (Fig. 4) (**Euroleon, Protohermes**). In cross sections the rhabdoms are usually star shaped with 2 - 3 layers of cells. In no case is there a typical basic ommatidium but always modified larval ommatidia. To derive these stemmata from ommatidia in Neuropteroidea then I can say that the basic situation must have been: 7 eyes which are normal eucon larval ommatidia. In the further course of evolution the Raphidioptera and Megaloptera have doubled the number of cell elements in each ommatidium, the Planipennia have also increased the number of cells but not doubled. With respect to Planipennia a study of the newly hatched larvae might reveal that their eyes might correspond to the basic larval ommatidia which would be altered in the further developmental stages.

3. PHYLOGENETIC AND SYSTEMATIC CONCLUSIONS

Even though a small number of species were investigated, it is possible to make some statements about the systematic position of Neuropteroidea. First we consider the idea that Neuropteroidea and Coleopteroidea are sister groups. Earlier (PAULUS 1979) I considered that the multilayered retinula of the stemmata was a possible synapomorphic character for both superorders. This assumption was based on the literature information only about adephagean Coleoptera and the scarce data on Neuropteroidea. In the meantime I have investigated numerous larvae of Coleoptera (especially the Polyphaga). In contrast to this previous belief we have found that the basic situation even in Coleoptera is: the stemma is composed of 8 retinula cells forming a monaxonal rhabdom and an aconic 4 parted crystalline cone. This aconic crystalline cone is a derived feature in Coleoptera with

Insect order	Number of ocelli	Semper-cells	Retinula cells	Remarks
Mecoptera	30 - 45	4 eucon *	8	slightly modified adult ommatidia, small facetted eye
Raphidioptera	7	8 eucon	20-25	type of double stemmata
Megaloptera	6(+1)	8(9) eucon	ca 40	type of double stemmata, one rudimentary eye
Planipennia	6(+1)	5-7 eucon	15	type of double stemmata, one rudimentary eye
Trichoptera	7	3 eucon	7	6 stemmata in derived groups, one of them a double stemma
Lepidoptera	6	3 eucon	7	3 large unpigmented primary pigment cells
Diptera	5	4 eucon	8	**facetted larval** eyes in Culicidae or Chaoborus are the later **facetted adult** eyes!
Coleoptera	6 **	4 acon	8	most species lack crystalline cones
Strepsiptera	5	pseudo-con	many?	adults with facetted eyes composed of stemmata
Hymenoptera	1	-	8	unicorneal **facetted** eye without crystalline cones

Table 1: Basic larval eye situation in the different Holometabola orders

Literature: Paulus (1978) (Mecoptera); Paulus & Lehn (1986) (Neuropteroidea); Paulus & Schmidt (1978) (Trichoptera, Lepidoptera); Paulus & Wortmann (1986) (Coleoptera); Meyer-Rochow (1973), Paulus (1978) (Hymenoptera); Wachmann (1972) (Strepsiptera); Paulus & Bauer (1986), Constantineanu (1930) (Diptera).

** Only in Dytiscini larvae there are 6 (+ 1)stemmata

* type of crystalline cone

respect to the basic larval ommatidium (PAULUS & WORTMANN 1986). For this reason the assumed synapomorphy is really a result of convergence. But the Neuropteroidea are more primitive than Coleopteriodea because they have the original number of 7 stemmata (which is only completely retained in Raphidioptera) (Fig.1b) and because their crystalline cone is of the eucon type. Synapomorphic characters for the Neuropteroidea are the cell multiplication of the cone cells as well a the retinula cells and the loss of typical primary pigment cells. The sister-group relationship between Coleopteroidea and Neuropteroidea cannot be supported simply by eye structure.

Within Neuropteroidea it is remarkable that the Raphidioptera are the only group with all 7 stemmata fully developed, whereas in Megaloptera (**Sialis, Protohermes**) and in Planipennia one of these stemmata has become a rudiment (Fig. 1 a, c). Whether this rudimentation represents a synapomorphic feature, is not possible to determine. If it were a synapomorphy then this would mean a sister-group relationship between Megaloptera and Planipennia. In opposition to this idea there are (1) common characters between Raphi-

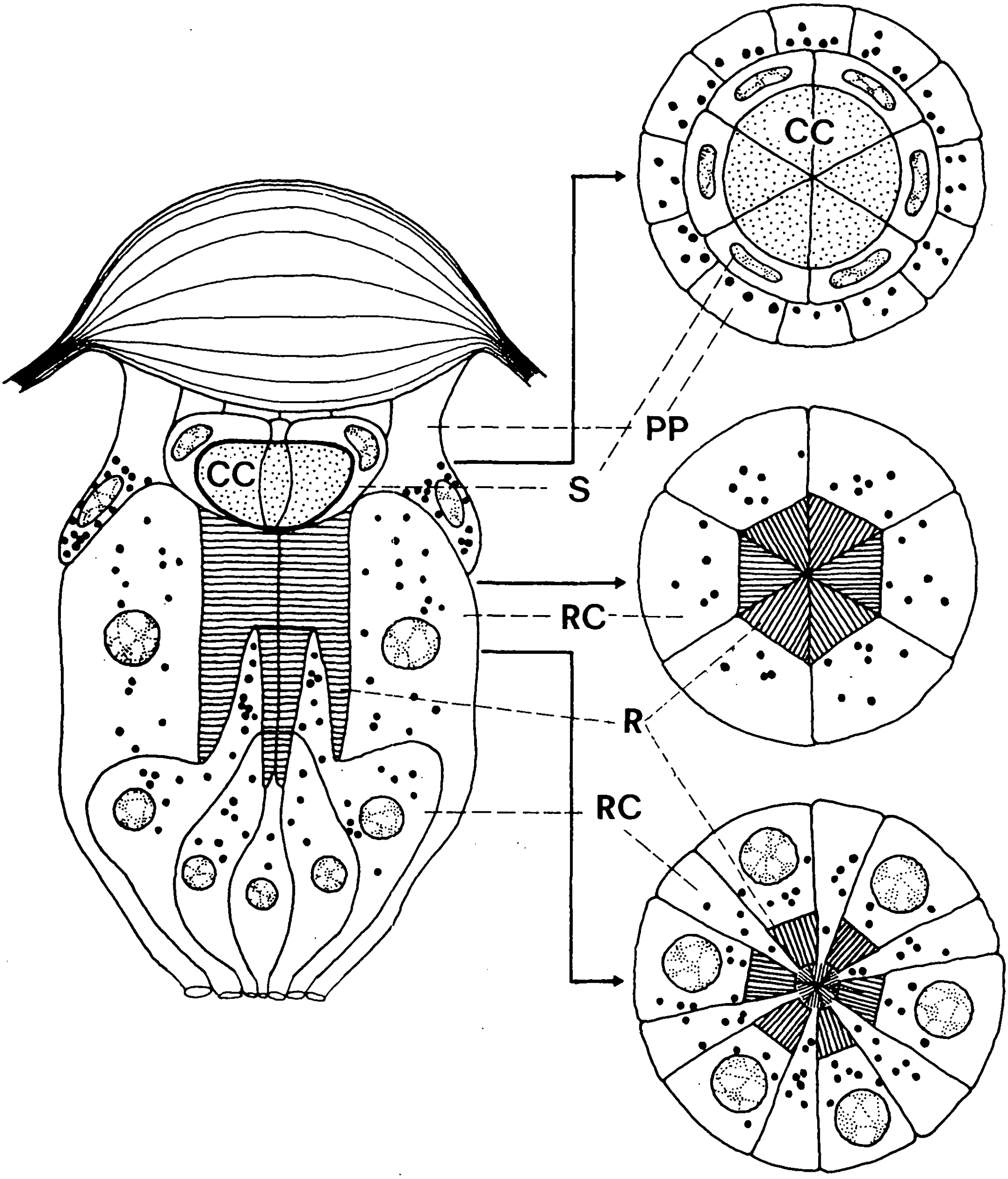

Fig. 6: Stemma of **Hemerobius** sp. (Planipennia). The crystalline cone is composed of 6 parts. About 20 retinula cells are arranged at two or three levels.

dioptera and Megaloptera, namely, the double number of cone cells (8) and one single retinula cell in the proximal part of central rhabdom and (2) even within Raphidioptera the Inocelliidae have 6 stemmata. Whereas in Planipennia there are only 5 - 6 crystalline cone cells and no such central rhabdom cell. To confirm or disconfirm the assumed sister-group relationship, more detailed information on larval eyes of more species is necessary.

Acknowledgements:

Technical assistance by Christine Gutmann with transmission and scanning electron microscopy preparations is gratefully acknowledged. The research was supported partly by DFG (Pa 163/2).

REFERENCES

CONSTANTINEANU, M. J., 1930: Der Aufbau der Sehorgane bei den im Süßwasser lebenden Dipteren-Larven und bei Puppen und Imagines von Cuolex. - Zool. Jb. Anat., 52: 253-346.

DEMOLL, R., 1917: Die Sinnesorgane der Arthropoden, ihr Bau und ihre Funktion. - Vieweg, Braunschweig, pp. 243.

GRENACHER, H., 1879: Untersuchungen über das Sehorgan der Arthropoden. Göttingen.

HESSE, R., 1901: Untersuchungen über Organe der Lichtempfindung bei niederen Tieren. VII. Von den Arthropodenaugen. - Z. wiss. Zool. 70: 347-473.

JOKUSCH, B., 1967: Bau und Funktion eines larvalen Insektenauges. Untersuchungen am Ameisenlöwen. - Z. vgl. Physiol. 56: 171-198.

MEINERTZHAGEN, J. A., 1973: Development of the compound eye and optic lobe in insects (pp. 51-104). In: Young, D. (ed.): Developmental Neurobiology of Arthropods. Cambridge Univ. Press.

MEYER-ROCHOW; V. B., 1973: Structure and function of the larval eye of sawfly Perga (Hymenoptera). - J. Insect Physiol. 20: 1565-1591.

PAULUS, H. F., 1975: The compound eye of apterygote insects (pp. 1-20). In: Horridge, G. A. (ed.): The compound eye and vision of insects. Clarendon Press, Oxford.

PAULUS, H. F., 1979: Eye structure and the monophyly of the Arthropoda (pp. 299-384). In: Gupta, A. P. (ed.): Arthropod phylogeny. Van Nostrand Reinhold, New York.

PAULUS, H. F. & SCHMIDT, M., 1978: Evolutionswege zum Larvalauge der Insekten. I. Die Augen der Trichoptera und Lepidoptera. - Z. zool. Syst. Evolutionsforsch. 16: 188-216.

PAULUS, H. F. & BAUER, J., 1986: Evolutionswege zum Larvalauge der Insekten. III. Die Augen der Dipterenlarven. - (manuscript).

PAULUS, H. F. & LEHN, K., 1986: Evolutionswege zum Larvalauge der Insekten. IV. Die Augen der Neuropteroidea. - (manuscript).

PAULUS, H. F. & WORTMANN, E., 1986: Evolutionswege zum Larvalauge der Insekten. V. Die Augen der Coleoptera. - (manuscript).

WACHMANN, E., 1972: Zum Feinbau des Komplexauges von Stylops (Strepsiptera). - Z. Zellforsch. 123: 411-424.

WEBER, H., 1933: Lehrbuch der Entomologie. G. Fischer, Jena.

YAMAMOTO, K. & TOH, Y., 1975: The fine structure of the lateral ocellus of the Dobsonfly larva (Megaloptera). - J. Morphol. 146: 415-430.

Address of the author: Prof. Dr. Hannes F. Paulus
Institut für Biologie I (Zoologie)
Albertstraße 21 a
D-7800 Freiburg, West Germany