Phylogenetic and Functional Implications of the Rhabdom Patterns in the Eyes of Chrysomeloidea (Coleoptera)

MICHAEL SCHMITT, UWE MISCHKE and EKKEHARD WACHMANN

Institut für Allgemeine Zoologie, Freie Universität, Berlin, GFR

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Ultrastructural data from 108 species of Chrysomeloidea show that all rhabdom-patterns can be assigned to one of two basic patterns. The insula-pattern: two central rhabdomeres (Rh 7/8) are spatially isolated from the six peripheral ones (Rh 1-6). The ponticulus-pattern: Rh 7/8 fuse at two sites with the ring of Rh 1-6. The distance between the two systems may prevent optical or electrical coupling in the insula-p. The structure of the ponticulus-p may allow electrical coupling as well as contrast-intensifying lateral filtering. Potential relative polarization and absolute sensitivities differ interspecifically between homologous cells and intraspecifically between Rh7/8 and Rh 1-6, and between Rh 7 and Rh 8. The Bruchidae show only the insula-p, the Chrysomelidae and Cerambycidae both. The distribution of the two patterns is subfamily-specific within the Chrysomelidae, but not in the Cerambycidae. Identical patterns must have developed convergently within the Chrysomeloidea. Both basic patterns are subdivided in different subfamilies or tribes.

1. Introduction

The compound eyes of the Chrysomeloidea are built up of numerous ommatidia, which are structurally separated from each other by their secondary pigment cells. Each ommatidium possesses a diopptic apparatus consisting of the crystalline cone and the corneal lens. The crystalline cone is formed by the four Semper-cells and is surrounded by the two primary pigment cells. A retinula made up of eight retinula cells lies below each diopptic apparatus. Each of these cells develops a rhabdomere, composed of tubular protrusions of the cell membrane (microvilli). All rhabdomeres together are called the rhabdom. In insects, the rhabdom can be closed or open. In the latter case, the central rhabdomeres of retinula cells 7 and 8 are separated from the peripheral ones by larger or smaller distances (Fig. 2m, n) or they are in contact with only some of them (Fig. 2 u-y) (cf. Eakin 1972; Elofsson 1976; Gokan & Hosobuchi 1979a,b).

As Wachmann (1977) has shown, open rhabdoms are found among the Coleoptera not only within the superfamily Chrysomeloidea, but also within other species, which all belong to the Cucujiformia. This taxon comprises—according to Crowson (1967)—the Cleroidea, Lymexyloidea, Cucujoidae, Chrysomeloidae, and the Curculionoidea.

The open rhabdoms found in the Chrysomeloidea show a variety of forms which differ from each other particularly in the alignment of the microvilli in the central rhabdomere-systems. These alignments of the microvilli are perceptible in cross-sections examined by electron microscopy (Figs. 3-5). All rhabdoms of the Chrysomeloidea can be assigned to two clearly distinguishable basic patterns.

First the rhabdom forms of the Chrysomeloidea will be described in detail. Then, the possible significance of the rhabdom structures for the phylogeny of the Chrysomeloidea and, finally, the consequence of the various rhabdom patterns will be discussed. The methods of investigation, morphological details and lists of the species studied may be found in two earlier publications (Wachmann 1977, pp. 99-100; 1979, pp. 22 and 44). These also include data on retinomotoric adaptations and on the normal distribution of the visual cell nuclei at different levels. In this paper the results pertaining to Callosobruchus maculatus Fabricius (Bruchidae), Hispa testacea L., Hispella atrata L. (Chrysomelidae), Agapanthia dahli Richter and A. violacea Fabricius (Cerambycidae) are published for the first time.

In order to avoid misunderstandings, the endings of names, the roots of which are used in different taxonomic levels, will be given in italics. For the same reason, for taxa below the family level, the corresponding family will be noted as an abbreviation in parentheses.

2. Results

In the first basic pattern (= insula-pattern; this corresponds to the “Grundmuster 1” of earlier publications) the Chrysomelidae, Bruchidae, Cerambycidae.
Fig. 2. Ommatidia with open rhabdoms of the Chrysoidea.

- Fig. 2a. Ommatidium with insula-pattern.
- b-h. Cross-sections at various levels.
- i. Ommatidium with ponticulus-pattern; b, c, e, i, k, g, h. Corresponding cross-sections.
- m-o. Insula-pattern with the different subpatterns (m-o) of the two central rhabdomeres 7/8; m, peripheral rhabdomeres isolated from each other; n, peripheral rhabdomeres laterally fused.
- u-z. Ponticulus-pattern with its different formations showing the lateral contact between central and peripheral rhabdomeres, which is absent in the insula-pattern.

A, aperture; Ax, axons; BM, basement membrane; C, cornea; PP, primary pigment cells (surrounding secondary pigment cells omitted); N, nucleus (N7, nucleus of cell 7); pR, peripheral rhabdomere; CR, central rhabdomere; l-6, peripheral retinula cells PR; 7 & 8, central retinula cells.
rhabdomeres Rh 7 and Rh 8 form a central system of round or oval cross-section. This is separate from rhabdomeres Rh 1-6 over its whole length. The rhabdomeres Rh 1-6 are arranged in a cylinder around the central system. They may have contact with each other at their narrow edges and thus form a complete cylinder or, alternatively, there may be intervals between them, so that in cross-sections the rhabdomeres are isolated (Figs 2 m, n; 3).

In the second basic pattern (ponticulus-pattern, "Grundmuster 2") the rhabdomeres Rh 7/8 form a central system which appears elongated in cross-section. At least in the distal zone of the rhabdom's narrow edges contact the rhabdomeres Rh 1 and Rh 4 (Figs 2 u-z; 5 d, e).

The insula-pattern was found in all families of the Chrysomeloidea, the ponticulus-pattern only in Cerambycidae and Chrysomelidae. The probable phylogenetic relationships within the Chrysomeloidea are shown in Fig. 1 (after Suzuki 1969). (For numbering of retinula cells: see Wachmann 1979, p. 21).

The descriptions of the forms of the insula- and ponticulus-patterns are based on light and electron microscope studies of the eyes of 108 species from 71 genera of European Chrysomeloidea.

2.1. The insula-pattern

The peripheral rhabdomeres Rh 1-6 encircle the central rhabdomeres Rh 7/8 and are distinctly shorter than these in all species studied, i.e. in Cassida vibex Rh 1-6: approx. 13 μm, Rh 7/8: 50 μm; Stenopterus ater Rh 1-6: 1-3 μm, Rh 7/8: 75 μm.

Distally, the peripheral rhabdomeres Rh 1-6 begin at a more proximal level than the central rhabdomeres Rh 7/8. There are only a few species in which the peripheral rhabdomeres are very close together (e.g. a few Clytrinae and Megalopodinae; see Wachmann 1977) but in most cases the peripheral rhabdomeres are actually touching (Table I; Fig. 2 n). In some species Rh 1-6 are separate from each other at a more proximal level (Table I; Fig. 2 m). The rhabdomeres Rh 1-6 may be isolated from each other along their entire length (e.g. in all Lepturinae, Ceramb.). Usually, they then lie closer together distally than proximally. This means that the distances separating the central rhabdomeres from the peripheral ones increase from distal to proximal. As a rule, the rhabdomeres Rh 1 and Rh 4 are somewhat longer than the other peripheral rhabdomeres.

The peripheral system of rhabdomeres is reduced in some cases. Whereas all rhabdomeres are found in Stenopterus flavicornis and S. rufus, a few are missing in S. ater (Ceramb.). In Tetrops praeusta, all peripheral rhabdomeres are missing. In this species the appropriate cells are present but do not form rhabdomeres.

In cross-sections the peripheral system can have the form of a circle, rectangle or hexagon. The area of the cross-section and the volume of the peripheral rhabdomeres varies to some extent from species to species. Rh 2 and Rh 5 in some Lepturinae have a cross-sectional area that is nearly twice that of the others.

A. The microvilli of a particular cell of the central rhabdomere system are arranged in parallel. They are normally also parallel to those of the other central cell. Whether or not the microvilli are also arranged parallel to each other at all proximo-distal levels cannot be decided from the present results (Figs 2 o, 3 a).

B. The rhabdomere of one of the two central cells is divided into two regions. The microvilli in each of the regions are orientated so that they either diverge from or converge to the centre of the ommatidium (Table I; Figs 2 p, q; 5 a). Within each of the two regions the microvilli are parallel to each other. The microvilli of the other central cell are also parallel to each other. Since the present observations were based upon cross-sections, the precise orientation of the microvilli with respect to the transverse axis remains unknown.

C. Both central rhabdomeres are subdivided into two rhabdomere regions with microvilli converging towards the centre. Generally the angle between the two subregions is about 90° (Table I; Fig. 2 r).

D. Each of the two central rhabdomeres is divided into three or even four subregions. The microvilli of the different regions converge towards the centre (Table I; Figs 2 s, 3 b). In these cases, the number of regions as well as the angle between them can vary along the longitudinal axis of the ommatidium (Wachmann 1977).

E. The microvilli converge in one central cell and diverge in the other (Table I; Figs 2 t, 5 b).

A study of the taxon specificity of the insula-pattern (see Table I) shows the following: Of the Cerambycidae, all Lepturinae, some Cerambycinae and a few Laminae have this basic pattern. However, different subpatterns were found within these subfamilies. In some cases, even the genera of a tribus do not have the same subpattern (for example, Stenocorus and Gaurotes: Stenocorini: Lepturinae). In the family Bruchidae, which contains few species, only the insula-pattern was found. The arrangement of the microvilli in the central rhabdomeres is shown in Fig. 2 o and 2 p.

Among the Chrysomelidae, the ommatidia of all subfamilies show the insula-pattern, with the exception of the Chrysomelininae. All species of each subfamily with the insula-pattern show the same subpattern. In one case (the Clytinae), a subfamily that was recently established by Crowson (1967) was verified by their having a special subpattern in common. In another case, the subfamily could not be verified: the species of Crowson's subfamily Hispinae showed two different subpatterns. The classical Cassidinae are represented by Fig. 2 s, the classical Hispinae by Fig. 2 o.

2.2. The ponticulus-pattern

As in the insula-pattern, the peripheral rhabdomeres also encircle the two central rhabdomeres Rh 7/8. Also, in all cases the peripheral rhabdomeres are clearly shorter than the central ones (e.g. Agapanthia villosoridescens, dorsal eye region, Rh 1-6: 14 μm, Rh 7/8: 36 μm; ventral eye region, Rh 1-6: 18 μm, Rh 7/8: 60 μm; Leptinotarsa decemlineata, Rh 1-6: 25-30 μm, Rh 7/8: 35-40 μm) and usually begin distally somewhat deeper. In various species of the Cerambycidae, however, the peripheral rhabdomeres begin distal to the central rhabdomeres Rh 7/8 and form a cap. Here they merge totally for a short distance (e.g. Asemum: Aseminae; Molorches, Phymatodes, Pyrrhidiun: Cerambycinae). This fused region is maximally 5 μm long. Below it, the rhabdomeres
form a typical ponticulus-pattern, in which the central rhabdomeres are connected at their narrow sides with those of Rh 1 and Rh 4 (Table I; Fig. 2 u, y).

Usually, all peripheral rhabdomeres are in contact with each other on their narrow sides so that a tube is formed, the cross-section of which can be circular, nearly rectangular or hexagonal.

In contrast, a different form was found in two genera of the Cerambycidae. In the ventral portion of the deeply emarginate eyes of Agapanthia villosolividescens and A. dahli, rhabdomeres Rh 1 and Rh 4 have no structural contact with the other peripheral rhabdomeres (Figs 2 x, 4 a).

The rhabdomere arrangement in the dorsal section (at least in A. villosolividescens and A. violacea) is shown in Fig. 2 u. The rhabdomeres of Agapanthia cardui are further modified and fused over their whole length (Figs 2 z, 5 e). On the other hand, in one of two individuals of Molorchus minor (Ceramb.) studied, the peripheral rhabdomeres were separate from each other (Fig. 2 y; detailed description in Wachmann 1979). However, the typical rhabdomeric connections between Rh 7/8 and Rh 1/4 were present. There are clear differences among different species in the arrangement of the central rhabdomere system in eyes with the ponticulus-pattern.

Table I. Rhabdom patterns in the Chrysomeloidae

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Basic pattern</th>
<th>Subpattern Rh 1–6</th>
<th>Subpattern Rh 7/8</th>
<th>N</th>
<th>Notes</th>
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<tr>
<td><em>Cerambycidae</em></td>
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<tr>
<td>Subfam. Priioninae</td>
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<tr>
<td>Priionus, Ergates</td>
<td>P</td>
<td>u</td>
<td>w</td>
<td>2</td>
<td>After Gokan &amp; Hosobuchi 1979b</td>
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<tr>
<td>Subfam. Disteniinae</td>
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<tr>
<td>Subfam. Lepturinae</td>
<td>P</td>
<td>u</td>
<td>u</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>(a) Rhagium, Guarotis, Acmaeops, Grammoptera, Allosterna, Leptura, Judolia, Strangalia</td>
<td>I</td>
<td>m</td>
<td>o</td>
<td>18</td>
<td></td>
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<tr>
<td>(b) Stenocorus</td>
<td>I</td>
<td>m</td>
<td>t</td>
<td>1</td>
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<td>Subfam. Aseminae</td>
<td>Asemum, Arhopalus, Spondylis</td>
<td>P</td>
<td>u</td>
<td>w</td>
<td>3</td>
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<tr>
<td>(a) Cerambyx, Obrium, Molorchus, Pyrrhidium, Phymatodes</td>
<td>P</td>
<td>u</td>
<td>w</td>
<td>7</td>
<td>Special arrangement of central rhabdomeres in the 3 latter genera (see 2.2.D.)</td>
</tr>
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<td>(b) Hylotrupes, Xylocthes, Clyton, Plagionous, Chlorophorus, Anaglyptus</td>
<td>I</td>
<td>n</td>
<td>o</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>(c) Stenoperus</td>
<td>I</td>
<td>n</td>
<td>t</td>
<td>3</td>
<td>In <em>S. uier</em>: peripheral rhabdomeres extremely short, partly lacking</td>
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<tr>
<td>Subfam. 1aminae</td>
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<tr>
<td>(a) Tetrops, Oberea</td>
<td>I</td>
<td>m</td>
<td>o</td>
<td>2</td>
<td>In <em>Tetrops</em> without peripheral rhabdomeres</td>
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<tr>
<td>(b) Dorcadion, Monochamus, Agapanthia</td>
<td>P</td>
<td>u</td>
<td>u</td>
<td>6</td>
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<td>(3 spp.)</td>
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<tr>
<td>(c) Agapanthia cardui</td>
<td>P</td>
<td>z</td>
<td>z</td>
<td>3</td>
<td>Rhabdom completely fused!</td>
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<tr>
<td>(b) Dorcatypus, Morimus, Liopus</td>
<td>P</td>
<td>u</td>
<td>w</td>
<td>3</td>
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<td><em>Chrysomelidae</em></td>
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<td>Zeugophora</td>
<td>I</td>
<td>n</td>
<td>p</td>
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<tr>
<td>Orsodacne</td>
<td>I</td>
<td>n</td>
<td>q</td>
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<td>Donacu, Platiumaris</td>
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<td>n</td>
<td>o</td>
<td>2</td>
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<td>Subfam. Cricoterinae</td>
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<tr>
<td>Cricoteris, Lilicosiris, Lema</td>
<td>I</td>
<td>n</td>
<td>o</td>
<td>5</td>
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<td>Subfam. Clytrinae</td>
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<tr>
<td>Clytra, Gynaurophalma, Coptocepheala, Lachnus, Labocestidae, Cryptocephala</td>
<td>I</td>
<td>n</td>
<td>r</td>
<td>8</td>
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<td>Subfam. Chrysomelinae</td>
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<tr>
<td>(a) Timarcha</td>
<td>P</td>
<td>u</td>
<td>w</td>
<td>3</td>
<td></td>
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<tr>
<td>(b) Phyiodecta</td>
<td>P</td>
<td>u</td>
<td>u + v</td>
<td>1</td>
<td>u + v in the same eye</td>
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<td>(c) Chrysonela, Dloclytra, Lepinotarsa, Melasoma, Phyllopecta, Gastroidea, Phardon, Chrysochloa</td>
<td>P</td>
<td>u</td>
<td>u</td>
<td>13</td>
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<td>Subfam. Galericninae</td>
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<td>Galerius, Galeruccia, Agelastica, Phyllophrotica, Sormylasai, Luperus, Chalcoidea, Halica</td>
<td>I</td>
<td>n</td>
<td>t</td>
<td>11</td>
<td>In <em>Lochmene</em>: central rhabdomeres as in t and o (within the same eye)</td>
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<td>Adoxus</td>
<td>I</td>
<td>n</td>
<td>o</td>
<td>1</td>
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<td>Subfam. Hipiptinae</td>
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<tr>
<td>(a) Hispa, Hipippa</td>
<td>I</td>
<td>n</td>
<td>o</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>(b) C. isida</td>
<td>I</td>
<td>+</td>
<td>s</td>
<td>2</td>
<td>Peripheral rhabdomeres similar to Fig. 2 x</td>
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</table>


Small letters in the columns "subpatterns" correspond to Fig. 2.

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Fig. 3.—a. Cross-section through the retinula cells of an ommatidium of *Anaglypta mysticus* (Cerambycidae). In this region all peripheral rhabdomeres (PR) are present. The microvilli of the two central rhabdomeres (CR) are aligned in parallel.—b. Cross-section through some ommatidia of *Cassida* (Chrysomelidae). In this part of the retinula only rhabdomeres 7 & 8 (each with several microvilli directions) and the peripheral rhabdomeres 1 & 4 are present.

M, mitochondria; N, nucleus of corresponding cell; P, pigment granule; PR, peripheral rhabdomeres; CR, central rhabdomeres. \( a \) 18400×; \( b \) 5400×.
Fig. 4. Cross-sections through several ommatidia showing the ponticulus-pattern of *Agapanthia villosoviridescens* (Cerambycidae).—a. Distal part of rhabdoms with central (CR) and all of the peripheral rhabdomeres of cells R1–R6. Notice the connection of central rhabdomeres with the peripheral rhabdomeres of R1 & R4, which are isolated from the others.—b. Cross-section proximal from a, in the nuclear region of peripheral retinula cells R2, 3, 5, & 6.

NP: nuclear region of secondary pigment cells, isolating ommatidia in several layers. *a* & *b* 3900×.
Fig. 5. — a. Retinula cells of Callosobruchus (Bruchidae) with insula-pattern. Central rhabdomeres surrounded by numerous pigment granules. Four of the 6 peripheral rhabdomeres can be seen. Zonulae adhaerentos in the squares.— b. Central rhabdomeres of cells R7 & R8 of Stenopterus ater (Cerambycidae) with insula-pattern.— c. Strangalia nigra (Ceramb.) with insula-pattern; peripheral rhabdomeres isolated from one another.— d. Leptinotarsa decemlineata (Chrysomelidae) with ponticulus-pattern.— e. Completely fused rhabdom of Agapanthia cardui (Ceramb.) with derived ponticulus-pattern (see Fig. 2 z).

M, mitochondria; P, pigment granule; arrows indicate alignments of microvilli. a 19000 x; b 23750 x; c 8000 x; d 5400 x; e 13500 x.

A. From observations of ommatidial cross-sections the microvilli of the central system were shown to be arranged exactly parallel to each other in many species (Table I; Fig. 2 u). Furthermore, serial cross-sections of Leptinotarsa (Chrys.) have shown that the rhabdomeres Rh 7/8 are not twisted along the longitudinal axis (with the exception of very few ommatidia).

B. The microvilli of cell 7 are often divided into several regions with different alignments of microvilli. One region is associated with the rhabdomere Rh 8. The other two
regions are associated with the rhabdomeres Rh 1 and Rh 4 (Fig. 2 v). Among the Chrysomelidae this arrangement is only found in Timarcha. Among the Cerambycidae, many only distantly related taxa show this type of pattern (Table I).

C. In some species of the Cerambycidae (for example Cerambyx cerdo and C. scopolii), only cell 7 of the central pair can be found in the distal area next to the peripheral rhabdomeres. Its microvilli are built into various outer rhabdomeres (usually Rh 1 and Rh 4). Cell 8 and its rhabdomere are located more proximally, with only a single microvilli alignment. The rhabdomere Rh 7 is no longer found at this level (Table I; and Wachmann 1977).

D. A similar proximo-distal order exists in the eyes of the genus Asemum (Ceramb.: Aseminae) and of some Cerambycinae. Cell 7 lies distally, in the form of a narrow, at most 1 μm thick, fingershaped appendix, between the peripheral rhabdomeres. Cell 8 appears at a slightly more proximal level (see also Wachmann 1979). The functional consequence of this arrangement is that all rhabdomeres form a common light guide (see Section 3.2.1; Table I).

E. In cross-sections of some ommatidia in Phytolecta viminalis (Chrys.), the two central rhabdomeres form a “V” shaped pattern (Fig. 2 v). The angle between them can vary. The peripheral end of the rhabdomeres are connected with the rhabdomeres Rh 1 and Rh 4 and/or with those of Rh 2 and Rh 3. This V-shaped arrangement does not appear in all ommatidia and is not distributed regularly throughout the eye. The other ommatidia have the rhabdomere arrangement described in Section 2.2.A. (Table I; Fig. 2 u).

3. Discussion

3.1. Phylogenetic implications

As many genetically and functionally independent characters as possible must be examined for an analysis of the phylogeny of a group of organisms. Such an analysis is not the goal of the present paper. Rather we wish to discuss how characters of the rhabdom patterns of the Chrysomeloidae can be exploited for an analysis of the phylogeny of this group, starting with the morphological results.

Before discussing this point, the most important terms used will be defined. This is in order to avoid misunderstandings, to make our statements comparable to those of other authors and to facilitate the reading of this paper.

3.1.1. Definitions. Systematic comparison is the search for and categorization of similarities among hereditary characters.

Similarity is a likeness of characters which is based on identical subcharacters, that is, a partial but not total identity which is usually integrally perceived.

There is no general rule concerning the number of identical subcharacters necessary for one to conclude that the structures are similar. Therefore, there will be borderline cases in which individually differing judgements will lead to different decisions as to similarity or non-similarity of characters (see Dohle 1976).

Homology is a similarity that stems from a single original form in the last common ancestor of the individuals carrying the characters being compared. From a single original form derivatives have emerged which retain similarities.

In contrast, convergence is a similarity that stems from multiple independent processes in the course of phylogeny so that different features become similar. “Convergent” and “analogous” are often used interchangeably (e.g. Riedl 1975). We use analogy as a term for similarity of characters which developed convergently as a result of identical selection pressures.

Homology denotes the similarity between homologous characters which have been transformed convergently. Such characters are homologous and convergent at the same time. This paradox is solved if one differentiates according to descriptive levels.

The raptorial legs of Manis and Manispa are homologous as insect legs and analogous as predatory instruments. Thus, the sequence of the joints and their general structure have been taken over from the last common ancestor, whereas the bent tibiae, which can be folded against the toothed femur, have been acquired independently in the two groups. Hence, the last common ancestor of praying mantids and lacewings had forelegs that had the same “Bauplan”, but these were not raptorial legs. (The terms “homology” and “parallelism” are often used synonymously, especially in British and American literature.)

Remane’s (1952) homology criteria usually serve to distinguish between homologies and convergencies. We concur with Dohle’s argument and employ his methodological criterion: “Similar structures can be considered to be homologous when their structural identity (position of the substructures in the whole, specific characters of the substructures, ontogenetic differentiation of the structure) is so extensive and so complex, that a convergent development is extremely unlikely” (Dohle 1980; translated by the authors).

Homologous characters have originated evolutionarily in one species in the past. Among the descendants of this species a homologous character occurs in the original condition (a, b) or in a derived condition (a’, b’, or transformed again: a”, b”). We will call the characters or character conditions from which transformation started (a, b) in a monophyletic group plesiomorphous, and the derived conditions (a’, a”, b’, b”) apomorphous. Simple reflection shows that these are relative concepts: the characters a and a” are both apomorphous compared with character a, but a is plesiomorphous compared with a’. We will call the presence of plesiomorphous characters in different species symplesiomorphous, the presence of apomorphous characters synapomorphous, always with the assumption that the compared characters belong to one and the same transformation series” (Hennig, 1966, p. 89).

Only synapomorphies can be used to substantiate sister group relationships between taxa, that is, to reconstruct the phylogeny (Hennig 1950; Schlee 1971).

In addition to Hennig’s (1966, pp. 95–98) criteria, Hennig & Schlee (1978) provide further reference points to decide whether or not a character can be considered to be synapomorphic:

(a) structural abundance and functional properties of character expression;

(b) distribution of the feature among the taxa (see also Dohle 1980; but note the arguments of Watrous & Wheeler 1981);

(c) degree of contradiction with the evidence of other characters.

It must be kept in mind that, since “synapomorphy” is not a “property” of particular features, but can only be used in comparison, its recognition cannot be defined in a simple way. Rather several items must be considered in order to decide whether a structure is synapomorphic or not (after Schlee 1976).

Very helpful and detailed statements are included in Bock (1977; 1981). It is important for the methodology of phylogenetic systematics to be aware of convergent transformation on all levels of complexity and decision, as Bock emphasizes.

We use “monophyletic” as defined by Hennig (1966, p. 73): “A monophyletic group is a group of species descending from a single (stem) species, and which includes all species descended from this stem species”.

3.1.2. Discussion of characters. A basic assumption of our discussion is the homology of the rhabdomeres of the various species. We consider this extremely likely, because all rhabdms studied are made up of an equal number (8) of retinula cells, arranged in the same manner in relation to each other and having the same substructures (position of the nuclei; rhabdomeres). The only two exceptions are the Cerambycidae species Stenopterus ater and Tetrops praeusta, where the peripheral rhabdomeres are partially or totally reduced (see Section 2.1). Further-
more, the occurrence of these rhabdoms is always coupled to the presence of acone ommatidia.

The major difficulty of a phylogenetic analysis is in recognizing whether the formation of a basic pattern in a particular group took place only once. The instances of the insula-pattern and the ponticulus-pattern, respectively, are therefore either homologies or true homologies. This applies also to the various forms within each basic pattern.

The rhabdom patterns of the Chrysomeloidea stem phylogenetically with high probability from the open rhabdom of the stem species of the Cucujiformia. Consequently, the character "open rhabdom" is homologous in all Chrysomeloidea. However, we cannot decide whether the stem species of the Cucujiformia possessed the ponticulus- or the insula-pattern, or a different pattern altogether. The specific conformities of all instances of the insula-pattern as well as those of the ponticulus-pattern are of low complexity. Thus we cannot state that within the Cucujiformia one of the two basic patterns emerged once. Moreover, we must assume that within the Chrysomeloidea each basic pattern emerged more than once: The ponticulus-pattern is found in certain Cerambycidae and in certain Chrysomelidae. The latter are with high probability a monophyletic taxon (Chůjů 1953 a), itemizes characters which can tentatively be considered to be synapomorphies of the Chrysomelidae: head without projecting muzzles; submentum not arising basally from a narrow stalk; larval and adult stages are plant-feeders.

Even if the Cerambycidae cannot be shown to be monophyletic taxon with complete certainty (see below), some unifications of Cerambycidae-subfamilies can be treated as well substantiated (Crowson 1967, pp. 145–149). These groupings do not allow the assumption that one of the two basic patterns could have emerged only once within the Chrysomeloidea.

In the following account we shall discuss the phylogenetic implications of the rhabdom patterns for the subfamilies of the Chrysomelidae in the sequence suggested by Crowson (1967). We thereby start from the monophyly of Crowson's subfamilies.

The Megalopodinae and Orsodacninae, which include only a few species, possess specific subpatterns of the insula-pattern. These subpatterns show remarkable conformities (Fig. 2 p, q). We tentatively treat these two subfamilies as sister groups. The synapomorphy of this taxon would be that one rhabdomere in the central system has one microvillus alignment and the other has microvilli orientated in two directions. This is unique among the Chrysomelidae. Since only one species out of each subfamily has been studied, this conclusion has to be tentative at this stage.

Donacinaceae and Criocerinae have the same subpattern (Fig. 2 o) as the Eumolpinae and the Hispinae (and the Bruchidae and many Cerambycidae). No phylogenetic conclusions can be drawn, because this is the subpattern which possesses the fewest substructures and the distribution of which among the Chrysomelidae also does not coincide with the distribution of other characters.

The Clytrinae sensu Crowson correspond to the Camptosomata (including the Lamprosomini which are not studied here) of the earlier entomologists (e.g. Reitter 1912).

As far as the Clytrini and the Cryptocephalini of the earlier entomologists are concerned, their unification in one taxon is supported by the occurrence of a common rhabdom subpattern which is an exclusive characteristic (Fig. 2 r). This subpattern is therefore considered to be a synapomorphy of the Clytrinae sensu Crowson; it cannot be ascertained which is the corresponding plesiomorphic alternative. In other words, we cannot determine which is the sister-group of the Clytrinae. The rhabdom characters appear to substantiate a dichotomy as proposed by Monró (1959) (Megalopodinae as sister-group of the Clytrinae). But, as long as systematic classifications like Monró's are made without mention of the corresponding character, one can only speculate on their validity.

The Chrysomelinae are the only subfamily of the Chrysomelidae which displays ommatidia with a ponticulus-pattern. Since the Chrysomelidae are assumed to be a monophyletic taxon (see above), there is no objection to considering the ponticulus-pattern within this taxon to be a synapomorphy of the Chrysomelinae.

According to Crowson (1967, p. 145) the Chrysomelinae are a "well characterised group", however, only few characters which can be seen as a synapomorphy of this taxon can be found in literature (form of tarsi: Reitter 1912; Mohr 1966; clypeus divided into two parts: Gressitt & Kimoto 1961; larval characters: Henning 1938; Steinhausen 1966).

Therefore, the ponticulus-pattern is an important indication of the monophyly of this taxon.

The results of developmental studies (Wachmann & Pfannenstiel in preparation) allow this conclusion, but they do not explicitly support it. Since the development of the insula-pattern of other Chrysomelidae has not been studied, we can only state that the ponticulus-pattern of the Chrysomelidae does not develop by way of an insula-like preliminary stage.

As for the Clytrinae, the sister-group of the Chrysomelinae cannot be determined at this time. Study of the rhabdom patterns does not help to resolve the issue.

Some authors consider the Galerucinae (that is the Galerucini plus Halticini; e.g. Chen 1964; Chůjů 1953 b), whereas others consider the Eumolpinae plus Lamprosominae (e.g. Gressitt & Kimoto 1961; Mohr 1966) to be the most closely related groups.

Crowson unites the classical Galerucinae and Halticinae in the one group Galerucinae. This classification is substantiated by our finding that all Galerucinae (sensu Crowson) studied so far have the same insula-subpattern (Fig. 2 f). This subpattern either first emerged within the Chrysomelidae (it would then be a synapomorphy of the Galerucinae and convergent to the corresponding subpattern of Stenocorus and Stenopterus, both Ceramb.) or it emerged earlier and then it is plesiomorphic for the Chrysomelidae. At present we cannot decide between these possibilities. Crowson's taxon Hispinae corresponds exactly to the old group Cryptostomes (the classical Hispinae plus Cassidinae). The observations concerning rhabdom structures are consistent with this grouping. However, they force us to conclude that either the sub-
pattern of the Hispini (Fig. 2 a) or that of the Cassidini (Fig. 2 s) was formed by transformation within the Hispinae. We prefer the assumption that the subpattern of the Hispini is relatively more primitive and therefore plesiomorphic for the Hispinae and that of the Cassidini is relatively recently derived and therefore apomorphic for this latter taxon.

The sister-group can be determined neither from the available literature nor from our data. One of the taxa within the Chrysomelidae with the sub-pattern 2 o would seem to be most probable.

On the basis of the present knowledge of rhabdom ultrastructures, no sister-group relationships of the type proposed by Hennig can be established. However, the hypothesis that the established subfamilies sensu Crowson represent monophyletic taxa can be confirmed in some cases. Further information can be gained only by continuing analysis of the fine structure of other Curculioniformia rhabdoms (in particular those of the Curculionoidea).

Some authors (e.g. Chen 1964; Monróś 1959) treat the Bruchidae as a subtaxon of the Chrysomelidae. Our results neither disprove, nor necessarily support this conclusion. Chen (1964) states that the “antennae (are) not inserted on prominent tubercles, not reflexive over body” in the Bruchidae and Chrysomelidae. We uphold the assumption that the Chrysomelidae are a monophyletic taxon, since from Chen (1964) it cannot be ascertained unambiguously where the Bruchidae should be placed in a phylogenetic system of the Chrysomelidae. In turn, the monophyly of the Bruchidae is well substantiated morphologically (e.g. Crowson 1967; Chen 1964) and ecologically (cf. Southgate 1979).

The present results do not yet permit a judgement concerning plesiomorphic or apomorphic stages of the character “central rhabdomere system” within the Cerambycidae. It is possible that after careful analysis of other characters the conclusion will be drawn that the Cerambycidae are not a monophyletic taxon. Crowson also considers this to be probable (personal communication 1979).

Two aspects of the data obtained for the Cerambycidae suggest areas that warrant further phylogenetic investigation of this group. First, there must be more studies to establish whether or not the presently accepted subfamilies of the Cerambycidae are genuinely monophyletic. Second, the findings obtained for Agapanthia cardui (Figs. 2 z; 5 e) should promote interest in detailed investigations into the means of formation and biological role of a fused rhabdom. Possibly the rhabdom of A. cardui is analogous to other closed rhabdoms. However, the phylogenetic development of the rhabdom of A. cardui from a typical ponticulus-pattern is quite plausible (see figs. 11 and 13 in Wachmann 1979), since all closely related Laminae show the ponticulus-pattern.

3.2. Functional implications

The theoretical and empirical investigations of vision in invertebrates show that structural differences in the rhabdoms affect the spatial, absolute, spectral and polarization sensitivities of the retinula cells.

3.2.1. Functional consequences of structurally coupled rhabdomeres. The morphologically coupled RH 7/8—and in the ponticulus-pattern also RH 1 and RH 4—could be structural prerequisites for optical and electrical coupling of retinula cells as discussed by Snyder et al. (1973) for insect eyes with fused rhabdoms.

In the insula- and ponticulus-pattern, the central rhabdomeres (in many species also the peripheral ones) are structurally connected to each other (Table 1; Fig. 2). Because of the dense membrane stacking, the rhabdomeres have a higher refractive index than the surrounding retinula cell cytoplasm, and thus work as light guides (Kirschfeld & Franceschini 1969; Seitz 1968; Stockhammer 1956). Where rhabdomeres of adjacent retinula cells are linked together, they operate as a single light guide. In this way, several retinula cells form a functional unit.

Shaw (1969a) has suggested that morphologically coupled microvilli of adjacent cells could be the site of electrical interreceptor coupling.

3.2.1.1. On the ponticulus-pattern. Provided that the coupled RH 1, 4, 7, and 8 are of two or more spectral types, they can act as lateral filters. The effects are narrow spectral sensitivity curves and high absolute sensitivity of the retinula cells (Snyder et al. 1973). ERG records of Chrysomelidae show two peaks (Section 3.2.1.2), so different spectral types of retinula cells seem possible. The microvilli of RH 7/8 are orientated roughly orthogonally to those of RH 1 and 4 (Fig. 2 u-z). Therefore, the rhabdomeres can act as lateral polarization filters analogously to the spectral sensitivity (see Section 3.2.2). Electrical coupling would decrease the difference of spectral and polarization sensitivity between the adjacent cells but increase the absolute sensitivity. If electrical coupling is a dynamic effect which decreases with increasing light intensity and is switched off at high intensities (as Snyder et al. 1973 discuss), then these cells have the maximal advantage of lateral filtering.

The cross-sectional area (and therefore the relative volume) of the rhabdomeres containing photopigment molecules is relatively larger for the ponticulus-pattern than for the insula-pattern. The absorption probability for incident quanta is consequently higher. Therefore, species with the ponticulus-pattern should be capable of better visual orientation in lower light intensities. The fact that the twilight- and nocturnal-active longhorn beetles Ergates faber, Priorus coriarius, Cerambyx cerdo, Morimus asper, Arhopalus rusticus (Wachmann 1979), as well as Priorus insularis (Gokan & Hosobuchi 1979a) and probably other Japanese species (Koyama et al. 1975) have a ponticulus-pattern substantiates this conclusion. However, not all species with the ponticulus-pattern are nocturnal, nor are all species with the insula-pattern diurnal.

3.2.1.2. On the insula-pattern. Assuming that the microvilli of adjacent rhabdomeres are the site of electrical coupling between retinula cells, then the insula-pattern could be the result of an evolutionary strategy towards electrical isolation of RH 1 and 4 from RH 7/8.

As a consequence of light guide properties, cross talk
can occur between morphologically isolated rhabdomeres. When there is only a small distance between neighbouring rhabdomeres, they can be optically coupled, because a part of the electromagnetic energy is in the medium surrounding the light guide (Kirschfeld & Franceschini 1969; Wijngaard & Stavenga 1975). Thus the optically effective diameter of a rhabdomere is larger than its structural diameter. Therefore, for the insula-pattern of the Chrysomelidae it must be ascertained whether the structural separation of the peripheral and central systems is sufficient to produce an optical separation. From cross-sections of the distal rhabdom area (in similar positions in neighbouring ommatidia, the Semper cells were still present) the shortest distances between the two systems were measured as follows: Xylotrechus arvicola 250 nm, Plagionotus arcuatus 350 nm, Clytus arietis 350 nm (Cerambycinae), Strangalia nigra 450 nm (Lepturinae: Cerambycidae), Cassida vibex 730 nm (Hispanae: Chrys.).

A geometric-optical analysis of the size of the optically effective rhabdomere area includes the consideration of refractive indices of the media, as well as the angle of incidence and wave-length of the radiation (Kirschfeld & Franceschini 1969). In this context only radiation of a wavelength which can be absorbed by the rhabdomeres is of interest.

Electro-retinograms of Leptinotarsa decemlineata, Cassida viridis and Galeruca tanacetii (Chrys.) recorded for the purpose of ascertaining the spectral sensitivity of the retinula cells show a sensitivity in the range of 320–610 nm with maxima at 360 and 510 nm (Mischke 1982). Since the optically effective area grows with the wavelength of the incident light, an analysis of the immediate surrounding area must be based first on the longest wavelengths. The refractive indices of the media (rhabdomere, cytoplasm) with maxima at 360 and 510 nm (Mischke 1982). Since the retinula cells show a sensitivity in the range of 320–610 nm with maxima at 360 and 510 nm (Mischke 1982).

In the distal region the distances are very small between Rh 7/8 and Rh 1 on one hand, and Rh 4 on the other, and optical cross-talk seems possible. The best-known open rhabdom is that of the flies. Here it is known that the rhabdomeres are optical waveguides (Kirschfeld & Snyder 1975). For a quantitative analysis it is necessary to know the fundamental waveguide parameter V (Biemson & Kinsley 1965, cit. after Stavenga 1975) which is given by

\[ V = \frac{2\pi d}{\lambda} \left[ n_1^2 - n_2^2 \right]^{1/2} \]

where \( d \) is the radius of the fibre, \( \lambda \) the wavelength in vacuum, and \( n_1 \) and \( n_2 \) are the refractive indices of the medium within and outside the waveguide. Two problems arise in solving the equation. First, there is no physiological method known which exactly analyses the refractive indices and is generally practicable for interspecific comparisons. Second, the above formula is only valid for cylindrical systems and not all Rh 7/8 and Rh 1 and 4 of the Chrysomelidae are of this shape (Fig. 2). Whether or not one of the above-mentioned alternatives apply would have to be tested for each individual case. In view of the problems mentioned above, this has been deemed impracticable for the present.

3.2.2. Polarization sensitivity. Besides intensity and colour contrasts, the environment contains polarization patterns which can be used by invertebrates for orientation purposes (cf. Waterman 1981). As shown in Fig. 2, the subpatterns of leaf-, longhorn- and seed-beetles differ in the alignments of their microvilli. It has already been noted that these alignments may be special adaptations for polarized light detection (Wachmann 1977, 1979).

Retinula cells are polarization sensitive if the absorption of light (of constant intensity and spectral composition) varies with the orientation of the oscillation plane of the electric vector (E) or if they have a varying degree of polarization (relation of polarized radiation to total intensity) (cf. Snyder 1973; Bernard & Wehner 1977; Waterman 1981).

Polarization sensitivity is a result of the E-vector dependence (dichroically) of the individual photopigment molecules in the microvillus membrane which is in turn a consequence of the physico-chemical properties of these molecules (Dartnall 1972; Täuber 1975). If selection for high polarization sensitivity in a retinula cell occurs, then the photopigments in the microvillus will be aligned parallel to each other so that the chromophore groups in the molecules are orientated perpendicularly to the direction of light incidence (see Moody & Parris 1961; Laughlin et al. 1975). Therefore, in a cell which is highly sensitive to the plane of polarization, one would expect the rhabdomere microvilli to be aligned in parallel and perpendicular to the direction of light incidence.

As in other beetles, the microvilli of the Chrysomelidae are aligned perpendicularly to the direction of light incidence. Therefore, to begin with, one can assume that all retinula cells with only one alignment of microvilli are polarization sensitive (cf. Sections 3.2.2.1 and 3.2.2.2). In the Chrysomelidae, generally the peripheral...
rhabdomeres, and in many cases the central ones, are of this type (Table I; Fig. 2).

A comparison of these retinula cells with parallel microvilli reveals a significant difference in the lengths of the rhabdomeres Rh 1-6 (often ≤30 μm) and Rh 7 and Rh 8 (≤70 μm) (Fig. 2). In order to explain this discrepancy, further factors must be taken into consideration. Under natural conditions, there is no completely linear polarized light, but rather only partially polarized radiation, which may vary in the degree of polarization (e.g. blue skylight, reflected light from water surfaces) (see Waterman 1981). Furthermore, the photopigments are not ideal dipole molecules. Absorption is also possible for light which does not oscillate parallel to the longitudinal axis (however, with only a small probability) (cf. Laughlin et al. 1975). If non-polarized (e.g. direct sunlight) or partially polarized radiation is incident to the rhabdomere, the distal pigments will absorb selectively according to their alignment (dichroic absorption). Therefore, the composition of the incident light reaching pigment at proximal levels is different from that received more distally. The consequence will be that the proximal molecules will absorb light with a less than optimal E-vector inclination to a greater extent than the distal molecules. Because of this property, which is called self-screening (Snyder 1973; Gribakin 1973; Laughlin et al. 1975), the dichroic absorption of the short rhabdomeres (Rh 1-6) of the Chrysomeloidea should be better than that of the long ones (Rh 7/8). Therefore, the polarization sensitivity of cells with short rhabdomeres should be better than that of the long ones. A particularly high dichroic absorption would be expected for the extremely short rhabdomeres of Stenopterus ater (length: 1-3 μm), as well as for those of S. rufus and S. flavicornis (Table I; Fig. 2 r, all Ceramb.). This probable high dichroism of the short rhabdomeres is at the cost of the absolute sensitivity (see Section 3.2.2.2), since the photopigment molecule content of the short rhabdomeres will be less than that of the long rhabdomeres.

3.2.2.1. Attenuation of the polarization sensitivity. Dichroic absorption and thus polarization sensitivity may be reduced by structural considerations (see Section 3.2.2). If several different microvillus alignments exist in a plane perpendicular to the direction of light incidence (e.g. Rh 7 or Rh 8 of Galeruca tanaceti, Orsodacne cerasi, Cassida viridis and Timarcha (Chrys.), as well as Stenopterus ater and Stenocorus meridianus (Ceramb.), then the relative polarization sensitivity of these cells will be comparatively low (Table I; Fig. 2).

Structural arrangements limit polarization sensitivity, independent of information as to photopigment orientation (aligned or not aligned), if divergent microvillus alignments occur in various planes of a rhabdomere (vertical twisting; cf. Menzel & Blakers 1975; Wehner et al. 1975; Wehner & Meyer 1981; Smola & Wunderer 1981). Serial cross-sections of Leptinotarsa decemlineata tend to refute the possibility of vertical twisting (Wachmann 1977).

Besides morphological considerations, polarization sensitivity could be considerably limited at the molecular level by random orientation of photopigment molecules (as in the discs of the retina cells of Vertebrata) or by orientation of the molecules at 45° to the direction of incident light (Laughlin et al. 1975).

Furthermore, electrical coupling (Shaw 1969a) or neuronal coupling (Schloes 1969; Kirschfeld & Snyder 1975) could limit the polarization sensitivity of two or more cells each of which absorbs maximally at different E-vectors.

3.2.2.2. Absolute sensitivity and polarization sensitivity. The polarization sensitivity of a receptor cell could be a byproduct of the optimizing of absolute sensitivity (general absorption probability) for nonpolarized radiation (Snyder et al. 1975). For instance, it is possible that more photopigment molecules could be built into a microvillus if they are all orientated in a similar fashion perpendicular to the incident light, than if they were orientated at random. Even if the same number of molecules occurs in each of these arrangements, the absolute sensitivity in the regular arrangement is higher for short rhabdomeres. The dichroic absorption of the rhabdomeres would therefore also be a byproduct (cf. Laughlin et al. 1975). Presumably, at least the peripheral rhabdomeres (Rh 1-6 less than 30 μm) of the Chrysomeloidea are to be considered short types in this sense (compare fly Rh 1-6 approx. 250 μm; Trujillo-Cenoz & Melamed 1966). Whether or not the central rhabdomeres (Rh 7/8 about 70 μm) of the leafhoppers and seed-beetles are also generally short in this sense cannot be judged, because the influence of self-screening may be quite significant here.

The polarization sensitivity of receptor cells in insects can be eliminated in principle by electrical and neuronal coupling of the second order neurons. Thus, an undesirable polarization sensitivity can be excluded before it becomes behaviourally effective (see Section 3.2.2.1).

Data concerning polarization-dependent behaviour of Coleoptera exist only for taxa other than the Chrysomeloidea (review: von Frisch 1965; Frantsevich et al. 1977; Gribakin 1981). Thus it is not known if the presumably high polarization sensitivity of some receptor cells of the Chrysomeloidea represents a further physiological mechanism for perceiving optical contrasts in the environment and using them for orientation.

For the purposes of a phylogenetic analysis, one may deduce from a comparison of polarization and absolute sensitivity that identical rhabdomere organizations may be the result of diverse physiological optimizing strategies.

In this connection a further indication of the possible existence of diverse neuronal strategies during polarization-dependent behaviour may be seen in the fact that, depending on the type of neuronal analysis, the responses of a varying minimum number of receptor cells must be evaluated by the nervous system. Thus, the signals of at least three retinula cells must be simultaneously compared for successful menotaxis of worker bees with respect to a section of the polarized sky. In the case of an ambiguous or successive analysis, one polarization sensitive receptor is sufficient (Kirschfeld 1973).

3.3. Conclusions

Phylogenetic investigations that are carried out on relatively closely related taxa may lead to the pitfall of in-
cluding homoiologies in the analysis, which are then incorrectly determined to be synapomorphic homologies. In the case of Chrysomeloidea rhabdoms, the findings must be interpreted in the following manner. The open rhabdom of all Chrysomeloidea are homologous as open rhabdoms. The two basic patterns and several of the sub-patterns of the insula-pattern must have developed convergently within the Chrysomeloidea.

"Homoiologous", "homologous" or "convergent" are, just as "apomorphic" or "plesiomorphic", only relative conditions of characters and not their inherent properties. For this reason, homoiologies (parallels) can be employed in the analysis of phylogeny depending on the integration level (compare Bock 1977, p. 881) but provided that their homologous and convergent portions are considered separately (see the Schle/Brundin controversy in Brundin 1976; Srether 1979; Schlee 1978). The "open rhabdom" feature of the rhabdom pattern of the Chrysomelinae can be considered to be a symplesiomorphy for this group, because it may be regarded as synapomorphy of the Cucujiformia within the Coleoptera (Wachmann 1977). The "ponticulus-pattern" feature of the rhabdom pattern can be considered as a synapomorphy of the Chrysomelinae within the Chrysomelidae, but its occurrence in the Chrysomelinae and certain Cerambycidae must be due to convergence. Similar conclusions can be reached for the insula-subpattern of the Clytinae or the Cassidinae, as stated in Section 3.1.2.

We regard the rhabdomeres in the compound eyes of the Chrysomeloidae as a system in which the environmental selection pressure influences the "biological role" of the union of form + function ("faculty": Bock & von Wahlert 1965). The fact that rhabdom patterns of different Chrysomeloidae vary could mean that the cells which are identically positioned in different species (particularly in the central system) are responsible for diverse "biological roles", and/or that different selection pressures influence the homologous cells of various species.

The consideration of the rhabdomeric organization in the compound eyes of beetles in terms of photoreceptor optics has shown that essential physiological properties are dependent on ultrastructural form. The causes of these patterns are to be found in the optimizing of different optical and/or electrical coupling (see Section 3.2.1) of the insula- and ponticulus-patterns, as well as in the different polarization and absolute sensitivities of the retinula cells 1–6 and 7/8, and of the various subpatterns (see Section 3.2.2).

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