Detectors for Polarized Skylight in Insects: A Survey of Ommatidial Specializations in the Dorsal Rim Area of the Compound Eye

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ABSTRACT   Apart from the sun, the polarization pattern of the sky offers insects a reference for visual compass orientation. Using behavioral experiments, it has been shown in a few insect species (field crickets, honey bees, desert ants, and house flies) that the detection of the oscillation plane of polarized skylight is mediated exclusively by a group of specialized ommatidia situated at the dorsal rim of the compound eye (dorsal rim area). The dorsal rim ommatidia of these species share a number physiological properties that make them especially suitable for polarization vision: each ommatidium contains two sets of homochromatic, strongly polarization-sensitive photoreceptors with orthogonally-arranged analyzer orientations. The physiological specialization of the dorsal rim area goes along with characteristic changes in ommatidial structure, providing actual anatomical hallmarks of polarized skylight detection, that are readily detectable in histological sections of compound eyes. The presence of anatomically specialized dorsal rim ommatidia in many other insect species belonging to a wide range of different orders indicates that polarized skylight detection is a common visual function in insects. However, fine-structural disparities in the design of dorsal rim ommatidia of different insect groups indicate that polarization vision arose polyphyletically in the insects. *Microsc. Res. Tech. 47:368–379, 1999.*   © 1999 Wiley-Liss, Inc.

INTRODUCTION

The sky appears bright and not black because on its way through the atmosphere the light that is radiated by the sun is scattered by air molecules. As a result of this scattering, skylight is partially plane-polarized, i.e., in any point of the sky a particular orientation of the electric vector (e-vector) dominates. The e-vector distribution in the sky follows the rule of tangential polarization, whereby the prevailing e-vector is oriented orthogonal to an imaginary straight line connecting an observed point in the sky and the sun (Strutt, 1871; for graphical representations of the polarization pattern, see Figs. 1 and 2 in Wehner, 1997). Since solar position and e-vector pattern are linked together, directional information in the sky is independent of the visibilty of the sun, provided that at least small parts of the sky are visible (Labhart, 1999a). The e-vector in the zenith is evaluated most easily because it is at all times oriented exactly 90° to the azimuth of the sun, i.e., independent of solar elevation.

Thus, skylight polarization offers polarization-sensitive organisms an attractive reference for visual compass orientation. The use of skylight polarization for long-range navigation was demonstrated by training experiments in honey bees and desert ants (Duelli and Wehner, 1973; von Frisch, 1948, 1949). Studying a spontaneous orientation response to polarized light, polarization vision was also shown in field crickets and house flies (Brunner and Labhart, 1987; von Philipsborn and Labhart, 1990). Further behavioral tests with these insects indicated that e-vector detection is mediated by a group of specialized ommatidia at the dorsal margin of the compound eye, termed the dorsal rim area (DRA) (bees: Wehner and Strasser, 1985; ants: Fent, 1985; crickets: Brunner and Labhart, 1987; Herzmann and Labhart, 1989; flies: von Philipsborn and Labhart, 1990). The dorsal rim ommatidia of these insects share a number of physiological properties that make them especially suitable for polarization vision, such as strongly polarization-sensitive photoreceptors (see below).

Is polarization vision a common sensory function in insects or is polarization vision a speciality of certain species or groups of insects? Apart from the four species discussed above, only a few other insects have been subjected to the strict behavioral tests necessary to prove e-vector detection (locust *Schistocerca*: Eggers and Weber, 1993; tenebrionid beetle *Parastizopus*: Bisch, 1999; fly *Drosophila*: Wolf et al., 1980). A number of other reports present circumstantial or preliminary evidence for polarization sensitivity (e.g., the scarab beetles *Melolontha*: Couturier and Robert, 1956; *Geotrupes*: Birukow, 1953; *Lethrus*: Frantsevich et al., 1977; wood ant *Formica*: Jander 1957; mosquitoes: Wellington, 1974; for a review, see Waterman, 1981). The reasons for the lack of hard evidence in all but a few insects may be that systematic behavioral experiments are difficult and time-consuming, or often not possible for technical reasons.

Histology	+++	+++[a]	+/-		-	+/---	- +++[b]	+++[c]	+++[d]
Electrophysiology		++				+	++		++
Behavior		++					++		+
Receptor type		B(2)				G(1)	UV(2)		UV(3)

Taxa (left to right): Collembola, Protura, Diplura, Archaeognatha, Zygentoma, Ephemeroptera, **Odonata**, Plecoptera, Embioptera, **Orthoptera**, Grylloblattaria, Dermaptera, **Blattodea**, Mantodea, Isoptera, Zoraptera, Psocoptera, Phthiraptera, Coleorrhyncha, **Heteroptera**, Stenorrhyncha, Auchenorrhyncha, Thysanoptera, Strepsiptera, **Coleoptera**, Raphidioptera, Megaloptera, **Neuroptera**, **Hymenoptera**, Trichoptera, **Lepidoptera**, Mecoptera, Siphonaptera, **Diptera**

Holometabola 300 Mio
Neoptera 325 Mio
Pterygota 350 Mio
Dicondylia 400 Mio
Insecta 450 Mio
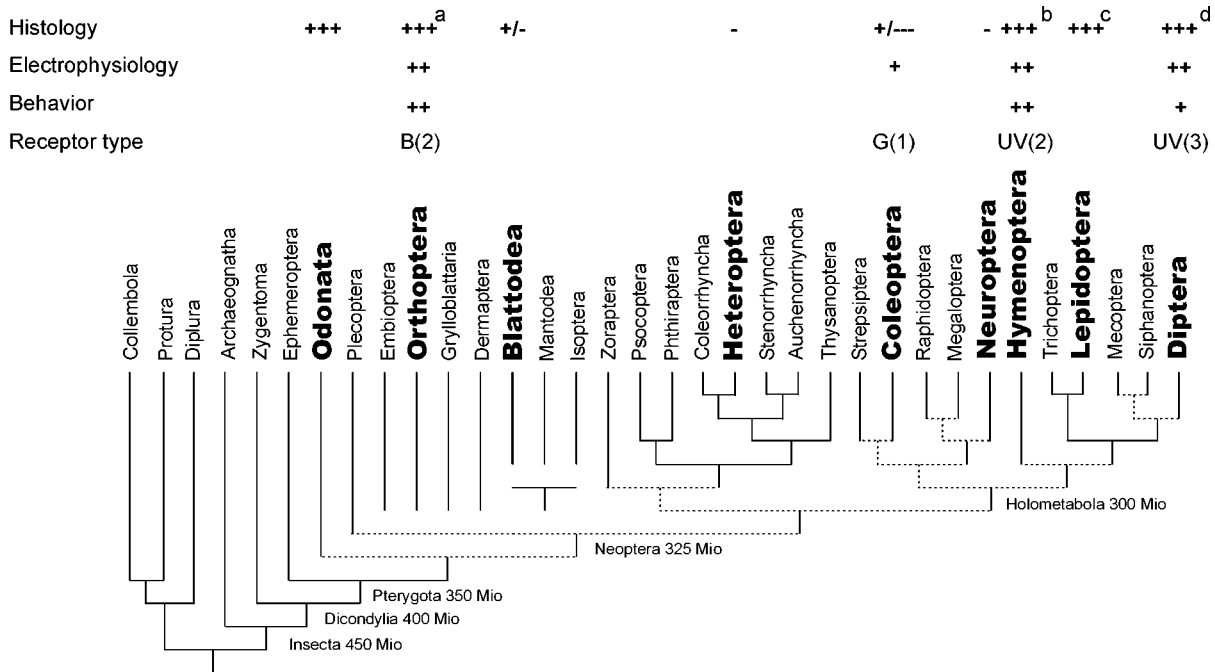
Fig. 1. A survey of specialized dorsal rim areas in insect eyes. Histology: evidence based on histological observations of the retina (for details see text); Electrophysiology: evidence based on high polarization sensitivity of the photoreceptors as opposed to low polarization sensitivity in other eye regions; Behavior: evidence based on behavioral tests indicating that the dorsal rim area is the eye region that mediates polarization vision. Plus signs indicate positive evidence: +, representatives of one family, ++, two families, +++, ≥3 families of a given order; minus signs indicate negative findings: -, representatives of one family,---, three families. Negative findings of Burghause (1981) for some orthopteran species are not included (see text). Receptor type: spectral type of photoreceptor that is used for polarization vision (electrophysiological and/or behavioral evidence); UV ultraviolet, B blue, G green, the number indicating the number of families. **a–d:** insect orders in which the retinal histology of a considerable number of families was studied: a, 7 families; b, 5 families (in 3 more families optical specializations of the cornea were observed, but no retinal data are available); c, 5 families; d, 13 families of brachyceran flies. Cladistic family tree modified after Kristensen (1981).

Fortunately, in accordance with the principle that "form follows function," the functional specialization of the DRA in bees, ants, crickets, and flies, i.e., in insects in which polarization vision was clearly shown behaviorally, goes along with characteristic changes in ommatidial structure representing actual hallmarks of polarized skylight detection, such that the specialized DRA can readily be recognized in histological preparations. Finding the characteristic anatomical traits of polarization vision in any other insect strongly suggests that polarized skylight plays a significant role in spatial orientation behavior of that species.

In this article, we review the occurrence of specialized DRAs in the insects relying on both published and previously unpublished data. According to the histological evidence, polarization vision seems to be a common visual function in insects. However, the failure of finding anatomically specialized DRAs in some species suggests that polarized skylight orientation is not omnipresent. Based on comparative aspects of DRA design in different insect groups, we present evidence that polarized skylight orientation in insects arose polyphyletically.
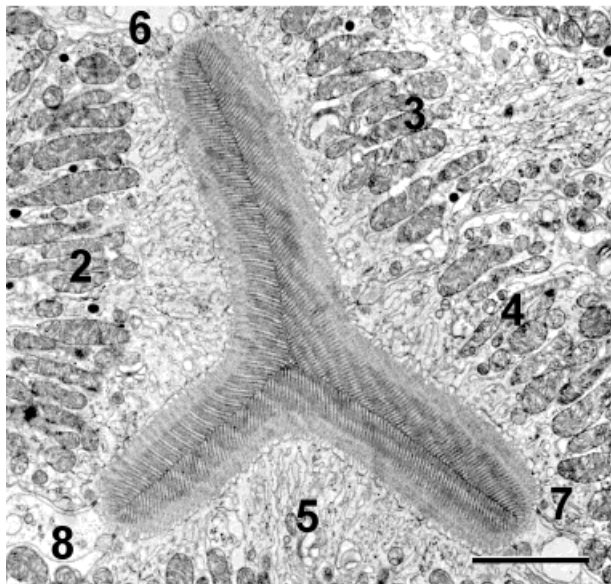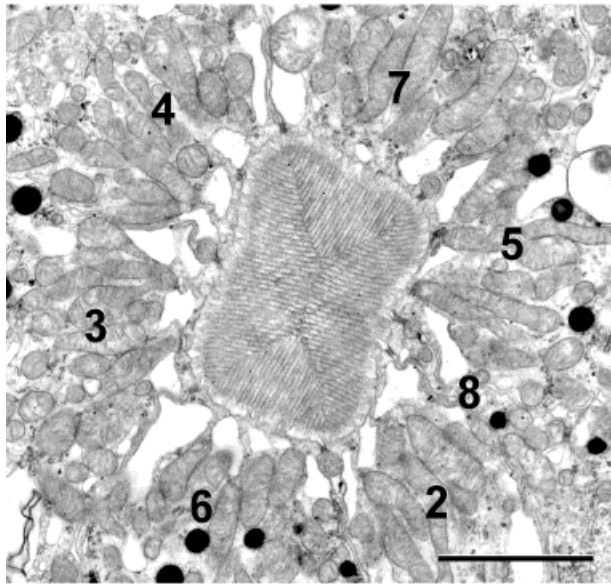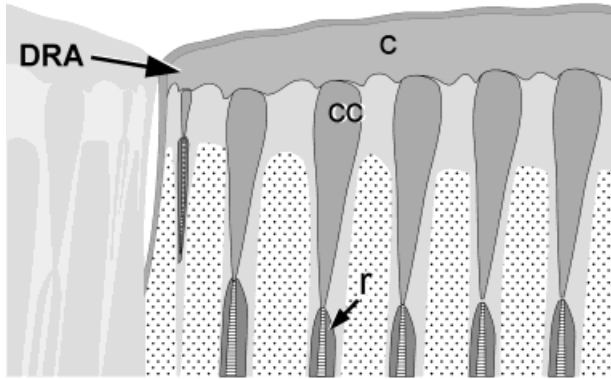
FUNCTIONAL ANATOMY OF SPECIALIZED DORSAL RIM AREAS

The key function of the dorsal rim area (DRA) of the compound eye for e-vector perception has been demonstrated in four insect species by behavioral experiments (honey bees *Apis mellifera*: Wehner and Strasser, 1985; desert ant, *Cataglyphis bicolor*: Fent, 1985; house fly, *Musca domestica*: von Philipsborn and Labhart, 1990; field cricket, *Gryllus campestris*: Brunner and Labhart, 1985). As shown by electrophysiological recordings, the dorsal rim ommatidia of these species share a number of physiological properties that makes them especially suitable for the detection of polarized skylight: each ommatidium contains two sets of homochromatic, strongly polarization-sensitive photoreceptors with orthogonally arranged analyzer directions (*Apis:* Labhart, 1980; *Cataglyphis:* Labhart, 1986; *Musca:* Hardie, 1984, 1985; *Gryllus:* Labhart et al., 1984). The functional specialization of the DRA in these species is reflected by the following specialized anatomical and optical properties of the ommatidia:

1. Optical axes: As suggested by the position in the eye, the optical axes of the dorsal rim ommatidia are directed upwards. In fact, as studied in *Apis, Cataglyphis,* and *Gryllus*, the visual field of the DRA has an elongated shape extending from upper front to upper back and with the center directed somewhat to the contralateral side (*Apis*: Labhart, 1980; Sommer, 1979. *Cataglyphis*: Labhart, 1986; Wehner, 1982. *Gryllus*: Labhart et al., 1984; Labhart, unpublished data).
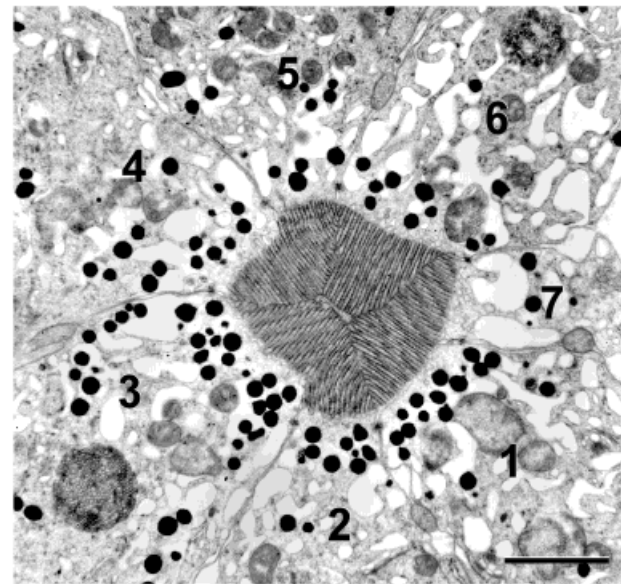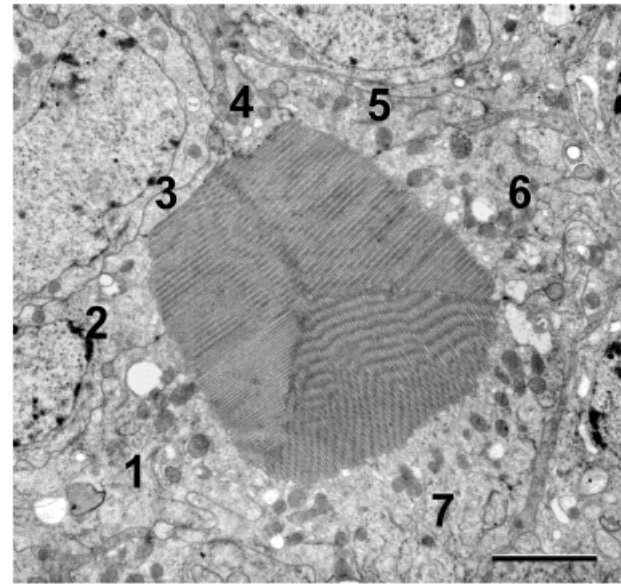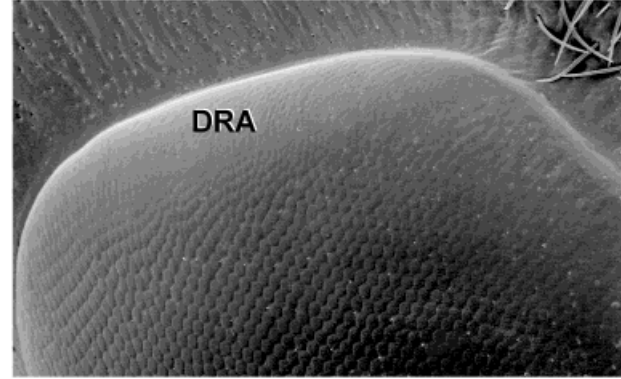
Fig. 2. Comparison between regular ommatidia and specialized ommatidia in the dorsal rim area (DRA) of the compound eye in different insects. Top row, optical properties of dorsal vs. dorsal rim ommatidia; center row, electron micrographs of cross-sections through ommatia of the DRA; bottom row, electron micrographs of cross-sections through regular ommatidia of the dorsal part of the eye. **A:** Dragonfly *Sympetrum striolatum* (Odonata). The schematic drawing of a longitudinal section through the dorsalmost part of the eye (top) shows that the dorsal rim ommatidia are strongly reduced in length and lack proper corneal lenses. c, cornea; cc, crystalline cone; r, rhabdom. The rhabdoms of the DRA (center) are rectangular with orthogonal microvilli as opposed to the lobed rhabdoms of the dorsal area (bottom). **B:** Field cricket *Gryllus campestris* (Orthoptera): The scanning electron micrograph of the dorsalmost eye part (top) shows strongly reduced and irregular facets in the cornea of the DRA. A right eye is depicted with the frontal direction to the right (same for C–F top). Dorsal rim retinulae (center) lack screening pigment and the rhabdoms have a characteristic trapezoidal shape with orthogonal microvilli.
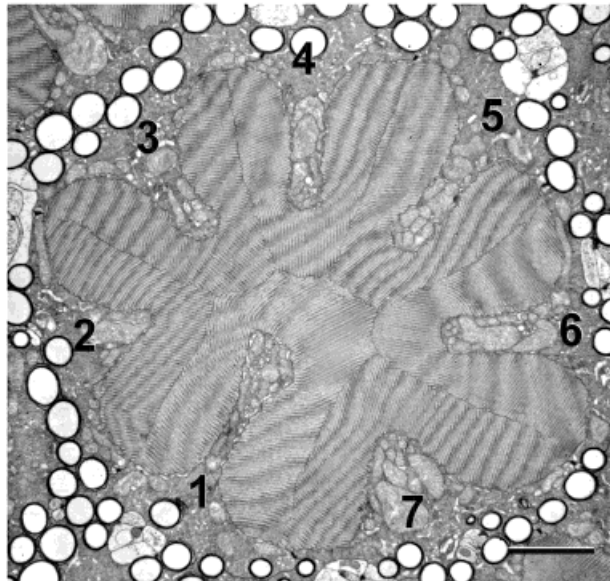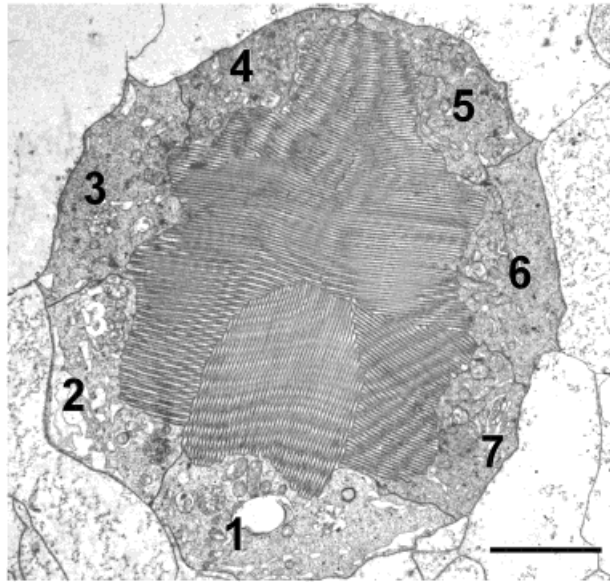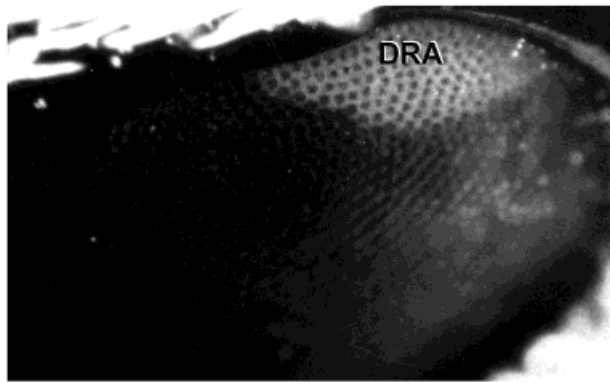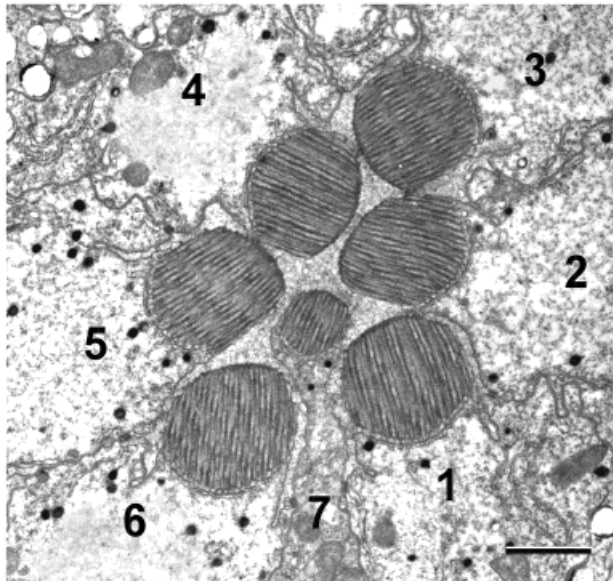
C Melolontha (Coleoptera)   **D** Drosophila (Diptera)
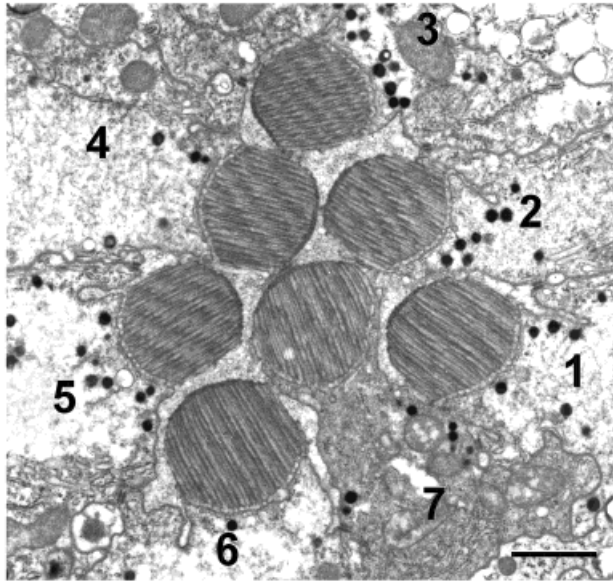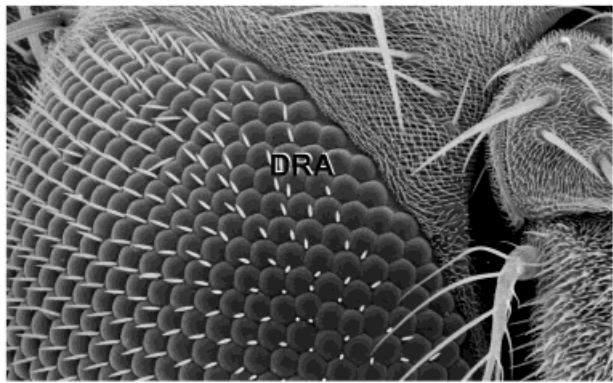
Fig. 2.   (Continued.) **C:** Cockchafer *Melolontha melolontha* (Coleoptera): The dorsal eye part of an intact eye as seen with incident illumination (top) reveals light-scattering bubbles in the cornea of the DRA. Dorsal rim retinulae (center) lack screening tracheoles and the rhabdoms have a compact shape with orthogonal microvilli as opposed to the regular retinulae with lobed rhabdoms (bottom). **D:** Fruit fly *Drosophila melanogaster* (Diptera): The scanning electron micrograph of the dorsalmost eye part (top) reveals no optical specializations in the DRA. The UV-sensitive, central photoreceptors (R7,8) of the dorsal rim ommatidia (center) have enlarged rhabdomeres and their microvilli are orthogonal to each other. Since R7 and R8 are arranged in tandem, only the distal R7 is visible in these sections.

E Apis (Hymenoptera)
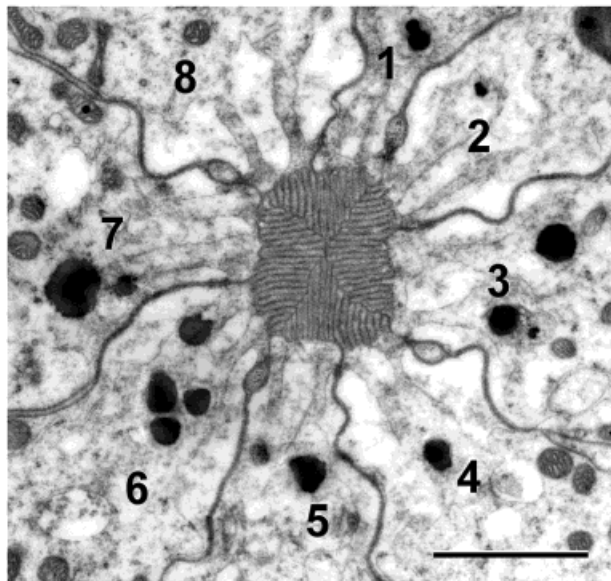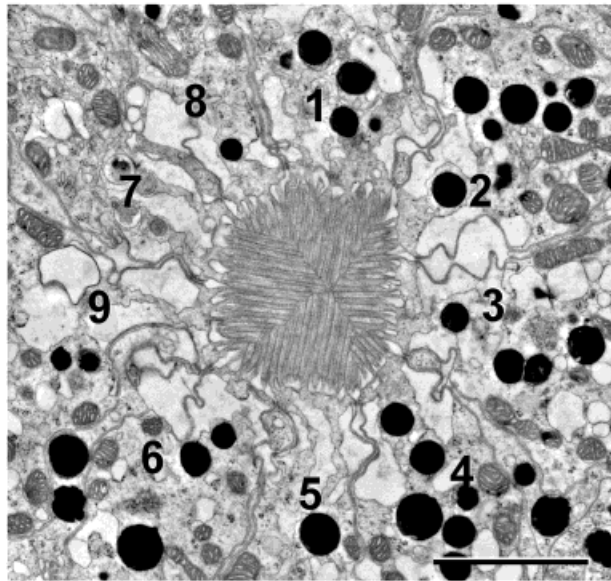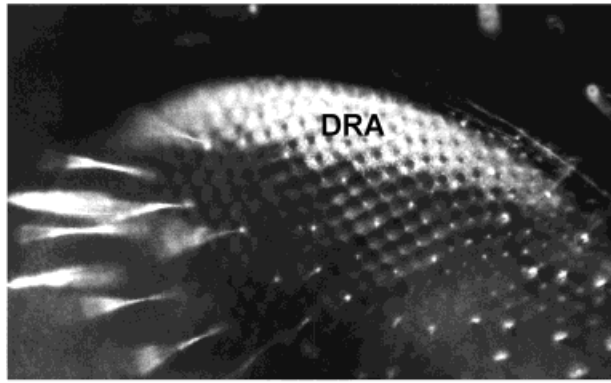
F Cataglyphis (Hymenoptera)
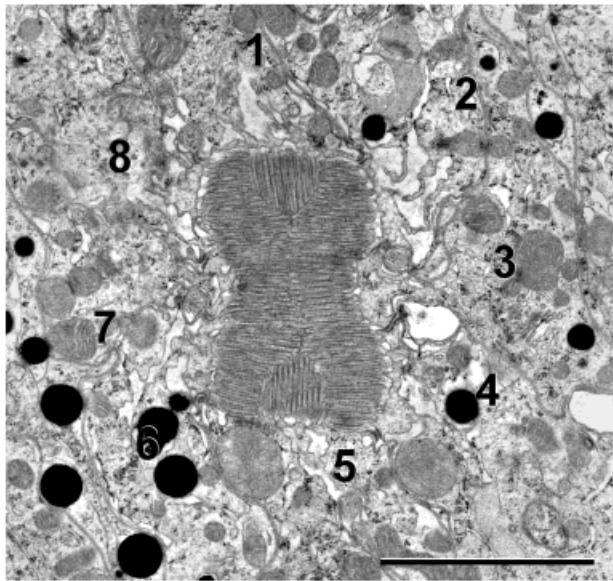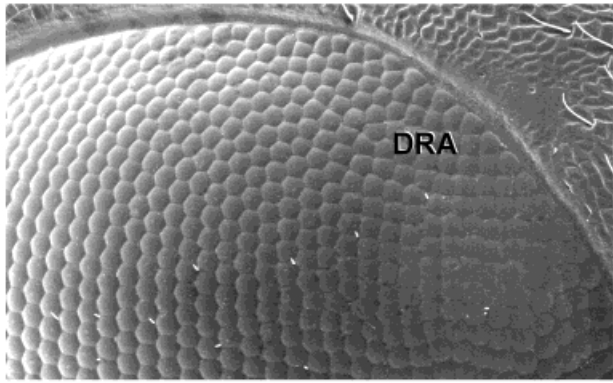
Fig. 2. (Continued.) **E:** Honey bee *Apis mellifera* (Hymenoptera): The dorsalmost eye part of an intact eye as seen with incident illumination (top) reveals light-scattering pore canals in the cornea of the DRA. Dorsal rim retinulae (center) contain nine (instead of eight) long receptor cells, the UV-cells of which have their microvilli oriented strictly orthogonal to each other (R1, 5 vs. R9). **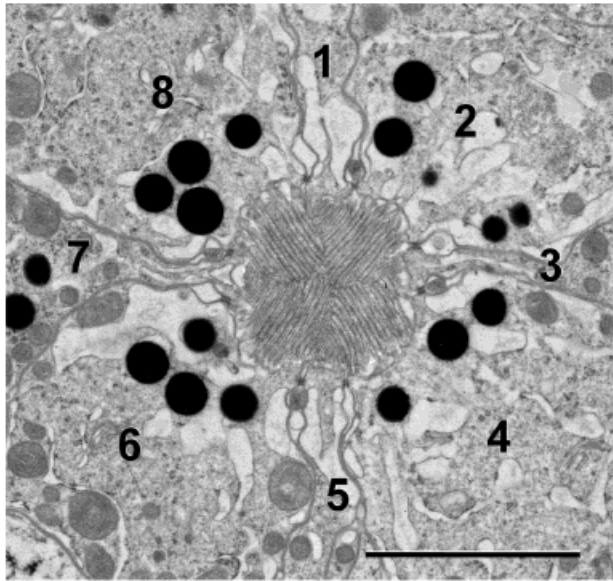F:** Desert ant *Cataglyphis bicolor* (Hymenoptera): The scanning electron micrograph of the dorsalmost eye part (top) reveals no optical specializations in the DRA. Dorsal rim rhabdoms (center) have characteristic dumb-bell shapes and exhibit just two orthogonal microvilli orientations as opposed to regular ommatidia (bottom). Note: Although photoreceptors with mutually perpendicular microvilli may also be present in the regular ommatidia of some of these species (*Gryllus, Apis, Cataglyphis*), the photoreceptors of regular ommatidia are only weakly polarization-sensitive because the microvilli are misaligned, either within each section plane (*Melolontha*) or along the rhabdomeres (*Gryllus, Apis, Cataglyphis*), or due to self-screening in the long rhabdoms (*Sympetrum*). Calibration bars = 2 µm. (A [center and bottom] reproduced from Meyer and Labhart, 1993, with permission of the publisher; C reproduced from Labhart et al., 1992, with permission of the publisher; E [top] reproduced from Meyer and Labhart ,1981, with permission of the publisher).

2. Rhabdom shape: The rhabdoms differ in shape, length, and width from those of regular ommatidia. More specifically, the rhabdoms are shorter and have a larger cross-sectional area. This is because the rhabdomeres of the polarization-sensitive photoreceptors (i.e., those receptors of the ommatidium that mediate polarization vision) are relatively wide and short. The differences in rhabdom shape are due to the large polarization-sensitive receptors and (in *Gryllus* and *Apis*) due to different numbers of receptors contributing microvilli to the rhabdom compared to the regular ommatidia (Fig. 2 B,D–F and Fig. 3) (*Apis*: Schinz, 1975; Sommer, 1979. *Cataglyphis*: Herrling, 1976; Nilsson et al., 1987; Räber, 1979. *Calliphora*: Wunderer and Smola, 1982a,b. *Musca*: Wada, 1974a. *Gryllus*, Burghause, 1979; Nilsson et al., 1987). Shortening the rhabdomere of a photoreceptor favors polarization sensitivity by reducing self-screening, whereas widening the rhabdomere increases sensitivity (Nilsson et al., 1987).

3. Microvilli orientation: The polarization-sensitive photoreceptors come in two sets that have their microvilli oriented 90° to each other (Fig. 2B,D–F and Fig. 3) (*Apis*: Schinz, 1975; Sommer, 1979; Wehner et al., 1975. *Cataglyphis*: Herrling, 1976; Räber, 1979. *Calliphora*: Wunderer and Smola, 1982b. *Gryllus*: Burghause, 1979). Polarization sensitivity in invertebrate photoreceptors is based on the absorption properties for polarized light of the microvilli that compose the rhabdomere. By still unknown mechanisms, the visual pigment molecules are aligned within the microvillar membrane in such a way that linearly polarized light is maximally absorbed when the oscillation plane (e-vector) is parallel to the long axis of the microvilli (Goldsmith and Wehner, 1977; Hardie, 1984; 1985; Israelachvili and Wilson, 1976; Kirschfeld, 1969). The orientation of the microvilli is, therefore, a convenient indicator for the e-vector to which a photoreceptor is tuned. Thus, dorsal rim ommatidia contain two types of e-vector analyzers that are tuned to mutually orthogonal e-vectors. There is both electrophysiological (*Gryllus, Cataglyphis*) and behavioral evidence (*Apis*) that the two analyzer channels feed antagonistically into comparator neurons (polarization-opponent neurons) (Labhart, 1988, 1999b; Rossel and Wehner, 1986). The antagonism enhances sensitivity for e-vector contrast and makes the system independent of ambient light intensity (Labhart, 1988, 1999a).

4. Microvilli alignment: In the polarization-sensitive receptors, the microvilli are well aligned along the whole rhabdomere. In the ommatidia of other eye regions, the microvilli are misaligned by twisting the whole retinula (*Apis*), by twisting the rhabdomeres (*Musca, Calliphora*), or by random misalignment *(Gryllus, Cataglyphis)* (*Apis*: Wehner et al., 1975. *Cataglyphis*: Meyer and Domanico, 1999; Räber, 1979. *Musca, Calliphora*: Wunderer and Smola, 1982a,b. *Gryllus*: Nilsson et al., 1987). Strict alignment of the microvilli within the rhabdom is an important requirement for high polarization sensitivity (Nilsson et al., 1987; Wehner et al., 1975).

5. Optics: In *Apis* and *Gryllus*, the optical properties of the ommatidia are also affected. In bees, the cornea of the DRA contains light scattering pore canals (Meyer and Labhart, 1981), whereas crickets lack

both outer corneal facetting and screening pigment (Burghause, 1979; Ukhanov et al., 1996) (Fig. 2B,E). These properties degrade the optics of the dorsal rim ommatidia, which increases the visual field of the photoreceptors (Labhart, 1980; Labhart et al., 1984; Nilsson et al., 1987). Large visual fields are of advantage because optical integration over a large area of the sky reduces the effect of irregularities in the polarization pattern that are caused by clouds (Labhart, 1999a).

OCCURRENCE OF SPECIALIZED DORSAL RIM AREAS IN THE INSECTA

Obviously, the ommatidia of an eye part dedicated to polarization vision have to meet other requirements than those ommatidia that mediate spatial vision or color vision. For instance, to avoid interference between e-vector and color information, the analyzers (photoreceptors) of a polarization vision system should be highly polarization-sensitive and homochromatic, but those of a color vision system must be polychromatic and polarization-insensitive for optimal performance. This explains the rhabdom twist, i.e., the extreme microvillar misalignment, in the regular, delicately color-sensitive part of the honey bee compound eye on the one hand, and the strict microvillar alignment in the DRA on the other hand (Wehner and Bernard, 1993). Thus, optimizing the ommatidia for polarization vision imposes characteristic structural modifications, which are detectable in histological sections. The presence of these anatomical hallmarks of polarized skylight detection in the DRA of an insect is strongly indicative for polarization vision, just as in those species in which polarization vision was demonstrated directly by behavioral experiments (see above). In the following, we review the occurrence and properties of specialized DRAs in different insect orders. We will briefly summarize the findings for each insect order, presenting details only when necessary. For more detailed information, including the full names of the different species studied, please refer to the cited original literature.

Our standard procedure for identifying specialized dorsal rim ommatidia was to inspect first the intact eye for obvious peculiarities of the optics. Then, light microscopical sections were examined for a first estimation of rhabdom shapes and sizes, of pigmentation, and of the optical properties of the dioptric apparatus. Finally, the structural details including the orientation of the microvilli were studied by electron microscopy. Histological procedures were as given in our previously published work (Meyer and Labhart, 1993; Labhart et al., 1992). Other authors often do not comment on the optical quality of the cornea such that this information is missing for several species. For a summarizing graphical representation of our survey see Figure 1.

Odonata

In all five studied genera of the Odonata (belonging to three families), the ommatidia of the DRA differ markedly form the regular ommatidia of the dorsal eye region (Meyer and Labhart, 1993). They are strongly reduced in length and the untiered rhabdom is rectangular in cross-section exhibiting just two orthogonal microvilli orientations. In the dragonfly *Sympetrum*, the contrast between the short, compact-shaped dorsal rim rhabdoms and the 10 times longer and lobed

	Sympetrum (Odonata)	Gryllus (Orthoptera)	Melolontha (Coleoptera)	Apis (Hymenoptera)	Cataglyphis (Hymenoptera)	Drosophila (Diptera)
dorsal rim ommatidia						
optical specializations	no proper lens	- altered lens structure - no screening pigment	- turbid lens (bubbles) - no screening tracheoles	turbid lens (pore canals)	none	none
spectral type of receptors [a]	n.d.	blue	green	UV	UV	UV
number of homochromatic receptors [a]	n.d.	5	7	3	6	2
number of microvillar types of receptor [a]	n.d.	4/1	6/1	2/1	4/2	1/1
structure						dist. prox.
regular ommatidia						
structure						

Fig. 3. Comparison between optical, spectral and structural details of the specialized ommatidia in the dorsal rim area of different insects. Where present, the optical specializations increase the visual field of the photoreceptors. Schematic drawings represent cross-sections through specialized dorsal rim ommatidia (**top**) and regular dorsal ommatidia (**bottom**). Colors indicate spectral receptor type; violet stands for UV. [a]Spectral type of receptor that mediates polarization vision, not counting a possible small, proximal receptor.

regular dorsal rhabdoms is dramatic (Fig. 2A). In addition, in *Sympetrum* the optics of the DRA was found to be degraded since the ommatidia lack proper corneal lenses (Meyer and Labhart, 1993).

Orthoptera

In the Orthoptera, the presence of a specialized DRA seems to be the rule. Most genera studied belong to the Grylloidea (Burghause, 1979, 1981; Egelhaaf and Dambach, 1983). As shown in *Gryllus*, specialized ommatidia are present from the first larval instar (Labhart and Keller, 1992). Although Burghause (1981) reports the absence of a specialized DRA in the two grasshopper genera (*Tetrix*, Tetrigidae; *Chorthippus*, Acrididae, Caelifera) and the one bushcricket genus (*Conocephalus,* Tettigonoidea, Ensifera) he studied, all orthopteran species examined by us had a specialized DRA. In fact, we did find a DRA in *Chorthippus sp.*, in the bushcricket *Pholidoptera griseaptera,* and in *Bullacris membracoides* (Pneumonidae, Caelifera), and a DRA was also reported for the locust *Schistocerca* (Acrididae, Caelifera) (Eggers and Gewecke 1993a; Paech et al., 1997). In orthopteran insects, the presence of a specialized DRA is already apparent in the intact eye by its pale appearance, indicating reduced or missing screening pigment, and by irregular and reduced corneal facets. Due to a marked size reduction or even inactivation (no microvilli) of two receptor cells (R3 and R4; see Figs. 2B and 3), the dorsal rim rhabdoms typically become triangular or trapezoidal in cross-section and contain just two orthogonal microvilli orientations. As shown in *Gryllus*, the microvilli are strictly aligned along the rhabdomeres of DRA ommatidia, which results in a much higher polarization sensitivity of the photoreceptors than in other eye regions (Labhart et al., 1984; Nilsson et al., 1987; Zufall et al., 1989). Both behavioral and electrophysiological experiments with *Gryllus* and *Schistocerca* indicate that polarization vision in the Orthoptera is mediated by blue-receptors, although also a small number of UV-receptors were found in the locust DRA (Eggers and Gewecke, 1993a,b; Herzmann and Labhart, 1989; Labhart et al., 1984; Zufall et al., 1989).

Coleoptera

Most species of the Coleoptera that were studied belong to the family of Scarabaeidae. This family is heterogeneous both regarding the presence of a specialized DRA and the architecture of the rhabdom. Whereas the dorsal rim rhabdoms of *Melolontha* (European cockchafer), *Anoplognatus*, *Pachysoma,* and *Onthophagus* are of a "simple" structure by containing just two microvillar blocks with orthogonal microvilli orientations (see Figs. 2C and 3) (Labhart et al., 1992; Gokan, 1990; Dacke et al., 1999), in *Geotrupes* the two microvillar types of rhabdomeres form a conspicuous herringbone pattern (Gokan, 1989). In *Amphimallon solstitiale,* we found no specialized DRA: all ommatidia contained rhabdoms of the lobed type similar to those in the regular ommatidia of *Melolontha.* Optical specializations in the form of light-scattering bubbles in the cornea and the missing of tracheal sheaths around the ommatidia have been reported for *Melolontha*, the latter trait also being present in *Anoplognatus* (Labhart et al., 1992). Regarding single species of two other families, in the tenebrionid *Parastizopus*, all 200 ommatidia of the eye have the same structure containing

untwisted rhabdoms of an elaborate theta-shape (Bisch, 1999), and we found no specialized ommatidia in the DRA in the buprestid *Melanophila accuminata*. Electrophysiological recordings from the DRA of *Melolontha* suggest that polarization vision is mediated by green-receptors (Labhart et al., 1992). Behavioral experiments with the tenebrionid *Parastizopus* also point to a long-wave receptor (Bisch, 1999).

Hymenoptera

In all species of the five Hymenoptera families studied, the DRA contained specialized retinulae (Aepli et al., 1985; Schinz, 1975). In specimens of three further families, light scattering structures in the cornea of the DRA were observed in the intact insects (Aepli et al., 1985). In the species other than ants, the specialization of the dorsal rim retina is not very conspicuous since the overall shape and the size of regular and dorsal rim rhabdoms differ little. There are, however, characteristic differences in fine structure: whereas a regular retinula is composed of 8 long receptors (R1–8) and one short proximal receptor cell (R9), a dorsal rim retinula contains 9 long cells with R9 strongly increased in size (Aepli et al., 1985). As revealed in the honey bee *Apis mellifera*, this modification arises because it is the three UV-receptors R1,5,9 that mediate polarization vision in the bee, forming large rhabdomeres with orthogonal microvillar orientations (see Figs. 2E and 3) (Helversen and Edrich, 1974; Labhart, 1980; Sommer, 1979). In addition, the DRA of *Apis* has straight retinulae as opposed to the regular retinulae that are twisted about their long axis (Sommer, 1979; Wehner et al., 1975). Light scattering structures in the cornea of the DRA were frequently found and always indicated the presence of specialized retinulae (Aepli et al., 1985; Meyer and Labhart, 1981). In all of the 10 ant genera (Formicoidea) studied, the DRA is clearly discernible by a marked difference in rhabdom shape, and the microvilli are oriented orthogonal to each other. However, in none of the ants were any optical specializations observed (Aepli et al., 1985; Herrling, 1976; Wehner, 1982; Meyer, unpublished results: *Myrmecia gulosa, Paraponera clavata*). As studied in *Cataglyphis*, the UV-receptors, that mediate polarization vision also in the ant, form microvilli that are oriented 90° to each other (R1,5 vs. R2,4,6,8; see Figs. 2F, 3) and the microvilli are better aligned than in the other eye regions (Duelli and Wehner, 1973; Labhart 1986; Meyer and Domanico, 1999; Räber, 1979). In both *Apis* and *Cataglyphis,* the strict alignment of the microvilli along the rhabdom was shown to boost polarization sensitivity of the UV-receptors (Labhart, 1980, 1986).

Lepidoptera

In the Lepidoptera, representatives of five families were studied and all exhibited specialized DRAs. The rhabdoms are characterized by their special shapes and the presence of two strictly orthogonal microvilli orientations. As demonstrated in *Pararge* and *Aglais*, the microvilli are well aligned along the rhabdomeres, in contrast to other eye regions, where the microvilli orientation of most retinula cells shows considerable scatter (Hämmerle and Kolb, 1996; Kolb, 1985, 1986; Meinecke, 1981).

Diptera

In all 30 genera of the 13 families of flies (Diptera, Brachycera) studied, the rhabdomeres of the central photoreceptors R7 and R8 are significantly enlarged in the dorsal rim ommatidia (Hardie et al., 1989; Strausfeld and Wunderer, 1985; Wada, 1974a,b; Wunderer et al., 1990; Wunderer and Smola, 1982a,b; Meyer, unpublished results: *Eristalis sp.*, *Myiatropa sp.,* Syrphidae; *Ormia ochracea*, Tachinidae). For a typical representative of the flies, see Figure 2D. As studied in *Calliphora*, the increase of rhabdom width goes along with a loss of rhabdomeric twist, which results in strong polarization sensitivity of these cells, and the microvilli of the distally located receptor R7 are orthogonal to those of the proximal cell R8 (Hardie, 1984; Wunderer and Smola, 1982b). R7 and R8 are both UV-sensitive (as shown in *Musca, Calliphora,* and *Drosophila*) and their key role in polarization vision was demonstrated by behavioral experiments with *Musca* (Fortini and Rubin, 1990; Hardie, 1984; von Philipsborn and Labhart, 1990). Except for the most marginal dorsal rim ommatidia of *Calliphora*, which seem to have poor focussing properties (Strausfeld and Wunderer, 1985), no optical specializations have been reported for the DRA of flies. Interestingly, the specialized ommatidia of most dipteran species were described before a functional explanation for their existence was available (Wada, 1974a,b). In this early study, the relative orientation of the microvilli of R7 and R8 was not assessed but the demonstrated size increase of the central rhabdomeres is as characteristic as it is in the better studied species (Strausfeld and Wunderer, 1985; Wunderer and Smola, 1982b). The small eye of the only nematoceran species of Diptera studied (*Psychoda cinerea*) contains only about 100 very short ommatidia. Although the dorsal ommatidia differ slightly from the ventral ones in rhabdom structure, both types are untwisted (Seifert et al., 1985).

Other Insect Orders

In three further insect orders, so far just one or two species have been tested for a specialized DRA. In the Blattodea, we found a well-developed DRA in the wood cockroach *Ectobius silvestris*, whereas in the German cockroach *Blattella germanica* all ommatidia are similar (Fig. 4). In *Ectobius,* dorsal rim rhabdoms are enlarged, appearing elongated rather than square or trapezoidal in cross-section, and they contain a set of six retinula cells that form two microvillar blocks with orthogonal microvilli orientations (in two further cells microvillar orientation is variable). In one heteropteran species (*Notonecta glauca*) and one neuropteran species (*Chrysopa sp.*) we did not find a specialized DRA (confirmed for *Notonecta* by Schwind, unpublished data).

DISCUSSION
Cases With Positive Evidence for a Specialized Dorsal Rim Area

Specialized dorsal rim areas (DRAs) in the compound eyes are widespread in the class Insecta. In five well-studied insect orders, the presence of a specialized DRA seems to be the rule. In the Blattodea and Coleoptera, at least some species exhibit specialized DRAs.

As argued above, histological evidence for a specialized DRA strongly suggests the ability of celestial polarization vision. It also indicates that e-vector detection follows the same principle in a wide range of insect orders: polarized skylight is analyzed exclusively by the dorsalmost ommatidia of the compound eye and seems to involve a polarization-opponent process, as suggested by the orthogonal microvilli orientation of the photoreceptors. We are aware that the histological evidence is no true replacement for the direct behavioral demonstration of e-vector detection. However, we are confident that a specialized DRA is quite a reliable indicator for polarization vision. In addition, compared to a proper behavioral study, the "DRA test" is not only economical but may in many cases be the only practicable approach.

Cases With Evidence Against a Specialized Dorsal Rim Area

In a number of species, we have found no histological indication for a specialized DRA. As elaborated below, negative findings have to be treated with care, as they are open to a number of different interpretations. First, the absence of specialized ommatidia could indicate that a species is unable to perceive skylight polarization. This conclusion seems plausible if one compares the two cockroach species studied. Whereas characteristic dorsal rim ommatidia are present in the outdoor-living *Ectobius silvestris*, we have found no such specializations in the house-dwelling *Blattella germanica*. On the other hand, it seems strange that the June bug *Amphimallon solstitiale* should lack polarization vision while the cockchafer *Melolontha melolontha* is equipped with a marked DRA since both of these closely related beetles (Melolonthinae) fly at dusk when sky polarization is most prominent. An alternative interpretation of negative histological evidence is that strong, histologically detectable specializations of dorsal rim ommatidia may not always be necessary for polarized skylight detection. As long as the regular ommatidia contain photoreceptors with orthogonal microvilli that are reasonably aligned within each rhabdom, they may well be suitable for polarization vision. The difference between the polarization detecting and the form or color sensitive eye parts may just reside in the spectral properties of the retinula (monochromacy vs. polychromacy) and in the synaptic organization in the optic lobe (antagonism vs. summation of signals from different tuning types of receptor), both of which are undetectable in histological sections. In addition, the challenging task of assessing the exact degree of microvillar alignment in the DRA, as compared to other eye regions, has only been undertaken in a few species (*Gryllus, Apis, Cataglyphis, Calliphora*), and the presence of specialized ommatidia may have simply been overlooked in other species. Such cases may be the buprestid beetle *Melanophila accuminata* and the tenebrionid *Parazistopus armaticeps*. Histologically, both species contain just one kind of untwisted ommatidium in their eye, although for *Parazistopus* there is behavioral evidence for e-vector navigation (Bisch, 1999). On the other hand, in several species the enhanced polarization sensitivity of the dorsal rim photoreceptors can easily be appraised by just comparing the gross shapes of the rhabdoms. Both strongly lobed (e.g., in *Melolontha*) and very long (e.g., in *Sympetrum*) rhabdoms prohibit useful polarization sensitivity, as opposed to the short and compact rhabdoms of the DRA. A third way to interpret the absence of an anatomically distinct DRA is that obvious anatomical specializations can only be expected if such an eye region is used exclusively for polarization vision.
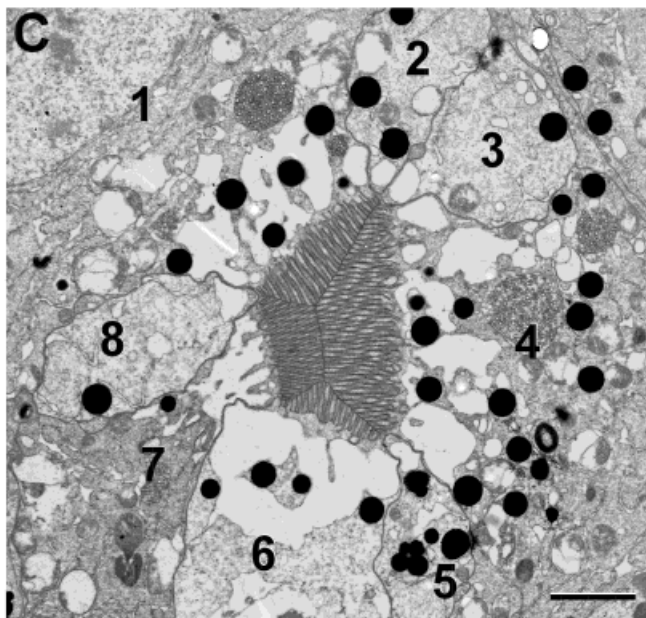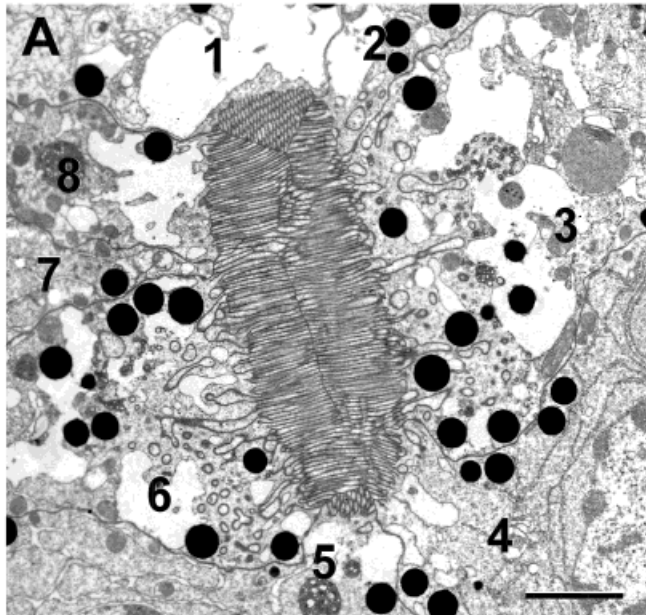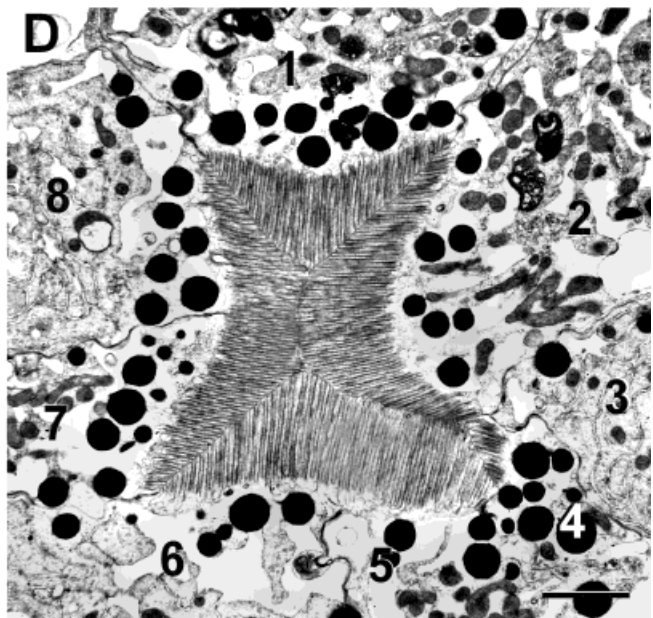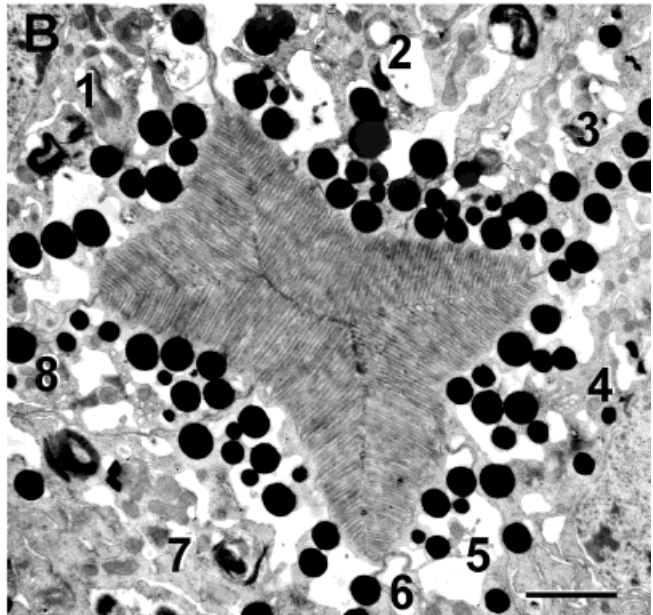
Ectobius (Blattodea)

Blattella (Blattodea)

Fig. 4. Comparison between ommatidia in the dorsal area and ommatidia in the dorsal rim area (DRA) of the compound eyes of two cockroach species (Blattodea). Electron micrographs of cross-sections through the retinula. Top (**A,B**) dorsal rim area, Bottom (**C,D**) dorsal area. Left (**A,C**) Wood cockroach *Ectobius silvestris*: The rhabdoms of the DRA (A) are characteristically elongated with the microvilli of receptor 1 orthogonal to those of receptors 2, 3, 6, 7, and 8 (microvilli orientation in R4 and R5 is variable). Right (B, D) German cockroach *Blattella germanica*: The rhabdoms of the DRA have the same shape as those of the dorsal area. Calibration bars = 2 μm

The conspicuous specializations would not be possible if the DRA also served spatial vision and/or color vision. The lack of any obvious DRA could, thus, also result from form and color vision being too important to be sacrificed in this part of the eye. Conversely, polarization sensitivity may not be restricted to the dorsalmost part of the eye. In this context, it is interesting to note that certain tabanid flies (Tabanidae, Diptera) have untwisted central rhabdomeres with well-aligned microvilli in the whole eye (Smith and Butler, 1991). Apart from celestial orientation, polarization vision has been shown to aid the detection of objects such as prey

organisms or bodies of water (e.g., Schwind, 1991; Shashar et al., 1998; Wildermuth, 1998).

Evolution of Polarized Skylight Detection

Although the dorsal rim ommatidia found in the representatives of different insect orders are functionally similar, they differ in detail. Based on the properties of the species presented in Figure 3, we will consider these differences in the following. (1) Although homochromatic in all cases studied, the spectral ranges within which skylight polarization is evaluated are different. Thus, polarization vision can either be medi-

ated by the blue-receptors (*Gryllus*), the green-receptors (*Melolontha*), or the UV-receptors (*Apis, Cataglyphis, Drosophila*). (2) The number of homochromatic photoreceptors representing the different (supposedly antagonistic) analyzer orientations ranges from 6/1 (*Melolontha*) to 1/1 (*Drosophila*). (3) The transition between regular and specialized ommatidia also differs strongly between species. For instance in *Sympetrum*, the regular dorsal rhabdoms are strongly lobed, contain three microvilli orientations, and are formed almost alone by four receptor cells. The dorsal rim rhabdoms have a compact shape with just two microvilli orientations and are formed by all but one of the eight retinula cells. Like in *Melolontha*, the conspicuous change of rhabdom shape serves to accommodate the two orthogonal microvilli orientations (Labhart et al., 1992). In contrast to *Sympetrum*, in *Gryllus* the number of rhabdomeres is decreased in the DRA. (4) Optical specializations (where present) include the degradation of the dioptric apparatus by deformation of the corneal lenses (*Sympetrum, Gryllus*), induction of a cataract-like turbidity in the cornea (*Melolontha, Apis*), and abandoning optical isolation between the retinulae (*Gryllus, Melolontha*).

Do the fine-structural differences between the dorsal rim ommatidia of the six insect species (Fig. 3) just represent differences between these species or are they characteristic for the whole taxonomic group to which these insects belong? More specifically, do at least some of the characteristic traits of each species also appear in other families of its order? In the Odonata (represented by *Sympetrum* in Fig. 3), the dorsal rim rhabdoms were found to be untiered, i.e., formed at all levels by the same seven receptor cells, in all families studied, in contrast to the regular, typically tiered rhabdoms. In the Orthoptera (see *Gryllus* in Fig. 3), reduction or loss of corneal facetting and pigment screen and the inactivation of receptors R3 and R4 were regularly observed. Blue-sensitivity was found in two different caeliferan families (*Gryllus*, Gryllidae; *Schistocerca*, Acrididae). In the hymenopteran suborder Apocrita, dorsal rim retinulae with nine long receptor cells seem to be the rule (see *Apis* in Fig. 3), however excluding the ant *Cataglyphis* (Formicoidea), which shows a different pattern (see Fig. 3). UV-sensitivity is common to bees (*Apis*, Apidae) and ants (*Cataglyphis*, Formicidae). The open rhabdom, a typical feature of the Diptera, is retained in the DRA and shows the characteristic increase of the central rhabdomeres in all of the many brachyceran families studied. As shown in representatives of three families (*Musca*, Muscidae; *Calliphora*, Calliphoridae; *Drosophila*, Drosophilidae), UV-sensitivity seems to be typical in the flies. Although similar rules for the fine structure of the dorsal rim ommatidia might exist in other groups, they could not be established for the Coleoptera, the Lepidoptera, and the Formicoidea (Hymenoptera) since the DRAs of most species in these groups have not been studied in sufficient detail.

Our analysis shows that there are indeed group-specific fine-structural differences in the design of dorsal rim ommatidia. The range of morphological solutions suggests that the ability to exploit skylight polarization for navigation has developed independently in different insect groups. The mechanism of polarization-opponency seems to be powerful enough to arise in all (of the well-studied) insect orders. Thus, the phylogenetically primitive dragonflies and damselflies (Odonata) use principally the same mechanisms for e-vector detection as the comparatively young group of the flies (Diptera), but precisely how these mechanisms are implemented depends on the basic *bauplan* of the ommatidium of each group.

Microvillar photoreceptors are inherently polarization-sensitive: even if the visual pigment molecules were not aligned but randomly oriented with respect to the microvillus axis, a polarization sensitivity of almost 2 would result just because of the cylindrical shape of the microvilli (form dichroism) (Laughlin et al., 1975; Moody and Parriss, 1961). Therefore, even primitive microvillar photoreceptors possibly lacking visual pigment alignment were preadapted to serve e-vector detection. Thus, although microvillar photoreceptors with their inherent polarization sensitivity are common to all arthropods, the development of specialized e-vector-detecting organs seems to be polyphyletic.

ACKNOWLEDGMENTS

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