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# Dimensional limits for arthropod eyes with superposition optics

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## Abstract

An essential feature of the superposition type of compound eye is the presence of a wide zone, which is transparent and devoid of pigment and interposed between the distal array of dioptric elements and the proximally placed photoreceptive layer. Parallel rays, collected by many lenses, must (through reflection or refraction) cross this transparent clear-zone in such a way that they become focused on one receptor. Superposition depends mostly on diameter and curvature of the cornea, size and shape of the crystalline cone, lens cylinder properties of cornea and cone, dimensions of the receptor cells, and width of the clear-zone. We examined the role of the latter by geometrical, geometric-optical, and anatomical measurements and concluded that a minimal size exists, below which effective superposition can no longer occur. For an eye of a given size, it is not possible to increase the width of the clear-zone  $cz = d_{cz}/R_1$  and decrease  $R_2$  (i.e., the radius of curvature of the distal retinal surface) and/or  $c = d_c/R_1$  without reaching a limit. In the equations ‘ $c$ ’ is the width of the clear-zone  $d_{cz}$  relative to the radius  $R_1$  of the eye and  $c$  is the length of the cornea-cone unit relative to  $R_1$ . Our results provide one explanation as to why apposition eyes exist in very small scarabaeid beetles, when generally the taxon Scarabaeoidea is characterized by the presence of superposition eyes. The results may also provide the answer for the puzzle why juveniles or the young of species, in which the adults possess superposition (= clear-zone) eyes, frequently bear eyes that do not contain a clear zone, but resemble apposition eyes. The eyes of the young and immature specimens may simply be too small to permit superposition to occur.

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## 1. Introduction

There are three basic types of compound eye in arthropods (Land, 1981): (i) the apposition eye, in which light from the small field of view of a single ommatidial lens (facet) is received by the retinula cells of that same ommatidium. (ii) The superposition eye, in which a parallel beam of light entering through many facets combines to form an erect image on the photoreceptor layer. (iii) The neural superposition eye, in which light from a parallel beam of light stimulates different receptors in adjacent ommatidia.

Ever since Grenacher (1879) and Exner (1891) anatomically examined and compared the compound eyes

of numerous species of crustaceans and insects more than a 100 years ago, it was the superposition eye (re-named “clear-zone eye” by Horridge in 1975 to avoid any premature functional interpretation) that became associated with a nocturnal life style and certain arthropod taxa. This type of eye is generally seen as a characteristic and typical feature of the Euphausiacea, Mysidacea, and Natantia as well as Reptantia, some anomurans, shrimps, and syncarids amongst the malacostracan crustaceans (Land, 1981; Nilsson, 1990) and scarab beetles (Caveney, 1986) as well as skipper butterflies (Horridge, Giddings, & Stange, 1972), fireflies (Horridge, 1969), mayflies (Zimmer, 1897), sphingid, noctuid, and other moths (Yagi & Koyama, 1963) amongst the insects.

There is good reason to believe that the presence of a clear-zone can improve an eye’s overall sensitivity to light. Migratory movements of screening pigments in and out of the clear-zone and simultaneous

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electrophysiological recordings of an eye's sensitivity to light (e.g., Bernhard & Ottoson, 1960; Meyer-Rochow & Horridge, 1975) have provided convincing evidence that a clear-zone devoid of screening pigments can improve sensitivity by up to three log units. The greater sensitivity of the proximally placed receptor cells in clear-zone eyes depends on the way the distally located dioptric structures channel light into the eye: the two main methods described involve (a) refraction in corneal lens cylinders and/or crystalline cones and (b) reflection of light from the vertical inner faces of crystalline cones that have square outlines (Land, 1981). With both methods (the latter favoured by crustaceans, the former by insects) the clear-zone allows light that has entered the eye through many facets to be focused on one single proximally-placed photoreceptor. In eyes without a clear-zone, like apposition eyes for instance, light that enters through one facet does not cross into neighbouring facets, but is perceived in the retinal cells of the same facet it entered.

In those relatively few cases in which clear-zone eyes are not developed in taxa in which they are expected to occur, a range of explanations for these exceptions has been offered. It has been suggested, for instance, that some immature malacostracan crustaceans possess apposition eyes, because ontogenetically an apposition eye, according to Richter (1999) representing the "archaic principle", precedes the clear-zone eye (Meyer-Rochow, 1975; Nilsson, Hallberg, & Elofsson, 1986). Alternatively, sometimes an absence of clear-zone eyes in taxa in which they are generally diagnostic has also been interpreted as a sign of erroneous taxonomic placement of a species or as an aberrant, degenerate, and isolated abnormality (Meyer-Rochow & Nilsson, 1999).

Inspired by an anatomical and ultrastructural comparison of eye organizations in 78 species of scarab beetles, covering a wide range of body (and eye) sizes (Gokan & Meyer-Rochow, 2000), we wondered whether dimensional limits (based on optical requirements) could be mathematically defined for the effectiveness of clear-zone eyes, if the latter were to function as significant improvers of photic sensitivity. In beetles of the family Scarabaeidae well-developed clear-zone eyes are the rule, but since the smallest species consistently appear to be those that lack a proper clear-zone in their eyes, we felt a functional rather than an ontogenetic or taxonomic reason could be behind this. Since only for the group of the scarab beetles a comparative study of eye anatomies involving a wide range of species existed, our raw data are based on the eyes of this taxon. However, the conclusions reached, are applicable to all kinds of clear-zone eyes anatomically resembling those of scarab beetles and operating on the principle of refraction optics, irrespective as to whether they function in water or air.

## 2. Materials and methods

In our model calculations we used an ideal superposition eye defined with the following features (for notations see Fig. 1A): (i) The eye consists of an array of identical and equally placed hexagonal facets with interommatidial angle  $\varphi$ . (ii) Only those ommatidia are involved in the gathering of light, the angular distance of which is not greater than  $\gamma$ , and it is these and only these ommatidia that focus all the incident rays of light (without any loss of energy) onto the central rhabdom, defined as the rhabdom that belongs to the ommatidium looking into the direction of the light source. One consequence of this is that  $\gamma = \delta - 2\mu$  (Fig. 1A). The relationship between angle of incidence ( $\eta = \gamma/2$ ) and angle of refraction ( $\mu$ ) follows from the geometry and is:

$$\mu = \arctan[(R \cdot \sin \eta)/(1 - c - R \cdot \cos \eta)], \quad (1)$$

where  $c = d_c/R_1$  (length of the cornea-cone unit relative to  $R_1$ ), and  $R = R_2/R_1$  (radius of curvature of distal retinal surface relative to  $R_1$ ) are the geometrical parameters of the superposition eye represented, together with  $R_2$ , in Fig. 1A. (iii) Only the central rhabdom absorbs the focused light and no spread of light is possible between the neighbouring rhabdoms. The width of the clear-zone was determined from the geometry by the expression

$$\begin{aligned} d_{cz} &= R_2 \cdot \sin(\mu_{\max} + \gamma/2) / \sin \mu_{\max} - R_2 \\ &= R_2 \cdot (\sin \delta/2) / \sin \mu_{\max} - R_2 \\ &= R_2 \cdot (\sin \delta/2) / \sin(\delta/2 - \gamma/2) - R_2. \end{aligned} \quad (2)$$

For derivation of Eq. (2), please see Appendix A.

In Eq. (2)  $\mu_{\max}$  is the maximal possible  $\mu$  refracting angle of the cornea-cone optical system. This expression allows us to calculate the smallest possible clear-zone size  $cz_{\min}$  for a given eye. The value of  $cz_{\min}$  was obtained from  $\mu_{\max}$  and  $\gamma$  in the following way: (i) The maximum angle of refraction  $\mu_{\max}$  usually ranges between  $15^\circ$  and  $30^\circ$  (for example in *Anoplagnathus pallidicollis*  $20^\circ$ – $24^\circ$ : Meyer-Rochow & Horridge, 1975 or in *Onitis westermanni*  $17^\circ$ : McIntyre & Caveney, 1998). (ii) According to the definition of a superposition eye  $\gamma \geq 2 \cdot \varphi$ , that is at least seven facets (a hexagonal arrangement is assumed) should be involved in image formation. If this requirement is not satisfied superposition is not possible. (iii) Using (i) and (ii) together with the expression of  $d_{cz}$ , one can calculate the minimal relative clear-zone width  $cz_{\min} = d_{cz}(\mu_{\max}, \gamma = 2 \cdot \varphi)/R_1$  for a given  $R_2/R_1$  ratio. The  $\delta(\gamma)$  relationship could also be obtained from expression (2) using  $R_2 = R_1 - d_c - d_{cz}$  (Fig. 1).

Although superposition eyes are, indeed, optimized for extended light sources, in our ideal model superposition eye the light intensity present at the central receptor was calculated as a function of given geometrical parameters of an eye, which is looking at a point

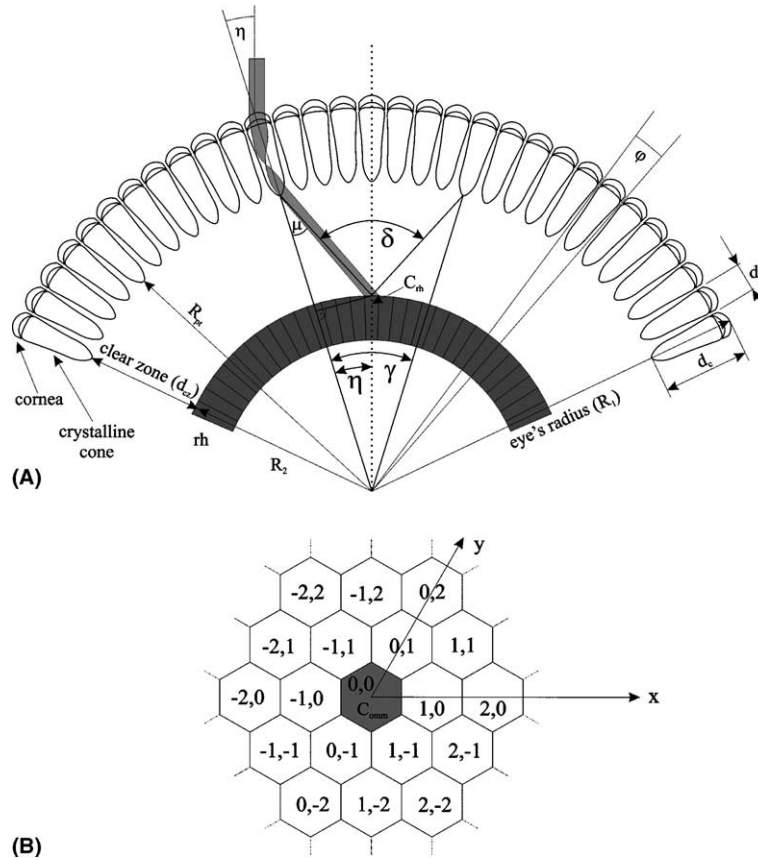


Fig. 1. Schematic drawing of our model superposition eye (A) and abbreviations of the main anatomical parameters: rh, rhabdom layer; C<sub>rh</sub>, central rhabdom (which belongs to the ommatidium looking in the direction of the light source); R<sub>1</sub>, the eye's radius; R<sub>2</sub>, radius of curvature of the distal retinal surface; R<sub>pt</sub>, radius of curvature of the surface formed by the proximal tips of cones; d, diameter of corneal facet; d<sub>c</sub>, length of the cornea-cone optical system; d<sub>cz</sub>, width of clear zone; γ, angular field of view of light gathered by C<sub>rh</sub>, measured from the centre of the eye; δ, receptor acceptance angle of light gathered by C<sub>rh</sub>, measured from the central rhabdom; φ, interommatidial angle; η, angle between the incident light and the optical axis of the ommatidium; μ, angle between the refracted light and the optical axis of the ommatidium. (B) The coordinate system used to describe the position of the facets. The ommatidium looking in the direction of the light source is the central ommatidium C<sub>omm</sub>.

source of light at infinity (this means parallel incident beams of light). If the maximal light collecting ability of a superposition eye needs to be optimized for the maximum amount of light collected by the optical system, then parallel rays of light should be considered (parallel rays of light are optically equivalent to a point source at infinity). Once the optical system (as in the superposition optics) collects the maximally possible intensity from a parallel beam of light, the eye itself will also be optimized for extended light sources, because extended light sources can be considered to represent superposition (in a physical sense) of point sources of light of the extended object: Huygens' principle, cf. website (<http://id.mind.net/~zona/mstm/physics/waves/propagation/huygens4.html>). Light energy focused onto the central rhabdom in the model eye that we use is equal to the sum of light energies *e* of illumination, entering the individual corneal facets that are within the angle γ

$$E(\gamma) = \sum e(x, y),$$

where (x, y) are the coordinates of facets within the angle γ.

The coordinate system shown in Fig. 1B was used to describe the position of a given facet in the eye. The illuminating energy of a given facet at the position (x, y) is

$$e(x, y) = e_o \cdot \cos \Theta(x, y)$$

where *e<sub>o</sub>* is the illuminating energy entering the central ommatidium,  $\Theta(x, y) = \varphi \cdot \sqrt{(x^2 + y^2 + x \cdot y)}$  is the angular distance of the facet from the origin, and φ is the interommatidial angle of the eye (Fig. 1). This allows us now to define the intensity enhancement factor *G* (further on referred to as 'gain') as follows:  $E(\gamma)/e_o = G(\gamma)$ . Using expression of *d<sub>cz</sub>*, one can calculate the relative clear-zone width  $cz_G = d_{cz}(\mu_{max}, \gamma = [G(\gamma)]^{-1})/R_1$  for a given *G*.

### 3. Results

To form a perfect image in a spherically symmetrical refractive superposition eye the following conditions must be met: there has to be an accurate and repetitive

geometrical arrangement of the anatomical units and there has to be an appropriate light-refracting ability of the cornea-cone optical system. Together they form the basis for the relationship (see Section 2) between angle of incidence  $\eta$  and angle of refraction  $\mu$ . The simple linear relationship between  $\mu$  and  $\eta$  (called Exner's line by Horridge, 1975) is applicable only for small angles, i.e.,  $\gamma = 0^\circ$ – $10^\circ$ . For the more distal, off-axis angles less light-bending than is predicted by Exner's line is needed. The relationship between  $\eta$  and  $\mu$ , calculated from Eq. (1), depends on  $R$  and  $c$  (Fig. 2). The cornea-cone optics in a superposition eye with a relatively weakly curved retina (i.e.,  $R = R_2/R_1$  is large) should bend the light rays more, because of the larger  $\mu$  at a given  $\eta$ , than in a superposition eye with a strongly curved retina (i.e.,  $R$  is small).

The main advantage of superposition vision when compared with the apposition mechanism, is the considerable enhancement of sensitivity through the gain in intensity of light focused on the retina. This intensity enhancement  $G$  in our model superposition eye can be calculated as a function of  $\gamma$  and the interommatidial angle  $\varphi$  (Fig. 3A). The radius  $R_1$  of an eye and the diameters  $d$  of its corneal facets determine the interommatidial angle through the relationship (cf., Fig. 1A):

$$\varphi = 2 \cdot \arcsin d / (2 \cdot R_1)$$

The interommatidial angle  $\varphi$  in scarab species investigated ranges between  $2^\circ$  (*Paraphytus dentifrons*) and  $7^\circ$  (*Euoniticellus africanus*). For a given  $\gamma$ , it follows that the smaller the interommatidial angle the more facets become involved in collecting the light. Thus, compared with an eye of similar size, but operating with the apposition mechanism, an increasing number of rays can be focused on the central receptor. In Table 1 numerical values are shown for relative intensity enhancements of  $G = 10$ ,  $G = 100$ ,  $G = 1000$  and  $G = 10000$  (cf. Fig. 3A).

The larger the  $\gamma$ , the greater the enhancement in intensity of the light focused onto the central receptor. However, for a larger  $\gamma$ , a larger receptor acceptance angle  $\delta$  is needed, and given a receptor acceptance angle of  $\delta$ , it holds true that the wider the clear-zone (i.e., the larger  $d_{cz}$ ), the wider  $\gamma$  of the eye.

Fig. 3B shows the dependence of  $\delta$  on  $\gamma$  for different relative clear-zone sizes ( $cz$ ), calculated for  $c = d_{cz}/R_1 = 0.2$ , which is the average value found in the scarab species studied in this paper ( $c$  varies from 0.11 up to 0.4). The average relative width of the clear-zone in the investigated species is  $cz = 0.2$  and ranges between 0 and 0.54. For example, in the eye of the small scarab *Eubrittoniella gestroi* (formerly known as *Ciphopisthes gestroi*: Ballerio, 2000) no clear-zone is present, i.e.,  $cz = d_{cz}/R_1 = 0$  (Fig. 4A), but the much larger scarab species *Anoplagnathus pallidicollis* and *Onitis vanderkelleni* possess eyes with much bigger clear-zones, i.e.,  $cz = 0.36$  and  $cz = 0.54$ , respectively (Fig. 4B).

The results of our calculation concern any kind of spherically symmetrical refracting superposition eye, but in this paper the model was applied only to forms within the taxon Scarabeoidea, and more specifically to 31 scarab species listed in Table 2, for which complete anatomical data were available. The width  $d_{cz}$  of the clear-zone in the eyes of scarab beetles shows a positive correlation with body length (Fig. 5). Although this correlation does not necessarily prove the existence of an exact linear dependence between  $d_{cz}$  and body size, it is nonetheless obvious from Fig. 5 that the width of the clear-zone in crepusco-nocturnal *Onitis* species depends more steeply on body size than in diurnal, crepuscular or nocturnal scarab species. Scarab beetles without any proper clear-zone present in their eyes may be active in daytime (e.g. *Aesalus asiaticus*) or at night (e.g. *Eubrittoniella gestroi*), but they are generally small-sized species ( $\leq 10$  mm, cf. points on abscissa in Fig. 5).

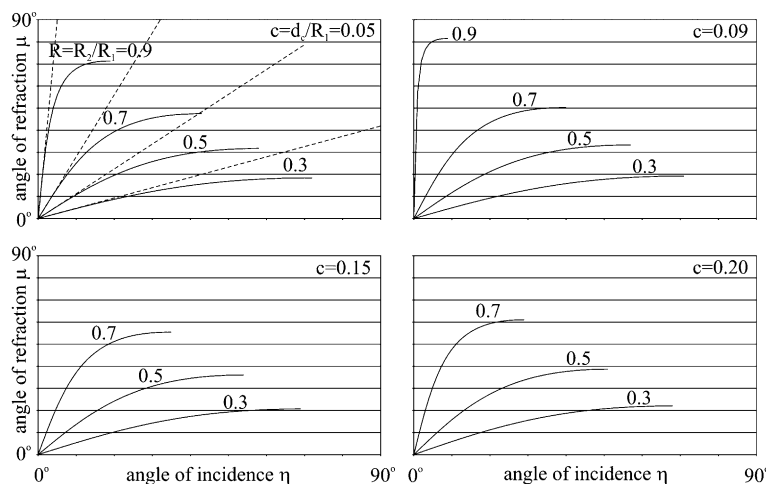


Fig. 2. Relationship between angle of incidence and angle of refraction for different values of the geometrical parameters  $c = d_{cz}/r_1$  and  $R = R_2/R_1$  of the model superposition eye, calculated from Eq. (1). The dashed lines correspond to Exner's line defined by  $\mu/\eta \ll 1$ . Abbreviations as in Fig. 1.

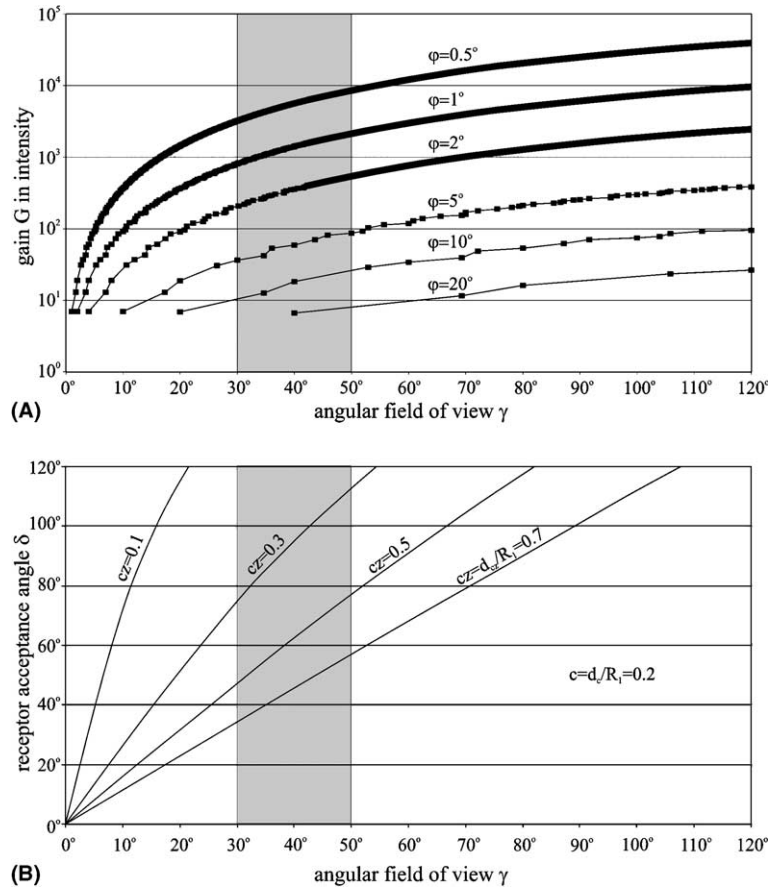


Fig. 3. Graph of maximum possible superposition gain  $G$  in light intensity on the receptor central to the incident parallel beam of light relative to that of an apposition eye as a function of  $\gamma$  for different interommatidial angles  $\phi$  (A). The relationship between  $\gamma$  and  $\delta$ , calculated for different relative clear-zone sizes  $cz$  in the superposition eye (B). The interval of  $\gamma$ -values typically occurring in superposition eyes is shaded in grey. Notations as in Fig. 1.

Table 1

The minimal values of  $\gamma_{\min}$  required to reach a given gain  $G$  in light intensity of an ideal superposition model eye relative to the intensity collected by a single facet

$G$	$\phi(N)$						
	20°	15°	10°	5°	2°	1°	0.5°
10	69° (13)	52° (13)	35° (13)	17° (13)	7° (13)	3° (13)	2° (13)
100	–	–	122° (139)	53° (109)	21° (109)	11° (109)	5° (109)
1000	–	–	–	–	70° (1111)	33° (1027)	17° (1003)
10000	–	–	–	–	–	123° (13 693)	54° (10 591)

In this ideal superposition model eye all rays of a parallel light beam passing through the eye under the angle of  $\gamma_{\min}$  are focused exactly onto a single photoreceptor. In brackets are the number of those facets  $N$  (corresponding to  $\gamma_{\min}$ ), which should contribute to the collecting of light rays in order to obtain a given gain, calculated for different values of the interommatidial angle  $\phi$ . Although no scarab beetle in our collection had even close to 10000 facets, the scarab *Polyphylla fullo* apparently has at least 12000 (Kahmann, 1947).

The width  $d_{cz}$  of the clear-zone in the investigated scarab species appears to exhibit a linear dependence on relative clear-zone width  $cz = d_{cz}/R_1$  (with linear regression square 0.7; Fig. 6). Nocturnal or crepuscular species, which are active in dimmer light conditions than the diurnal species, have larger clear zones than the exclusively diurnal or crepuscular species.

However, the narrower the clear zone (i.e., the smaller the  $d_{cz}$ ), the smaller its relative width 'CZ' in the eye, suggesting that other elements of the eye (for example, the photoreceptive cells and their rhabdoms) become more prominent at the expense of the clear-zone. The narrowest clear zone with  $d_{cz} = 38 \mu\text{m}$  in the investigated species belongs to the diurnal *Ochodaeus*

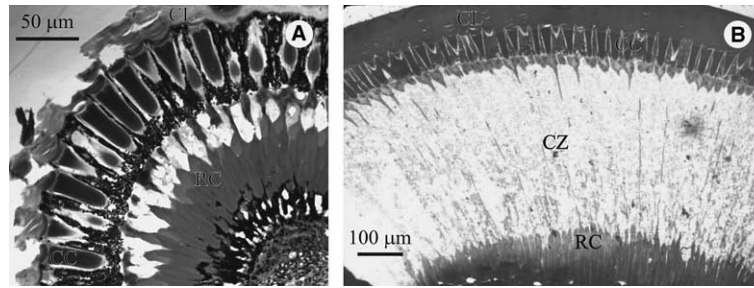


Fig. 4. Light micrographs of longitudinal sections through the eyes of two species of scarab beetles of very different body size: the eye of *Eubrittoniella gestroi* (body length: 3.5 mm) without a clear-zone (A) and *Anoplognathus pallidicollis* (body length: 27 mm) with a wide clear-zone (B). Abbreviations used: CC, corneal cones; CL, corneal lenses; and CZ, clear-zone; retinula cells.

Table 2  
Anatomical parameters of various scarab beetle eyes

Species	Body length (mm)	$R_1$ ( $\mu\text{m}$ )	$d_{\text{cz}}$ ( $\mu\text{m}$ )	Activity	Reference
<i>Eubrittoniella gestroi</i>	3.5	245	0	N	This paper
<i>Paraphytus dentifrons</i>	5	182	0	N	This paper
<i>Aesalus asiaticus</i>	5	184	0	D	Gokan, Meyer-Rochow, Nakazawa, and Iida (1998)
<i>Trox mitis</i>	5.5	336	57	D	Gokan, Meyer-Rochow, and Nagashima (1987)
<i>Paraserica grisea</i>	8	246	0	C	Gokan (1982b)
<i>Maladera orientalis</i>	8	301	0	C	Gokan (1982b)
<i>Serica nigrovariata</i>	8	250	55	D	Gokan, Nagashima, and Meyer-Rochow (1987)
<i>Serica takagii</i>	8	250	55	C	Gokan et al. (1987)
<i>Sericesthis geminata</i>	8.5	800	175	C	Meyer-Rochow (1977)
<i>Nicagus japonicus</i>	9	284	64	D	Gokan and Masuda (1998)
<i>Ochodaeus maculatus</i>	9	309	38	D	Gokan (1989a)
<i>Euoniticellus africanus</i>	9	980	120	D	Meyer-Rochow (1978)
<i>Platycerus acuticollis</i>	10	219	0	D	Gokan et al. (1998)
<i>Onitis ion</i>	13	480	118	D	McIntyre and Caveney (1998)
<i>Onitis westermanni</i>	14	600	162	NC	McIntyre and Caveney (1998)
<i>Anomala rufocuprea</i>	14.5	559	121	D	Gokan (1982a)
<i>Onitis alexis</i>	15	750	280	NC	McIntyre and Caveney (1998)
<i>Figulus boninensis</i>	17	627	59	N	Gokan et al. (1998)
<i>Onitis caffer</i>	17	800	415	NC	McIntyre and Caveney (1998)
<i>Geotrupes auratus</i>	19	710	127	D	Gokan (1989b)
<i>Onitis pecuarius</i>	19	925	360	NC	McIntyre and Caveney (1998)
<i>Onitis tortuosus</i>	19	1011	425	NC	McIntyre and Caveney (1998)
<i>Onitis vanderkelleni</i>	20	850	460	NC	McIntyre and Caveney (1998)
<i>Onitis aygulus</i>	21	1000	447	NC	McIntyre and Caveney (1998)
<i>Onitis belial</i>	21.5	676	180	D	McIntyre and Caveney (1998)
<i>Lucanus gamunus</i>	25	845	111	D	Gokan et al. (1998)
<i>Anoplognathus pallidicollis</i>	27	950	340	N	Meyer-Rochow and Horridge (1975)
<i>Nipponodorcus rubrofemoratus</i>	30	788	123	C	Gokan et al. (1998)
<i>Lucanus maculifemoratus</i>	30	800	231	C	Gokan et al. (1998)
<i>Prosopocoilus inclinatus</i>	34	886	241	C	Gokan, Nagashima, and Narita (1986)
<i>Aceraius grandis</i>	45	1202	255	N	Gokan and Meyer-Rochow (2000)

$R_1$  = eye radius;  $d_{\text{cz}}$  = absolute clear-zone width; C = crepuscular; D = diurnal and N = nocturnal.

*maculatus*, (body size: 9 mm) and the widest with  $d_{\text{cz}} = 460 \mu\text{m}$  to the crepusco-nocturnal *Onitis vanderkelleni* (body size: 20 mm) (Figs. 5 and 6 and Table 2). As pointed out earlier (see above) the very smallest species of scarabs investigated, i.e., *Eubrittoniella gestroi*, *Paraphytus dentifrons*, and *Aesalus asiaticus* lacked clear-zones altogether.

The relative (CZ) and absolute ( $d_{\text{cz}}$ ) widths of the clear-zone and the radius  $R_1$  of curvature of the eyes in the investigated scarabs are summarized in Fig. 7. In diagrammatic form we also represent the minimal width  $d_{\text{cz, min}}$  of the clear-zone and its relative value  $\text{cz}_{\text{min}}$ , as well as the size of the clear-zone necessary for intensity gains of  $G = 100$  and  $G = 1000$ . Fig. 7A shows that

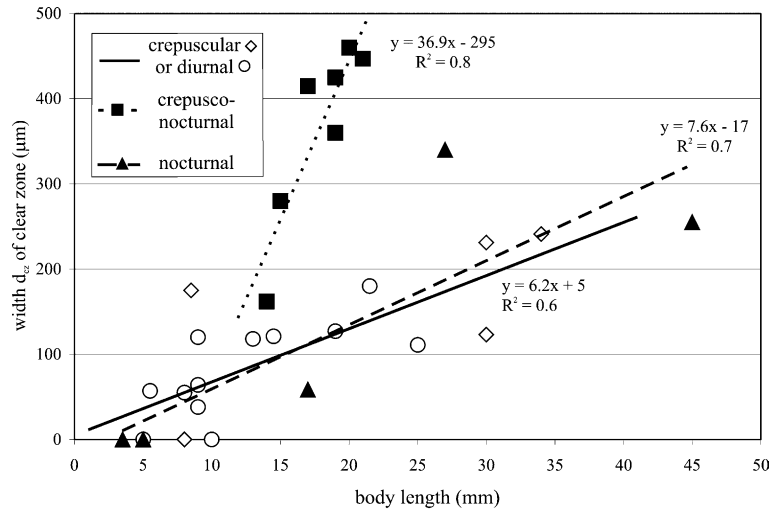


Fig. 5. Body lengths and clear-zone widths  $d_{cz}$  in the different scarab species investigated. The lines correspond to the best linear fit of the data points: crepuscular or diurnal species (continuous line with empty rhombi or circles), crepusco-nocturnal species (dotted line with black squares) and nocturnal species (dashed line with black triangles). Note, that the crepusco-nocturnal species all belong to species of the genus *Onitis*.

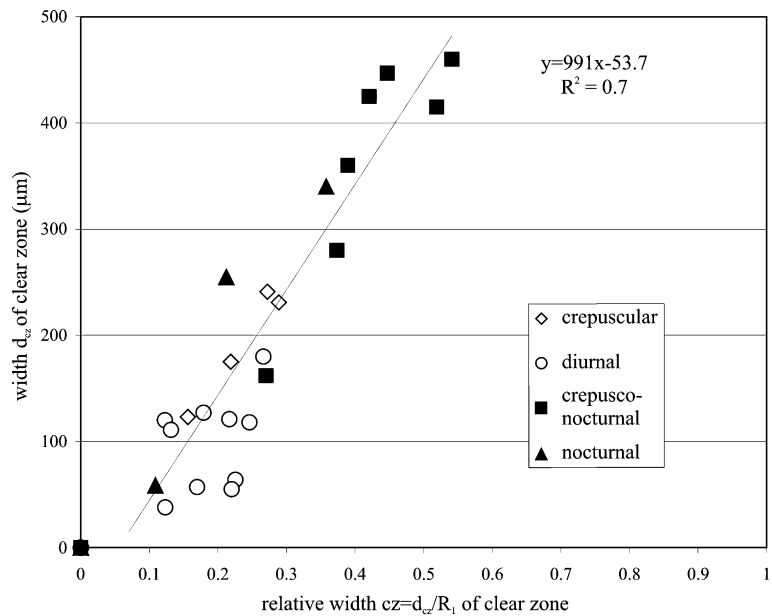


Fig. 6. Width  $d_{cz}$  of the clear-zone and *relative* clear-zone widths ( $cz = d_{cz}/R_1$ ) in the different scarab species investigated. Species without a clear-zone ( $d_{cz} = 0$ ) are located at the origin (left hand corner).

when  $cz_{min}$  is larger than 0.2, no clear-zone can be found in the eye. With an eye radius  $R_1$  smaller than about 250  $\mu\text{m}$ , little intensity enhancement is possible and the presence of a clear-zone would actually be counter-productive. If the eye radius  $R_1$  ranges between 250 and 350  $\mu\text{m}$ , a 100-fold intensity enhancement ( $G$ ) is theoretically possible, but does not seem to be realized in species representative of this size range. However, for  $R_1 > 650 \mu\text{m}$  there are some species, whose clear-zone width lies within the range of the  $G = 100$ -fold intensity gain. If the radius of the eye  $R_1$  exceeds 450  $\mu\text{m}$ , then a  $G = 1000$  fold intensity enhancement is theoretically

possible, but this appears to be realized only for some of the largest beetles with eye radii greater than about 800  $\mu\text{m}$  (Fig. 7B).

#### 4. Discussion

##### 4.1. The role of geometrical and optical parameters

For the formation of a perfect image by any spherically symmetrical refractive superposition eye, not only accurate geometrical arrangements of the anatomical

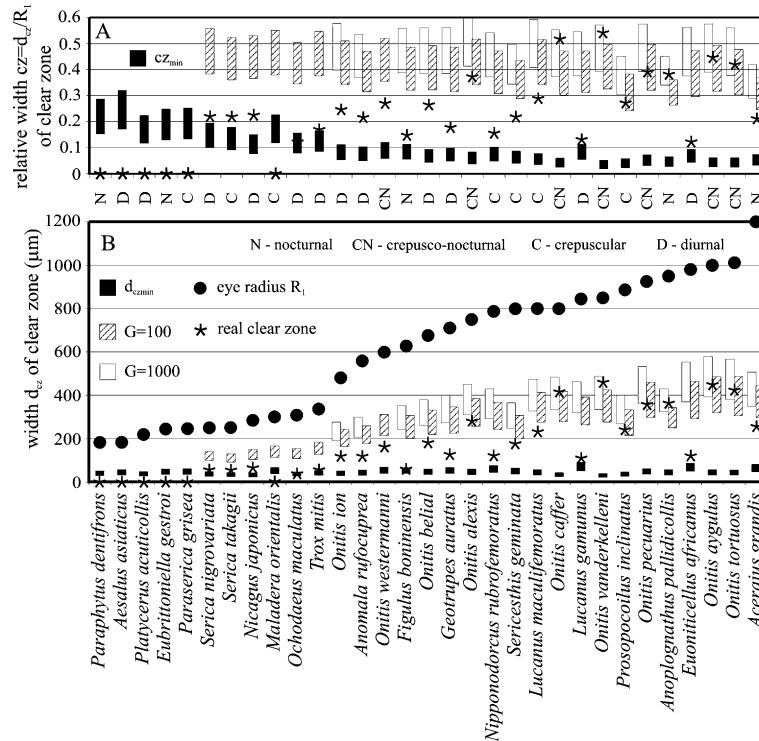


Fig. 7. Relative width  $cz = d_{cz}/R_1$  of clear-zone (A) and absolute width  $d_{cz}$  of clear-zone in  $\mu m$  (B) in different species of scarab beetles. The range of clear-zone widths needed for sensitivity gains  $G = 100$  (hatched bar) and  $G = 1000$  (white bar) to a point source of light in infinity (calculated for  $\mu_{max} = 15^\circ\text{--}30^\circ$ ) are compared with the real widths of the clear-zone (star) as well as with  $R_1$ , i.e., the radius of curvature of the eye surface (grey column). The minimal clear-zone width  $cz_{min}$  (definition see in text) is also indicated. The bottom ends of the hatched and white bars correspond to  $\mu_{max} = 30^\circ$ , while the top ends correspond to  $\mu_{max} = 15^\circ$ . In those species, in which hatched or white bars are not present,  $G = 100$  or  $1000$  sensitivity enhancements are not possible, because the eye is too small. Daily activity peaks of the species are indicated by assigning them to N, nocturnal; CN, crepusco-nocturnal; C, crepuscular and D, diurnal groups (abbreviations between graphs (A) and (B)).

units are required, but an appropriate light refracting ability of the cornea-cone optical system is equally essential. This can be expressed through the relationship between the incident angle  $\eta$  and the angle of refraction  $\mu$ . For small off-axis angles  $\eta$ ,  $\mu(\eta)$  could be approximated with a linear function (dashed lines in Fig. 2), whereas for larger off-axis angles  $\eta$  the real relationship deviates from the linear. If the geometrical surfaces (e.g., corneal surface, surface formed by the proximal tips of the cones, and the surface of the distal rhabdom) are not exactly concentrically arranged in a superposition eye, then the  $\mu(\eta)$  relationship will, of course, be different (Warrant, Bartsch, & Günther, 1999). Although slight disalignments in the position of the centre of the curvature were observed in the investigated scarab species, these disalignments are below the uncertainty level in the determination of the radius of curvature and although Warrant et al. (1999) observed considerable departures from spherical symmetry in the superposition eye of the hummingbird hawkmoth *Macroglossum stellatarum*—with far bigger eyes than most of the species studied by us—, the investigation of non-spherical superposition eyes is considered to be beyond the scope of this work.

A maximum refraction angle of  $15^\circ\text{--}30^\circ$ , which is the most probable range of  $\mu_{max}$  (Land, Burton, & Meyer-

Rochow, 1979; McIntyre & Caveney, 1985), was assumed, because for larger angles of refraction the optical aberrations are also larger, and for smaller  $\mu_{max}$  the light-collecting ability of the eye fails, i.e.,  $G$  decreases. From the lens cylinder model we know that  $\mu_{max} = \sqrt{1 - (n_{min}/n_{max})^2}$ , where  $n_{min}$  is the index of refraction at the periphery of the cone and  $n_{max}$  is the index of refraction in the centre of the cone (Saleh & Teich, 1991). If we use values like  $n_{min} = 1.35$ ,  $n_{max} = 1.55$ , which have been determined experimentally for insect eyes, including scarabs (cf. Meyer-Rochow, 1973, 1978; Meyer-Rochow & Horridge, 1975), then we obtain  $\mu_{max} = 28^\circ$ . Any focusing of the light beams due to much larger refractive angles is not likely to be possible with simple corneal-cone optical systems.

In order to obtain as intensive a light as possible, focused onto the central rhabdom of the eye, one requires as large a  $\gamma$  as possible. However, the larger the  $\gamma$ , the larger the receptor acceptance angle  $\delta$  (Figs. 1 and 3B), and therefore—although in superposition eyes of low  $F$ -numbers several different solutions are found to maintain incident light rays within the target rhabdom (Warrant & McIntyre, 1991)—the wider the  $\mu$ , the higher the chance of light spreading into the rhabdom layer. Greater spread and scattering of light in the



photoreceptor layer lead to a deterioration of image quality and a decrease in light absorption of the target rhabdom. This means that the animal should use the maximally possible  $\gamma$  combined with the smallest possible  $\delta$ . A compromise is achievable with a relatively wide clear-zone and smaller values of  $R_2$  and  $c = d_c/R_1$  (Fig. 3B).

The dimensions of the different components in the eyes, however, have a minimum limit beyond which these components cannot effectively function. Such limits exist for the corneal-cone optical system (limit of geometrical optics) as well as for the length of the rhabdoms (anatomical limit). We can estimate the minimal width  $d_c$  of the corneal cone unit using an approximation of the lens cylinder model (Saleh & Teich, 1991):  $d_c \geq \pi/2 \cdot d/\sqrt{1 - (n_{\min}/n_{\max})^2}$ . This gives us  $d_c \geq 32 \mu\text{m}$  (if we assume  $n_{\min} = 1.35$ ,  $n_{\max} = 1.55$  and a diameter of a facet in a superposition eye not much smaller than about  $10 \mu\text{m}$ ). It is also possible to estimate the smallest possible rhabdom length  $l_{\text{rh}}$  on the basis of the absorption expression (Warrant & McIntyre, 1993: relative absorption =  $1 - \exp(-k \cdot l_{\text{rh}})$ ). This describes a limit rhabdom length of  $l_{\text{rh}} \geq 16 \mu\text{m}$  assuming that  $k = 0.0067 \mu\text{m}^{-1}$  (Bruno, Barnes, & Goldsmith, 1977) and at least 10% of incident light is absorbed in the rhabdom (without any sheaths of reflective tapetal structures). For an eye with a given size, it is, therefore, not possible to increase  $\text{cz} = d_{\text{cz}}/R_1$  and decrease  $R_2$  and/or  $c = d_c/R_1$  without reaching a limit. On the other hand, the smaller the clear-zone width  $d_{\text{cz}}$ , the smaller its relative proportion  $\text{cz} = d_{\text{cz}}/R_1$  in the eye (Fig. 6) Rather than to increase the intensity of the collected light on the retina by increasing the width of the clear-zone at the expense of the size of other organs, it appears to be more important to retain the functionality of the different components of the eye (those, for instance, involved in focusing, absorbing, and/or perceiving the light).

#### 4.2. Applicability of the model superposition eye

Although the relative sizes  $\text{cz}$  of the clear-zones in all of the investigated species (with clear zones of non-zero width) are larger than  $\text{cz}_{\min}$  predicted by our model (Fig. 7), the approximations used in our model eye may have led to some differences between reality and model. In our calculations of  $\text{cz}_{\min}$  and  $\text{cz}$  for different  $G$ -values we assumed that the cornea-cone optical system of every facet focused light from the incident parallel beam of light onto the central ommatidium. In reality, due to imperfect geometry and optics, the presence of screening pigments, scattering and spread of light in the eye as well as lack of 100% absorption of light by the photoreceptors, all of these decrease the light energy absorbed by the target rhabdom (Warrant & McIntyre, 1991). Therefore the value of  $d_{\text{cz}}$  should be somewhat higher than the one our model predicts. For example, in *Onitis*

*alexis*, as estimated by Warrant and McIntyre (1993), probably more than 90% of the light intended for the central rhabdom from a point source is absorbed by its neighbours. Yet, the intensity enhancement factor  $G$  in *Anoplagnathus pallidicollis*, in agreement with our calculation, lies within the 1000-fold range (Fig. 7). This improvement in absolute sensitivity, measured electrophysiologically through intracellular recordings by Meyer-Rochow and Horridge (1975), and the value predicted by our calculations are, thus, remarkably congruent and this demonstrates that our superposition model eye can, indeed, serve as a reliable approximation of the situation in real eyes of this kind.

Applying our model to the reflection type of superposition eyes is not immediately possible, because in such eyes the light through the aperture of the central cone will tend to follow a straight pass without any reflection (Land, 1976). Such rays will not be focused on the central rhabdom (e.g. crayfish; Bryceson & McIntyre, 1983) and therefore the criterion (ii) described in Section 2 is not satisfied. However, considering clear-zone widths (that is  $\text{cz}_{\min}$ ,  $\text{cz}$ ), one can predict that sensitivity gains of  $G = 100$  and  $1000$  in a reflection superposition eye with similar geometry than those resulting from the model presented, require wider clear-zones. This may explain, why eyes based on superposition by reflection are generally larger than those based on refraction.

A concentric and matched arrangement of the corneal lenses, crystalline cones, and rhabdoms is also one of the prerequisites of our model. Eyes of some species with superposition optics (e.g., some deep-water Euphausiids: Land et al., 1979 or the hummingbird hawkmoth: Warrant et al., 1999) do not have these concentric features. To cover also such cases, modifications to the model presented here are needed. Finally, we need to stress that only fully dark-adapted states were considered in our calculations. During the day and following an exposure to light many superposition eyes react with screening pigment migrations, changes in cell shapes, the creation of narrow light-guides and crystalline threads (cf. review by Meyer-Rochow, 1999), all of which would preclude the use of our calculations on sensitivity enhancements.

In a given superposition eye a clear-zone less wide than that, which is predicted by our model, is theoretically also possible. However, in such a case the superposition mechanism would not convey any advantage over apposition optics for an animal, considering enhancement of its light-gathering capacity. Our findings are not in conflict with the view that superposition eyes have evolved only in certain taxa and are characteristic for such taxa. What our results suggest is that smaller species of the aforesaid taxa (e.g., scarabaeid beetles) with less space for their eyes on the surface of the head would have little or no advantage from possessing a clear-zone and, therefore, have secondarily lost

the clear-zone feature. That this is a greater problem for insects than crustaceans, stems from the fact that the latter bear their eyes on stalks, but the former have to find space for them on their heads.

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We are grateful to Prof. Nobuo Gokan for having provided specimens of *Eubrittoniella gestroi* and *Paraphytus dentifrons* and Dr. Marina Bobkova for the preparation of ultrathin sections of the eyes of these species. Useful comments and suggestions by the reviewers helped us improve the paper.

## Appendix A

(Derivation of Eq. (2))

From Fig. 1 it is obvious, that

$$\tan \frac{\delta}{2} = \frac{(R_2 + d_{cz}) \cdot \sin \left(\frac{\gamma}{2}\right)}{(R_2 + d_{cz}) \cdot \cos \left(\frac{\gamma}{2}\right) - R_2}$$

and therefore

$$\begin{aligned} \tan \frac{\delta}{2} R_2 \cos \frac{\gamma}{2} + \tan \frac{\delta}{2} d_{cz} \cos \frac{\gamma}{2} - \tan \frac{\delta}{2} R_2 \\ = R_2 \sin \frac{\gamma}{2} + d_{cz} \sin \frac{\gamma}{2} \end{aligned}$$

$$\begin{aligned} d_{cz} \left( \tan \frac{\delta}{2} \cdot \cos \frac{\gamma}{2} - \sin \frac{\gamma}{2} \right) \\ = R_2 \left( \sin \frac{\gamma}{2} + \tan \frac{\delta}{2} - \tan \frac{\delta}{2} \cdot \cos \frac{\gamma}{2} \right) \end{aligned}$$

$$\begin{aligned} d_{cz} \left( \sin \frac{\delta}{2} \cdot \cos \frac{\gamma}{2} - \cos \frac{\delta}{2} \cdot \sin \frac{\gamma}{2} \right) \\ = R_2 \left( \cos \frac{\delta}{2} \cdot \sin \frac{\gamma}{2} + \sin \frac{\delta}{2} - \sin \frac{\delta}{2} \cdot \cos \frac{\gamma}{2} \right) \end{aligned}$$

$$d_{cz} = R_2 \frac{\sin \left(\frac{\delta}{2}\right) - \sin \left(\frac{\delta}{2} - \frac{\gamma}{2}\right)}{\sin \left(\frac{\delta}{2} - \frac{\gamma}{2}\right)} = R_2 \frac{\sin \left(\frac{\delta}{2}\right)}{\sin(\mu_{\max})} - R_2$$

because  $\frac{\delta}{2} - \frac{\gamma}{2} = \mu_{\max}$ .

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