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Solar-absorber antireflector on the eye of an Eocene fly (45 Ma)

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Antireflection structures on eyes potentially increase visual efficiency through increased photon capture for a given stimulus condition. We report an unusual surface grating on the compound eyes of an Eocene dolichopodid dipteran (45 Ma) known only from Baltic amber. By measuring the reflective properties of a flat model of this grating constructed from material of appropriate refractive index we show that this 'fly eye grating' is an efficient antireflector of white light at angles up to 60°, and a relatively good antireflector for angles beyond 60°. We calculate that such a grating would be particularly useful on a curved corneal surface as it would increase the transmission of incident light through the cornea compared with a smooth surface. This structure is also reported on the curved regions of the corneas of at least two extant dipterans. We argue that this grating probably derives from the previously described moth eye antireflection structure, which we also report here to occur in a silverfish, a 'primitive' insect. The fly eye grating is a more efficient antireflector than the moth eye structure only at angles greater than about 10° from the surface normal. A comparable antireflector is employed on solar absorbers.

Keywords: antireflector; grating; solar absorber; fly; eye; amber

1. INTRODUCTION

In addition to colour pigment cells (e.g. Voigt 1935), metallic colours have been found in fossilized animals (e.g. Towe & Harper 1966; Wuttke 1992). Some of these involve diffraction gratings consisting of periodic, parallel ridges with spacings greater than or equal to the wavelength of human visible light (comparable with diffraction gratings in extant animals (e.g. Parker 1995)). The effect on light waves of smaller ('sub-wavelength') structures in extinct animals has not been studied previously.

Most material surfaces cause considerable reflection of light. For example, we can clearly see reflections from a glass window-pane. A regular sub-wavelength structure formed on a given surface can significantly reduce reflection from that surface. Decreased reflection of white light results in more photons available for absorption as, for example, a stimulus for vision in eyes or a source of energy in solar absorbers.

There are three principal known types of antireflection structures. The first is widely observed on the corneas of some moths (Miller *et al.* 1966; Clapham & Hutley 1973). Here, antireflection results at the sub-wavelength structure formed by an array of protuberances, typically of about 200 nm height and spacing (Miller *et al.* 1966; Clapham & Hutley 1973). In generalized terms the structure is equivalent to a gradual change in refractive index between the material of the cornea and the air. The moth eye structure is now employed to reduce reflection from multiple glazed windows in Scandinavia, for example. An antireflector consisting of numerous thin layers is used on glass lenses, such as those of cameras. A third type of antireflector consists of parallel ridges with a rectangular profile and is employed on solar absorbers (Thornton 1975), where angle-independent antireflection properties are required. We report a structure comparable to the solar-absorber antireflector on the corneal surfaces of certain flies.

Many extinct insects have been preserved in amber in exceptional detail. The principal aim of this study was to test the reflection properties of the corneal surface of an Eocene dolichopodid dipteran (undetermined genus, see Mierzejewski (1976)), from Baltic amber (45 Ma). This species has particularly well-preserved eyes, showing possible antireflection structures. Extant dolichopodids are brilliantly coloured flies (Bernard 1971), and in addition to courtship and combat (Steyskal 1938, 1947), vision is an important factor in locating and catching prey (Bishop & Hart 1931). We also tested for comparable structures on the eyes of some extant insects, including (distant) 'relatives' of the above fossil.

2. MATERIALS AND METHODS

The corneal surfaces of six ommatidia from the Eocene fly were examined in the scanning electron microscope (SEM) after the amber matrix surrounding an eye was removed by polishing and levering (Mierzejewski 1976). The precise

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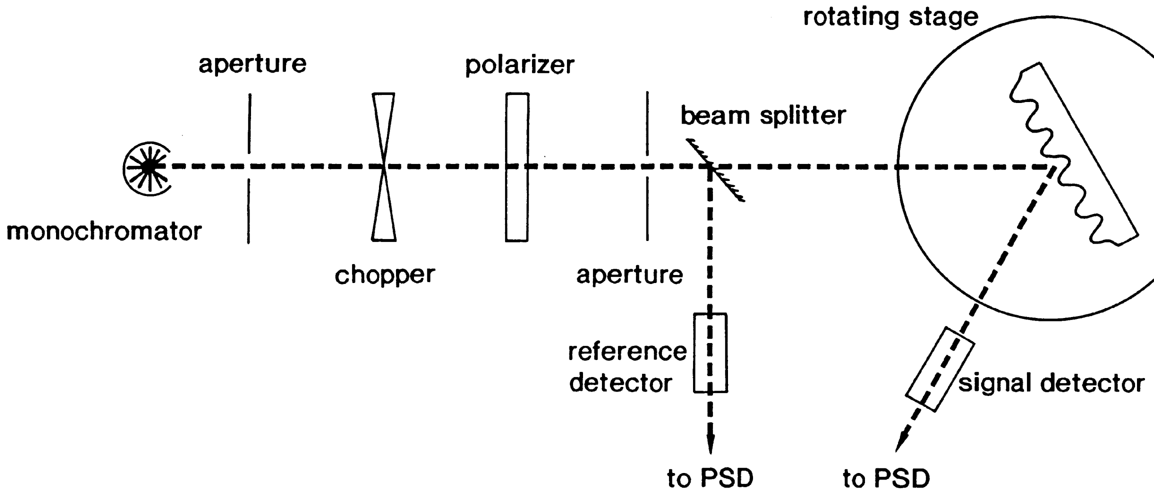

Figure 1. The apparatus used in recording reflectivity measurements from the manufactured fly eye grating, shown diagrammatically.

topography of the corneal surface was determined from lateral views of the broken edges of the corneas of two ommatidia. In each case the periodicity and amplitude of ten grooves of the grating (see § 3) were measured and averaged.

To test the reflection properties of the Eocene cornea we produced a model of the surface in bulk material of similar refractive index with an extremely similar relief profile and dimensions. The cornea itself could not be tested for reflection from its surface because it is extremely fragile and may possess an internal multilayer reflector comparable with the corneas of extant dolichopodids (Bernard 1971), which would interfere with the surface reflection results. The fly eye surface (grating; see § 3) was manufactured in Shipley AZ-1805 photoresist according to the general method for manufacturing deep gratings (Mello *et al.* 1995; Wood *et al.* 1995).

Reflectivity measurements were recorded using the apparatus shown diagrammatically in figure 1. A monochromator was used to illuminate the grating. This beam was passed through two apertures to produce a well-collimated beam with an area of about 1 mm^2. The polarization of the incident beam was set to an accuracy of ±0.05°. The beam splitter reflected about 5% of the incident radiation into the reference detector. The main signal was later divided by this reference signal to correct for small fluctuations in beam intensity. The detectors were photomultipliers. Phase sensitive detectors (PSDs) were used to extract the component of the detected signal that was modulated at the chopper frequency of about 1.2 kHz. Absolute reflectivities were obtained by measuring the amount of light incident upon the surface of the grating by allowing the incident beam to fall directly onto the signal detector; dividing the signal by the reference gave a normalization constant, which is a function of wavelength. The recorded reflectivities were then divided through by this normalization constant, giving absolute reflectivities, with typical noise levels of about 1.0% and a scaling uncertainty of ±1%. Normal incidence was set to an accuracy of ±0.02° by ensuring that the reflected beam passed back down the incident beam, and the azimuth was set to an accuracy of ±0.05° by ensuring that all the diffracted orders lay in the plane of incidence. This was achieved by ensuring that at the Littrow angles the respective diffracted beams did pass back down the path of the incident radiation.

The reflectivity data were recorded as a series of wavelength scans from 450 to 700 nm (set by the limitations of the apparatus) in 1 nm steps, for each of the two orthogonal linear polarizations (where the polarization was defined as being transverse electric or transverse magnetic with respect to the plane of incidence). Nine of these scans were recorded for incident angles ranging from 0° to 80° in 10° steps, where the plane of incidence was set to be parallel to the grating grooves. For comparison, a similar set of reflectivity data was recorded from a bulk photoresist sample. Once obtained, the reflectivity data was corrected for the wavelength dependence of the device, and the mean reflectivity across the specified spectral window was obtained, for each incident angle, by finding the mean of the reflectivity data.

The grating was subsequently cleaved and its relief profile was imaged in a SEM to test for accuracy of reproduction of the fly eye surface.

For comparison, we examined the compound eyes of six other insect taxa, in a SEM, to test for surface structures. We selected three extant dipterans from different families: *Neurotexis primula* (Neurochaetidae), *Zalea minor* (Canacidae) and *Amenia* sp. (Calliphoridae). To make a more diverse correlation we also selected representatives from other insect orders. These were the bee, *Apis* sp. (Hymenoptera: Apidae), the spiny leaf insect, *Extatosoma tiaratum* (Phasmatodea: Phasmatodae), and the silverfish, *Ctenolepisma* sp. (Thysanura: Lepismatidae). A representative from Thysanura was chosen because this order evolved early in the history of insects and therefore possesses many plesiomorphic characters (Kukalova-Peck 1991).

3. RESULTS

At the cornea–air interface of the Eocene dolichopodid eye exists a series of parallel ridges (figure 2) with an approximate sine-wave profile, which we will refer to as the fly eye grating. The ridges are equal in height (145 nm) and periodicity (240 nm), and can therefore be approximated by a regular grating. The constant spacing is possible on the curved surface because many independent gratings are formed, each occupying a small area, which lie at angles to each other, forming a cross-hatched pattern on the ommatidium.

The periodicity of the model, determined from SEM examination, was 240±2 nm, while the depth of the grooves was 146±10 nm. This is extremely close, if not

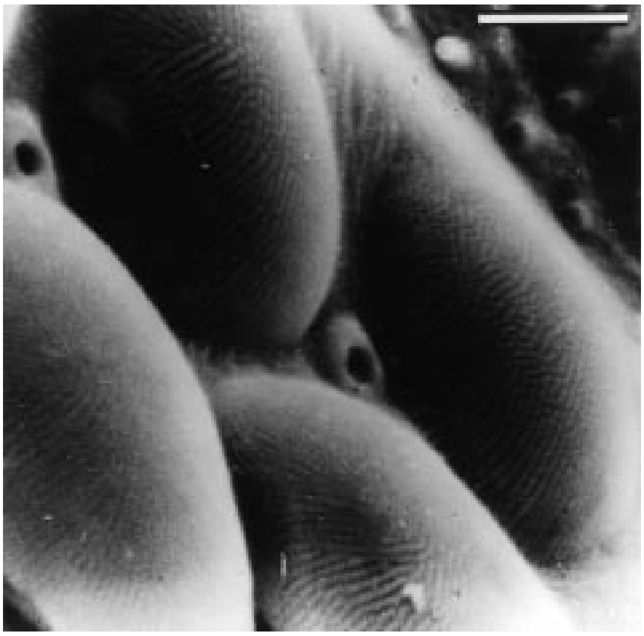

Figure 2. Scanning electron micrograph of the corneal surface of an Eocene dolichopodid fly preserved in Baltic amber. Four ommatidia are shown, each bearing surface gratings. Micrograph by P. Mierzejewski. Scale bar represents 3 μm.

equal, to the corresponding dimensions of the fly eye grating. The photoresist had an approximate refractive index of 1.58. The material of dipteran eye corneas is chitin with an average refractive index of about 1.548 (Bernard & Miller 1967); the difference regarding the effect on antireflection here is negligible. The reflectance properties of the model and of a smooth surface on the same bulk photoresist, i.e. the mean of the corrected reflectivity data plotted as a function of angle of incidence, are shown in figure 3.

We also found the fly eye grating, with the same profile and dimensions, on the corneas of two extant species of Diptera: *N. primula* (figure 4*a*) and *Z. minor* (figure 4*b*). In addition, these flies possess the cylindrical protuberances (moth eye structure) on the flattened central, 'polar' region of each ommatidium. It was noted that other parts of the bodies of these species reflect white light, so that the flies appear conspicuous to the human eye in all spectral colours. The corneal surface of *Amenia* sp. is smooth at the sub-micron level.

The eyes of *Apis* sp. and *E. tiaratum* also possess corneas that are smooth at the sub-micron level. *Ctenolepisma* sp. possesses protuberances of the moth eye type on its corneal surface.

4. DISCUSSION

(a) *Antireflection*

An important property of the fly eye grating is that it is a good antireflector at angles of incidence up to 60°, and a relatively good antireflector at angles between 60° and 80°, for light of wavelengths 450–700 nm. The above 'relative' values refer to comparisons with (i) a smooth surface from the same bulk photoresist, (ii) a multilayer-type antireflector, and (iii) the moth eye structure (see graphs in Wilson & Hutley (1982)). Although the multilayer and moth eye structures are generally improved antireflectors at normal incidence, they have a high angular sensitivity. In fact, the eyes of *N. primula* and *Z. minor* possess cylindrical protuberances on the flattened region of each ommatidium (e.g. figure 4*b*). The Eocene dolichopodid has no flattened region on the cornea of each ommatidium, and also possesses no cylindrical protuberances (figure 2). This evidence further suggests that the moth eye protuberances are the more efficient antireflector at normal incidence, whereas the fly eye grating is more efficient at angles greater than about 10° from the surface normal, such as on curved corneal surfaces.

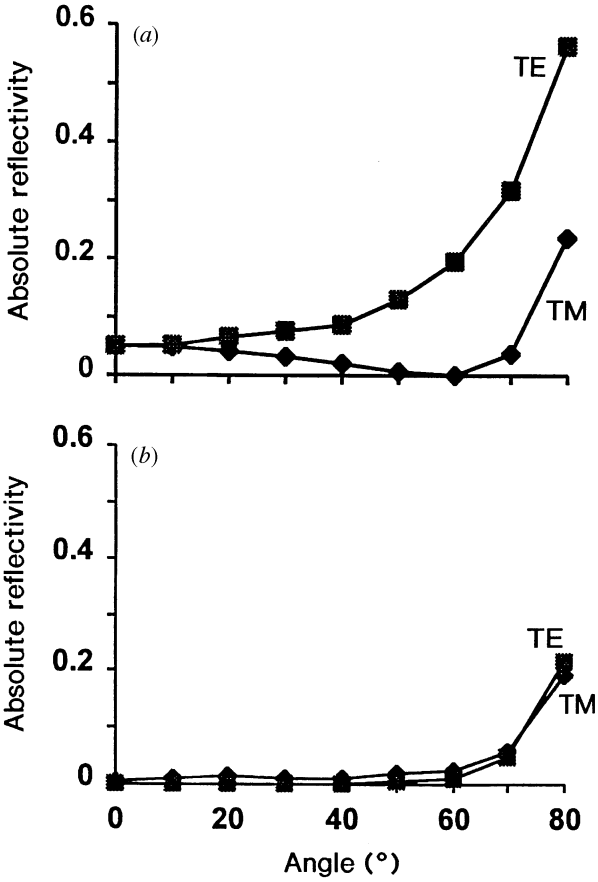

Figure 3. Mean reflectivity data for the wavelength range 450–700 nm recorded from: (*a*) bulk Shipley AZ-1805 photoresist with a smooth surface; (*b*) a surface relief grating of groove depth 146 nm and pitch 240 nm, manufactured in Shipley AZ-1805 photoresist. The two polarizations (TE and TM) are plotted for each surface. For the grating the plane of incidence was perpendicular to the grooves. Typical noise levels are about 1.0% and the scaling uncertainty is ±1%.

The fly eye grating additionally reduces the difference in reflectivity between the two polarizations of incident light (figure 3), whereas the moth eye protuberances show a similar polarization sensitivity to the smooth surface (see graphs in Wilson & Hutley (1982)). This effect could be beneficial to the fly because polarized light is analysed at the photopigment molecules in the rhabdomeric microvilli (Moody & Parriss 1960). Thus, a cornea with a fly eye grating would have little influence on, or interference with, polarization analysis compared with a cornea with a smooth surface or cylindrical protuberances.

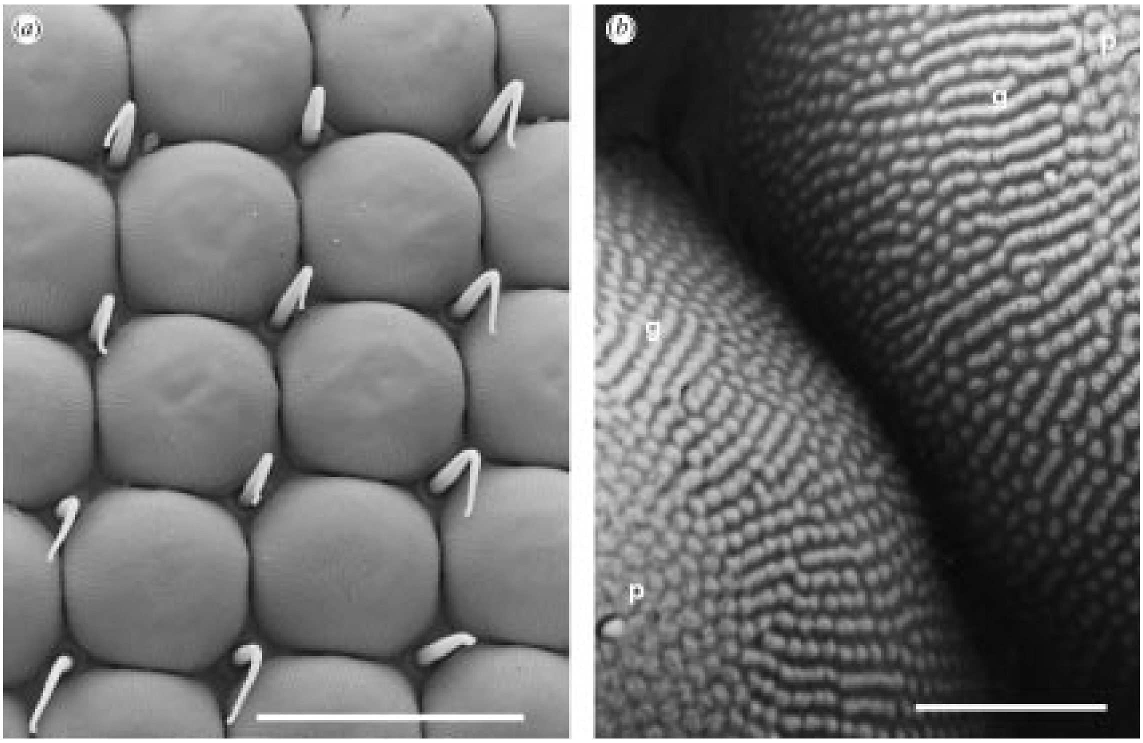

Figure 4. Scanning electron micrographs of the corneal surfaces of two extant dipterans. (*a*) Many ommatidia of *Neurotexis primula* with setae (ommatrichae) between. (*b*) Detail of two adjacent ommatidia of *Zalea minor*, showing grating on each; 'g' represents grating zone, 'p' represents cylindrical protuberances zone. Bar: (*a*) 20 µm; (*b*) 2 µm.

Other parts of the bodies of *N. primula* and *Z. minor* are efficient reflectors of white light, and so the structures on their eyes are not part of a comprehensive stealth strategy (that the moth eye protuberances provide antireflection to continue visual camouflage of the body has been hypothesized (see review by Gale (1989)) but not tested). Instead, the fly eye grating probably provides antireflection at the surface of the eye to induce a greater incidence of photons on the light detection apparatus beneath, and thus enhance vision. Therefore, it appears that Nature has anticipated the reflection problems facing solar absorbers and evolved a comparable antireflector.

(b) *Diversity and evolution of the grating-type antireflector in insects*

Bernard (1971) alleged that the moth eye protuberances are present on the cornea of an extant dolichopodid (*Dolichopus gracilis*) and the horsefly *Hybomitra lasiophthalama* (Diptera: Tabanidae). However, from the sections illustrated (Bernard 1971), it appears that these species do not possess cylindrical protuberances on their corneas but rather the fly grating, with a sine-wave profile and periodicity of about 220–250 nm, i.e. approximately consistent with the surface of the extinct dolichopodid, described here. It has subsequently been brought to our attention that the fly eye grating is also present in the fern fly, *Auster pteridii* (Diptera: Teratomyzidae), as evident in a published SEM of ommatidia of this species (McAlpine & De Keyzer 1994). Determination of dimensions, however, is difficult from this illustration. It is interesting to note that *D. gracilis*, *H. lasiophthalama* and *A. pteridii* all possess curved corneal surfaces on each ommatidium; a possible factor in the diversity of the fly eye grating.

Diptera evolved in the Triassic (possibly Upper Permian); Dolichopodidae first appeared in the Lower Cretaceous, Calliphoridae possibly in the Cretaceous, Canacidae in the early Tertiary, and Neurochaetidae are further derived (Kukalova-Peck 1991). Thysanura (silverfish) are less-derived insects, evolving in the Upper Carboniferous (Kukalova-Peck 1991). Considering that a silverfish possesses the cylindrical protuberances, we regard protuberances as the ancestral-type antireflector. In addition, the fly eye grating is not a degenerative form of the protuberances but is rather physically developed. The evidence therefore suggests that the fly eye grating has evolved to provide relatively angle-independent antireflection properties.

The fly eye grating is not common to all Diptera. It appears to have evolved along a lineage that includes Dolichopodidae, Canacidae, Neurochaetidae and Teratomyzidae, but has been lost in at least a clade including Calliphoridae (see dipteran classification of McAlpine (1989)). A further, comprehensive study of the diversity of the fly eye grating is required before significant conclusions on evolution can be drawn.

The moth eye structure was found to be optimal, in terms of shape and size, for the protuberance-type design (Ma & Robinson 1983). Maybe natural selection, spanning at least 45 million years, has resulted in an optimal form of the grating-type design on the eyes of certain Diptera.

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