

probably the only dedicated one in *Drosophila*. Although we cannot yet exclude additional central-clock functions for dCRY, the abrogation of constant-light effects in *cry<sup>b</sup>* mutant flies indicates that this cryptochrome makes a unique contribution to *Drosophila* circadian photoreception.

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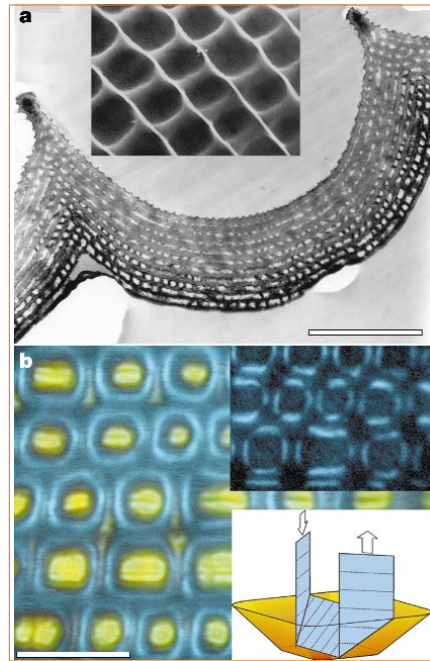
Structural colour

## Colour mixing in wing scales of a butterfly

Green coloration in the animal kingdom, as seen in birds' feathers and reptile integument, is often an additive mixture of structurally effected blue and pigmentary yellow<sup>1</sup>. Here we investigate the origin of the bright green coloration of the wing scales of the Indonesian male *Papilio palinurus* butterfly, the microstructure of which generates an extraordinary combination of both yellow and blue iridescence. The dual colour arises from a modulation imposed on the multilayer, producing the blue component as a result of a previously undiscovered retro-reflection process.

Scanning electron micrographs of scales taken from the wings' coloured regions show that their surfaces comprise a regular two-dimensional array of concavities, of about 4–6 μm in diameter and 0.5–3 μm at the greatest depth. Transmission electron micrographs of these scales in cross-section reveal the multilayering that causes the iridescence as well as a modulation that leads to retro-reflection (Fig. 1a).

The variation in colour across each concave surface modulation is evident from optical microscopy. In reflection, for normally incident light, the flat regions between and



**Figure 1** Modulated multilayering leads to dual colour in *P. palinurus*. **a**, Transmission electron microscope image showing a cross-section through one concavity on a *P. palinurus* iridescent scale. Inset; a scanning electron microscope image of the surface of an iridescent scale. Scale bar, 1 μm (inset, 7 μm). **b**, Real-colour image showing the dual-colour nature of the reflectivity from the surface of the *P. palinurus* iridescent scale, taken using unpolarized light in an optical microscope. Top inset, image of the same region taken with crossed polarizers. Bottom inset, illustration of the mechanism by which polarization is converted through double reflection from orthogonal sides of a concavity. Scale bar, 12 μm (inset, 6 μm).

in each concavity appear yellow, and the inclined sides of each concavity appear blue (Fig. 1b). It is the juxtaposition of these yellow and blue regions that synthesizes the green coloration perceived by the human eye, as they are too small to be resolved individually. Such spatial-averaging colour-stimulus synthesis<sup>2</sup> has been reported in beetles<sup>3</sup>, and it also forms the basis of colour-television pictures and pointillistic painting.

The blue component cannot be back-reflected from a single multilayer system inclined at 45° to the incident direction. The effect is in fact caused by a pair of orthogonal multilayer surfaces that lie on opposite sides of each concavity. Light incident along the scale perpendicular, reflected from one surface inclined at 45°, is directed across the concavity to the opposite, orthogonal surface, where it is returned back along the incident direction. These pairs of inclined surfaces with almost identical multilayering have matched spectral reflectivity characteristics; this causes intense blue reflectivity through this double reflection.

Support for this retro-reflection mechanism comes from evidence of polarization conversion in the reflection from these scales. When we cross an input linear polarizer with an exit analyser while viewing the sample

under normally incident light, all yellow reflected light is extinguished, but a substantial amount of blue reflected light remains, indicating that the blue reflected light has undergone polarization conversion. This effect occurs after double reflection from a pair of orthogonal surfaces when the wavevector of the incident light is at 45° to the reflecting surface and the polarization vector is at 45° to the plane of incidence.

Under diffuse white light, humans see the wing's green coloration in a limited solid angle about the wing normal. Outside this perspective, the wing colour changes predictably, becoming bluer as observation approaches grazing incidence<sup>4</sup>. The retro-reflection from pairs of opposite sides of each concavity is then less effective because their angle-dependent spectral reflectivity characteristics become mismatched. However, increasingly non-normal incidence observation is facilitated through large-angle reflections from the bottom and single sides of each concavity.

The purpose of this mechanism of colour generation is unclear. Structural colours can provide higher visibility<sup>5</sup> than pigmentary colours and can, given the appropriate microstructure<sup>6</sup>, create colour-dependent polarization and angle effects. Conspecific and predator photoreceptor sensitivity must also be considered. Species whose spectral-vision sensitivity spans the two reflected structural colours may perceive a third by colour-stimulus synthesis. Polarization sensitivity associated with such photoreceptors<sup>7</sup> would provide further detail from wing reflectivity about species type and even wing orientation.

The mechanism by which *P. palinurus* produces its bi-colour and polarization effects is optically rare (although similar but less pronounced polarization effects and colour-stimulus synthesis of green have been identified in the other *Papilio* butterflies, *P. crino*, *P. buddha* and *P. blumei*). Through simple modulation of an otherwise uniform multilayer system, it synthesizes a very different colour stimulus in certain visual systems. The structure shows strong local polarization conversion of only one of the colours, through the mechanism we term orthogonal-surface retro-reflection.

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