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Mechanisms of structural colour in the *Morpho* butterfly: cooperation of regularity and irregularity in an iridescent scale

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Structural colour in the *Morpho* butterfly originates from submicron structure within a scale and, for over a century, its colour and reflectivity have been explained as interference of light due to the multilayer of cuticle and air. However, this model fails to explain the extraordinarily uniform colour of the wing with respect to the observation direction. We have performed microscopic, optical and theoretical investigations, and have found that the separate lamellar structure with irregular heights is extremely important. Using a simple model, we have shown that the combined action of interference and diffraction is essential for the structural colour of the *Morpho* butterfly.

Keywords: structural colour; iridescence; *Morpho* butterfly; interference; diffraction

1. INTRODUCTION

Colouring in nature mostly comes from the inherent colours of materials, but it sometimes has a purely physical origin, such as diffraction or interference of light. The latter, called 'structural colour' or 'iridescence', has long been a problem of scientific interest. The peacock feathers, the stripes of *Neon tetra* (fish), the brilliancy of pearl, the electric blue wing of the *Morpho* butterfly—all these brilliant colours have a structural origin. It is well known that these colours are due to the presence of surprisingly minute structures that cannot be attained even by means of ultramodern nanotechnology.

Hooke (1665) and Newton (1730) reported the structural colours of insect and peacock feathers. However, it was not until the end of the 19th century that the scientific approach began to elucidate the mechanism of structural colour (Rayleigh 1888). Since then, many scientists (Michelson 1911; Rayleigh 1918, 1923; Merritt 1925; Anderson & Richards 1942; Denton 1971; Land 1972; Huxley 1976; Tabata *et al.* 1996; Vukusic *et al.* 1999; Parker 2000) have followed up their work, making further contributions to our understanding of this phenomenon. Mason (1927) performed careful investigations on various insects and compared their iridescence with that of thin films. Ghiradella performed structural and developmental investigations on iridescent lepidopteran scales (Ghiradella *et al.* 1972; Ghiradella 1974, 1991, 1998). She classified iridescent scales morphologically and explained the development of some iridescent scales in terms of elastic buckling. Recently, Vukusic *et al.* (2000) showed a new mechanism of colour mixing in the *Papilio* butterfly. It is now well known that submicron structures are responsible for the structural colour through light interference in layered or lattice structures and also Tyndall scattering (Huxley 1976).

The *Morpho* species of butterflies are some of the most well known iridescent creatures living in South and Central America and have been extensively studied for over a century. However, their structural colours have been simply explained as interference due to alternate layers of cuticle and air using a model of multilayer interference. What are the inherent characteristics of the *Morpho* wing? From a physical viewpoint, the answer to this question can be summarized as follows: (i) very high reflectivity in a particular wavelength range, (ii) uniform blue reflection in a broad angular range, (iii) glitter-like laser speckles, and (iv) variations of colours among species. It is evident that the simple multilayer interference model explains (i) and partly (iv), but neither (ii) nor (iii). In this sense, the physical elucidation of the structural colour in the *Morpho* butterfly is just beginning, although its application has already been progressing in the automobile and textile industries.

Here, we report detailed investigations of two typical male *Morpho* butterflies, *M. didius* and *M. sulkowskyi*, which show quite different hues: the former shows cobalt-blue wings, while the latter displays translucent pearly colouring with blue brilliancy. In the following, we elucidate the physical origin of the structural colour in the *Morpho* butterflies referring to these two species.

2. MATERIAL AND METHODS

Samples of male *M. didius* and *M. sulkowskyi* were purchased from the Nawa Insect Museum and Mushi-sha, Japan. The scales and their microscopic structures were observed by an Olympus BX50 fluorescence microscope and also by a JEOL JSM-5800 scanning electron microscope (SEM). The SEM images were also taken in Osaka JEOL Research Center, Japan. The cross-section of the scale was observed by a JEOL JEM-1200EX transmission electron microscope (TEM). The TEM samples were prepared according to the conventional method (Satoh *et al.* 1997).

The optical properties of the wing and scale were examined by the following three methods: (i) the diffuse reflection and transmission spectra were measured using a Shimadzu UV-240 spectrophotometer equipped with an integrated sphere because the reflected and transmitted light from the wing was distributed

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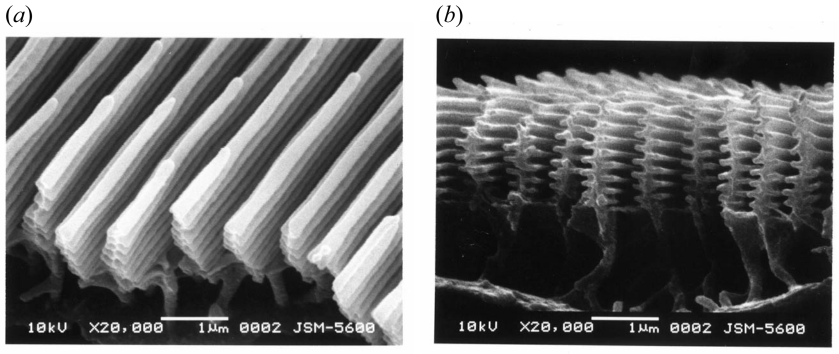

Figure 1. Scanning electron microscope images of (*a*) an oblique view and (*b*) a cross-section of a ground scale of the male butterfly *Morpho didius*.

over a broad angular range; (ii) the angular dependence of the reflected light intensity from the wing was measured under monochromatic light illumination. One end of an optical fibre was placed at a distance of 10 cm from the sample and was rotated slightly below a plane of incidence, while the other was attached to a photomultiplier; (iii) the angle- and wavelength-resolved reflection and transmission spectra of a single scale were measured using a xenon lamp of high luminosity as a light source. The light emitted from the lamp was first focused into a pinhole of 50 μm diameter and then focused into a scale attached to the tip of a needle through an achromatic lens having a 100 mm focal length. The reflected or transmitted light was collected by an optical fibre on a rotating stage and spectrally analysed by an Ocean Optics USB2000 monochromator.

3. RESULTS

We first performed a microscopic investigation using a SEM. The wing of the male *M. didius* is covered with two kinds of scales: cover and ground scales. Both cover and ground scales have many minute ridges with intervals of 1.4 μm and 0.6–0.7 μm, respectively. Like ordinary *Morpho* butterflies, *M. didius* mostly owes its iridescence to the ground scales (Ghiradella 1991; Tabata *et al.* 1996). In fact, the SEM observation confirms that the cross-section of a ridge of a ground scale consists of lamellae in six to eight layers with an interval of *ca.* 0.20 μm (figure 1). It was also observed that the lamellae are not precisely regular. Furthermore, each layer of a lamella runs obliquely with respect to the plane of the scale and the ends of the layers are randomly distributed on the ridges (figure 1*a*). These features are responsible for the irregularity in the heights of the ridges observed in cross-section. The wing of the male *M. sulkowskyi* consists of regularly arranged cover and ground scales, both having ridges with an interval of 0.7–0.8 μm, and the lamellar structures of both scales are similar to those of the ground scale of *M. didius*.

We then measured the diffuse reflection and transmission spectra of the intact wings of the two *Morpho* species to investigate the differences in their hues. The results, shown in figure 2, demonstrate that we can successfully divide the optical response of the wing into three parts (reflectance, transmittance and absorption) assuming that the fluorescence is ignored. It is evident that the reflectivity reaches a maximum value of 55% at 460 nm for *M. didius* and of 70% at 460 nm for *M. sulkowskyi*. Conversely, the minimum reflectivity at around 600 nm reaches 10% and 30%, respectively. The marked difference between the two species lies thus in the amount of absorption and/or background reflection at around 600 nm.

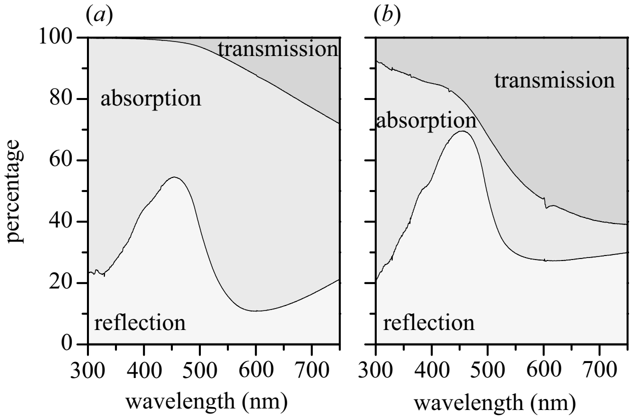

Figure 2. Percentages of transmission, absorption and reflection for the wings of (*a*) *Morpho didius* and (*b*) *Morpho sulkowskyi* measured by a spectrophotometer equipped with an integrated sphere.

Next we show the angular dependence of the reflected light intensity. Since the iridescence of *M. didius* is due mostly to the ground scales, we removed cover scales using adhesive tape. Even if the incident light is nearly monochromatic, the reflected light spreads widely in a plane transverse to the ridges and no apparent diffraction spot is observed. The reflection in a plane normal to the scale and containing a ridge is limited to a range of 20°. As shown in figure 3*a*, the angular dependence transverse to the ridges measured under normal incidence tends to reach a maximum value around the direction normal to the wing at longer wavelengths, while it shows three peaks around 0 and ±50° at shorter wavelengths. Conversely, the measurement on the intact wing shows that the reflected light is intense towards the normal for a wider wavelength range, while the reflection in the other plane becomes somewhat distributed over 40°. Thus, the cover scales in *M. didius* may have a mechanism that reduces the anisotropy of the reflection. The angular dependence of the *M. sulkowskyi* wing is similar to that of *M. didius* without cover scales.

In order to investigate the optical properties of each scale, we conducted a single-scale angle- and wavelength-

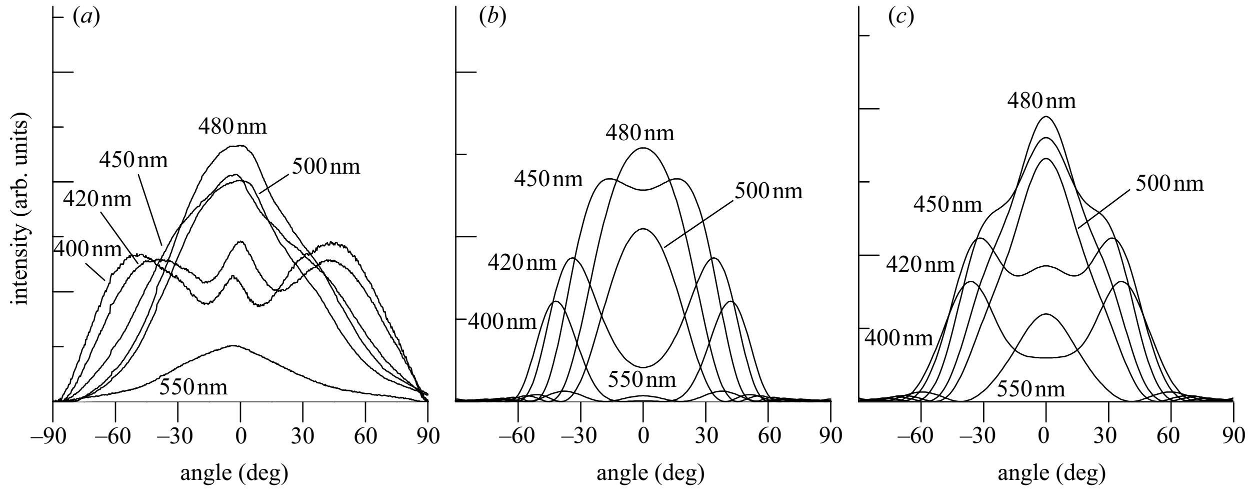

Figure 3. Angular dependence of the reflected light intensity from a wing of the male butterfly *Morpho didius* without cover scales under normal incidence at various wavelengths. (*a*) Experimental data and (*b*) calculated results obtained under the assumption that a plane wave incident on six layers each infinitely thin and 300 nm in length with a 235 nm interval is diffracted at each layer and interferes in the far-field region. These value are obtained from TEM images of the scale of *M. didius* and calculated using the refractive index of cuticle 1.6. (*c*) The angular dependence calculated for four layers by taking the spatial correlation of the ridge height into account. The correlation length is assumed to be 0.4 of the ridge separation with the Gaussian correlation function. The other parameters are the same as (*b*).

resolved experiment. The typical result of the *M. sulkowskyi* scale is shown in figure 4. The data obtained agree basically with that of the intact wing in the reflection region. Under normal incidence, the reflected light towards the normal direction has a peak at 440 nm. With an increasing angle of observation, the relative intensity at shorter wavelengths increases and the angular range reaches ±80°. It was also observed that the reflection around 600 nm was quite low, which is in contrast with that of the intact wing of 30%. In the transmission region, the first-order diffraction spots due to the periodic ridge structure are clearly resolved and its peak shifts with the angle of observation, which is in good agreement with that expected from the multi-slit interference due to periodic ridge structure (figure 4*c*). The single-scale experiments on *M. didius* show similar results in the reflection region, but the transmission spectra show a marked difference (Vukusic *et al.* 1999). That is, the diffraction spots up to the third order are clearly observed for a cover scale, while in a ground scale, only the first-order spot is visible with a complex transmission pattern observed above 500 nm.

4. DISCUSSION

We are now in a position to explain the above results through simple theoretical studies. First, we discuss the effect caused by the separate positioning of the lamellae of a finite size. The difference between the *multilayer interference model* and the actual lamellar structure is evident, namely, the lamellae of a finite size standing perpendicular to the ridge cause the diffraction of light as well as the interference within the lamella. However, if all the ridge heights were equal to each other at any cross-section, extra interference would occur among ridges as in multi-slit interference and would cause the diffraction spots. Since the ridge heights are determined by obliquely running cuticle layers, we have investigated the ridge height distribution at several cross-sections using the distribution of the ends of lamellar layers. From this investigation, it was deduced that the heights are almost randomly distributed within the layer interval of 0.2 μm without any spatial correlation longer than the ridge separation. A simple simulation shows that the interference of the diffracted light emanating from the ensemble of such lamellae cancels out, and hence the wavelength and angular dependence of the light reflected from a scale can be considered to originate essentially from the incoherent sum of single-lamella diffraction.

To elucidate the angular dependence of the reflection from the *Morpho* wing, we consider a simple model in which a plane wave illuminates a lamella under the assumption that the cuticle layers are infinitely thin with the optical path length of the layer interval equal to that of the actual lamella, and that the incident and diffracted light is not subjected to reflection or refraction while passing through the other layers. Under these assumptions, the light diffracted from each layer interferes in the far-field region. Although this simplified model does not take account of multiple reflections, it creates a basis from which to analyse the characteristics of structural colour while retaining the physical essence, and also reflects the slightly irregular structure of the actual lamella.

In figure 3*b*, we show the calculated results under normal incidence. It is clear that the simulated data reproduce the angular dependence moderately well in addition to the wavelength dependence. In particular, the different behaviours around 480 and 400 nm are well reproduced. Thus, the peaks of 0° around 480 nm and of ±50° around 400 nm can be explained in terms of constructive interference. The simple model detailed above, however, fails to explain the peculiar features such as the peak around 0° at 400–420 nm and the shoulders around ±30–40° at 450–500 nm. The peak observed at the angle of incidence can be partly explained in terms of the coherent backscattering (Van Albada & Lagendijk 1985; Wolf & Maret 1985), as it appears even under a 30°-inclined incidence.

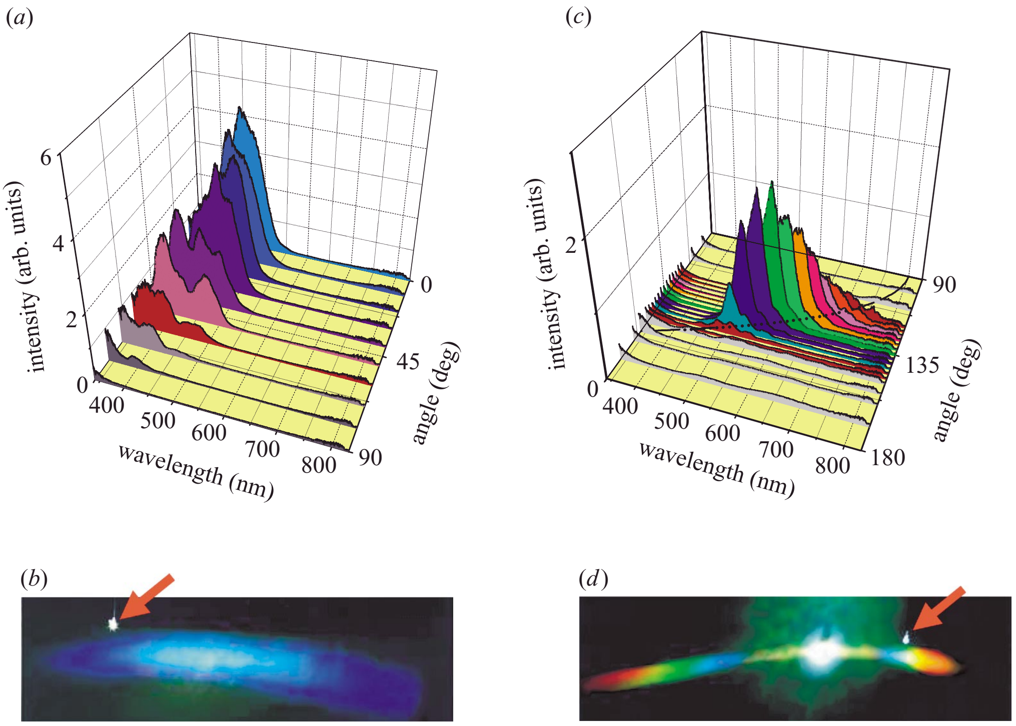

Figure 4. Single-scale angle- and wavelength-resolved experiment on a scale of *Morpho sulkowskyi* under normal incidence (0°) in (*a*) reflection and (*c*) transmission directions. The calculation for the positions of the diffraction spots due to the periodic ridge structure having a 0.8 μm interval is shown as a solid–dotted line in (*c*). The light emanating from a scale spreads transversely to the ridges as shown in (*b*) and (*d*). The arrows indicate a *Morpho* scale under the illumination of a xenon lamp.

We have found the agreement between the experiment and simulation is improved if we incorporate a very small degree of spatial correlation into the ridge height distribution and reduce the number of effective lamellar layers, as shown in figure 3*c*. The incorporation of the spatial correlation causes a modulation corresponding to the diffraction spots due to the interference between neighbouring ridges, while the decrease in the number of effective layers is related to the transmission loss at the other layers. The remaining difference of the large angular range in the experiment may be due to the spread of the tilt angles of the ridges (Vukusic *et al.* 1999).

The random distribution of the ridge heights also contributes to the glittering speckles visible to the eye. That is, the ridges with random heights behave as incoherent scatterers and the scattered light accidentally interferes in space at a sufficient distance from the wing, resulting in the observed spatially inhomogeneous pattern in intensity and colour.

The reflectivity of the periodically arranged lamellae can be qualitatively considered as uniform alternate layers of air and an averaged dielectric layer (Bernhard *et al.* 1968), the refractive index of which is estimated by the spatial average of cuticle layer and air between ridges. According to this model, we calculate the reflectivity against the ridge separation using the transfer matrix method (Pendry 1994). The maximum reflectivity corresponding to the ground scale of *M. didius* is calculated to be 70%, which agrees fairly well with our single-scale observation of 50–60%. Thus the reflectivity is deeply related both to the number of cuticle layers and to the ratio of the ridge width and separation.

Finally, we consider the difference of hues between *M. didius* and *M. sulkowskyi*. Although the microscopic lamellar structures of the two are similar to each other, the apparent wing colours of these species are completely different. The marked difference is found in the optical responses shown in figure 2. Since the lamellar structures of both species equally contribute to the blue reflection, at around 400–500 nm, the major difference comes from the amount of the absorption and/or background reflection at around 600 nm. We have investigated the scales in detail and have found that the pigmentation in the ground scale of *M. didius* is responsible for the difference. The pigments responsible for the absorption are believed to be melanins (Ghiradella 1998) and from the microscopic observation, we have found that these are distributed on the lower region of the scale. Thus, the presence of the pigment contributes to the absorption of the green to red region and enhances the contrast of blue colouring. From the difference in the optical responses of the scale and wing of *M. sulkowskyi*, it is deduced that the pigmentation is effective in reducing the effect of backward light scattering at the wing membrane and the ventral scales, and also in reducing the transmitted light from the underside of the wing.

The mechanisms responsible for the structural colour in the *Morpho* butterflies can be summarized as follows. (i) Lamellar structure in a ridge offers constructive interference, which results in the strong reflection within a selective wavelength range. (ii) The irregularity in the ridge height eliminates the interference among the ridges, which results in the diffuse and broad reflection of a uniform colour. Thus, the combined action of interference and diffraction due to the separate lamellar structure is essential for the structural colour. (iii) High reflectivity is realized owing to the presence of multiple layers in a lamella and a sufficiently small separation between adjacent lamellae. (iv) The irregularity in ridge height also results in the accidental interference of scattered light in space, manifesting as the glittering speckles. (v) The pigmentation in the scale absorbs the extraneous green to red light and enhances the blue colouring.

From a biological viewpoint, the *Morpho* wings exhibiting high brilliancy may function in display such as courtship (Ghiradella 1998; Vukusic *et al.* 1999). As described above, the irregularity makes it possible to maintain the wing colour against the large inclination of the wing. This may confer the particular hue to each species and may also be important in mutual recognition. Conversely, the interaction of light with microstructures is closely related to recent developments in photonic technology. However, a photonic crystal requires a complete structure in order to ensure the presence of a photonic band gap, whereas the structural colour actively incorporates the irregularity into the structure to create a diffuse reflection. Thus, the understanding of structural colour in the *Morpho* butterfly is of profound interest in terms of both its biological and physical aspects.

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