Photophysics of Structural Color in the *Morpho* Butterflies

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Abstract. The *Morpho* butterflies exhibit surprisingly brilliant blue wings originating from the submicron structure created on scales of the wing. It shows extraordinarily uniform color with respect to the observation direction which cannot be explained using a simple multilayer interference model. We have performed microscopic, optical and theoretical investigations on the wings of four *Morpho* species and have found 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 color. It is also shown that the presence of pigment beneath the iridescent scales greatly enhances the blue coloring by reducing the unwanted background light. Further, variations of color tones and gloss in the *Morpho* wings are discussed in terms of the combination of cover and ground scales with various structures and functions.

1. Introduction

Coloring in nature mostly comes from the inherent colors of materials, but it sometimes has a purely physical origin, such as diffraction or interference of light. The latter, called *structural color* or *iridescence*, has long been a problem of scientific interest (Pᴀʀᴋᴇʀ, 2000). Newton had already noticed the colors of peacock feathers as due to the thin-film interference (Nᴇᴡᴛᴏɴ, 1730). From 19th to 20th century, the structural color was a subject of stimulating discussion (Lᴏʀᴅ Rᴀʏʟᴇɪɢʜ, 1888, 1918, 1923; Mᴀʏᴇʀ, 1897; Mɪᴄʜᴇʟsᴏɴ, 1911; Oɴsʟᴏᴡ, 1921; Mᴇʀʀɪᴛᴛ, 1925). The color of butterfly wing, covered with scales having many vertical vanes (ridges), was one of the most extensively studied subjects. However, the origin of the iridescence in the butterfly wing was controversial at that time. The theories accounted for its metallic color fell into the following categories: 1) diffraction of light due to a grooved structure, 2) thin-film interference, 3) light scattering, 4) selective reflection of light such as metals and colored crystals.

Mason performed careful investigations on the scales of the *Morpho* butterfly and concluded that the color-producing lamellae were present within the vane on the upper

surface of the scale and inclined toward the root of the scale (MASON, 1927). Anderson and Richards first performed the electron microscopic investigation on the wing of *Morpho cypris* and found hundreds of vanes possessing linear thickenings 0.2 μm apart on the scale (ANDERSON and RICHARDS, Jr., 1942). They considered that the diffuse and multicolored reflection was due to a variation of their intervals and thickness. Ghiradella performed structural and developmental investigations on iridescent lepidopteran scales (GHIRADELLA *et al.*, 1972; GHIRADELLA, 1974, 1991, 1998). She classified iridescent scales morphologically into 1) thin-film lamenae, 2) diffraction lattice, 3) Tyndall blue (HUXLEY, 1976), 4) microrib-satin, 5) microrib thin-film, and 6) lamellar thin-film. She also explained the development of some iridescent scales in terms of elastic buckling. Recently, VUKUSIC *et al.* (2000) showed a new mechanism of color mixing in the Papilio butterfly.

The *Morpho* species are some of the most well-known iridescent butterflies living in South and Central America, and have been extensively studied for over a century (MAYER, 1897; MICHELSON, 1911; LORD RAYLEIGH, 1918; ONSLOW, 1921; SÜFFERT, 1924; MERRITT, 1925; MASON, 1927; ANDERSON and RICHARDS, Jr., 1942; LIPPERT and GENTIL, 1959; GHIRADELLA, 1974; BINGHAM *et al.*, 1995; TABATA *et al.*, 1996; VUKUSIC *et al.*, 1999). However, their structural color has been simply explained as interference due to alternate layers of cuticle and air using a model of multilayer interference. The optical characteristics of the *Morpho* wing are summarized as follows; 1) very high reflectivity in a selective wavelength range, 2) uniform blue reflection in a wide angular range, 3) variations of color tones and gloss among species. It is evident that the simple *multilayer interference model* explains 1), but neither 2) nor 3). In this sense, the physical interpretation of the structural color in the *Morpho* butterfly is just beginning, although its application has already been progressing in the painting, automobile, cosmetics and textile industries.

Here we report the detailed investigations on the microscopic and optical properties of four typical male *Morpho* butterflies, *M. didius*, *M. rhetenor*, *M. adonis* and *M. sulkowskyi*, which are known to show quite different color tones and structures. Using a simple model, we will elucidate the physical origin of the structural color in these *Morpho* butterflies (KINOSHITA *et al.*, 2002) and will discuss the difference of tones and gloss in terms of the combination of cover and ground scales with various structures and functions.

2. Experimental Procedure

The samples of the male *Morpho* butterflies were purchased from the Nawa Insect Museum and Mushi-sha. The scales and their microscopic structures were observed by a fluorescence/transmission optical microscope (Olympus BX50) and a scanning electron microscope (SEM; JEOL JSM-5800). The SEM sample was evaporated by gold to maintain good electric conductivity. The cross section of the scale was observed by a transmission electron microscope (TEM; JEOL JEM-1200EX). The TEM samples were prepared according to the conventional method (SATOH *et al.*, 1997).

The optical properties of the *Morpho* wing were examined by the following methods:

1)   Diffuse reflection and transmission spectra were measured using a Shimadzu UV-240 spectrophotometer equipped with an integrated sphere. The integrated sphere was employed because the reflected and transmitted light from the wing is distributed in a wide
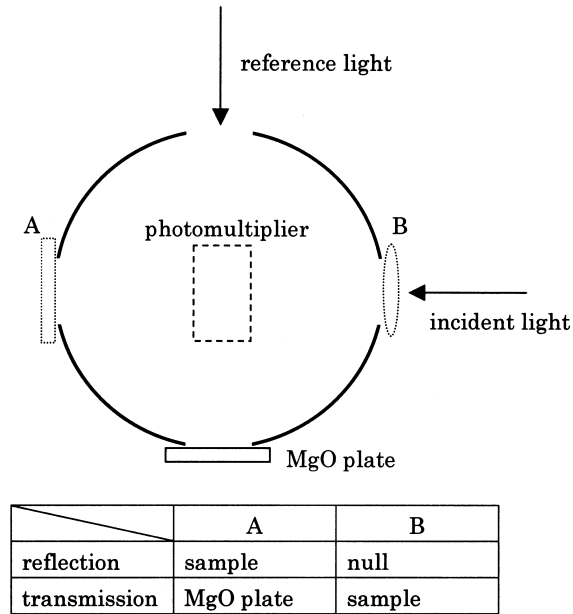
Fig. 1. Schematic diagram of an integrated sphere attached to a spectrophotometer. The absolute transmission and reflection spectra of a diffusely scattering sample are measured in comparison with the reflection of the reference light by a MgO plate.

	A	B
reflection	sample	null
transmission	MgO plate	sample

angular range. The transmission and reflection spectra were measured by placing a piece of the wing before and after the integrated sphere, respectively, so that the scattered light in a wide angular range could be collected in a quantitative manner (Fig. 1). In order to measure the absolute reflectivity, we placed a Shimadzu MgO plate at the sample position as a standard of reflection. In the transmission arrangement, we placed the sample at the input of the integrated sphere and the MgO plate at the output. From these measurements, we could determine the absolute transmission and reflection spectra of the wing.

   2)   The angular dependence of the reflected light intensity from the wing was measured under monochromatic light illumination. In this case, we put one end of an optical fiber at a distance of ~10 cm from the sample and rotated it in a plane slightly below a plane of incidence, while the other end was attached to a photomultiplier.

3. Experimental Results

3.1. Microscopic observation

   In Fig. 2, we show an overview of four kinds of butterflies examined here: *M. didius* shows somewhat dull, cobalt-blue wings, while *M. rhetenor* and *M. adonis* show glossy blue wings. On the other hand, *M. sulkowskyi* displays translucent pearly coloring with blue brilliancy. The microscopic observation shows that the wing of the male *M. didius* is covered with two kinds of scales; a cover scale of a slender shape and a slightly overlapping
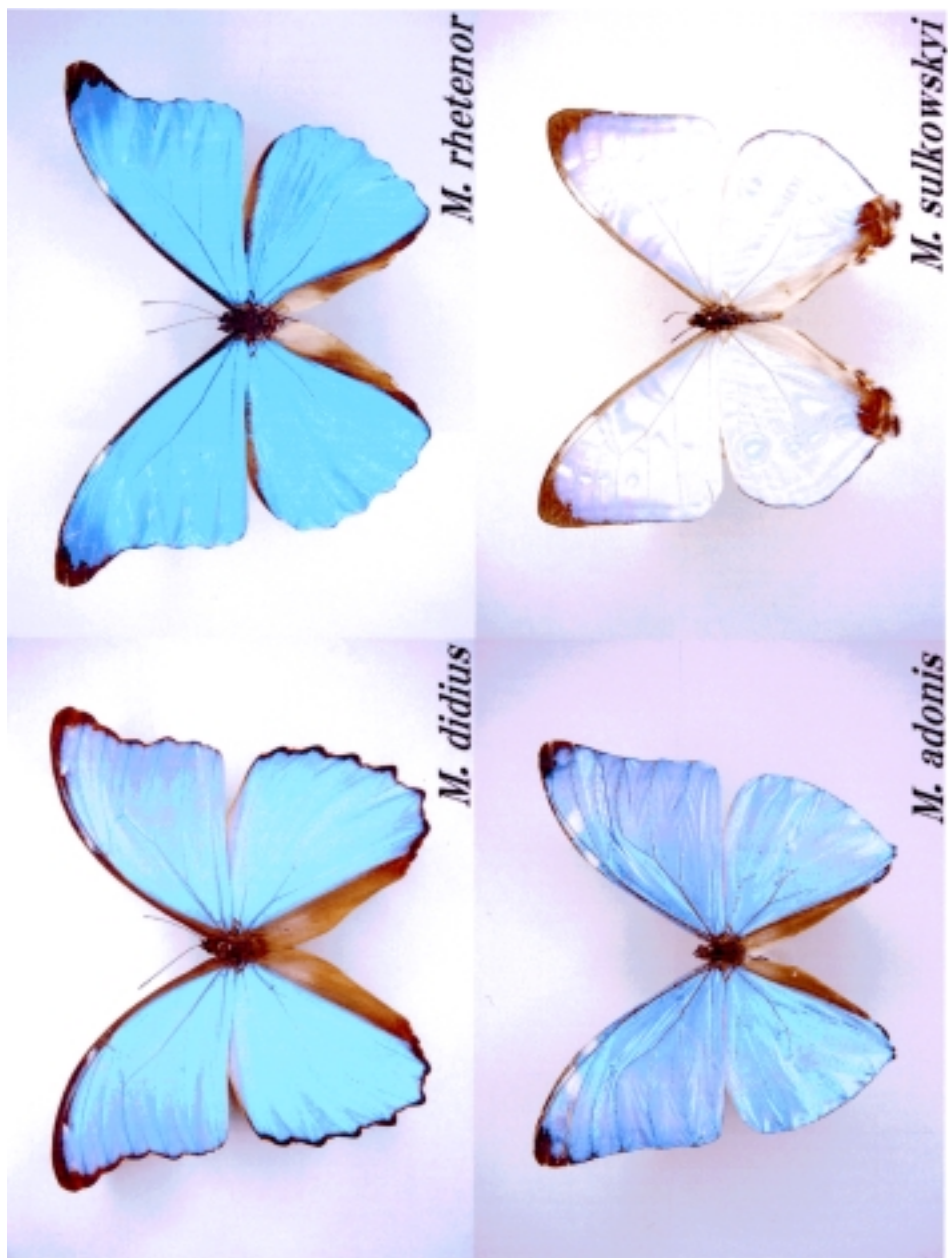
Fig. 2. Photographs of the male *Morpho* butterflies, *M. didius*, *M. rhetenor*, *M. adonis*, and *M. sulkowskyi*.
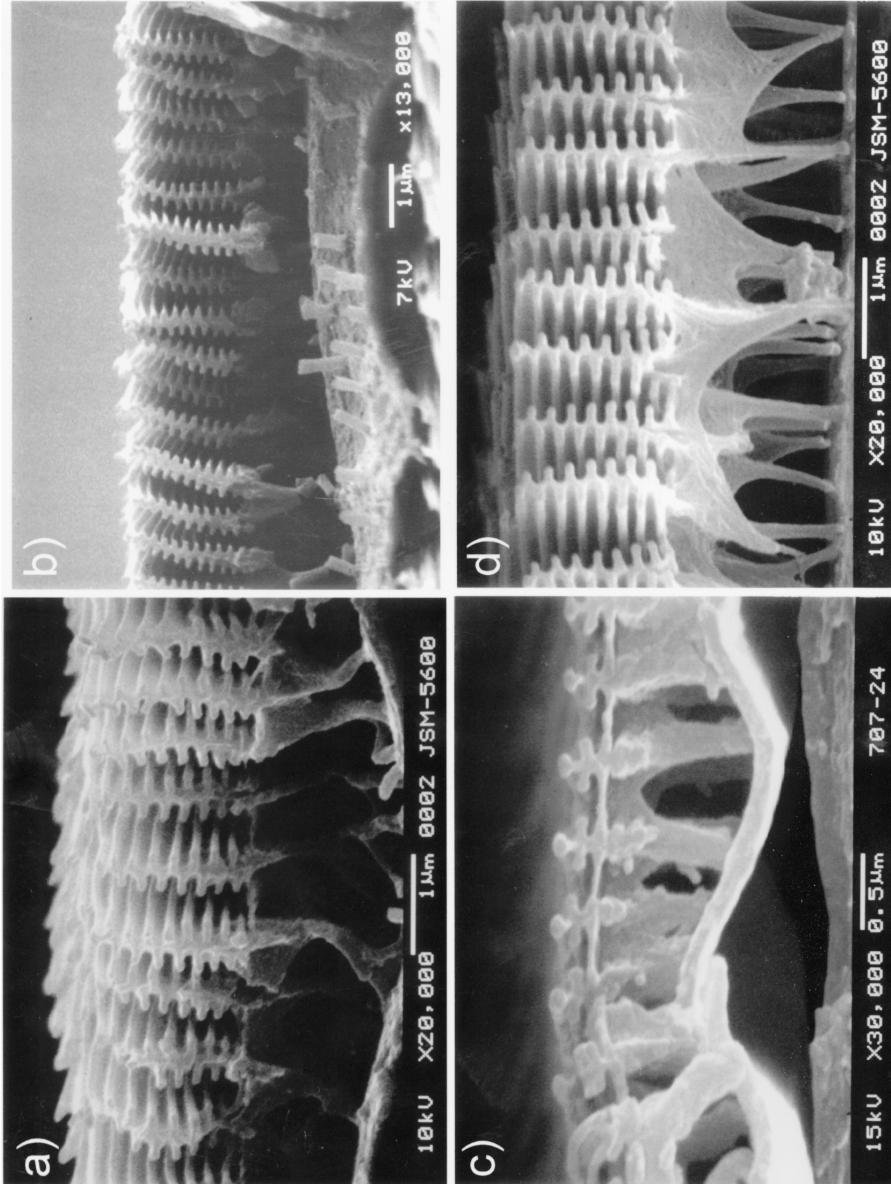
Fig. 3. Scanning electron microscope images of the cross sections of the iridescent scales of *Morpho* butterflies: (a) a ground scale of *M. didius*, (b) a scale of *M. rhetenor*, (c) a cover scale of *M. adonis* and (d) a scale of *M. sulkowskyi.*

ground scale of a rectangular shape. Each of the cover and ground scale has many minute ridges with a pitch of 1.4 and 0.6–0.7 μm, respectively. As shown in Fig. 3a, the cross section of a ridge consists of a lamellar structure of 6–8 layers, which is known to consist of alternate layers of cuticle and air. The TEM observation reveals that the thickness of cuticle and air was approximately 0.055 and 0.15 μm, respectively. The structural difference between the cover and ground scales lies mainly in the density of ridges, and further the development of the lamellar structure seems poor in the former. These facts suggest that the ground scale is mainly responsible for the structural color in *M. didius*. It is also noticed that the cover scale is transparent, while the ground scale contains the pigment making the whole wing brownish.

The wing of the male *M. sulkowskyi* consists of alternatively arranged scales of normal and slightly slender shapes, both having many ridges with a pitch of ~1.0 μm. The lamellar structure is essentially equivalent to that of *M. didius*, although it is somewhat more regular (Fig. 3d). In *M. sulkowskyi*, both scales are nearly transparent, slightly overlapping, and seem to contribute equivalently to the structural color. As for *M. rhetenor*, one of the two types of scales seems to degenerate to a small flake, and the remaining scale which possesses many ridges with the spacing of 0.7–0.8 μm is mainly responsible for the structural color. It sometimes shows a peculiar structure in which most of the ridges are combined here and there at the edge with neighboring ridges so that a considerable number of ridges stand obliquely with respect to the plane of the scale. The lamellar structure of *M. rhetenor* is more complete than the former two and consists of 8–10 cuticle layers (Fig. 3b). The wing of *M. adonis* shows a very different form: the wing is covered with transparent, broad cover scales of an oval shape, on which the smooth ridges are spaced 0.5–0.6 μm apart. The scale possesses a peculiar lamellar structure which consists of only 2–3 cuticle layers with the third layer tied together as shown in Fig. 3c. The scales remarkably overlap one after another, which may have a function to increase the reflectivity of the wing. *M. adonis* seems to owe its structural color mostly to the cover scale, while a rectangular ground scale, containing the pigment, contributes to the structural color only slightly. The microscopic observation reveals that the bright cover scales are somewhat rainbow-colored, while the ground scales have a deep blue tinge.

The scales responsible for the structural color thus show variations. Besides, it is clear that the overall structure is not highly regular in an optical sense. For example, the heights of the neighboring ridges are distributed in spite of seemingly regular lamellar structure standing separately with each other. This is clearly seen from the SEM images that each cuticle layer run obliquely with respect to the base plane of the scale, while the ends of the layers are randomly distributed on the ridges as shown in Fig. 4. We have investigated the ridge height distribution at several cross sections using the distribution of the ends of cuticle layers in the SEM image of *M. didius*. Under the assumption that the ends of cuticle layers have an equal height and that the average length of the end-to-end distance corresponds to the layer interval of 0.2 μm, we determine the ridge height distribution and calculate its spatial correlation function. From this investigation, it is concluded that the ridge heights are randomly distributed within a range of a layer interval and no trace of spatial correlation longer than the ridge spacing is found to exist. These features are responsible for the optical irregularity described later.
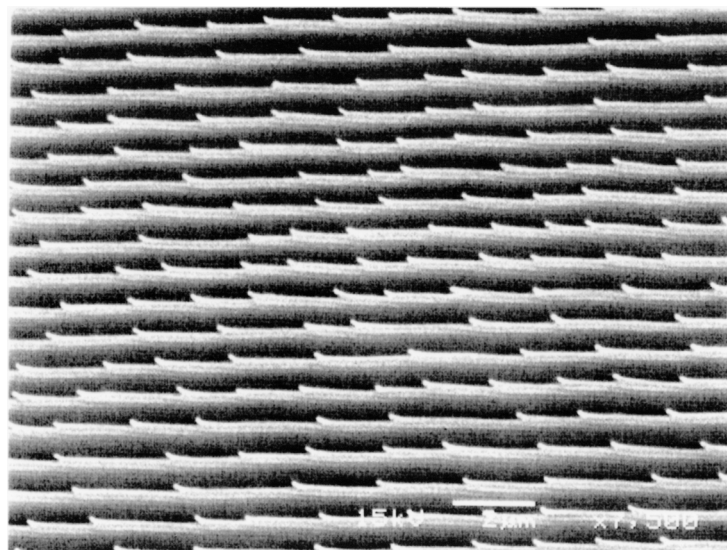
Fig. 4. Oblique view of the scanning electron microscope images of the ground scale of *M. didius*.

3.2. Diffuse reflection and transmission measurements

Next, we show the diffuse reflection and transmission spectra of various wings using a spectrophotometer equipped with an integrated sphere. Since the optical response of matter is generally expressed by the sum of transmission, reflection and absorption of light, we divide the response of the wing into the above three parts under the assumption that the fluorescence process is neglected. This assumption is valid for the butterfly wing because the absorption owes mostly to pigment of melanin (GHIRADELLA, 1998), which is known to be less fluorescent.

In Fig. 5, we show the typical results for the above four species. It is evident that the reflectivity reaches a maximum value at around 460 nm for *M. didius* and *M. sulkowskyi*, and 450 nm for *M. rhetenor*, while that in *M. adonis* is 400 nm with a broad bandwidth of 300 nm, which is about twice that of the other three. The maximum reflectivity amounts to 55, 70, 45 and 60%, while the minimum reflectivity at around 600 nm reaches 10, 27, 3 and 13%, respectively. The high reflectivity of *M. sulkowskyi* seems to owe mostly to the high background reflectivity. Considering this, we deduce that the net reflectivity due to the lamellar structure for these four species show essentially the same value of ~45%.

The transmittance of the wings of *M. didius*, *M. adonis* and *M. rhetenor* is very weak below 500 nm and increases toward a near-infrared region, while that of *M. sulkowskyi* shows an extraordinarily large value especially above 500 nm. Thus the difference of color tones between *M. sulkowskyi* and the other species comes from the differences of the transmission/absorption properties and also of the background reflection in the green to red region of 500–700 nm.
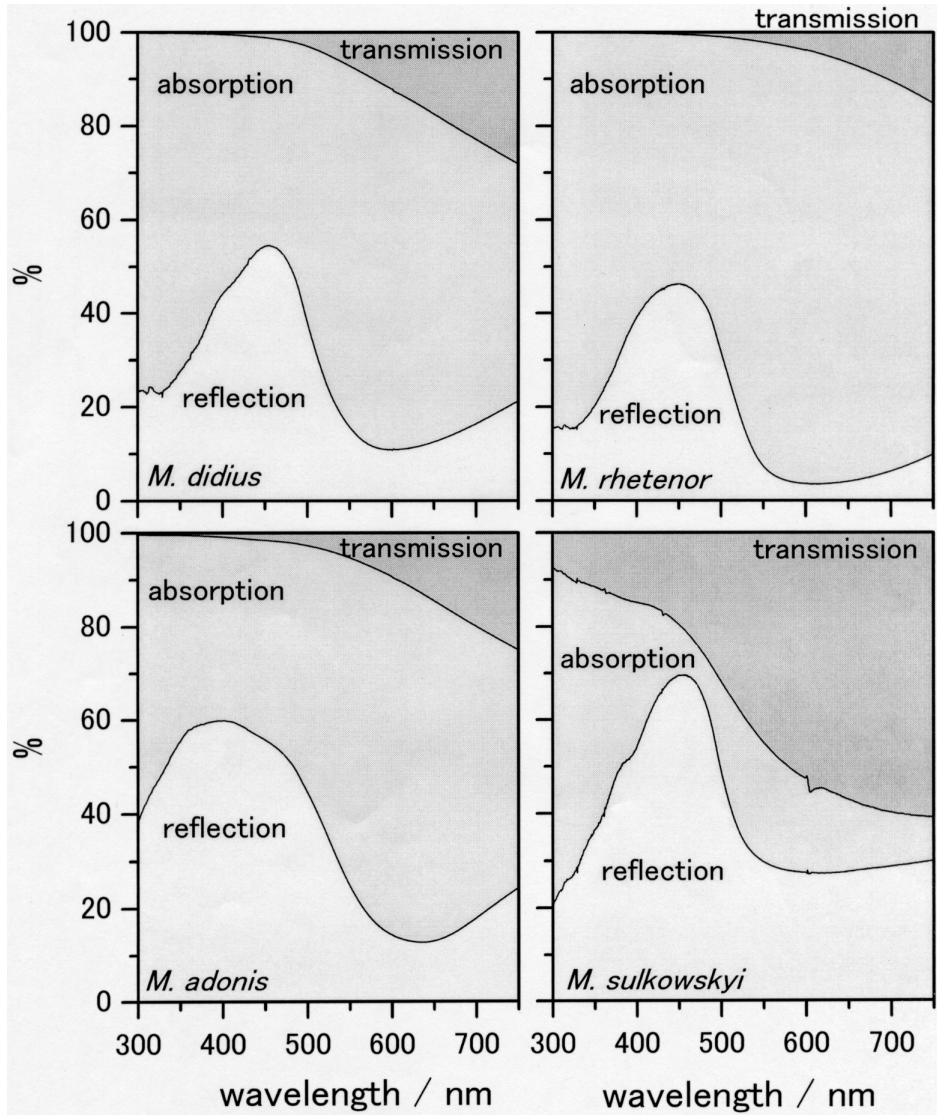
Fig. 5. Percentages of transmission, absorption and reflection of the wings of a) *M. didius*, b) *M. rhetenor*, c) *M. adonis* and d) *M. sulkowskyi*.

3.3. Angular dependence of reflected light intensity from the Morpho wings

Finally we show the angular dependence of the reflected light intensity from a wing of *M. didius*. Even if the incident light is nearly monochromatic, the reflected light is widely distributed in a plane nearly perpendicular to the ridges and no trace of diffraction spots is observed. We measured the angular dependence at various exciting wavelengths. The
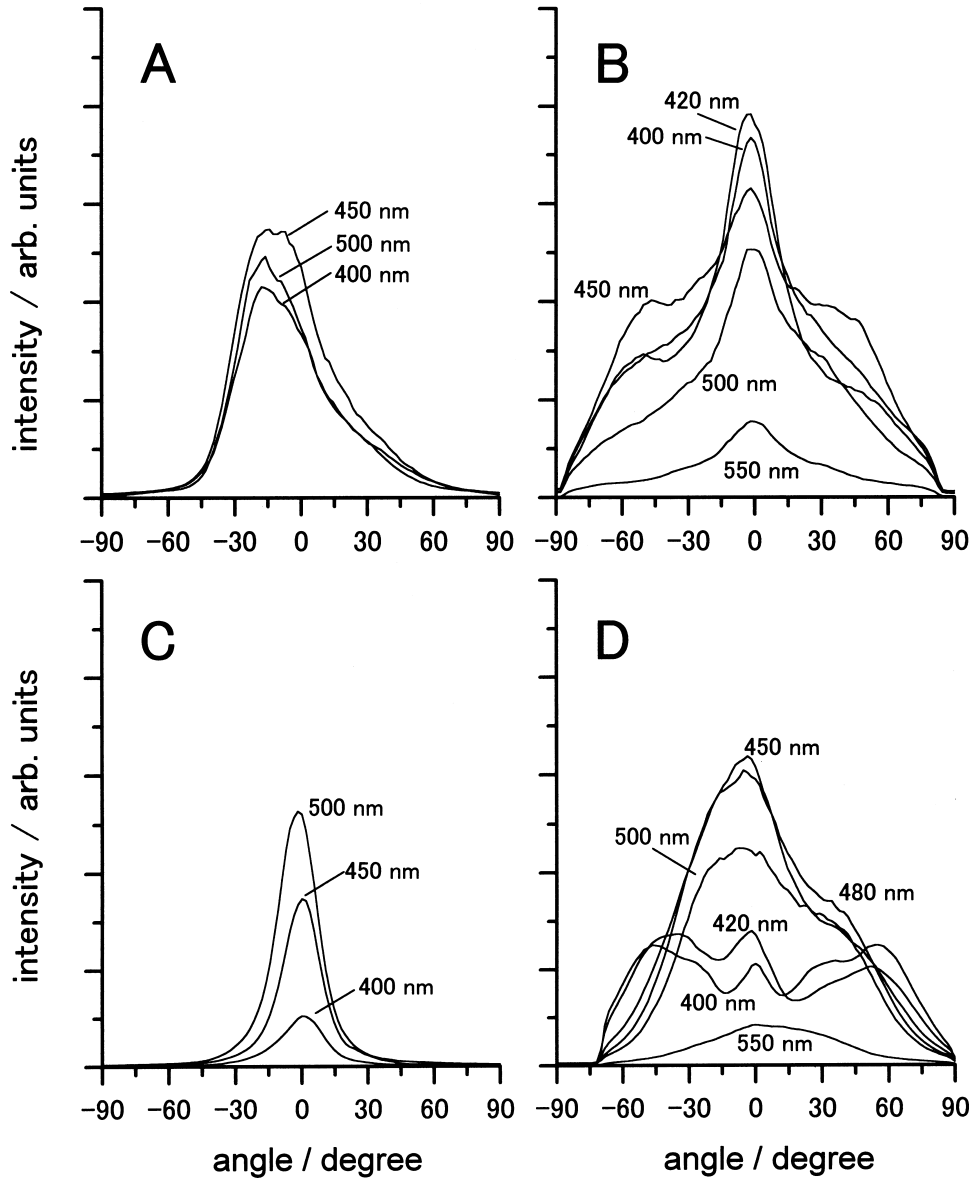
Fig. 6. Angular dependence of reflected light intensity in a plane perpendicular to the ridges for various wavelengths from B) an intact wing and D) a wing without cover scales of the male *M. didius* under normal incidence. Also shown is the angular dependence of reflected light intensity in a plane parallel to the ridges for A) an intact wing and C) a wing without cover scales.

results are shown in Fig. 6B. It is noticed that the reflected light under normal incidence is intense toward the normal direction and is widely distributed regardless of the wavelength. It is also noticed that for the observation angle of 50° or larger, the reflection at 450 nm is rather intense. These results support our observation that the color of the *Morpho* wing does not change largely with the observation direction except for that close to the wing plane.

Since the wing of *M. didius* is covered with two types of scales, we investigated the roles of these two different scales through the angular reflectivity. For this purpose, we removed cover scales using adhesive tape and measured the angular dependence of reflectivity for the wing covered only with ground scales, because the ground scales are mainly responsible for the *Morpho* coloring in *M. didius*. As shown in Fig. 6D, the angular dependence in a plane perpendicular to the ridges tends to reach a maximum value at around the normal direction for longer wavelengths, while it shows a peak at around ±50° for shorter wavelengths.

The light reflected in a plane parallel to the ridges is confined within a small angular range of ±10° as shown in Fig. 6C. Actually, the center of the reflection is inclined from the normal of the wing. This inclination was reported as due to that of the scale with respect to the wing membrane and also of the obliquely running cuticle layers (MASON, 1927; ANDERSON and RICHARDS, Jr., 1942; TABATA *et al.*, 1996). The difference in the angular reflectivity for the directions perpendicular and parallel to the ridges originates from the diffraction effect due to the unidirectional structure of the ridge. In Fig. 6A, we show the angular dependence of the reflection parallel to the ridge for the intact wing. It is clear that the angular range becomes widely distributed and asymmetric as compared with that for the wing without cover scales. Thus, the cover scales in *M. didius* work as a diffuser and may have a function to reduce the anisotropy of the reflection. This hypothesis is experimentally confirmed by the measurement of the angular dependence for the other three species, because the iridescent scales of these species do not accompany diffuser scales. The experimental results show that the angular ranges of the reflectivity are within ±10° for the other three and are comparable to that without cover scales in *M. didius*.

4. Analyses and Discussion

4.1. A simple model based on light diffraction and interference

Now we are in a position to explain the above results in terms of a simple theoretical consideration. Firstly, we will discuss the effect that the lamellae of a finite size are positioned separately with each other along the direction perpendicular to the ridges as in *M. didius*, *M. sulkowskyi* and *M. rhetenor*. As is immediately understood, the separate lamellar structure causes the diffraction of light in addition to the interference within a lamella. However, if the heights of ridges at any cross section were equal, extra interference would occur among ridges as in multi-slit interference, which restricts the direction of light diffraction and causes diffraction spots. Experimentally, no diffraction spots are observed both for a wing and even for a single scale. This result is consistent with the fact described in the previous section that the ridge height is randomly distributed.

To elucidate the angular dependence of the reflection from the *Morpho* wing, we will propose a simple model in which a plane wave incident on *N* separate lamellae having a finite width in one direction and an infinite length in the other. Further, each cuticle layer
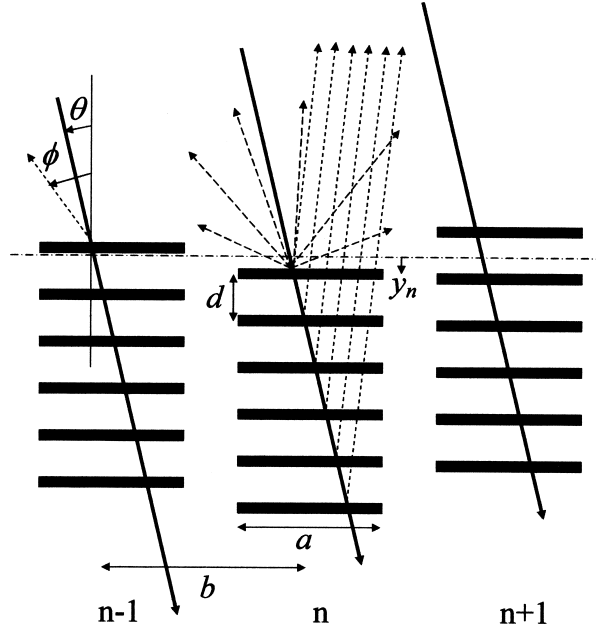
Fig. 7. A simple model for the lamellar structure on the scale. A plane wave is incident on N separate lamellae with different heights.

is assumed to be infinitely thin, and the incident and diffracted light is not subjected to reflection nor refraction while passing through the other layers as shown in Fig. 7. Then the light diffracted by each layer interferes in the far-field region. Although this simplified assumption does not take into account the multiple reflection, it offers an opportunity to analyze the characteristics of structural color without missing the physical essence and also partly reflects the slightly irregular structure of actual lamellae. In other words, this assumption is based on light scattering due to the polarization induced directly on each layer by the incident light field and corresponds to the first-order solution of the wave equation under the presence of complex dielectric materials.

Then the intensity of the diffracted light toward the direction of ϕ under the illumination of the incident light from the direction of θ is expressed as

$$I_\phi = \frac{a^2}{2} \cdot \frac{\sin^2(kdvM/2)}{\sin^2(kdv/2)} \cdot \frac{\sin^2(kau/2)}{(kau/2)^2} \cdot F_R \cdot I_\theta \cos^2\theta, \qquad (1)$$

with

$$F_R = \left| \sum_{n=1}^{N} \exp(ikbun + i\psi_n) \right|^2, \qquad (2)$$

where d, a, b, and M are the interval of cuticle layers, the width of a cuticle layer, the ridge separation and the number of cuticle layers, respectively. I_θ is the intensity of incident light per unit area and $k = 2\pi/\lambda$ with the wavelength of light λ. The factors u and v are expressed as

$$u = \sin\theta + \sin\phi$$

$$v = \cos\theta + \cos\phi.$$

ψ_n is the phase difference at the n-th ridge due to the height distribution of the lamella and is expressed as

$$\psi_n = ky_n v, \tag{3}$$

where y_n is the ridge height deviation from the average. If there is no spatial correlation among ridge heights, then the factor F_R reduces to

$$F_R = N\left\langle \left| \exp\left(ikbun + i\psi_n\right)^2 \right| \right\rangle = N, \tag{4}$$

and any interference term between different ridges disappears. This means that the diffracted light emanating from each lamella does not interfere coherently, and that the wavelength and angular dependence of the light reflected from a scale can be considered to originate essentially from the lamellar structure within a ridge. Thus the total diffraction results from the incoherent sum of single-lamella diffraction.

We calculate the angular dependence of the reflectivity under normal incidence according to the above relation. In Fig. 8, we show the results calculated for 3, 6 and 9 cuticle layers, which roughly corresponds to the iridescent scales of *M. adonis*, *M. didius* and *M. rhetenor*, respectively. It is evident that the increase in the number of cuticle layers enhances the effect of the interference and exhibits more pronounced angular dependence. The simulated data for 6 cuticle layers reproduce fairly well the angle and wavelength dependence of the reflection for the wing covered only with ground scales in *M. didius* (Fig. 6D). Particularly, the difference of the angular dependence for various wavelengths is well reproduced. It is concluded that the wavelength difference in the reflection to the normal direction can be explained in terms of constructive and destructive interference at 450–480 and 400–420 nm, respectively, while the peaks of ±50° at 400–420 nm can be explained in terms of constructive interference. In Fig. 9, we show the spectral distributions calculated for the reflection from various numbers of cuticles layers. With increasing the number of cuticle layers, the intensity of the spectrum becomes higher and the spectral shape becomes sharper. Thus the difference in the spectral widths observed for *M. adonis* and the other three are partly explained in terms of the number of the cuticles layers concerned. Anyway, the present model, although simplest enough, reproduces the angular dependence of the reflection, which can never be explained using the multilayer interference model. The neglect of multi-reflection at the cuticle layers offers a surprisingly good result. This may
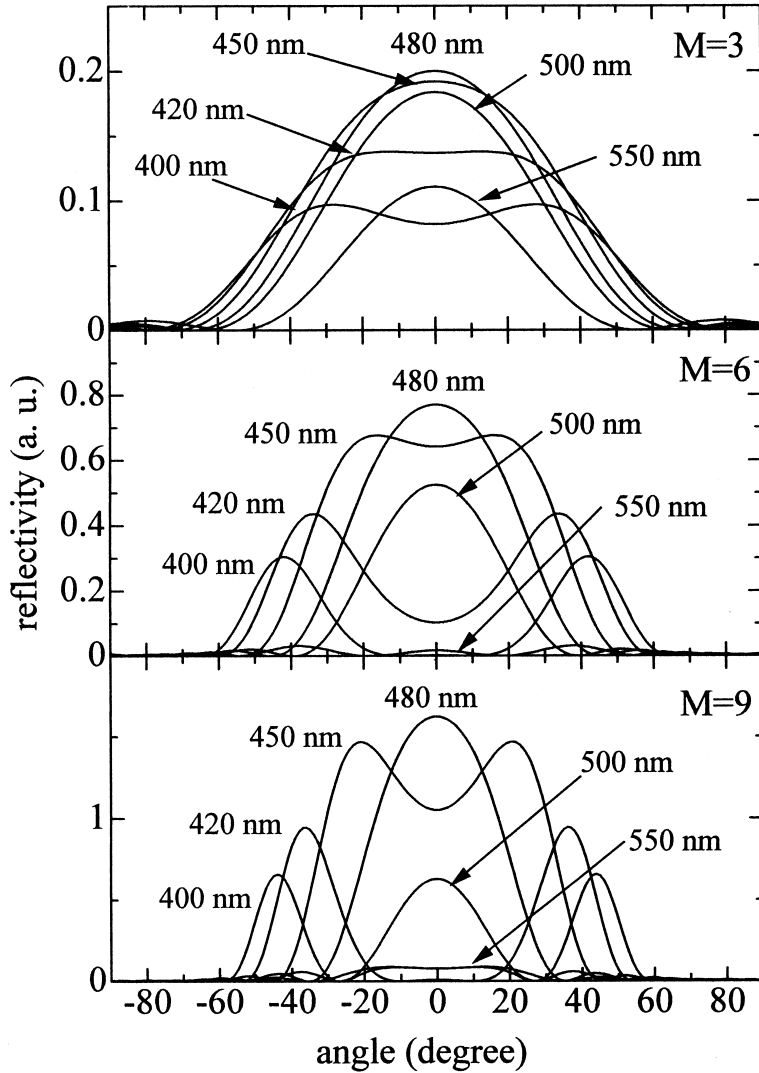
Fig. 8. Angular dependence of the reflectivity calculated under the assumption that a plane wave incident on 3, 6 and 9 layers each infinitely thin and 300 nm in length with a 235 nm interval is diffracted at each layer under normal incidence.

be due to the diffraction effect at each layer and also due to the irregularity in the actual lamellar structure.

The above simple model, 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
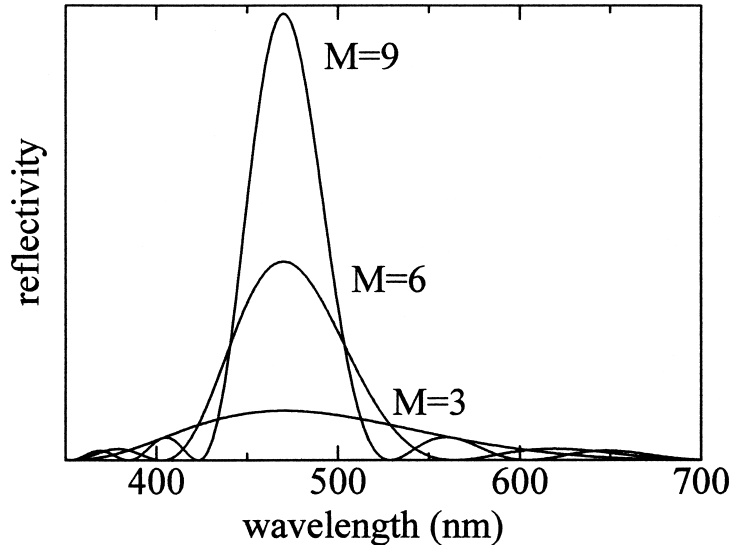
Fig. 9. Reflection spectrum calculated under the assumption that a plane wave incident on 3, 6 and 9 layers each
       infinitely thin and 300 nm in length with a 235 nm interval is diffracted at each layer under normal incidence.

backscattering (VAN ALBADA and LAGENDIJK, 1985; WOLF and MARET, 1985), as it
appears even under 30°-inclined incidence. It is worth mentioning that the agreement
between the experiment and the 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 (KINOSHITA *et al*., 2002). The incorporation of the spatial
correlation causes a modulation corresponding to the diffraction spots due to the interference
between neighboring 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 observed in the experiment may be due to the spread of the tilt angles of the ridges
(VUKUSIC *et al*., 1999).

4.2. High reflectivity

Secondly, we will consider the high reflectivity of the *Morpho* wing. Since the simple
geometrical inspection fails to explain when the ridge spacing is smaller than or comparable
to the wavelength of light, we will consider a general problem of the light reflectivity.
Because of the complexity of the actual lamellar and ridge structures, here we simplify the
model by assuming regularly spaced lamellae having equal heights. Although this model
differs considerably from the actual ridge structure with random height distribution, it may
offer the physical insight into the high reflectivity of the *Morpho* butterfly.

If we consider the spatial Fourier transformation of periodically arranged lamellae, it
is immediately understood that the incident field does not couple directly with the periodic
structure, unless the interval of the lamellae (ridge spacing) fits that of the wave fronts of
the incident light at the interface. In such a case, it couples only with the zeroth order
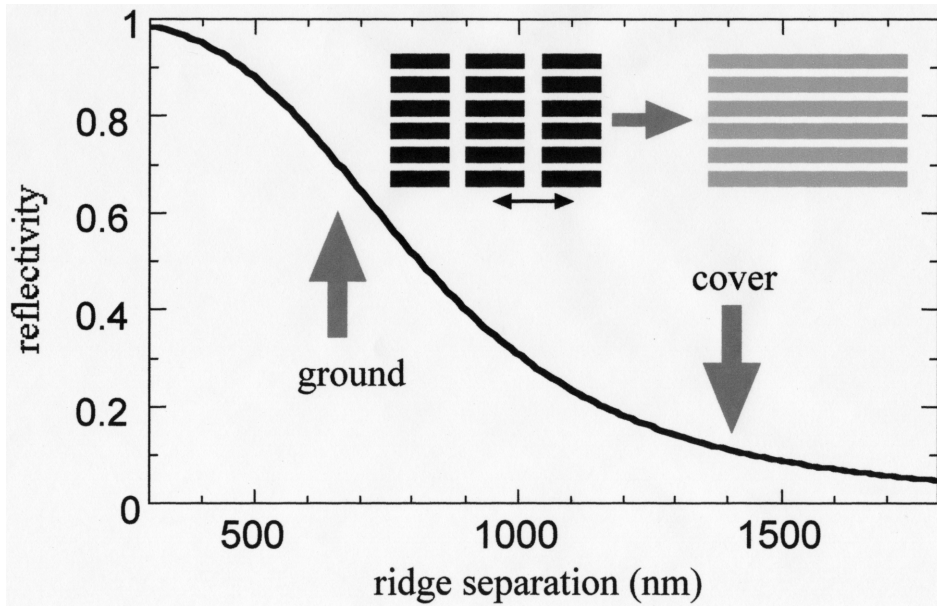
Fig. 10. Reflectivity at 480 nm calculated for alternate layers of air and an averaged dielectric layer corresponding to various ridge separations. The width of the air layer is 145 nm, while that of the averaged dielectric layer is 60 nm. The refractive indices of air and cuticle are taken to be 1.0 and 1.6, respectively. The length of the cuticle layers is assumed to be 300 nm. Arrows show the ridge separations corresponding to ground and cover scales of *M. didius*.

Fourier component of the dielectric layer, i.e. the layer having a spatially averaged dielectric constant (BERNHARD *et al*., 1968; PARKER, 2000). Thus, the *separate lamellae model* is reduced to the simple *multilayer model* with two alternate layers having averaged dielectric constants.

In Fig. 10, we show the reflectivity calculated against the ridge separation using a transfer matrix method (BORN and WOLF, 1975). In this calculation, we employ the width of a cuticle layer as 0.3 μm with the refractive indices of cuticle and air as 1.6 and 1.0, respectively. It is clear that the high reflectivity is maintained roughly to the intervals up to the wavelength of light. Beyond this, the reflectivity decreases quickly. Although the effect of the first- and higher-order diffraction is neglected in this treatment, it may increase the reflectivity slightly. Thus the reflectivity of the *Morpho* wing is determined both by the number of layers in a lamella and by the ratio of the ridge width and separation. A typical example of this effect appears as the difference in reflectivity of the cover and ground scales of *Morpho didius*, where the experimentally determined reflectivity for the former and the latter amounts to 30% and 60% at 480 nm, which are comparable with the present expectations of 10 and 70%, respectively.

The reason of the high reflectivity observed in *M. adonis* is still controversial. It is because its iridescent cover scale has only 2–3 cuticle layers with increasing widths, in

which ordinary discussion based on the ridge-lamella interference seems to be difficult. In fact, the reflectivity for 3 cuticle layers calculated using a simple model shows only one quarter of that for 6 cuticle layers as shown in Fig. 9. We deduce that the following three factors may affect the reflectivity of *M. adonis*. First, a relatively small ridge spacing of 0.5–0.6 μm partly compensates the deficient number of layers. In fact, a simple simulation shows 30% increase of the reflectivity by reducing the ridge spacing from 0.7 to 0.57 μm. Second, in case that cover scales are responsible for the iridescence and do not bear the pigment, the thin-film interference at the base plane of the scale considerably contributes to the reflectivity, which amounts to maximum 19% reflectivity for a layer of the refractive index of 1.6. Finally, the spatial overlap of cover scales piles up the reflectivity incoherently. Of course, it should be added that weakly iridescent ground scales partly contribute to the reflection. The extraordinarily broad reflection spectrum implies that the interference due to a small number of cuticle layers contributes to the spectrum and also the thin-film interference superposes it. However, to clarify its high and broadband reflectivity, further investigations are necessary.

4.3. Effect of pigment

Finally, we will consider the difference of color tones in the two types of *Morpho* species, *M. sulkowskyi* and the other three. Although both microscopic lamellar structures are similar to each other except for *M. adonis*, the apparent wing colors are completely different. The difference is also found in the optical response shown in Fig. 5. Since the lamellar structures of both species equally contribute to the blue reflection around 400–500 nm, the major difference comes from the amount of the absorption and/or background reflection above 530 nm. The absorption in the green to red region is due to the presence of pigment, which is believed to be melanin (Ghiradella, 1998) and is distributed in the base plane of the iridescent ground scale of *M. didius* (Onslow, 1921). The pigment is also distributed in the iridescent scales of *M. rhetenor* and in the weakly iridescent ground scales of *M. adonis*, while only a negligible amount of pigment is recognized in two kinds of iridescent scales of *M. sulkowskyi*.

Thus the presence of the pigment beneath the iridescent scale is important to exhibit the peculiar tones in the *Morpho* butterflies, because it contributes to the absorption of the green to red light and enhances the contrast of blue coloring. The absorption due to the pigment may be effective to reduce the scattering within the scale and at the wing membrane, and also to reduce the transmitted light from the back. Comparing the reflection measurements of an intact wing and a single scale of *M. sulkowskyi*, and also taking the reflection measurement on the wing without ventral scales, we deduce that the background reflection at about 600 nm in this butterfly comes from the light scattering at the wing membrane and ventral scales. Thus the whitish tone of *M. sulkowskyi* originates mainly from the background reflection due to its own structure.

5. Conclusions

The present model, although simplest enough, reproduces the angular dependence of the reflectivity fairly well, which cannot be explained by the multilayer interference model. The physical significance of the above results is summarized as follows (Fig. 11):
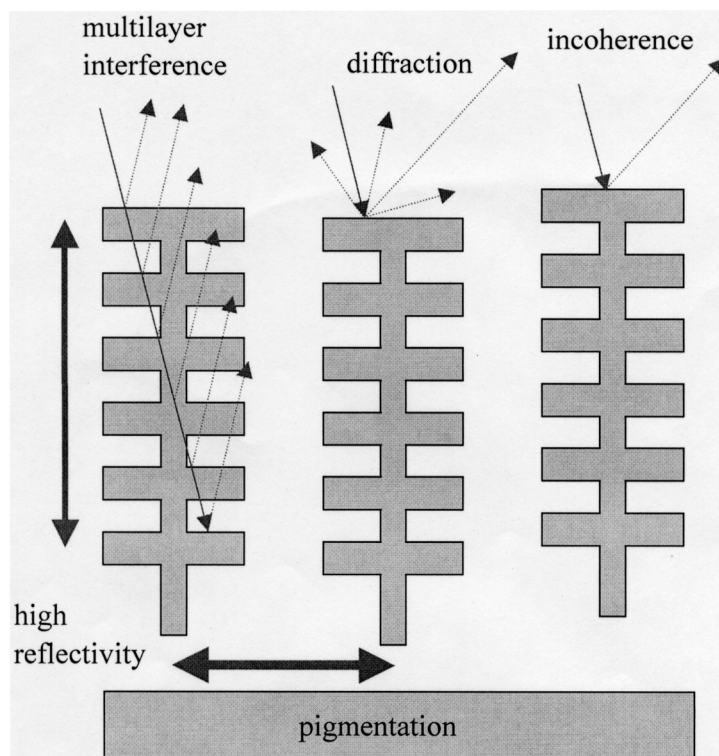
Fig. 11. Schematic view of the factors related to the structural color of the *Morpho* butterflies.

1) The structural color originates mainly from light interference within a lamella on the scale.

2) The irregularity in the ridge height destroys the interference among neighboring lamellae, which results in the diffuse and uniformly distributed reflectance in angle. Thus the combined action of interference and diffraction due to separate lamellae is essential for the structural color of the *Morpho* butterflies.

3) High reflectivity is realized owing to the presence of 6–10 layers in a lamella and sufficiently small separation between adjacent lamellae.

4) The pigment beneath an iridescent scale absorbs the unnecessary green to red light, which reduces the background reflection and enhances the blue structural color. However, the reflectivity and angular dependence in the *M. adonis* wings is still in question. Further investigations are necessary.

From the biological point of view, the wings displaying high brilliancy in a selective wavelength range regardless of the wing inclination are expected to confer the particular hue to each species and to play an important role in mutual recognition of the species. On the other hand, the interaction of light with micro structures is closely related to recent topics in photophysics such as photonic bands, photon localization, near field optics and

so on. Thus, the subject of structural color in the *Morpho* butterfly is of profound interest both in its biological and physical aspects.

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