

Role of photonic-crystal-type structures in the thermal regulation of a Lycaenid butterfly sister species pair

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One of the possible functions of the photonic-crystal structure found on the wing scales of some butterflies is investigated. The optical and electron microscopic investigation of two male butterflies—blue (colored) and brown (discolored)—representing a sister species pair and originating from different altitudes, revealed that the blue color can be attributed unambiguously to the fine, spongelike medium, called “pepper-pot structure,” present between the ridges and the cross ribs in the scales of the colored butterfly. Only traces of this structure can be found on the scales of the discolored butterfly. Other physical measurements, mainly optical reflectivity, transmission, and thermal measurements, are correlated with structural data and simulation results. The thermal measurements reveal that under identical illumination conditions the high-altitude butterfly reaches a temperature 1.3–1.5 times the temperature reached by the low-altitude butterfly. This is attributed to the photonic-crystal-like behavior of the pepper-pot structure, which significantly reduces the penetration of light with wavelength in the blue region of the spectrum into the body of the scales. This sheds some light on the adaptation that enhances the survival chance of the butterfly in a cold environment rich in blue and UV radiation.

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I. INTRODUCTION

Photonic crystals [1] have attracted recently much interest in the physicist community as an excellent tool to manipulate light [2,3] and as a potential route towards building ultrafast fully optical computers [4]. Present days microtechnology and nanotechnology is still in the process of learning how to produce large, defect-free photonic-crystal structures operating in the visible range [5,6].

Interestingly enough, photonic-crystal-like structures have been developed in several species of butterflies [7,8] and beetles [9] during their evolution. A recent review [10] gives an overview of several cases when photonic structures were found in a very wide variety of biological objects, from crabs [11] to 500×10^6 years old fossil animals [12]. Recently, photonic-crystal-like fibers were revealed in a sea mouse [13]. As these structures are the result of hundreds of thousands of years of evolution, it may well be that the animal designs are superior to our own [10]. Even more remarkable, butterflies can change their wing coloration depending on the particular period of the year in which they reach adult status or the geographic region they live in. The coloration of butterfly wings has two main sources: color arising from pigmentation and color arising from the nanostructure of their wing scales, often referred to as “physical color” [14]. Whether through pigmentation or structure, the coloration lies in the scales that cover the surface of the wings. Each scale is a flattened projection of cuticle from a single epider-

mal cell within the epithelial layer that makes up the surface of the wing. Typical scale dimensions are of the order of $50 \mu\text{m}$ by $200 \mu\text{m}$. The scales are built of chitin [15], a biopolymer with excellent mechanical properties, which, if it does not contain pigments, is colorless.

Certain populations of Lycaenid butterflies (Lepidoptera: Lycaenidae) show an interesting phenomenon described by Bálint and Johnson [16] as “discoloration.” In discolored populations the most striking character is that the males do not show bright upper surface structural coloration (iridescent blue, green, purple, or gold)—typifying sexual dimorphism in the family Lycaenidae—but, instead, have the warm brown pigmental color typical of females. The explanation given to the phenomenon of discoloration [16] is based on the thermal-regulation mechanism of butterflies, a crucial aspect for the survival of Lycaenid butterflies in extreme conditions, such as in mountainous regions at altitudes of 2000–2500 m. Male individuals of not discolored populations emerge several days earlier before the emergence of females for setting up perching area or patrolling routes. As butterflies do not possess internal thermal regulation like mammals, prior to their activities in the early morning hours they have to spend considerable time to heat their bodies using the energy of solar radiation. A likely explanation for the change of coloration at high altitudes is that discolored males have better survival rates and, therefore, the chance to reach the time of female emergencies, so that they can reproduce. The discolored males are able to use in a more efficient way the solar radiation, particularly the blue and UV part of the solar spectrum, which are the more intense ones under the condition under which the discolored populations live. The present work is dedicated to the verification of this hy-

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pothesis by physical methods, and to the investigation of the potential use of mechanically robust photonic-crystal-type structures built of materials of biological origin in thermal-regulation applications.

II. EXPERIMENT

Light microscopy was used to identify those scales responsible for the color of the upper side of the butterfly wing. Scanning electron microscopy (SEM) was used to study the fine structure of the scales. For SEM, the samples were covered by a thin, sputtered gold layer to avoid charging effects. Thermal measurements were done in a homemade setup, which is shown schematically as an inset in Fig. 5. Copper-constantan thermocouples were used in a differential mounting. Identical disks of white paper were fixed over the junctions using thermally conducting silicone paste. White paper was chosen as comparison because it is a thin, textured material, with good reflectance in the visible. Moreover, cellulose—the main component of paper—resembles chitin in some chemical and physical properties [15]. The wing pieces were placed over one of the white disks, while the other was left empty. The voltage output of the thermocouples was measured by a digital nanovoltmeter. The ratio of butterfly wing temperatures upon irradiation with artificial light as compared to white paper was calculated according to the equation

$$R(P_i) = \frac{T_{BR}(P_i) - T_{WH}(P_i)}{T_{BL}(P_i) - T_{WH}(P_i)}, \quad (1)$$

where $T_{BR}(P_i)$ is the temperature of the brown butterfly wing, $T_{BL}(P_i)$ is the temperature of the blue wing, $T_{WH}(P_i)$ is the temperature of the white paper, and P_i is the incident light power.

A dual beam fiber illuminator (Perkin Elmer, 41720-series, 150 W, quartz, halogen, color, temperature 3100–3400 K) with variable illumination intensity was used to illuminate under identical conditions the empty white paper disk and the one with the butterfly wing. A light power meter (Spectra Physics 404) operating in the wavelength range of 450–900 nm was used to check whether or not the two beams give equal illumination and to measure the incident power at a distance identical with the distance between the fiber-optic illuminator and the butterfly wing. The spectral distribution of illumination was measured at the lowest and at the highest light power output using a monochromator (SPM2 Zeiss) in combination with a Si detector (Hamamatsu). The transfer function of the monochromator was obtained using a Tungsram blackbody source. Colored glass filters were used to select the red, yellow, green, and blue spectral regions of light emitted by the source. UV-VIS transmission and reflection spectra of the butterfly wings were taken using a spectrophotometer (Perkin Elmer Lambda 15). IR transmission showed the absorption characteristics to melanine [17], no differences were evidenced between the wing pieces. This result, together with the UV-VIS transmission spectra, makes it unlikely that the differences in optical properties may arise from compositional differences.

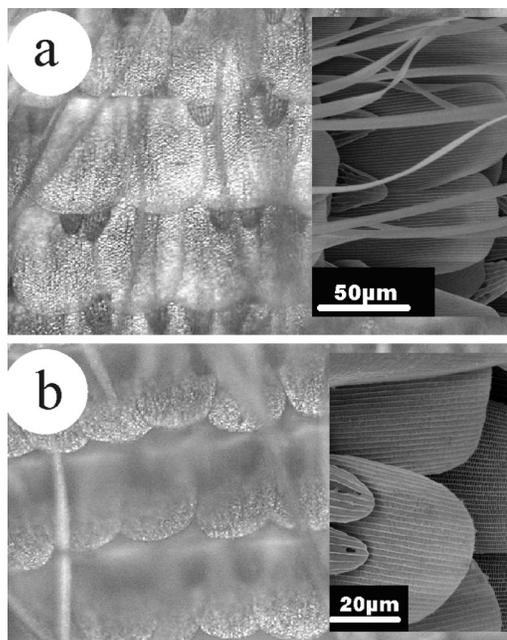


FIG. 1. Low magnification optical microscopy and SEM images (insets) showing the wing of the (a) blue (BL) male and (b) brown (BR) male. One may note that the morphology of the scales is identical.

For testing our hypothesis, we have selected a sister species pair of polyommata Lycaenids belonging to the Daphnis species group or subgenus *Meleageria* de Sagarra, 1925, represented by a nondiscolored and a discolored species.

Five butterfly specimens were investigated in detail: (a) blue-violet male, an Anatolian specimen of *Polyommatus daphnis* (Denis et Schifferemüller, 1775) (low altitude); (b) brown male, an Iranian specimen of *Polyommatus marcidus* (Lederer, 1872), restricted at the high altitude (over 2500 m) slopes of the Elbrus Mountains; (c) blue male, a Pannonian specimen of *Polyommatus daphnis* (Denis et Schifferemüller, 1775) (low altitude); (d) brown female associated with (a); (e) brown-blue female associated with (c). In the present paper the most typical physical similarities and differences between (a) and (b) will be discussed in detail.

The low (optical) and medium (SEM) magnification morphology of the scales of the blue (BL) and of the brown (BR) male butterflies are shown in Fig. 1. The scale morphologies are identical, i.e., both butterflies have the same kind of scales, with rounded ending, which is usually responsible for the blue coloration of male butterflies of the investigated family. By contrast, the female butterflies, usually of brown color, have more elongated scales with a deep zigzag ending, composed usually of three to five fingerlike features.

The medium magnification SEM images reveal that in the micron range the structures of the BL and BR scales are identical. However, the high-resolution SEM images, Fig. 2, show that the fine structure with typical dimensions on the scale of 100 nm is different. The BL scales, Figs. 2(a) and 2(b), exhibit a spongelike structure called “pepper-pot” structure by the entomologists [14,18]; while this structure is mostly absent from the BR scales [as seen in Fig. 2(c), only some very weak traces of the pepper-pot structure can be

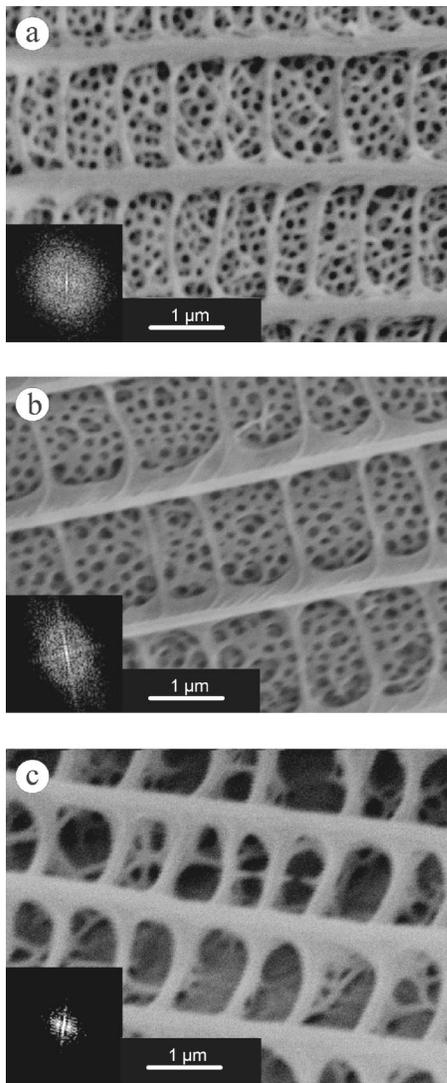


FIG. 2. High-resolution SEM images showing the fine structure of the scales with rounded ends: (a) blue (BL) male, blue region; (b) blue (BL) male, blue-violet region; (c) brown (BR) male. The insets in the lower left-hand corner show the two-dimensional, logarithmic Fourier power spectra of square areas selected from the images. Note that the structural differences between (a) and (b) are manifested as color difference visible to the naked eye, and that in (c) the Fourier spectrum is practically featureless.

found]. A systematic SEM examination of the BL scales revealed that the differences in coloration seen by the naked eye from blue to violet can be associated with morphological modifications of the typical scale structure, as shown in Figs. 2(a) and 2(b). A quantitative evaluation of these differences is given by the two-dimensional logarithmic Fourier power spectra of square areas selected from the images shown as insets in the images in Fig. 2, and by the data in Table I. Table I gives the average hole area, the deviation of the hole from circular shape, calculated as the ratio of largest diameter to smallest diameter, and the fill factor, which gives the fraction of the surface covered by the holes. The data show that the spectral maximum of the increased reflectance given by the photonic-crystal structure (pepper pot) can be finely

TABLE I. Average hole area, deviation from circularity, and (hole) fill factor of the pepper-pot structure on blue-violet and blue regions of the blue male butterfly as calculated from high SEM images.

Color	Average hole area (nm ²)	Average deviation from circularity	Average fill factor (hole)
Blue-violet	9520	1.29	0.802
Blue	11134	1.47	0.746

tuned by the morphology of the structure. The second point worth mentioning is that the investigated spongelike structure, as seen in Fig. 2, allows for relatively large long-range structural disorder without losing the photonic-crystal-like behavior. One may note that the Fourier power spectrum of the BR scale, Fig. 2(c), does not show the spread-out, diffuse ring (round or elongated) characteristic for the other two. It shows some features, which may be attributed to the ridge and cross-rib structure.

Spectroscopic measurements in the UV-VIS spectral range reveal the existence of a marked specular reflectance difference between the BL and BR butterflies. The specular reflectance was measured using white MgO powder as reference. Spectra were taken at several angles of incidence for the BL butterfly from 75° (lowest reflectance values) to 27.5°. The highest reflectance was found for 45°, with slightly lower and almost coincident values at 27.5° and 35°. The comparative measurements between different butterflies were carried out at 27.5°. The difference between the specular reflectance of the BL and the BR butterflies is shown in Fig. 3. The highest reflectance value $I/I_0=0.25$ was measured for BL at 830 nm. One may remark a significant difference between the BL and BR butterflies around 490 nm with an extended shoulder towards the red region. A not so pronounced maximum may be found around 790 nm. In specular reflection measurements only a fraction of the re-

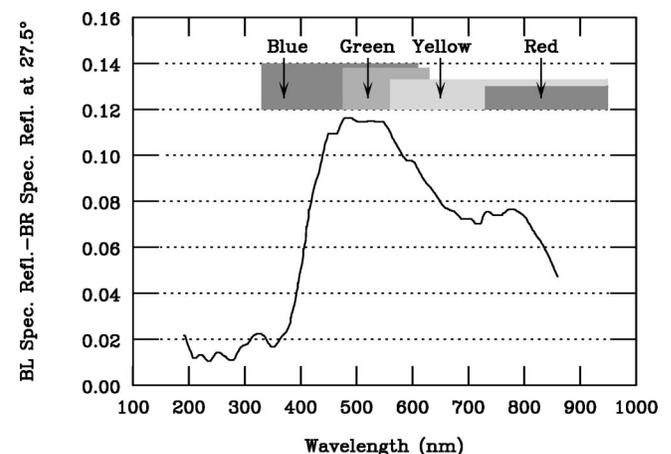


FIG. 3. Specular reflectance difference of the blue (BL) and brown (BR) male butterfly wings, measured at 27.5°. The spectral regions in which the colored glass filters have a transmission higher than 50% are indicated.

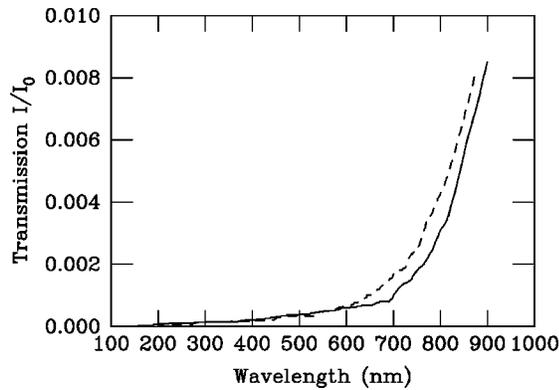


FIG. 4. Transmission spectra of the blue (BL) and the brown (BR) butterfly wings: Continuous line (BL), broken line (BR).

flected light is measured, namely, the fraction reflected under the particular angle under which the measurement is carried out. The blue color of the BL butterfly is seen for a wide range of observation angles from normal to almost glancing angle observation.

The transmission values cannot be interpreted in a straightforward way, taking into account only the scales on the upper side of the wing. The transmitted light must cross the upper scales, transmit through the wing membrane, and finally traverse the scales on the lower wing side. However, the differences in the transmission values of the BL and BR butterflies could show whether there was significant difference in the amount of the pigment contained in the wings. The transmission values measured are shown in Fig. 4; no significant differences are found. Both for the BL and the BR, the overall light intensity transmitted through the three-layer system is negligibly small. One may conclude that practically all the UV-VIS light incident on the upper wing is either reflected by the scales or absorbed by the melanin in the upper scales, the wing membrane, and the lower scales. The differences in the reflectance (Fig. 3) then indicate that, due to the higher reflectivity of the BL butterfly, the BR sample is absorbing a larger amount of energy.

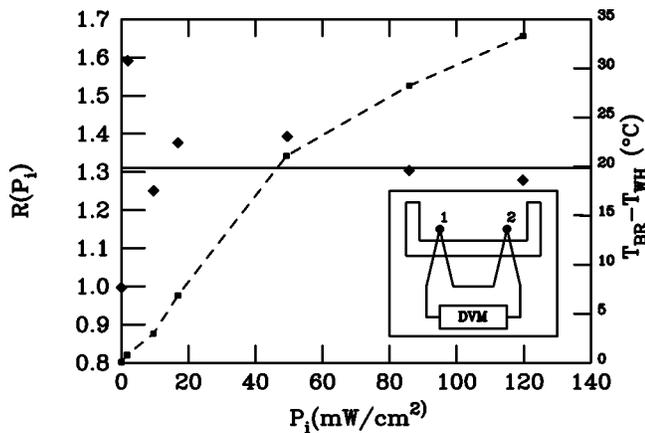


FIG. 5. $R(P_i)$ as measured with unfiltered, artificial light from the fiber-optic illuminator as a function of incident light power density. The temperature difference between the brown (BR) butterfly and white paper is shown on the secondary axis. The inset schematically shows the setup used for the measurement.

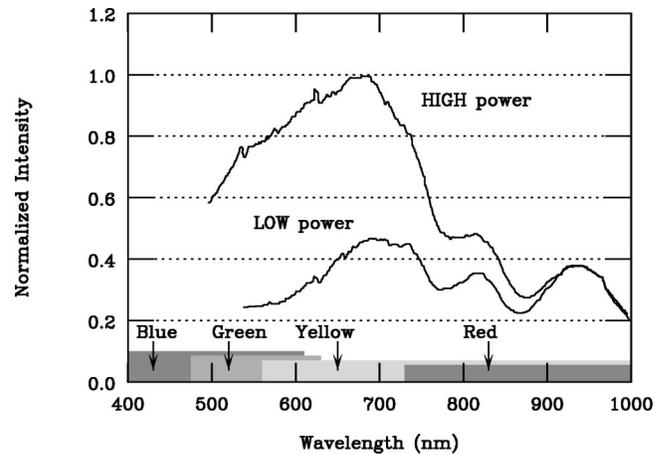


FIG. 6. Spectral distribution of the light from the fiber-optic illuminator at the lowest and the highest illumination intensities. The spectral regions in which the colored glass filters have a transmission higher than 50% are indicated.

To check the heating effect of the illumination on the two kinds of butterfly wings, thermal measurements were carried out using copper-constantan thermocouples in a setup shown in the inset of Fig. 5. After switching on the illumination, the samples were illuminated for 30 min to allow the thermal equilibrium to be established before reading the difference of temperatures. When using white light to illuminate the samples, it was found that the temperature ratio $R(P_i)$ was of the order of 1.3 irrespective of the intensity of illumination, except the lowest illumination intensity used (Fig. 5). The highest temperature difference achieved between the brown butterfly and the white paper was of the order of 32 °C. In order to avoid sample degradation, no higher intensity illumination experiments were carried out.

The spectral distribution of the dual beam fiber-optic illuminator at the lowest and at the highest illumination intensity used is shown in Fig. 6. One may note that when increasing the illumination intensity only a moderate shift in the position of the intensity maximum is found and the most significant variation of the intensity occurs in the green-blue range of the spectrum. The spectral ranges in which the different filters have a 50% transmission are indicated in Fig. 6.

The red, yellow, and green light illumination produced a maximum in the $R(P_i)$ temperature ratio according to Table II, followed by a moderate decrease in the $R(P_i)$ temperature ratio as the incident light power increases. For these three wavelength regions used to illuminate the samples, the $R(P_i)$ ratio showed a horizontal plateau at around 1.3 for

TABLE II. Incident light power values at which the maximum in the BR/BL temperature ratio is produced for red, yellow, and green illumination.

Filter color	Incident light power (mW)	$R(P_i)$ temperature ratio
Red	9.0	1.52
Yellow	2.2	1.45
Green	9.0	1.52

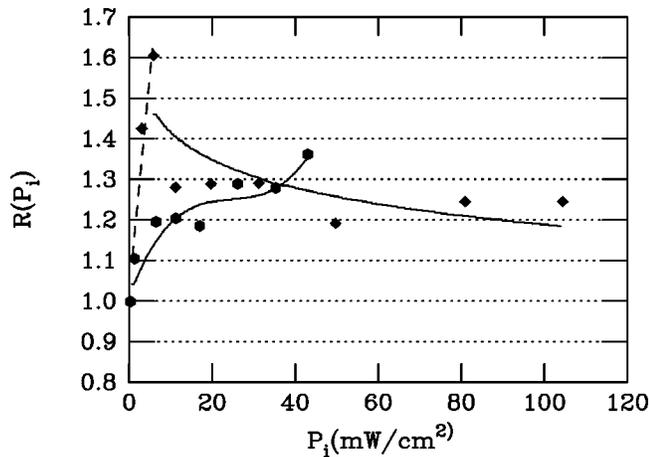


FIG. 7. $R(P_i)$ values for yellow (diamonds) and blue (heavy circles) light illumination, using the colored glass filters. Note that the blue illumination does not produce a maximum in the range of available light power densities.

light power densities higher than 20 mW/cm^2 . The blue illumination did not produce any maximum in the $R(P_i)$ ratio, and this ratio did not reach saturation in the range of available illumination intensities. The curves for yellow and blue light illumination are shown in Fig. 7.

III. DISCUSSION

The amount of energy that can be used to modify the sample temperature depends on the radiative energy penetrating into the material and the capacity of the material to absorb this energy. Melanins are organic pigments present in many living beings, including humans. These pigments absorb the light very efficiently in the near UV and visible [19,20]. In particular, the brown melanin present in butterfly wing scales [21] absorbs in the entire UV-VIS range as shown by the transmission data of Fig. 4. Therefore, the UV-VIS light, at wavelengths at which it can penetrate the material of the scales, will be absorbed. The penetration of light into the scale for certain wavelength regions can be reduced or even forbidden by the photonic-crystal-type structure seen in the high-resolution SEM images of Fig. 2. Even with low dielectric constants, perfect three-dimensional photonic crystals can have direction-dependent gaps in their transmission spectrum. In these regions and directions, the penetration of the electromagnetic waves is strongly limited by the evanescence of the fields, and therefore the pigments present in the structure produce very little absorption. According to theoretical calculations [22,23], the introduction of structural disorder may partially destroy this kind of photonic stop bands, with the consequence that the medium is more easily penetrable [24,25]. On the other hand, recent work has shown that amorphous photonic crystals may also have similar incomplete photonic gaps [26]. In the case of the BL butterfly, the increased reflectance in the visible and, in particular, in the blue region of the spectrum, Fig. 3, appears to be due to such an incomplete gap. This increase in the reflectance will result in a less efficient heating under

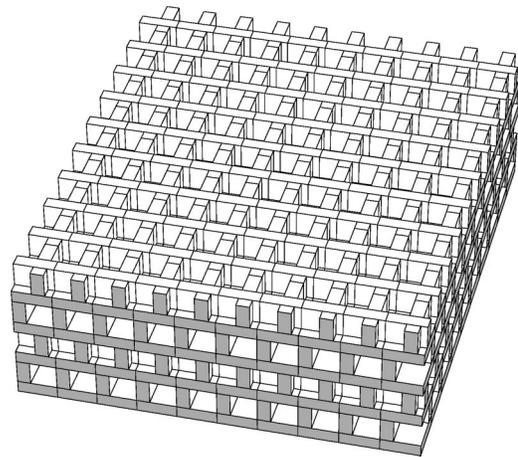


FIG. 8. Model structure built on the basis of high-resolution SEM images used in the computer simulation of the photonic crystal. The periodic structure is made of two identical layers, each $0.2 \mu\text{m}$ thick. All chitin walls (dielectric constant $2.25 + 0.1i$) are assumed to have a mean thickness of $0.066 \mu\text{m}$. The lateral unit cell is rectangular, $0.24 \mu\text{m}$ by $0.2 \mu\text{m}$.

identical illumination as compared with the BR butterfly, Figs. 5 and 7. Due to the fact that the pigment content of the butterfly wings does not differ neither in the visible nor in the IR region of the spectrum, the differences found in the reflectance, and consequently in the heating, can be attributed only to the presence of the fine structure observed between the ridges and the cross ribs in Figs. 2(a) and 2(b), and which is absent in Fig. 2(c). This structure acts as a photonic band gap material (PBG) that does not allow the deep penetration of the light in the structure in the wavelength region corresponding to the gap [27].

In support of the interpretation of the reflectance data reported in Fig. 3, a computer model was built and reflection coefficients computed from this model. The difficulty is that the geometry of the pepper-pot structure is strongly disordered. So, we will provide a reasonably ordered structure with average parameters, and check the result with an auxiliary model containing significant geometric variations. The theoretical structure, shown in Fig. 8, consists of a stack of four ordered layers, each $0.2 \mu\text{m}$ thick. Considering the average size of the holes in the pepper-pot sponge, the film is given a periodic structure in the lateral directions (parallel to the scales), with a rectangular unit cell of $0.2 \mu\text{m}$ by $0.24 \mu\text{m}$ (the latter along the light incidence plane). The two-dimensional unit cell is itself a two-story structure, with the upper layer identical to the lower layer, except for an overall half-period displacement in both lateral directions. This multilayer model was developed taking into account the structural data of Tilley *et al.* [18]. All chitin walls in this structure have been given a thickness of $0.066 \mu\text{m}$, with a refractive index of 1.5. A calculation of the reflectance of this layer has been performed using a transfer-matrix approach similar to that reported by Pendry and Mackunnon [28]. This provides the theoretical result shown as a solid line in Fig. 9, which should be compared to the experimental data given in Fig. 3. The dotted line, in Fig. 9, shows the reflectance of a variant model. Compared to the model shown in Fig. 8, the

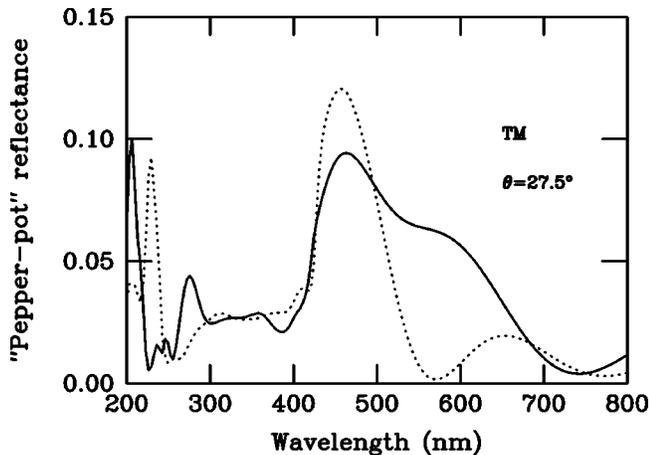


FIG. 9. Reflectance values (solid line) of the pepper-pot structure as calculated from the computer model (see Fig. 8), to be correlated with the measurements described in Fig. 3. The dotted line refers to a second, independent model, where parallelepipedic cavities are replaced by ellipsoids.

lateral periodicity has been conserved, and the parallelepipedic cavities have been replaced by hollow ellipsoids. Also, the layer thickness has been very slightly reduced (from 0.2 to 0.19 μm). The lateral half diameters of these ellipsoids are set to 0.087 μm (along the incidence direction) and 0.066 μm , while the vertical half diameter is 0.066 μm . The center of the ellipsoid lies one half diameter (0.066 μm) deep. The convergence of the results provided by these models, shown in Fig. 9, confirms that the coloration spectrum in Fig. 3 most likely originates from the pepper-pot structure.

The natural photonic band gap material (n -PBG) on the BL butterfly scale has a “filtering” effect for the incoming radiation. The efficiency of the filtering is determined by the selectivity of the filter. Qualitatively speaking, this efficiency may be characterized by the magnitude of the difference in reflectance between the BL and the BR scales at the wavelength of the incoming radiation, Figs. 3 and 9. In the case of nonmonochromatic illumination, the slope that characterizes the reflectance difference curve in the spectral range of the illumination used has a further influence on the filtering efficiency. When using low power illumination in combination with the colored glass filters, the n -PBG filter can achieve good selectivity. The increase in the incident light power will make the filtering by the n -PBG filter less efficient. This is mainly due to the fact that the increase of the power of the incident white light from the source can be associated with the broadening of the wavelength region in which light is transmitted through the filter. The smaller red slope of the curve showing the reflectance difference due to the n -PBG material, Figs. 3 and 9, in combination with the secondary maximum on the red side, Fig. 3, will decrease the selectivity. As a consequence, for the red, yellow, and green illumination, after a maximum is achieved in the temperature difference of the BR and BL butterfly wings at low illumination power, this difference is decreased at higher power illumination. An undiminished selectivity is found for the blue illumination.

The question of heat regulation, attributed to multilayer structures in butterfly wing scales of iridescent type, was briefly discussed by Roush [29]. Somewhat contradictory results were found between the species *Urania fulgens fulgens* (Lepidoptera: Uraniidae) and *Papilio palinurus* (Lepidoptera: Papilionidae): the scales from *Papilio palinurus* absorbed significantly more energy than those of *Urania fulgens*, although the chitin layers in *Papilio palinurus* are only 1/100 μm thinner [29]. These contradictory findings support the idea that not only the layer thickness may be important but the particular fine structure inside the layers, too, i.e., a full three-dimensional quasiperiodic structure, which is in certain sense similar to the structures needed to produce artificial PBG materials. The fine structure of scales of *Papilio palinurus* was discussed recently by Vukusic and co-workers [30]. They showed that the coloration is a result of reflection on a thin film multilayer structure, i.e., the light has to penetrate through the layers of the structure that allows for absorption. This may explain the observed differences [29] assuming that the color of *Urania fulgens* is produced by a PBG structure that does not permit light penetration into the scale, therefore no or less absorption may take place.

Coming to the question of the reason for which the discoloration of the male butterflies living at high altitudes is produced, one has to take into account that the male butterflies emerge several days before the emergence of females. The males living in the thermally hostile environment characteristic for alpine regions, the better they were able to use the blue and near UV radiation to accumulate heat, the higher survival chances they had till the moment they could reproduce. It is worth pointing out that for sunlight, the UV and blue light are best transmitted through cloudy skies and that at high altitudes the UV radiation is stronger than at sea level, so that the more efficient use of the radiation in this spectral range can constitute a successful survival strategy. This, along with the fact that the morphologies of isolated butterfly populations are often highly derived, suggests that, at least in the *Polyommatus* group of genera studied by Bálint and Johnson [16] (i) discoloration is a derived condition and (ii) discolored populations often greatly similar in external features, have generally arisen through adaptive convergence.

IV. CONCLUSIONS

The comparison of the nanostructure and of the optical spectroscopy data taken from the wings of the blue (BL) and brown (BR) male Lycaenid butterflies with computer simulation results showed that the blue color of the BL male is produced by the so-called “pepper-pot-” type fine structure, which is absent in the BR male. The pepper-pot structure acts as a natural photonic band gap (PBG) material causing the increased reflectance in the spectral range from blue to near UV. The absence of the pepper-pot structure reflects that the BR butterfly can absorb energy from the light falling on its wings in a more efficient way. It is believed that this adaptive modification in the color of the male Lycaenid butterflies

living at high altitudes is a consequence of better survival chances till reproduction takes place, associated with the more efficient energy absorption from solar radiation. The thermal characteristics of PBG materials have been less investigated up to now. Our results show that beyond their applicability in optical devices, PBG materials may find useful applications in thermal management too. Taking into account that the pepper-pot structure is far from being as perfect as artificially produced PBG materials, it is likely that the manufacturing conditions are less strict for PBG materials to be used in thermal applications. We also observed PBG-type behavior in a biopolymer, such as chitin, which is closely related to cellulose, which is an extensively used material. As potential practical applications in thermal management, one may think of mechanically robust and at the same time flexible thermal protection in hot environments such as deserts, or solar radiation shielding in space station and space suits, where the mass to be lifted into orbit is a critical issue.

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