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Iridescence and spectral filtering of the gyroid-type photonic crystals in *Parides sesostris* wing scales

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The cover scales on the wing of the Emerald-patched Cattleheart butterfly, *Parides sesostris*, contain gyroid-type biological photonic crystals that brightly reflect green light. A pigment, which absorbs maximally at approximately 395 nm, is immersed predominantly throughout the elaborate upper lamina. This pigment acts as a long-pass filter shaping the reflectance spectrum of the underlying photonic crystals. The additional effect of the filtering is that the spatial distribution of the scale reflectance is approximately angle-independent, leading to a stable wing pattern contrast. The spectral tuning of the original reflectance is verified by photonic band structure modelling.

Keywords: photonic crystal; Papilionidae; optical filtering; iridescence; biomaterials

1. INTRODUCTION

The brilliant body colours of many animals are due to the specific interaction of incident light with complex structured assemblies of biomaterial that have refractive index variations of the order of the wavelengths of visible light [1–3]. The structural colours are especially diverse in butterflies. Their wing scales have a wide variety of nanostructures with several levels of complexity [4]. The biological function of the structural colorations is mostly for communication and display [5] and also for camouflage [6].

The structural colours of a number of papilionids and lycaenids are produced by three-dimensional biological photonic crystals, which were recently identified as single-network gyroid-type photonic crystals [6–10]. The unit cell defining the crystal is composed of a network of the biomaterial chitin and air. The structure is defined by a minimal surface, the inter-material dividing surface, which divides the two interconnected networks. Gyroids are special in that their chiral structure gives rise to circular dichroism (CD), i.e. the reflectance of incident circular-polarized light depends on the handedness [9,11].

A beautiful representative of the butterflies with brightly coloured scales is the Emerald-patched Cattleheart,

Parides sesostris, native to the Americas (figure 1*a*). Earlier studies have unequivocally identified photonic crystals in the green cover scales. The crystals are assemblies with gyroid-type morphology [7,8] with a chitin filling fraction between 30 and 40 per cent and a cubic unit cell size in the range of 280–330 nm. The photonic crystals are covered by a thick lamellar structure, called a honeycomb [9]. The green scales reflect incident light diffusely and show no specific scale iridescence when illuminated from the side of the honeycomb, which is the case when the green scales are attached to the wing. However, clear iridescence is observed when an isolated green scale is illuminated from the opposite side [3]. Poladian *et al.* [9] suggested that the honeycomb functions in suppressing the iridescence of the photonic crystal by acting either as a collimating or a diffusing structure.

In the present paper, we revisit the photonic structure of *P. sesostris* scales and show that the suppression of the photonic crystals' iridescence is mainly achieved owing to a pigment immersed throughout the honeycomb structure which in addition acts as a scattering device, thus randomizing light propagation. By photonic band structure modelling, we show how the pigment narrows the intrinsic reflectance spectrum of the photonic structure.

2. MATERIAL AND METHODS

2.1. Animals

The investigated specimens of the Emerald-patched Cattleheart, *P. sesostris* (Cramer, 1779; Papilionidae),

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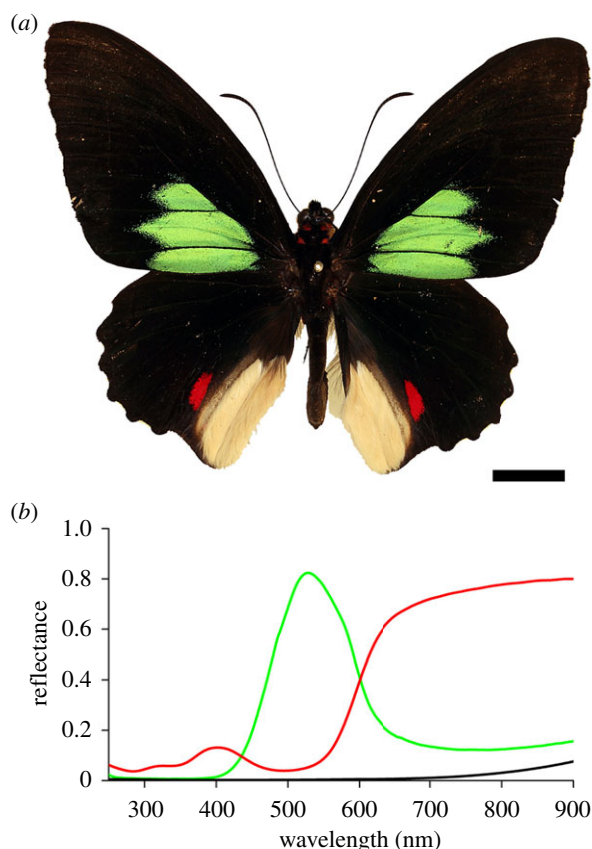


Figure 1. Emerald-patched Cattleheart, *Parides sesostris*. (a) Photograph showing the upper side of the butterfly with large, green-coloured spots on the forewing and smaller, red spots on the hindwing, framed by black borders. Scale bar, 1 cm. (b) Reflectance spectra of the green- and red-coloured wing patches and the black frame of the upper side of the butterfly wing. Green solid line, green patches; red solid line, red patches; black solid line, black patches.

caught in Satipo, Peru, were obtained through Tropical Butterflies and Insects of America (Tampa, FL, USA).

2.2. Photography

A specimen of *P. sesostris* of the Lepidoptera collection in the Natural History Museum Naturalis (Leiden, The Netherlands; curator Dr B. van Bekkum-Ansari) was photographed with a Canon EOS-30D camera equipped with an F70 macro-objective and a Nikon SB-800 flash (figure 1a). Details of the scale arrangement on the wings were photographed with a Zeiss Axioskop microscope (Carl Zeiss AG, Oberkochen, Germany), applying epi-illumination and using a Kappa DX-40 (Kappa optronics GmbH, Gleichen, Germany) digital camera. For fluorescence photographs, 450–490 nm or 510–560 nm excitation light was used and the emission was filtered by a 520 or a 590 nm high-pass filter, respectively.

2.3. Spectrophotometry

The absorbance spectrum of the pigment in the green wing scales of *P. sesostris* was calculated from transmittance spectra obtained from single wing scales, immersed in a fluid with refractive index 1.56 (Cargille

Labs, Cedar Grove, NJ, USA), and measured with a microspectrophotometer; a Leitz-Ortholux microscope with a 20/0.46 Olympus objective, connected to an AvaSpec-2048-2 spectrometer (Avantes, Eerbeek, The Netherlands). Reflectance spectra of intact wings were measured with a bifurcated probe (Avantes FCR-7UV200) connected to the AvaSpec-2048-2 spectrometer. The light source was a xenon or a Deuterium-Halogen (Avantes D(H)-S) lamp. For the reflectance measurements, a white diffuse reflectance tile (Avantes WS-2) served as a reference.

2.4. Imaging scatterometry

The far-field spatial distribution of the light scattered from single scales and wing patches, glued to the end of pulled micropipettes, was visualized with an imaging scatterometer (ISM). The scatterometer is built around an ellipsoidal mirror, which collects light from a full hemisphere around its first focal point where the sample is positioned [12]. A small piece of magnesium oxide served as a white diffuse reference object. Images were acquired with an Olympus DP-70 camera and were subsequently corrected for geometrical distortions using a Matlab-routine.

2.5. Scanning electron microscopy

The anatomical structure of the wing scales was investigated, after sputtering with palladium, with a Philips XL30-ESEM scanning electron microscope (SEM).

2.6. Photonic band structure modelling

We modelled the single-network gyroid structure using the MIT photonic band structure solver [13]. The filling function of a single-network gyroid lattice is given by Schwartz' G surface:

$$f(X, Y, Z) = \sin X \cos Y + \sin Y \cos Z + \cos X \sin Z,$$

where $X = 2\pi x/a$, $Y = 2\pi y/a$ and $Z = 2\pi z/a$, with x , y and z being the coordinates of the cubic basic structure with lattice constant a ; for the *P. sesostris* scales, we took $a = 310$ nm. A threshold parameter t defines the separation between the interconnected cuticle and air networks and thus determines the filling fraction of the material in the unit cell. In the case where the volume is filled with cuticle ($f(X, Y, Z) < t$), the refractive index of the material was set to $n(X, Y, Z) = 1.56$; for the air-filled volume areas ($f(X, Y, Z) \geq t$), the refractive index was $n(X, Y, Z) = 1$. The threshold was set to -0.3 , resulting in a cuticle filling fraction of approximately 40 per cent [3,7].

3. RESULTS

3.1. Optical appearance and scale fluorescence

The visual appearance of the butterfly *P. sesostris* is quite striking: while the overall colour of the upper side of the wings is jet-black, owing to highly melanized scales, large green spots dominate the forewings and smaller red spots mark the hindwings (figure 1a). The

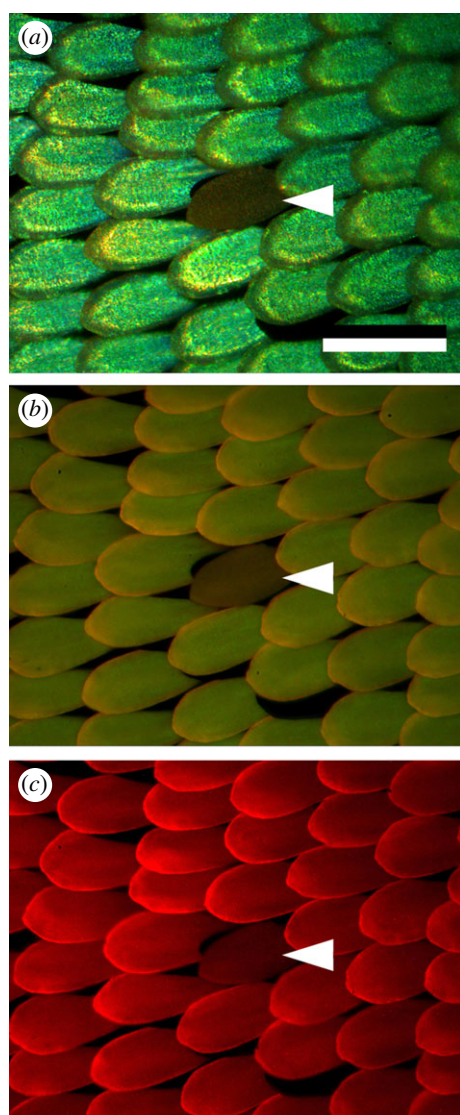


Figure 2. Reflection and fluorescence of the scales in the green wing area. (a) RGB photograph with white light epi-illumination. A dense lattice of green-coloured cover scales is seen above dark brown ground scales. An aberrant ochre scale is seen (white arrowhead). (b) Blue-induced green–yellow fluorescence. (c) Green-induced red fluorescence. The ochre scale fluoresces more weakly than the green scales. Scale bar, 100 μm .

green areas have a metallic appearance, clearly indicating a structural basis for the coloration, but the red spots display a more diffuse coloration. Spectral measurements with a bifurcated probe yield distinctly different reflectance spectra with shapes, suggesting that the green colour has indeed a structural basis and that the red colour is owing to a pigment that only absorbs in the short and middle wavelength ranges (figure 1b).

Observing the green wing areas with an epi-illumination microscope shows a dense lattice of green-coloured cover scales with black ground scales seen below them (figure 2a). The green colour remains virtually identical upon rotation of the wings, suggesting the presence of a diffusive structure. Very occasionally, aberrant ochre-coloured cover scales can be observed as part of the original scale assembly (white arrowheads in figure 2),

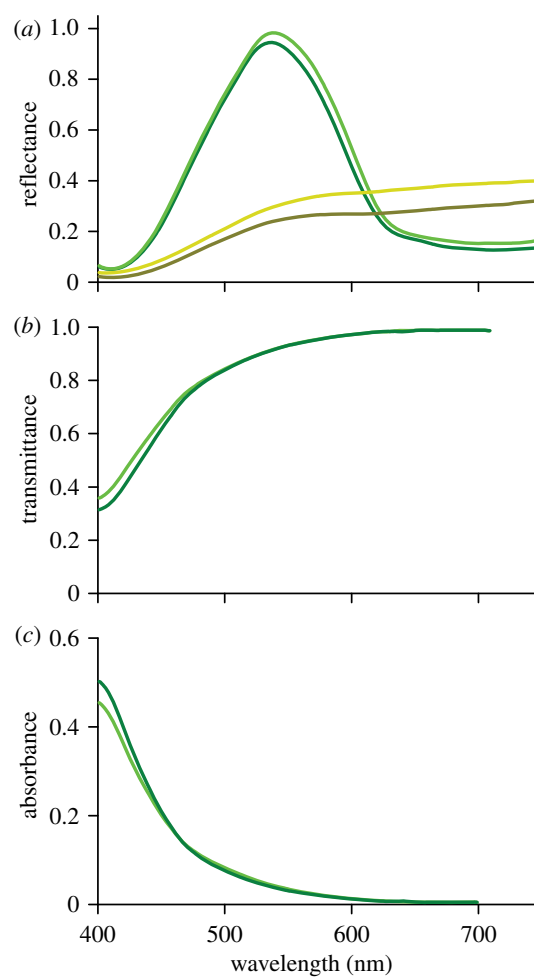


Figure 3. Reflectance and transmittance spectra of cover scales. (a) Reflectance spectra of two green and two ochre scales on an excised wing patch. (b) Transmittance spectra of two isolated green scales immersed in a fluid with refractive index $n = 1.56$. (c) Absorbance spectra calculated from the transmittance spectra.

indicating the presence of a short-wavelength absorbing pigment. We therefore further investigated the pigment distribution by using the fluorescence attachment of the microscope. Blue- and green-excitation light revealed that the cover scales distinctly fluoresce (figure 2b,c). The colours of the emission of the green and ochre scales observed with blue and green excitation light are very similar, although the fluorescence of the ochre scales is somewhat weaker. This indicates that the different scale types contain the same pigment, and that the amount of pigment is smaller in the ochre scales.

To characterize the pigment, we measured the reflectance and transmittance spectra of single cover scales with a microspectrophotometer (figure 3). The reflectance spectra of individual green cover scales have a peak wavelength $\lambda = 540 \pm 5$ nm and closely resemble the probe spectra (figure 1b). The reflectance spectra of the ochre scales are virtually flat above $\lambda \sim 550$ nm, but the reflectance decreases with decreasing wavelength, presumably owing to the short-wavelength absorbing pigment [14]. We measured transmittance spectra of isolated green cover scales immersed in a

fluid with refractive index $n = 1.56$; this value is close to that of butterfly scale chitin [15]. The measured spectra indeed revealed a distinct short-wavelength absorbing pigment. The transmittance spectra of the green cover scales and the reflectance spectra of the ochre scales have very similar shapes, confirming the assumption above that the same pigment is present in the green and ochre scales. The transmittance spectra, $T(\lambda)$, straightforwardly yield absorbance spectra, $A(\lambda)$, of the pigment via $A(\lambda) = -\log_{10}[T(\lambda)]$ (figure 3c).

3.2. Scale ultrastructure

We investigated the anatomy of the *Parides* scales with SEM (figure 4a; see also fig. 21 of Ghiradella [4]). Both cover and ground scales are composed of two laminae. The ground scales have a classical shape [4] with a thin, about flat lower lamina and a structured upper lamina with ridges and crossribs (arrowhead in figure 4a and electronic supplementary material, figure S2). The cover scales are very differently and much more elaborately structured. The upper lamina, thickness 3–5 μm , has a ‘honeycomb’ structure [9], which is basically a stretched and elaborated version of the upper lamina of the ground scales. The honeycomb consists of tall ridges connected by numerous crossribs [4]. The lower lamina is thin and about as flat as in the ground scales, but a prominent layer exists in between the upper and lower lamina of the cover scales. This layer, with thickness $4.0 \pm 0.3 \mu\text{m}$ [9], consists of domains of single-network gyroid photonic crystals [7,8]. We determined a typical domain size of approximately $5 \times 5 \mu\text{m}^2$ and for the cubic unit cell size of the gyroid photonic crystals $310 \pm 30 \text{ nm}$, in agreement with previous studies [7,8].

The presence of the crystal domains can also be demonstrated by light microscopy. When observing the cover scales from the adwing (under side) through an epi-illumination polarization microscope with crossed analyser and polarizer, differently coloured domains are strikingly visible (figure 4b). The intensity of the domain reflections strongly varies upon rotation of the scale. When scales are observed from the abwing (upper side), the domains are vaguely visible, apparently due to the filtering and diffusing effects of the honeycomb structure in the upper lamina (figure 4c; see also electronic supplementary material, figure S1).

3.3. Iridescence of the wing scales

We further investigated the effect of the honeycomb in the upper lamina on the reflection properties of the photonic crystal layer by imaging scatterometry. Single wing scales were glued to the tip of pulled glass micropipettes, and we then measured the spatial scattering profiles applying white-light illumination with variable apertures [12,16]. Figure 5a presents the scatterogram of a single cover scale owing to about normal, narrow aperture (approx. 5°) illumination with white light. The scattering pattern is very directional and marked by a green line. The line is presumably owing to diffraction at the raster of parallel ridges that extends out of the upper lamina, because

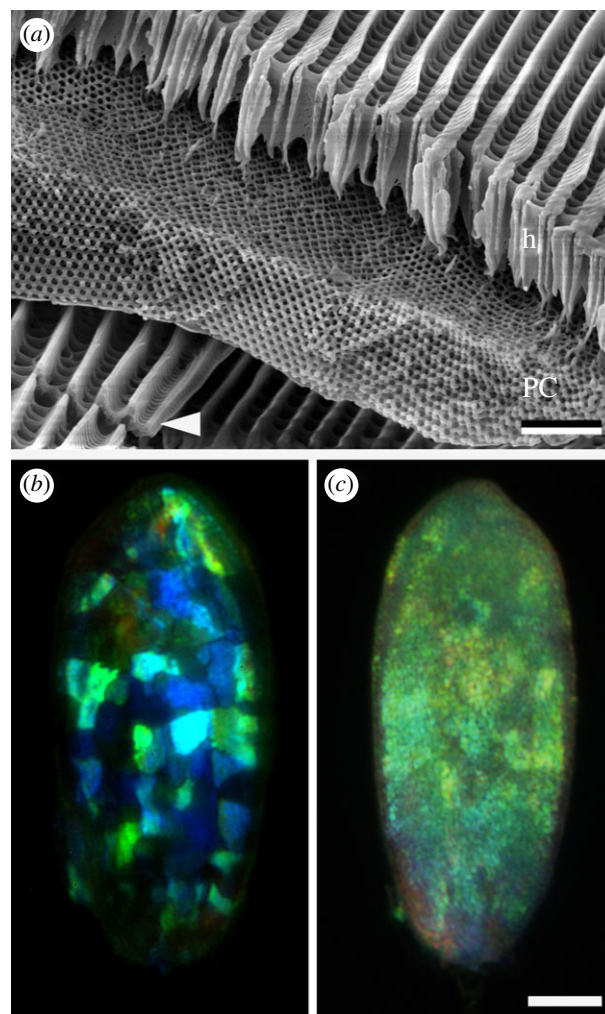


Figure 4. Anatomy of a cover scale and filter effects. (a) SEM of a fractured scale showing the structural composition of the scale. The approximately 5 μm thick single-network gyroid photonic crystal layer (PC) is covered by the approximately 5 μm honeycomb structure (h), acting as a pigment filter. Note the undifferentiated ground scale below the cover scale (white arrowhead). Scale bar, 2 μm . (b) A single scale upside-down observed through crossed polarizers. (c) A single scale upside-up observed through crossed polarizers. Single domains are clearly visible when the scale is upside-down (b), but are indiscernible in the normal scale orientation (c). Scale bar, 20 μm .

similar diffraction lines are seen in the scattergrams of other scales with clear ridges, notably in *Morpho* butterflies [12] and pierids [17,18]. The scatterogram additionally features a diffuse green background. This runs counter to what may be expected for ideal photonic crystals. When the domains are large, illumination with a narrow aperture beam creates a single prominent spot [19], and when the domains are small-grain, a diffuse scatterogram with discernible spots results [6]. Presumably therefore, the honeycomb in the upper layer of the green scales affects the reflection properties of the gyroid-type photonic crystals (figure 4b).

To further assess the effect of the upper pigment filter on the photonic crystal reflection, we illuminated the under and the upper side of a single scale with a wide-aperture white-light beam (figure 5b,c). The resulting scatterogram of the upper side is green and

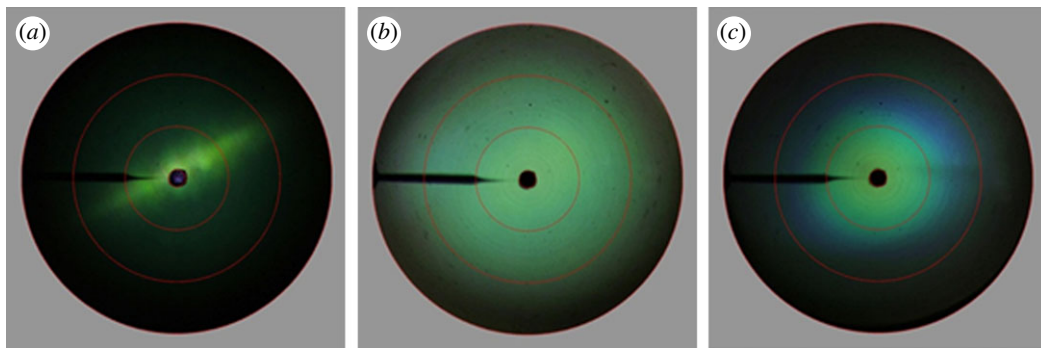


Figure 5. Scattering patterns of a single cover scale. (a) Narrow-beam white-light illumination. The scattering is primarily a restricted line. (b,c) Wide-aperture white-light illumination of the upper side (b) and the under side (c) of a single scale. The scattering by the scale upper (abwing) side is green and virtually angle-independent, while scattering by the under (adwing) side shows strong iridescence, i.e. a blue shift occurs with an increasing angle of light incidence. The red circles indicate scattering angles of 5° , 30° , 60° and 90° .

approximately angle-independent. Reflectance measurements from various spots in the scatterogram using an optical fibre [18,20] indeed showed no changes in the spectra with changes of the detection angle or polarization of the incident light. The under side of the scale however showed strong iridescence, i.e. the peak wavelength changed with the angle of light incidence and observation (figure 5c). The reflectance in the centre of the scatterogram is mainly green-coloured, identical to the reflected light with normal illumination of the upper side. For larger scattering angles, greater than 30° , the reflected colour is strongly blue-shifted. We hence conclude that the upper honeycomb layer acts as both a diffuser for the reflected light and a suppressor of the iridescence of the gyroid photonic crystals.

3.4. Photonic band structure diagram modelling

To understand the impact of the pigment filter on the ‘original’ photonic response of the photonic crystals, we simulated the photonic response of an ideal gyroid photonic crystal using a block-iterative frequency-domain solver for Maxwell’s equations [13]. We calculated the photonic band structure diagram (PBD) for a chitin-filling fraction of 40 per cent ($t = -0.3$), converted into wavelengths by using a unit cell size of $a = 310$ nm (figure 6). Constructive interference happens only for paths lying on the outer borders of the first Brillouin zone (FBZ) of the underlying unit cell structure, because Bragg’s law is fulfilled for these space points. For the gyroid morphology in the wing scales, the underlying unit cell is base-centred cubic and the FBZ thus has face-centred cubic symmetry [21,22].

The peak reflectance of the photonic crystals in the *P. sesostris* green scales strongly changes with their orientation. For the investigated crystal structure, the longest peak wavelength (the mid of the bandgap) of approximately 560 nm is predicted for a crystal oriented with point *N* upwards, while for a *H*-oriented crystal a multi-peaked reflectance with a minimal peak of approximately 395 nm is predicted. With a peak wavelength ratio of the lowest and highest wavelength of approximately 1.43 [9], this iridescence is quite strong for an unfiltered gyroid structure.

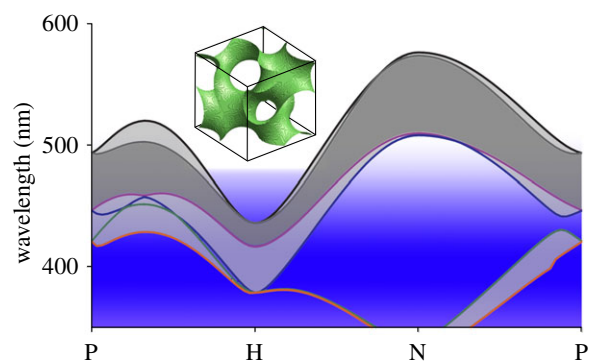


Figure 6. Photonic band structure diagram of the single-network gyroid PC of *P. sesostris* of which the lowest six bands are shown. The photonic bandgap opens between separated bands, causing reflection of incident light in the regime between the bands (grey shaded areas). The abscissa indicates the high-symmetry points of the first Brillouin zone determining the reflectance from the photonic crystal (see text). Further, the absorption range of the pigment filtering the reflection of the photonic crystal is indicated by the blue area. The inset shows the unit cell of the gyroid nanostructure used for modelling.

The measured reflectance spectra had peak wavelengths at 540 ± 10 nm, while the pigment in the upper layer absorbs below 450 nm (figure 6, blue band). Figure 6 illustrates that the pigment filter strongly suppresses the gyroid photonic crystal’s iridescence. The filtering narrows the reflectance spectrum to the wavelength range of 450–600 nm. Consequently, blue- and UV-reflecting crystals (figure 4b) do not contribute to the overall wing colour.

4. DISCUSSION

4.1. Function of the pigment filter

The scales in the brilliant green-coloured wing areas of *P. sesostris* have a special photonic system consisting of a layer with a honeycomb structure on the top of a layer with differently oriented gyroid-type photonic crystals (figure 4a). The honeycomb structure contains a pigment, absorbing in the UV- and blue-wavelength

range, which acts as a dense optical filter in front of the photonic crystals. The diffusive honeycomb causes approximately angle-independent scattering (figure 5 and electronic supplementary material, figure S1), confirming the hypothesis of Poladian *et al.* [9]. We furthermore demonstrated that the filter curtails the reflectance spectrum of the photonic crystal layer to the green wavelength range (figure 6; see also fig. 15 of Poladian *et al.* [9]). The filter effectively narrows the reflectance spectrum, and thus creates the brilliant metallic green colour observed on the intact wing (figure 1*a*). The PBD modelling thus shows that an angle-independent green colour using a multi-domain gyroid photonic crystal layer can be well achieved with selective spectral filtering.

A less obvious function of the absorbing pigment filter is the elimination of CD. For the topologically comparable gyroid-type photonic crystals of the Green Hairstreak, *Callophrys rubi*, a strong CD has been predicted to exist in the UV- and blue-wavelength ranges, from about 370 to 440 nm (*H*-orientated crystal, figure 6; [9–11]; see also fig. 2 of Saba *et al.* [11]). In the green scales of *P. sesostris*, these wavelength ranges are absorbed (and thus the CD is eliminated there) by the frontal pigment filter. Polarization-dependent spectral measurements from the scatterograms of scales illuminated from the upper side (figure 4*b*) indeed showed no significant polarization dependency.

4.2. Combination of structural and pigmentary coloration

Optical filtering of structural coloration by a frontal pigment layer very similar to that of *P. sesostris* was recently discovered in the *Papilio nireus* group [23,24]. In the butterflies of the *nireus* group, a frontal UV-absorbing filter tunes the reflectance of a thin film structure and, as in *P. sesostris* scales, suppresses the angle dependency of the reflectance spectrum. The same tuning principle of selective filtering the spectral reflectance of photonic structures appears to exist also in other butterfly groups, e.g. in Heliconiinae (A. J. M. Vey, B. D. Wilts & D. G. Stavenga 2011, unpublished data) and in birds [25]. The common, unstructured butterfly scales, which are built according to a basic *bauplan* [1,4], approximate ideal diffusers. When these scales contain a spectrally selective absorbing pigment, their diffusive properties result in a dull, angle-independent coloration, as in the typical papilionid ground scales (figure 4*a*, see also [4]), and in the red spots on the hindwings of *P. sesostris* (figure 1*a*).

4.3. Biological implications

The presented photonic mechanism produces angle-independent, green-coloured wing patches, which together with the intense black surrounding wing parts create a high-contrast signal [26] that provides a high within-pattern colour contrast contributing to the conspicuousness of the animals [27,28]. The green and red wing patches presumably serve as an aposematic signal, because *Parides* species are known to elicit aversive behaviour from bird predators [29].

Many insect species exhibit green coloration for camouflage [6,7], generally produced by structural coloration except for a few rare cases [30].

4.4. Photonic structures in butterflies

The three-dimensional gyroid-type photonic crystals in the wing scales of *P. sesostris* are not unique. All three-dimensional photonic crystals in butterflies have been identified to be of the gyroid type [7,8,10]. They occur in different families, e.g. the lycaenids and papilionids. Saranathan *et al.* [8] recently demonstrated that specific interactions of the cell plasma membrane and the intracellular smooth endoplasmatic reticulum initiate the development of the gyroid networks in the nascent wing scales by cubic membrane folding.

Interestingly, other minimal surfaces, as simple cubic-type (P) or the diamond-type (D) photonic crystals have not been found in butterflies. Diamond-type photonic crystals have been identified in beetles [1,19,31,32], but gyroid-type photonic crystals have not been discovered in beetles, so far. This suggests the hypothesis that the developmental pathways in different insect groups are fundamentally different, but it also poses the question if different crystal types, as gyroid- or diamond-type crystals with different iridescent and polarization characteristics have special advantages for the different insects. As mentioned above, the different crystal types seem to be developmentally constrained to different groups of insects. For butterflies, as *C. rubi*, it was shown that the gyroid-type photonic crystals are advantageous in foliaceous background for camouflage against predators but they simultaneously can serve as an identification signal to conspecifics [6].

The green-coloured wing areas of papilionids are realized with various optical mechanisms. While the Emerald-patched Cattleheart, *P. sesostris*, and the Kaiser-i-Hind butterfly, *Teinopalpus imperialis*, apply three-dimensional photonic crystals [7–9,33] to the Common Bluebottle, *Graphium sarpedon*, a stable green coloration is achieved by the sole use of a combination of different pigments in the wing substrate [30], and in the Peacock, *Papilio blumei*, the wing scales' lumen is filled with a stack of tilted multilayers, which result in additive mixing of yellow and blue colours to achieve a bright green coloration [34]. The diversity of optimized photonic structures present in butterflies and other animals [1,2,7,33] may provide a valuable source for bioinspired applications [31,35,36].

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