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Optical coloration mechanism of beetle elytra: a review

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Abstract: In nature, structural colors are widely observed in various living organisms, resulting from intricate nano-structural designs developed through evolution. Beetles, with over 350,000 species, exhibit a remarkable diversity of colors, many of which are structural rather than pigment-based. These structural colors arise from optical processes such as film interference, diffraction grating, light scattering and photonic crystals. Additionally, some beetle elytra can change color, aiding in survival through camouflage, communication, and environmental adaptation. This review explores the fundamental optical mechanisms of structural colors, and then survey three color change ways of beetle elytra. The summary of basic researches can help scientists to further investigate biomimetic materials about structural color.

1. Introduction

There are two main causes of color in the biological world: pigment color and structural color. On the one hand, pigment color usually refers to organic pigments. Pigment compounds exhibit different colors through selectively absorbing, reflecting and transmitting specific wavelengths of light. And the mechanism of color formation of pigment involves molecular orbital theory. The main pigments are carotenoids, melanin, indigo, quinones, porphyrins and so on which appear gorgeous colors. However, the pigments are unstable and easy to fade when exposed to light and oxidizing compounds. On the other hand, structural color is the color formed when light is reflected, scattered, interfered or diffracted in the microstructure [1,2]. That is to say, the structural color is generated by the microstructure, and the colors will not fade if the microstructures do not change. It is more environmentally friendly that the using of structural color instead of pigment coatings in industry, textile, printing, construction, aerospace, military and other fields. The color saturation generated by the microstructure is higher, giving wide ranges of application prospects in the functions of display, decoration, anti-counterfeiting, sensing and so on.

The beetle comes with more than 350,000 species (Coleoptera). After millions of years of survival evolution, they are not only different in shape and colour, but some beetles can also change their body colour [3, 4]. The forewings (also called elytra) of beetles are horny and the hind wings are membranous. The elytra cover the upper part of the beetle body, protecting its membranous hind wings and back, and the light weight and high strength of elytra can help improve its flight lift [5]. In addition, the beetle elytra have multiple functions such as deterring, intimidating opponents, attracting mates, camouflaging predators, regulating body temperature and preventing water evaporation in terms of colour, morphological structure and material properties [3, 6]. The colour of elytra changes in different ways, such as reversible colour changes, irreversible colour changes and angle dependent colour changes [7-9]. The colour appearances of many beetles are achieved by structural colors. In this paper we summarise the main mechanisms of optical coloration discovered in beetle elytra.

2. Fundamental Optical Mechanisms Related to Structural Colors

2.1. Interference

The structural colour formation mechanism of beetle elytra mainly includes thin film interference, grating diffraction, scattering and photonic crystal. Thin film interference includes single-layer thin film interference and multi-layer thin film interference. The single-layer thin film forms a single color and play low saturation, while multi-layer thin film structure formed a diverse and bright color. Because the refractive index of the multilayer is different, the light refracts into the multilayer film, and reflects at the upper and lower interfaces of each film, and the refracted light and the reflected light interfere with each other to form the interference of the multilayer film. According to the layer thickness and periodic arrangement of the multilayer structure, the interference of the multilayer film can be divided into three types: The first type is that the layer thickness of the layer pile does not change and the periodic distribution is uniform (Figure 1a); The second type is the layer thickness of the layer pile decreasing or increasing along the vertical direction of the film and is periodically distributed, which is called "chirped layer pile" (Figure 1b). The third type is the layer thickness of the layer pile, which changes irregularly and is randomly distributed, which is called "chaotic layer pile" (Figure 1c) [10].

The body surface of the Japanese beetle (*Chrysochroa fulgidissima*) shows a gorgeous rainbow color, and its body color changes when viewed from different angles, as shown in Figure 1d [11]. The color changes of the front, back and side body surface of beetles were observed from 0°, 20° and 30°, respectively. The body color of the front, back and side is green, orange and purple at 0°, respectively. The body color changes to dark green and blue, gold and yellow-green, red and orange at 20° and 30°, respectively. The cross-sectional microstructures of the green part on the front, the orange part on the back and the purple part on the side of the beetle were observed at 0°. It was found that the internal microstructures of these three parts were uniform multi-layer structures with different layer thickness, as shown in Figure 1e. The layer thickness and refractive index of the multilayer structures of the front, back and side sections of the beetle's body surface make it show different colors. When observed from different angles, the wavelength of light entering the human eye after light is reflected and refracted through these three different multilayer structures changes, so it shows different colors.

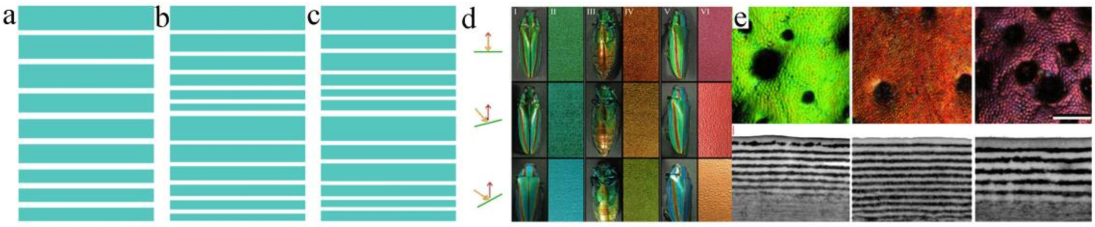

Figure 1: Interference structure of multilayer films, *Chrysochroa fulgidissima* and its cross-section microstructure: (a) non-varying layer thickness layer, (b) chirped layer and (c) chaotic layer [10]; (d) colour changes of the front, back, and side of the beetle at 0°, 20°, and 30° viewing angles and (e) microstructures of its front, back, and side elytra sections [11].

2.2. Grating Diffraction

Diffraction refers to the phenomenon that light waves deviate from the original straight-line propagation when they encounter obstacles. The diffraction of beetle elytra is mainly reflected grating diffraction (grating refers to the barrier formed by parallel slits of equal width and spacing). As shown in Figure 2a, multiple beams of light interfere with each other to form diffraction phenomenon after the monochromatic light and mixed light pass through each slit of the grating. The grating equation is $h \sin\theta_m = m\lambda$ for monochromatic incident light, and $h(\sin\alpha \pm \sin\theta_m) = m\lambda$ for mixed incident light (m is the order of diffraction spectrum; α is the incidence angle and θ_m is the diffraction angle. h is the grating constant, that is, the sum of the slit width p and the width w of the opaque part between the slit, λ is the wavelength).

The beetle (*Aglyptinus tumerus*) elytra surface has a diffraction grating structure, as shown in Figure 2b [3]. When white light is irradiated on the beetle elytra, the diffraction grating on its surface breaks down the white light and reflects and refracts light of different wavelengths from the grating at different angles to form an ordered rainbow color sequence. As a result, the elytra surface presents a brilliant rainbow color, as shown in Figure 2c [12].

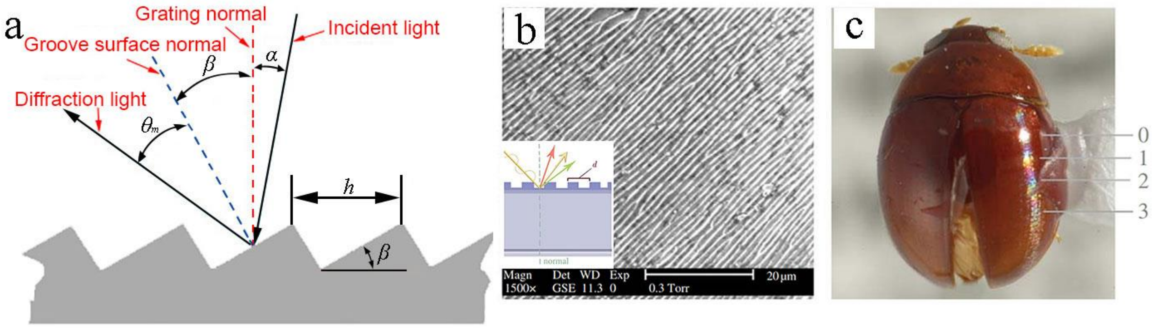

Figure 2: (a) Grating diffraction; (b) the surface microstructure and structure model of the beetle (*Aglyptinus tumerus*) elytra and (c) the iridescence of the beetle body surface [3].

2.3. Scattering

Scattering refers to the phenomenon that a light beam spreads out in all directions when it passes through an inhomogeneous medium. According to the different sizes of scattered particles, scattering can be divided into Rayleigh scattering, Mi scattering, large particle scattering and Raman scattering.

The relationship between the scattering particle linearity a and the wavelength of the incident light satisfies $a<0.1\lambda$. And the wavelength of the scattered light is the same as that of the incident light, and the intensity of the scattered light I is inversely proportional to the fourth power of the wavelength, that is, $I \propto \lambda^{-4}$.

The wavelength of the scattered light is consistent with that of the incident light, and the intensity of the scattered light fluctuates with the increase of the particle linearity, and the amplitude of the fluctuation decreases with the increase of the particle linearity. For large particle scattering, the scattering particle linearity is greater than 10 times the incident light wavelength, that is, $a>10\lambda$, and the scattering light intensity and wavelength are dull.

The beetle (*Cyphochilus*) is white, and its elytra surface is densely distributed with white scales 250 μm long, 100 μm wide and 7 μm thick, as shown in Figure 3. Observation of its internal microstructure reveals random cross-linked network filamentous structures (filamentous structures less than 1 μm long and about 250nm in diameter). Its duty cycle is about 60%); The filamentous network structure inside the scales scatter light which enters the elytra, causing irregular reflection and refraction of light of different wavelengths. After entering the human eye, the light in all visible wavelengths is fused together. Therefore, the elytra of the beetle are white in visual observation [13].

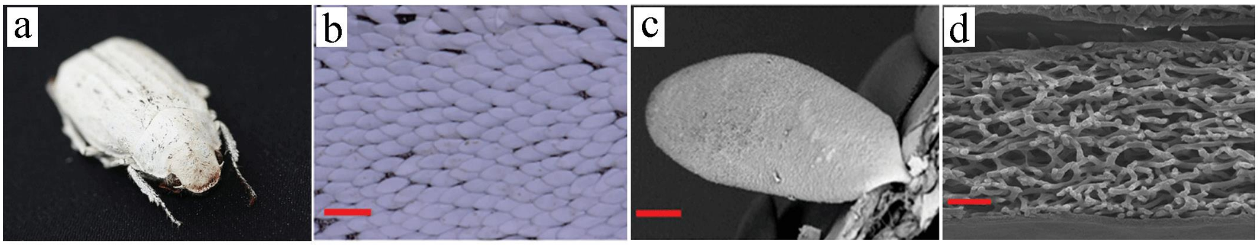

Figure 3: (a) The beetle (*Cyphochilus*); (b) densely distributed scales on the elytra; (c) individual scales; (d) internal structure of scales [13].

2.4. Photonic Crystal

Photonic crystals are composed of materials with different dielectric constants that are periodically arranged in space. When electromagnetic waves propagate in photonic crystals, they follow the principles of refraction, reflection and transmission. Periodic Bragg scattering of electrons modulates electromagnetic waves and forms an electron band. These bands are called photonic energy bands. Under the condition of suitable lattice constant and dielectric constant ratio, there can be a frequency region between the photonic bands of the photonic crystal, which makes the electromagnetic wave of certain frequencies completely impenetrable, and this frequency region is called photonic band gap. Photonic crystals can be divided into one-dimensional photonic crystals, two-dimensional photonic crystals and three-dimensional photonic crystals.

One-dimensional photonic crystal is a structure formed by alternating accumulation of two dielectric blocks with different dielectric constants (Figure 4a), such as the reflection/penetration film of optical multilayer in Fabry-Perot cavity. Two-dimensional photonic crystals are structures with periodic permittivity in two-dimensional space. The typical two-dimensional photonic crystal structure consists of some round or square dielectric columns arranged into hexagonal crystal system (triangular or graphite structure) in the air background, or air holes arranged regularly in the media background (Figure 4b). The dielectric constant of two-dimensional photonic crystals is a function of space period in the direction perpendicular to the dielectric column, but does not change with the spatial position in the direction parallel to the column. Therefore, two-dimensional photonic crystals are periodic in the X-Y plane and continuously invariant in the Z direction. Three-dimensional photonic crystal is a spatial periodic structure composed of squares of two media (Figure 4c), which has periodicity in the X-Y-Z plane, that is, it has a frequency cut-off band in three directions, rather than a photonic band gap in one or two directions, so it is called an omnidirectional photonic band gap.

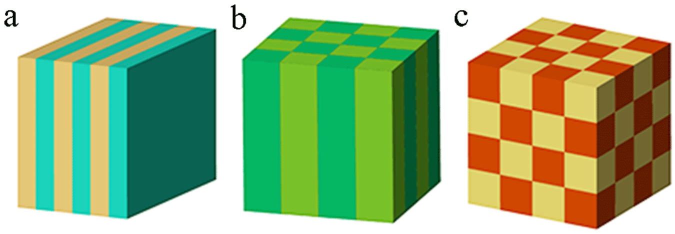

Figure 4: Photonic crystals: (a) one-dimensional photonic crystals; (b) two-dimensional photonic crystals; (c) three-dimensional photonic crystals [14].

There are few researches on one-dimensional photonic crystal in biological structure color. Two-dimensional photonic crystal structure mainly exists in bird feathers, while three-dimensional photonic crystal structure is mainly in beetle elytra. The elytron of the weevils (*Lamprocyphus augustu*) has a metallic orange-yellow color, but the edges appear green (Figure 5a). Observations under an optical microscope show that it is closely packed with scales (Figure 5b). The epidermis on the scale was excised with focused ion beam (FIB) and the internal microstructure was found to be inconsistent by scanning electron microscopy (SEM) observation (Figure 5c). With the white dotted line as the dividing line, the photonic crystal structure on the left and the right are arranged in different ways, and the photonic crystal structure on the left is tilted 60 ° compared to the right. The scale section was resected step by step, and it was found that the pattern of the holes on the surface changed every time the section was resected at 238 nm. The structures are all in regular arrangement. Therefore, the two photonic crystal structures observed under SEM are actually one photonic crystal structure. The structural units as shown in Figure 5d were established, and the structural units were regularly arranged by tilting 33.6 °, 37.5 °, 34.2 °, 88.2 °, 89.6 ° and 91.8 ° in six dimensions relative to the Z-axis, respectively. The structure model is shown in Figure 5e [15]. The photonic crystal structure arrangement of the model at different angles is basically consistent with the results observed under SEM.

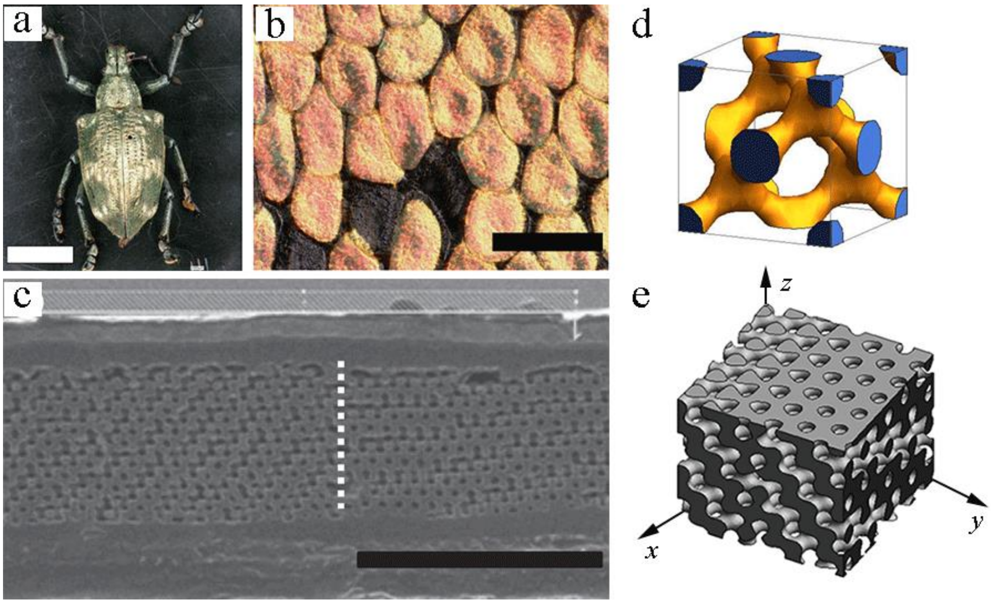

Figure 5: Weevils (*Lamprocyphus augustu*); (b) Scales on the elytra; (c) photonic crystal structure within scales; (d) photonic crystal structure unit; (e) Photonic crystal structure model [15].

3. Colour Changes of elytra

3.1. Reversible Colour Changes

The beetle (*Tmesisternus isabellae*) appears green in dry environments and red in high humidity environments [16]. There is multilayer structure with two different layers stacked alternately in the beetle elytra: the black layer is a homogeneous protein layer with a thickness of 100 nm-110 nm; the other layer is a mixed layer composed of melanin nanoparticles and air holes, with a layer thickness of 70 nm-80 nm. In a high humidity environment, the two different layer structures will absorb water and expand, then the air holes of the mixed layer will be filled with water. However, its melanin nanoparticles will not absorb water and expand. Therefore, the two factors that cause the color change of the beetle in a high humidity environment are as follows: the refraction index of the air part of the mixed layers changes from 1.0 to the refraction index of water 1.33 when the air part of the mixed layer fills with water; and the refraction and transmission of light incident to the layer are increased due to the swelling of the protein layer caused by water absorption.

When the beetle (*Charidotella egregia*) is stimulated, its cuticle color changes from gold to red within 30 s-120 s [17]. When the color changes from gold to red, the reflectance decreases continuously, and the peaks at 560 nm, 640 nm and 810 nm gradually disappear with the decrease of reflectance. The reflectance curves tend to be horizontal without peaks after 2 min. There is also multilayer structure with distributed pores in the beetle elytra. When there is no external stimulation, the pores in the multilayer structure are filled with body fluids, and the golden metallic luster on the body surface is caused by the reflection and interference of light between the multilayer structures. When the beetle is stimulated by the outside world, the body fluid in the pores disappears, the multilayer structure is in a dry state, the metal luster on the body surface disappears, and then pigment color appears with brick red.

3.2. Irreversible Colour Changes

Harmonia axyridis shows no significant difference between individuals from larva to pupal stage, and the body color changes after adults, which is irreversible [18]. The distribution of black spots on the orange or yellow surface of elytra was varied. The number of spots was also different, ranging from 0 to 20. In the optical testing, the reflectance curve of the black speckled part showed almost no fluctuation, while the reflectance curve of the orange part showed a peak value at 600 nm, indicating that the different wavelengths of light to the black part was almost same. In addition, the spectrum of the orange and black speckled part shows the peaks resulting from the action between the multilayer film and the light. When the beetle was soaked in hydrogen peroxide for 12 hours, its elytra were discolored, meaning the presence of pigment in the black spots and orange parts. It is well known that the color of pigment compounds will be faded after oxidizing. The microstructure of the black spots and orange parts of the elytra are both dense multi-layer structures. Therefore, the color formation of the different color parts of the elytra is mainly caused by the pigmented color and structural color of multilayer structure.

The beetle (*Ceroglossus suturalis*) has two distinct metallic sheen body colours, brown and green, which change irreversibly as adults [19]. Both brown and green beetles have ribbed structures with a series of convex hull and pits, and multilayer in cross-section. The epicuticle of the green beetle elytra is 9 layers structures with light and dark periods, and the thickness of the light and dark layers is 100 nm and 60 nm, respectively. The epicuticle of the brown beetle elytra is 20 layers with light and dark periods, and the thickness of the light and dark layers is 120 nm and 70 nm, respectively. According to the theoretical spectral calculation of the layer thickness of the multilayer structure, the reflectance peaks of the green and brown beetle elytra is 556 nm and 644 nm, respectively, which are consistent with their colors. Therefore, the metallic luster colors of the brown and green beetle elytra surfaces are the result of the integration of the multilayer structure and surface microstructure.

3.3. Angle-Dependent Colour Changes

The surface of *Chlorophila obscuripennis* elytra was observed under high-power optical microscope and SEM. It was found that the uplifted part was green and the depressed part was green-blue. Both of the uplifted and depressed parts are multilayer structures, but the layer thickness is different. The thickness of light layer is 90 nm and 78 nm for the uplifted and depressed parts, respectively. And the thickness of dark layer is 66 nm. Multi-angle optical tests were conducted on elytra at 0°, 20°, 40° and 60°, and the reflectance peaks were obtained at 520 nm, 506 nm, 477 nm and 446 nm of wavelength, respectively. The iridescence green-blue color of elytra and its angle-dependent color change are mainly formed by the interference of the multilayer structure in epicuticle [20].

The black beetle (*Lomaptera*) appears iridescent under strong diffuse lighting [21]. The sawtooth diffraction grating with a grating constant of 1.45 μm was found to be regularly distributed on the surface of elytron. Under the grating, there is an alternating light-dark multilayer structure (the thickness of the dark layer is 119 nm, and the thickness of the light layer is 67 nm), and the total number of layers is about 90. However, no reflectance curve consistent with the optical calculation of the multilayer structure was found in the test results. Therefore, the angle-dependent color change of the elytron is mainly caused by diffracted light on the grating and then forming rainbow color bands on the black surface.

4. Conclusions

The optical coloration mechanisms of beetle elytra exemplify nature's ingenuity in achieving vivid, dynamic, and durable colors through nano structural engineering. Structural colors, arising from film interference, diffraction gratings, light scattering and photonic crystals, offer significant advantages over pigment-based coloration, including higher saturation, resistance to fading, and environmental sustainability. Beetles leverage structural color not only for aesthetic purposes but also for critical survival functions with reversible, irreversible and angle-dependent colour changes.

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