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Role of Color Interference on the Insect's Cuticle Coloration

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Abstract: ***Interference colors result from the reflection of light from a series of neighboring interfaces that are separated by distances comparable with a quarter of the wavelength of light. .Interference colors are common in some adults of Lepidoptera insects. The integument layers producing interference are formed by modifications of the scales. Each of the blue scales of the Morpho rhetenor butterfly, for instance, consists of a flat basal plate carrying a large number of near-parallel vertically aligned ridges that run parallel with the length of the scale. Within each ridge are series of horizontal layers, separated by air spaces. Collectively, the horizontal layers in each adjacent ridge form a series of reflecting surfaces, which are spaced such that a blue color is produced by interference. Interference colors in other insects are produced by reflection at the interfaces of layers in the cuticle which differ in refractive index. The refractive indices of the alternating layers in the pupa of the danaid butterfly, Euploea mulciber, are 1.58 and 1.37. In jewel beetles, Chrysochroa fulgidissima Buprestidae and tiger beetles, Cicindela japonica (Cicindellidae), these layers are in the exocuticle, but in tortoise beetles (Cassidinae) and some butterfly pupae they are in the endocuticle. Interference is responsible for the iridescence of the membranous wings of many different insects, particularly Odonata.***

Keywords: Interference colors, insect integument, refractive index, cuticle layers

1. Introduction

Color is not an inherent property of objects; it is a perceptual attribute that depends on illumination, the spectral reflectance of an object and its surroundings, as well as the spectral receptor types and further neural processing in the animal in question. Thus the same object might appear differently colored to different viewing organisms. Insects are master chemists whose virtuosity is particularly evident in the design of the cuticle, the nonliving material that makes up the exoskeleton and serves as the boundary between the living animal and the outside world [1].

Cuticle, a composite of chitin fibrils and various proteins and lipids, can be tailored for strength, rigidity, flexibility, permeability, or elasticity, as needs dictate. It is also a technical and artistic medium with which insects, who are also master physicists and optical engineers, manipulate light to attire themselves with brilliant color on their bodies and wings. "Light" by definition involves wavelengths within the visible part of the electromagnetic spectrum. For humans it consists of wavelengths ranging from approximately 400 nm (violet) to approximately 725 nm (red). Many organisms, including insects, extend this range into the near ultraviolet (300^100nm). "White" light for a particular organism consists of all wavelengths visible to that organism. Colored light has an incomplete spectrum in which only some wavelengths are represented. Matter interacts with white light in various ways to produce color. The Color production in biological systems may be divided into two principle categories: the first is usually associated with chemical processes such as absorption and luminescence; the second relates entirely to coherent scattering processes that underpin the interaction of light with materials that have periodic variations in refractive index [2]. One way is by selective absorption of particular wavelengths by a chemical, or pigment. The absorbed wavelengths (which are determined by the pigment's molecular structure) are essentially subtracted from the total spectrum, whereas the rest are reflected or transmitted to produce the visible color. Because pigments subtract colors, as additional pigments are added to a mix, additional wavelengths are absorbed and lost to view, changing the perceived color. When all wavelengths of the visible spectrum are absorbed, we call the sensation "black." Pigmentary colors may be found in the cuticle or, if that is transparent, in the underlying tissues and even in the gut contents. A second basis for color is structural, caused by the interaction of white light with minute and precise arrays on or in the material. The effects depend on the architecture, rather than the chemical makeup of the material. Light may be reflected, refracted, diffracted or scattered, but it is not absorbed, and so structural colors are "additive": if two are combined, both sets of wavelengths are represented in the final effect. If all wavelengths of the visible spectrum are reflected, we call the sensation "white."

2. Insect Cuticle And Color Interference

Color is generated from white light incident upon an insect when some of the incident wavelengths are eliminated, usually by absorption in its pigmentation, and the remainder are scattered. These scattered wavelengths of the reflected or transmitted components determine the color observed. There are many mechanisms by which structural colors can be produced. All depend directly or indirectly on the fact that a particular piece of material scatters or refracts different wavelengths of light to different degrees. This property of the material can be expressed in terms of its index of refraction (n) a measure of the degree to which a given wavelength of light entering the material is "retarded" or slowed down. For insect cuticle (n) typically ranges from 1.5 for long-wave (red) light to 1.6 for short-wave (UV) light, although in special cases $n < 1.4$ has been reported (for comparison, n for air is by definition 1). Structural colors described so far in biological systems fall into two general classes, scattering and interference.

2.1. Color Scattering

Light may be scattered (i.e., reflected in all directions) by granules on, or irregularities in, a surface. (Fig. 2). At least some of the component wavelengths of the beam will be reflected in random directions, including toward the observer. If the scattering agents are relatively large (700 nm or more), all visible wavelengths are scattered, and the resulting color is a matte white (the color of whole milk is an example of such scattering). If the particles are smaller (in the 400 nm range), the short wavelengths are scattered to a much greater degree than the long ones, which tend to pass on through the system and not reach the eye of the observer. The resulting color, Tyndall blue, is commonly seen in blue eyes and blue jay feathers; in insects it occurs in blue dragonflies and in some blue butterflies. Often, the blue structure is underlaid by a layer of ommochrome pigments, which, as mentioned above, deepen and intensify the color by absorbing stray light.

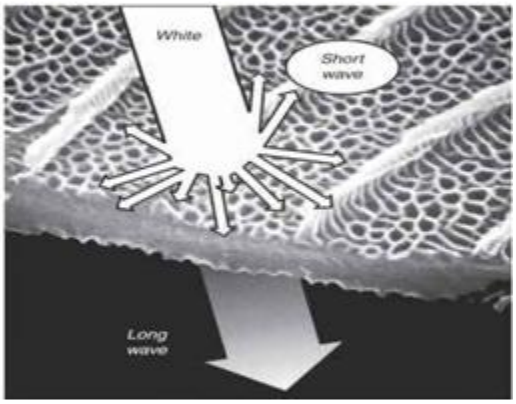

Figure 1: Scattering of white light

2.2. Color Interference

Interference colors result from the reflection of light from a series of neighboring interfaces that are separated by distances comparable with a quarter of the wavelength of light. As a result of wave superposition from these reflections, some wavelengths are reflected or transmitted in phase and are therefore reinforced, while others are out of phase and are cancelled out. The net result is that only certain wavelengths are reflected or transmitted and the surface appears colored. The general category of interference includes those situations in which the rays of a beam of white light are temporarily separated and then brought back together in such a manner that some have traveled a longer path than others. Depending on the geometry, when the rays recombine, certain wavelengths are in phase and reinforced ("constructive interference"); these will shine with particular brilliance. Others are out of phase and cancel each other ("destructive interference"). The results are the shimmering colors we call "iridescent." There are many ways of producing iridescence; this article considers only those of known importance in insects. In some butterflies, for example, layers of cuticle are intercalated with layers of air in order to generate efficient interference colours

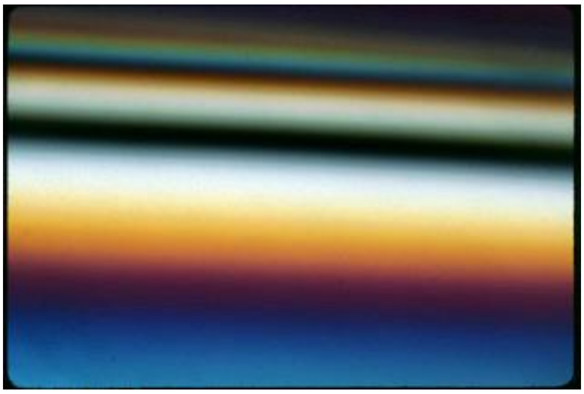

Figure 2: Color interference

Interference colors are common in adult Lepidoptera where the layers producing interference are formed by modifications of the scales. Each of the blue scales of the *Morpho rhetenor* butterfly (Fig. 3), for instance, consists of a flat basal plate carrying a large number of near-parallel vertically aligned ridges that run parallel with the length of the scale (Fig. 4). Within each ridge are series of horizontal layers, separated by air spaces. Collectively, the horizontal layers in each adjacent ridge form a series of reflecting surfaces, which are spaced such that a blue color is produced by interference. Various optical appearances are produced by a great variety of scale modifications in many different Lepidoptera. For instance, strong ultraviolet reflectance at a peak wavelength of approximately 345nm is generated in the butterfly *Colias eurytheme* by horizontal layered structures in its scale ridges that are 30–40% thinner that those typical of iridescent Morpho butterflies.

Figure 3:.Adult of *Morpho rhetenor* butterfly

2.3. Color Diffraction

Diffraction colors in insects was first described in *Serica sericea*, a Scarabaeid beetle [3]. The authors described striation 0.8μ apart on the elytra which were responsible for the diffraction grating effects. Diffraction occurs when light strikes the edge of a slit, groove, or ridge. Different wavelengths bend around the edge to different degrees and the spectrum fans out into its components. If many such grooves or ridges occur in a regularly spaced array light of different wavelengths is reinforced at different angles so that the colors change with the position of the viewer (e.g., consider iridescent bumper stickers and other shimmering plastic labels). Many insect cuticles have fine gratings etched into them; these and the ridge and crossrib structures of some lepidopteran scales and bristles produce diffraction colors. The diffraction grating was located in the epicuticle [4].

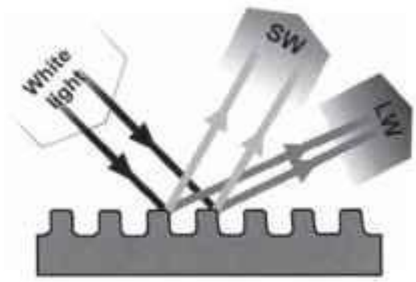

Figure 4: Color diffraction

2.4. Thin-Film Interference

Thin-film interference involves, as the name implies, the interaction of light with ultrathin films of a material. Newton had already noticed the colors of peacock feathers as due to the thin-film interference [5]. Light reflecting from the top surface of such a film interacts with that reflecting from the bottom surface (Fig. 5) and depending on the optical thickness of the film (n) its index of refraction, , (d) times its actual thickness,

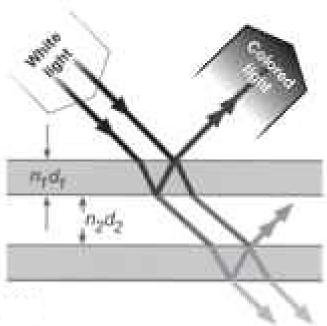

Figure 5: Thin film interference

3. Mechanism of Insect Coloration

3.1. In lepidoptera

The *Morpho* butterflies are among the largest in the world, with a wingspan of 7.5 to 20 cm. The males have beautiful metallic blue upper wings, while the females are drab. Their iridescence stems from the microscopic structure of their wings. Pilots flying over the rain forest can occasionally see brief flashes of blue as these butterflies travel above the forest canopy. The color of butterfly wing, covered with scales having many vertical vanes (ridges), was one of the most extensively studied subjects (Fig. 6). Their wings, however, amplify the effects of iridescence because they have many more layers for the light to pass through and thus many more opportunities for the light waves to reflect and magnify one another. As small as they are, butterfly wings are covered by thousands of microscopic scales (Fig. 7), split into two to three layers -- thus their Greek order name, Lepidoptera, meaning scaled wings. In turn, each scale has multiple layers separated by air. Rather than having just the constructive interference from the top and bottom layer that you have in a bubble, the many, equally spaced layers of butterfly wings 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. 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 [3]. When light hits the different layers of the butterfly wing, it is reflected numerous times, and the combination of all these reflections causes the very intense colors that you see in many species. Some butterfly displays even extend into the ultraviolet spectrum, which is visible to butterflies but not to humans. 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.

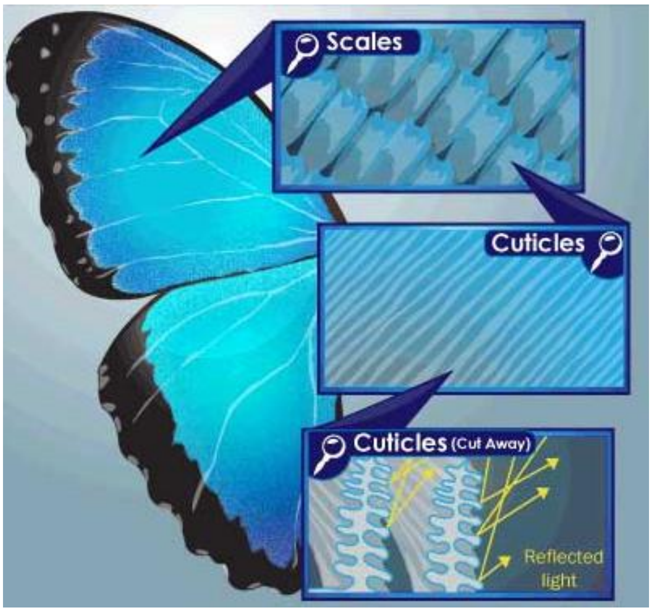

Figure 6: Butterfly wing

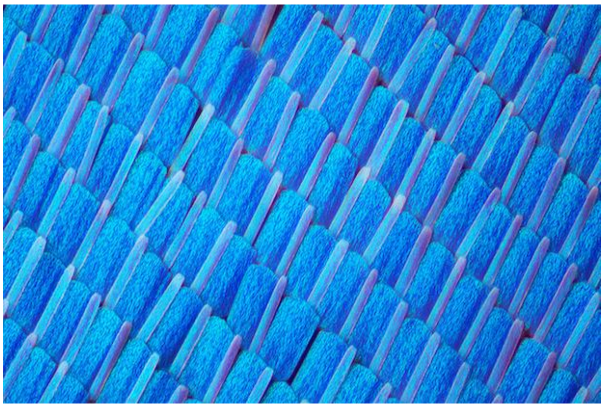

Figure 7: Scales of butterfly wing

The iridescence, or more specifically, structural colors are produced by refraction from microstructures smaller than the wavelength of light, such as the rainbow effect produced by compact discs [2]. The gorgeous blue in Morpho butterflies and the bright metallic gold of many tropical beetles are the result of submicron chitinous structures in the cuticle. These structural, refractive mechanisms of generating color are fundamentally different from the more familiar and intuitive mechanism of coloration via pigment, or the differential absorption of wavelengths of light by pigment molecules. In addition to being an important aspect of insect natural history, structural colors are of interest to physicists and materials scientists because many of the tiny structures responsible for some of the more impressive insect phenomena are still impossible to fabricate. In some cases, the study of insect structural colors has revealed optical phenomena that were never imagined or characterized by physicists. Berthier explores and explains color-generating structures and mechanisms in insects, as well as other relevant topics in natural history and biological optics.

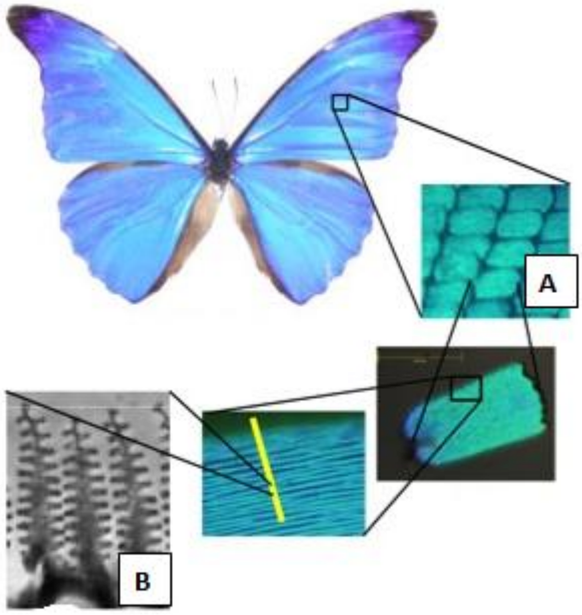

Figure 8: *Morpho* butterfly, its scales A, and electron microscopy image of the cross-section of the scales B.

The blue color of *Morpho* butterfly wings is resulted from nano-sized structures instead of pigments (Fig. 8) [6]. The ridges with ten layers of alternating shelves are densely arranged on the scales, which cover the whole wing of the *Morpho* butterfly. So far, various models have been proposed by simplifying the complicated structures and give us understanding that regularly arranged shelves are the key point for the blue coloring. However, these models cannot explain broad angular range of the reflection, which is essential for the Morpho blue. In order to improve this, we have simulated the light intensity reflected directly from the very structure obtained by electron microscopy using high-accuracy non-standard finite-difference time-domain (NS-FDTD) method. From the simulation, the following structural features are particularly important for the *Morpho* blue. Firstly, alternating shelves strongly suppress light reflected toward the normal direction and broaden the angular range of the reflection. Secondly, densely arranged ridges block the reflection toward large angles (Fig. 9), which restricts the wavelength range of the reflection within a blue region. These findings offer us a new insight in the mechanism of the blue coloring of the Morpho butterfly. This results confirmed that structural colors in *Morpho* butterfly are created by an optical effect (such as interference, refraction, or diffraction) rather than by a pigment. They arise from the arrangement of physical structures interacting with light to produce a particular color. Iridescent surfaces, such as butterfly wings, help animals to elude potential predators. When these insects fly, the upper surface of their wings continually changes from bright blue to dull brown (Fig. 10) because the angle of the light striking the wing changes. As the butterflies move their wings up and down during flight, they seem to disappear, and then reappear a short distance away, looking like ethereal flashes of bright blue light. The dark undersides of their wings strengthen this effect. Combined with an undulating pattern of flight, this ability to change color quickly makes them difficult for predators to pursue.

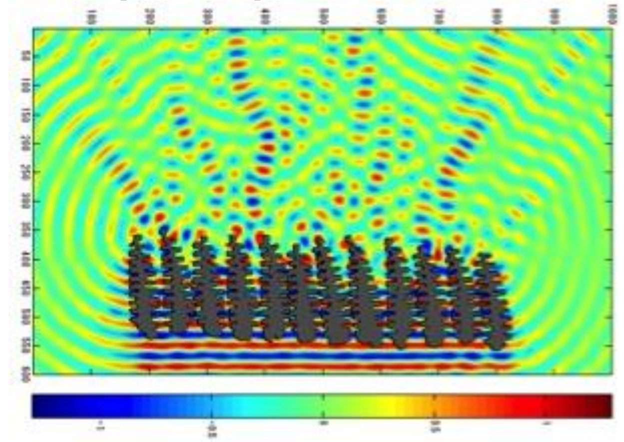

Figure 9: Ridges in insect wing and light reflection

Although it's true that the blue *Morpho's* wings look more blue because they contain blue pigments, this is not the main reason we see blue. A close look at the wing scales under an electron microscope reveals a regularly spaced array of biopolymer. The blue is because of the structure not because of the pigments [7]. It was pointed out earlier that some of the wings of butterflies and the cuticles of beetles produce brather remarkable colors using arrays of precisely fabricated structures, providing a striking example of pattern formation in biological systems. These elaborate architectures lead to structural colors that are seen in various insects and birds. Most of the colors are produced by either thin-film interference or diffraction or, as in the case of some beetles, by selective reflection of light. In the case of thin-film interference (which is known as thin-film reflectors), coloration is due to alternating layers of high and low refractive index materials. Such assemblies are usually referred to as Bragg reflectors in the physics literature. Such multilayer stacks or Bragg reflectors have been considered for use in optical limiting and switching applications, using the terminology of photonic band gap (PBG) crystals [8].

In general, the wings of butterflies and moths consist of a colorless translucent membrane covered by layers of scales (the name of the order is Lepidoptera, meaning "scaly wings"). Each scale is a flattened outgrowth of a single cell and is about 100 μm long and 50 μm wide. The scales overlap like roof tiles and completely cover the membrane, appearing as dust to the naked eye. The iridescence is caused by multiple slit interference. Sunlight contains a full range of light wavelengths. "Interference" occurs when light hitting the wing interacts with light reflected off the wing. Light is a wave. If the crests and the troughs of the waves are aligned, or in phase, they will cause constructive interference and iridescence is the result. One light wave hits the first groove, and a second light wave travels half of a wavelength to another groove, and is then reflected back in phase with the first. If the crest of one wave meets the trough of another wave (out of phase), they will cancel each other out, as destructive interference occurs.

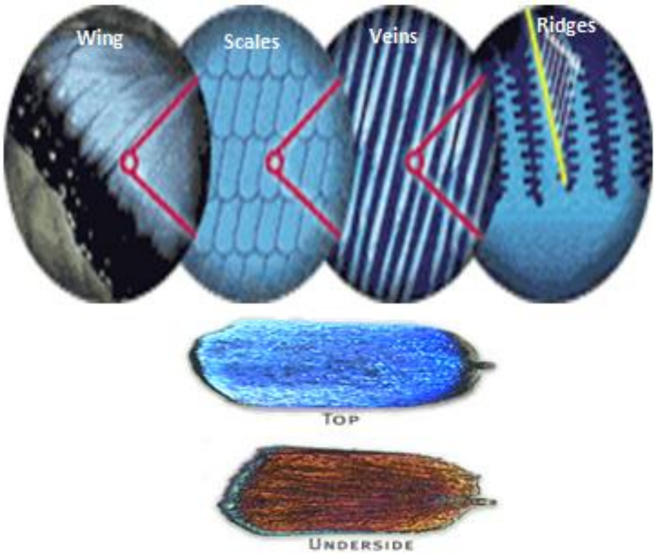

Figure 10: Wings parts and Scales from the top and bottom of a *Morpho* wing

Why does the *Morpho* appear blue?

Blue light has a wavelength range from 400 to 480 nm. The slits in the scales of the *Morpho* are 200 nm apart. Because the distance between slits corresponds to half of the wavelength of blue light, this is the wavelength that undergoes constructive interference. The slits are attached to a base of melanin, a material that absorbs light, further strengthening the blue image (Fig. 10).

Why are *Morphos'* wing undersides brown?

The scales on the underside of the Morpho's wing do not cause interference. This stems from normal organic pigments, rather than physical structure, and does not change with viewing angle. They resemble foliage, with lackluster browns, grays, blacks, and reds ((Fig. 10). The iridescence is more useful on the topside of the butterfly wing, where it can be used to elude their main predators: birds. These scales also protect the wing from physical contact. Each scale is about 70 by 200 µm, and is covered with thin parallel veins. The veins are much like ridges on a vinyl record. There are about 1,800 veins per millimeter. The texture forms a reflection grating. The veins are made of stacked chitin lamellae kept equidistant by fine braces. On the underside, the slits on the scales are 160 nm apart, less than half of any visible light wavelength, and thus do not cause visible interference. The Morpho microstructure was modeled in tree-like structure, which is schematically shown in Figure (11) [9]. The refractive index of chitin was 1.56 + 0.06i, in accordance and that the remaining regions were filled with air with a refractive index of 1.0. the authors denote the incident angle and viewing angles by a and b, respectively, as shown in Figure 11(a). The tree-like structure originated from a multilayer structure, as shown in Figure 11(b). The following multilayer parameters were used defined as: lamella height 560 nm, lamellae interval 5140 nm and number of layers 5 5. Three important parameters of the tree-like structure are shown in Figure 11(b): DR (width of ridge) 560 nm, DT (lamellae taper) 5 10 nm and DL (lamellae distribution) 5 0 nm, 100 nm, 0 nm, 100 nm. The same DL was used for each ridge for simplicity. Most of the aforementioned geometrical data were obtained from electron microscopy studies.

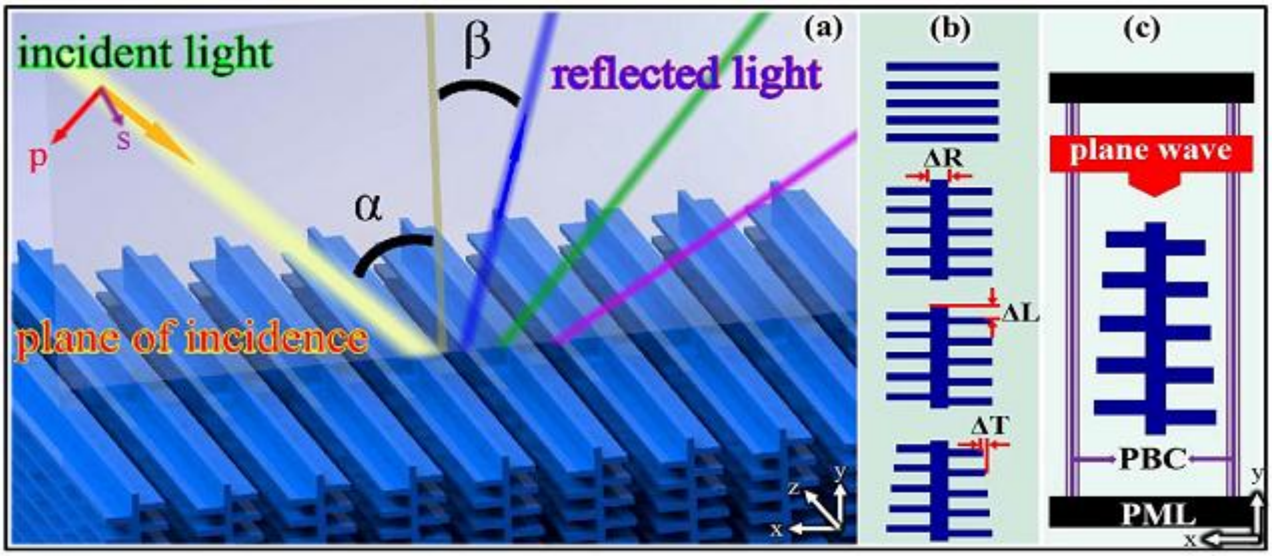

Figure 11: Computational model. (a) tree-like structure, incident light, reflected light, incident angle a, and viewing angle b; and (b) evolving the model from a multilayer to a tree-like structure by incorporating three parameters: DR (ridge width) 5 60 nm, DT (lamella taper) 5 10 nm, and DL (lamella distribution) 5 0 nm, 100 nm, 0 nm, 100 nm, ….; (c) the boundary condition in the vertical direction is absorbing (perfectly matched layer, PML), and the boundary condition in the horizontal direction is periodic (periodic boundary condition, PBC).

Figure 12: Coleoptera beetle

3.2. In Coleoptera

The members of the order Coleoptera are sometimes referred to as 'living jewels', in allusion to the strikingly diverse array of iridescence mechanisms and optical effects that have arisen in beetles (Fig. 12) [10]. A number of novel and sophisticated reflectance mechanisms have been discovered in recent years, including three-dimensional photonic crystals and quasi-ordered coherent scattering arrays. However, the literature on beetle structural coloration is often redundant and lacks synthesis, with little interchange between the entomological and optical research communities. Here, an overview is provided for all iridescence mechanisms observed in Coleoptera. Types of iridescence are illustrated and classified into three mechanistic groups: multilayer reflectors, three-dimensional photonic crystals and diffraction gratings. Taxonomic and phylogenetic distributions are provided, along with discussion of the putative functions and evolutionary pathways by which iridescence has repeatedly arisen in beetles.

The beetle cuticle has an outer epicuticle mainly composed of wax. It is multilayered and normally has a thickness of a micrometer or smaller [11]. The epicuticle can be seen as the top layer in Fig. 13 and at this location it has a thickness of less than 0.5 mm for this specimen. Under the epicuticle, the thicker exocuticle is found which is the color-generating part of the exoskeleton. The bottom (inner) part is the endocuticle which is more soft. It can further be seen that the exocuticle has a layered structure but the sublayer thickness varies throughout the exocuticle. The exocuticle is around 6-8 mm thick if the effect of an oblique cut is taken into account.

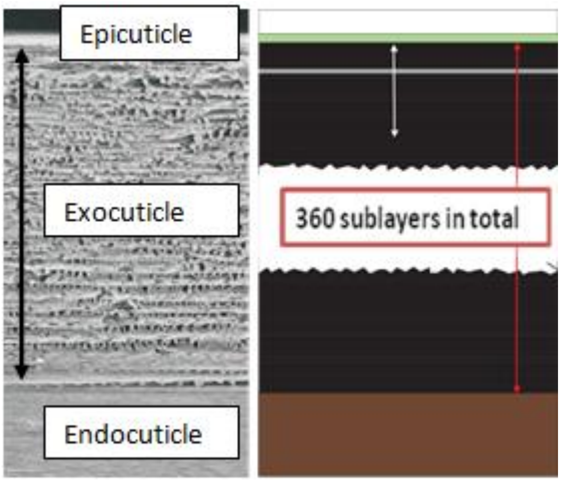

Figure 13: Cuticle of Scarab beetle

Multilayer reflectors are without question the most common and the best understood iridescence mechanism in beetles[12]. During the formation of insect integument, thin parallel layers of chitin (sometimes interspersed with other materials) that differ in refractive index are secreted by the epidermis and later harden during sclerotization. If the spacing of these layers approaches one-quarter the wavelength of visible light (approx. 380–750 nm), one or more colours will be produced by constructive interference [13]. The multilayer reflectors of beetles can be located at different layers within the integument (figure 14d–f) [14]. The beetle iridescence arose from different depths within the cuticle and could be removed from meloid, carabid and buprestid beetles by scraping the (epicuticular) surface; transmission electron microscopy (TEM) later revealed multilayer reflectors in the outer 1–2 mm of the exoskeleton of buprestids and carabids [14] [15]. Using electron microscopy and chemical analysis, Schultz and Rankin (1985) identified the reflectors of tiger beetles (Cicindelinae) as non-chitinous epicuticle laminated with ultra-thin layers of melanin was defined [16]. A similar epicuticular reflector occurs in the iridescent chrysomelid Plateumaris sericea [17]. Layers of chitin fibrils and protein in the exocuticle form the interference reflectors of many scarabs [1].

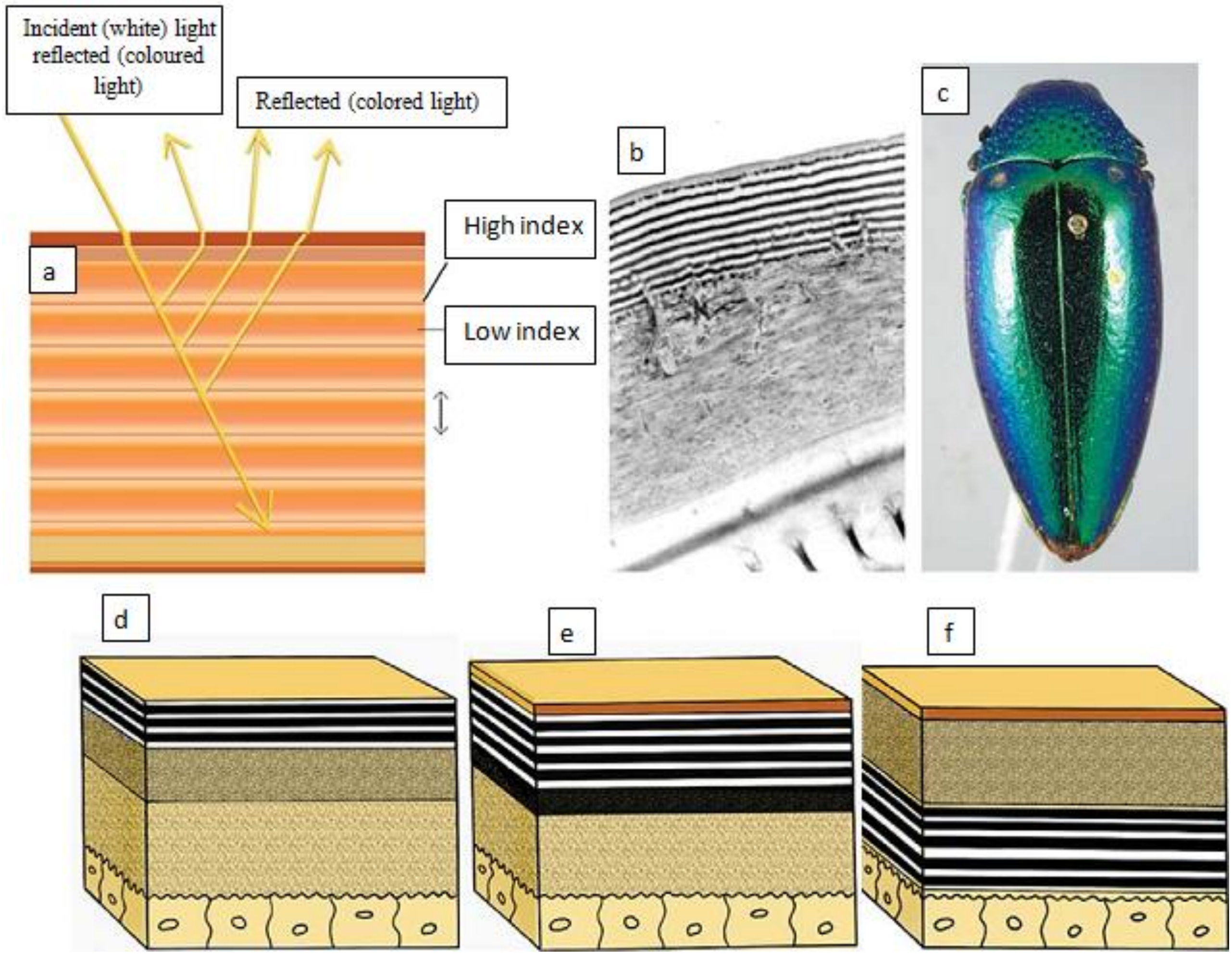

Figure 14: Multilayer reflectors. (a) A schematic of simple cuticular multilayer reflector, (b) Cicindela scutellaris, TEM cross section of cuticular reflector, (c) simple multilayer colour in a buprestid; schematic of (d) epicuticular reflector, (e) exocuticular reflector and (f) endocuticular reflector.

The color reflected by a multilayer structure depends on the refractive index of the component layers and their periodicity. Layers with a greater optical thickness reflect longer wavelengths than thinner layers and the peak $wavelength_{max}$ is equal to 2 ($n_a d_a + n_b d_b$), where n is the refractive index; d is the actual layer thickness; and a and b are the alternating layers in the eflector [13]

The apparent colour of a simple multilayer reflector also varies with the angle of observation; given a constant angle of illumination, as the angle of observation increases (i.e. deviates from normal), the reflected colour will undergo a 'blue shift' to a shorter wavelength, i.e. towards the blue end of the spectrum [18]. The colour shift occurs because reflected light rays are travelling a shorter distance through each layer, which means that constructive interference occurs for shorter wavelengths. This relationship between viewing angle and apparent hue results in a multicoloured appearance in convex beetles: when viewed from above, the lateral regions of the pronotum and elytra will be blue shifted with respect to the top of the segment (fig. 14c).

The diamond photonic structure is considered a special case due to it being the most isotropic periodic structure of the more commonly encountered crystal classes [19]. The multi-domained photonic crystal in the weevil *Lamprocyphus augustus*, was the first discovered example of this (Fig. 15D) [20]. Despite the limited RI contrast between chitin and air that form its system, there is a cumulative PBG (Photonic Band Gap) at green wavelengths for different crystal planes. The diamond photonic crystal arrangement has also been discovered in the scales of other beetles [21].

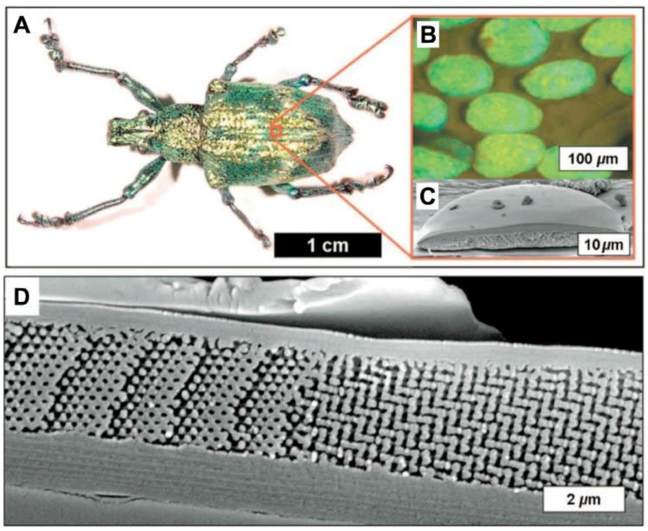

Figure 15: Brazilian beetle (A), photonic crystals (B) under electronic microscope (C) and 3D photonic crystal

Another beetle-based example of photonic crystals (Fig. 16) demonstrates the contrasting optical properties of highly ordered 3D structures versus quasi-ordered 3D structures. *Eupholus magnificus* exhibits two differently coloured bands (Fig. 16A) across its elytra, one of which is metallic in appearance due to highly specular reflection from ordered structure. The second coloured band is less intense and results from a more diffuse reflection from less ordered structure. Analysis of the associated scales shows that this difference arises from the 3D arrangements of across its elytra, one of which is metallic in appearance due to highly specular reflection from ordered structure. The second coloured band is less intense and results from a more diffuse reflection from less ordered structure. Analysis of the associated scales shows that this difference arises from the 3D arrangements of cuticle within the scales shown in Figure 16B and C [22]. The coexistence of these two contrasting forms of 3D structural order in the same species is uncommon in biological systems.

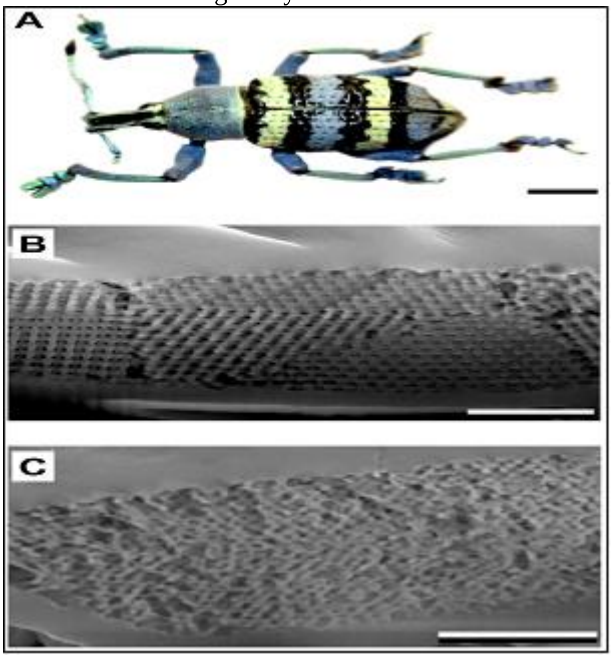

Figure 16: (A) Photograph of *E. magnificus* SEM images of a fractured: (B) yellow scale, showing the highly periodic 3D lattice, and (C) blue scale, showing the contrasting quasi-ordered structure.

4. Conclusion

Structural colors are created by an optical effect (such as interference, refraction, or diffraction) rather than by a pigment. They arise from the arrangement of physical structures interacting with light to produce a particular color. The structural color changes of biological organisms are based on changes in the refractive. Colors in some insects are produced by thin-film interference, a structural phenomenon; they have the property of being iridescent. This means that the apparent reflection off the insect wing surface changes dramatically in intensity and hue as the relative positions of the wing surface, viewer, and light source changes. In other words these colors are only apparent to receivers on specific conditions.

The epicuticle of insect integument, or outermost surface, of iridescent beetles is made of many stacks of slanting, plate-like layers, which are oriented in different directions. These layers bend, and then reflect the incoming light in the same way as the ridges of iridescent butterfly and moth scales. Similarly, they produce structural colors by interference in the same way as butterfly wings. A layer of pigment below the refractive plates of beetles and the ridges of iridescent butterfly scales enhances the effect of the iridescence. In some species, the epicuticle acts as a reflection diffraction grating to cause iridescence.

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