Structural origin of sexual dichromatic coloration and luster in the beetle *Goliathus cacicus*

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In the beetle *Goliathus cacicus*, male elytra show silky luster with iridescence while female ones appear lusterless white without iridescence to our perception. We revealed by structural characterizations and optical measurements that elytral coloration and luster of both male and female beetles stem from the tubular scales on the elytra, whose interior is filled with a random structure. Distinct differences between male and female scales reside in the cortex thickness and the filling fraction of the random structure, which are important factors in the determination of the sexual dichromatic luster and iridescence. In addition to reflection peaks in the visible range, spectral measurements indicate that both male and female elytra display also strong iridescent ultraviolet (UV) reflections. Scattering spectra show that both male and female elytra display UV luster, although it is absent for female ones in the visible range.

coloration, luster, tubular scale, random structure, sexual dichromatism

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In the biological world, coloration can be produced by pigments, microstructures, or their combination. Distinctly different from pigmentation, structural coloration is caused by the interactions of light with microstructures via optical effects, such as interference, diffraction, or scattering [1–5]. Ordered microstructures like single [6] and multi-layered thin films [7], and periodic photonic structures (photonic crystals) in two- [3,8] and three-dimensions [9–12] can produce iridescent structural coloration. On the other hand, amorphous photonic structures that possess only short-range order give rise to non-iridescent structural colors, found in bird feathers [13–17] and even in beetles [18,19]. Whiteness is ubiquitous in the biological world, but it cannot be generated by pigments. Instead, it results from disordered structures by broadband scattering or diffused reflection of light in the visible range [20].

In the animal kingdom, the male-female differences in

colors or marking patterns, sexual dichromatism, are widely spread, found in birds [21–26], fishes [27], butterflies [28], spiders [29], and even in toads [30], often ascribing to sexual selection [31]. There have been a number of reports devoted to sexual dichromatism via structural coloration in avian plumage, and resulting implications [21,24,26]. Discussions in other species such as insects are rather limited. It has been pointed out that many birds and insects can perceive ultraviolet (UV) light which cannot be seen by human being. As a result, not only visible but also UV reflections must be considered when discussing sexual dichromatism [21,24,29,32].

In most studies, structural colors have been assessed usually by their hue, saturation, and brightness. Luster, however, is also an important feature of a reflecting surface, produced by the dependence of reflection on viewing angles and varying with the structural nature of the surface. It has been widely used in the evaluation and grading of gemstones, and in characterizing fabrics. It has been suggested

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that the luster of human hair can even be used as an indicator of health and age [33]. Many animals like beetles, birds, and mammals have glossy appearance which depends on their integument's structure, order, and integrity [34,35]. The glossiness of avian plumage may even be related to signaling traits [36]. Compared with other features of structural colors, luster has been much less documented and studied.

Here, we studied the sexual dichromatic luster and coloration of the beetle *Goliathus cacicus* in both visible and UV ranges. Origin of the sexual dichromatic luster and iridescence was investigated by structural characterizations and optical measurements.

1 Material and method

1.1 Samples

Specimens of the beetle *G. cacicus* under study were purchased from the Shanghai Natural Museum, Shanghai, China. The beetle *G. cacicus* belongs to the Cetoniinae subfamily, within the scarab beetle family, and can be found in western equatorial Africa. Adult males are about 6 cm long and females are about 5 cm long.

1.2 Observation and structural characterization

Both male and female beetles were observed and recorded by a digital camera (Canon EOS 5D). Optical micrographs of elytra were observed and recorded by an optical microscope (Leica DM6000 M) which is connected to a CCD camera.

Elytra and scales were characterized by a scanning electron microscope (SEM) (Philips XL30 FEG). Microstructures of single scales were also characterized by a transmission electron microscope (TEM) (JEOL 100S). For SEM observations, scales were embedded in epoxy resin and then cut into 5- μm -thick slices by a slicer (Leica RM2255). Samples for TEM observations were prepared according to a conventional method [37].

1.3 Angle-resolved spectroscopy

Reflection spectra of elytra were measured by our homemade angle-resolved spectroscopy. The light source is a xenon lamp covering a wavelength range from 250 to 800 nm. A Polka-Dot beamsplitter (Edmund Optics) with square metallic coated apertures was used to split light beams (50R/50T) with wavelengths ranging from UV to near infrared. Two coaxial motorized rotary stages were used to control the rotating angles of the upper and lower stages independently. Samples were placed on the center of the upper stage. An optical fiber was put on the detection arm which was fixed on the lower stage. A high-resolution spectrometer (Ideaoptics PG2000pro EX) with a UV enhanced

back thinned CCD array was connected to the fiber. To obtain the absolute reflectance, a standard white board (Ocean Optics) was used as reference.

With our setup, we can measure both specular reflection and scattering spectra. By adding two Glan-Taylor polarizers with their pass axes parallel or perpendicular with each other, polarization effects can also be studied.

2 Results

2.1 Observation and structural characterization

To the human eye, the elytra of male beetles display silky luster (Figure 1(a)). Under oblique observing angles with respect to the elytral surface normal, they appear shallow greenish, showing some iridescence. On the other side, the elytra of female beetles are bright white with neither luster nor iridescence. Under optical microscopy, the elytral coloration stems from dense scales covered on the elytra (Figure 1(b)). Scales are oriented almost parallelly with each other.

SEM observations revealed that the elytra are densely imbricated with hair-like scales (Figure 2(a) and (b)). From SEM and TEM cross-sectional images, the scales are tube-like with an outer chitin cortex and a hollow interior (Figure 2(c)–(f)). The hollow interior is filled with randomly distributed chitin filaments (Figure 2(g)).

The differences of scales between male and female beetles lie in their size, the thickness of the outer cortex, and

Figure 1 Optical images of male (left column) and female (right column) *G. cacicus*. (a) Photographs of elytra. Male elytra show silky luster while female ones are lusterless white. (b) Close-up micrographs of elytra. Both male and female elytra are covered densely with hair-like scales.

Figure 2 SEM and TEM images of scales in males (left column) and females (right column). (a) and (b) SEM top-view images of elytra; (c) and (d) SEM cross-sectional images; (e) and (f) TEM transverse cross-sectional images; (g) SEM longitudinal cross-sectional image of a female scale.

the filling fraction of the random structure in the hollow interior. From TEM cross-section images, the average size of male scales is $1.5 \pm 0.4 \mu\text{m}$, while that of female scales is $2.0 \pm 0.5 \mu\text{m}$. The outer cortex of male scales has a larger thickness ($290 \pm 15 \text{ nm}$) than that of female scales ($260 \pm 12 \text{ nm}$). The filling fraction of the random structure for males is 0.22 ± 0.07 , while it is 0.32 ± 0.08 for females.

2.2 Specular reflection spectra

The specular reflection spectra of both male and female elytra were measured for unpolarized light at different incident angles with wavelength ranging from UV to near infrared, as shown in Figure 3. Two incident configurations were considered: one with the incident plane parallel to the long axes of the scales and the other perpendicular to. At normal incidence, there is nearly no difference between two incident configurations. Both male and female beetles were characterized by a broad visible peak and two UV peaks in the displayed wavelength range. For males the visible peak is centered at 585 nm, one UV peak at 360 nm and the other at 265 nm. For females the visible peak is centered at 535 nm and one UV peak at 325 nm. The other UV peak is obvious but its peak position seems below 250 nm, outside our detection range. For males the intensity of the visible and UV peaks is comparable. For females, however, the intensity of the visible peak is larger than that of the UV peaks. The intensity of the visible peak for males is much smaller

Figure 3 Measured specular reflection spectra of male and female elytra for unpolarized light at different incident angles. (a) and (b) Measured spectra with the incident plane parallel to the long axes of the scales (see inset); (c) and (d) measured spectra with the incident plane perpendicular to the long axes of the scales (see inset).

than that for females.

With increasing incident angles, all reflection peaks under both incident configurations undergo a blue shift in wavelength, and their intensities increase also. Meanwhile, the UV peak at short wavelength shifts outside the detection range of our spectroscopy, and a new reflection peak seems to emerge in near infrared. For females the reflection spectra between two incident configurations show a very small difference. For males, it is a bit different. At small incident angles, the reflection spectra of both incident configurations are very similar. Difference occurs at large incident angles. The shifts of reflection peaks toward lower wavelengths are much larger for the incident configuration with the incident plane perpendicular to the long axes of the scales than for the other incident configuration.

To explore the polarization effects, we also measured the reflection spectra of both male and female elytra under normal incidence by placing two Glan-Taylor polarizers in our spectroscopy. For two polarizers with their pass axes parallel or perpendicular with each other, the measured reflection spectra show a large difference (Figure 4). For parallel polarizers, the visible and UV reflection peaks for both male and female beetles still exist. For crossed polarizers, however, the reflection spectra are rather different, showing polarization effects to be discussed later.

2.3 Scattering spectra

To quantitatively access the elytral luster, scattering spectra of elytra at fixed incident angles were measured for different emergent angles, shown in Figures 5 and 6 for the incident plane parallel and perpendicular to the long axes of the scales, respectively. For the specular reflection, the reflectance is the highest as expected. For emergent angles different from specular reflection angles, the attenuation behavior of

Figure 4 Measured reflection spectra of both male (red lines) and female (blue lines) elytra under normal incidence for two Glan-Taylor polarizers with their pass axes parallel (solid lines) and perpendicular (dashed lines) with each other.

Figure 5 Measured scattering spectra in the color-scale form for the incident plane parallel to the long axes of the scales at incident angles of zero (left column) and 30 degrees (right column). Color scales on the right are in units of %. (a) and (b) Spectra for male elytra; (c) and (d) spectra for female elytra. Emergent angles are set to be with respect to the specular reflection angles.

scattering is different for males and females. For females the scattering attenuates much slowly than for males. In other words, in a wide range of emergent angles away from the specular reflection direction we can still perceive scattered light. Differences also exist for different incident configurations. This implies that different luster should be viewed at different viewing directions.

3 Discussions

3.1 Coloration and iridescence

As shown in Figure 2(a) and (b), elytra of both male and

Figure 6 Same as Figure 5 but for the incident plane perpendicular to the long axes of the scales.

female beetles were covered densely with hair-like scales. Elytral coloration comes thus from scales. Measured specular reflection spectra show a series of peaks with a nearly equal interval of frequency, similar to those of a thin film. Note that scales are tube-like and their sizes are much larger than the visible wavelengths. The dorsal side of the scale cortex may act effectively as a thin film to produce interference. The ventral side offers slight contributions to interference since randomly distributed filaments in the scale interior will destroy the interference, similar to the case in pigeon feathers [6].

For a thin film in air ambience, the wavelength of reflection peaks is given by [6]

$$\lambda_m = \frac{2d\sqrt{n^2 - \sin^2 \theta}}{m + 1/2},$$

where d and n are the thickness and refractive index of the thin film, respectively; θ is the incident angle; and m is the order index of the harmonic peaks. To test the above hypothesis, a refractive index of 1.56 was used for chitin [7] and the thickness of 290 nm for male and 260 nm for female was taken from the structural measurements. For normal incidence, the predicted peak wavelengths are 603, 362 and 258 nm for male, while for female the predicted values are 541, 324 and 237 nm. Obviously, these predicted values are consistent with the experimental data, implying that the elytral coloration stems indeed from the dorsal cortices of scales simply via thin-film interference.

Note that the thickness of the scale cortex varies with scales, and in the plane perpendicular to the long axes scales are aligned randomly. These may lead to the broadening of reflection peaks, which can be seen from the measured reflection spectra shown in Figure 2, especially for the visible peaks.

3.2 UV reflection

In addition to the visible reflections, both male and female beetles display strong UV reflections with prominent peaks. For both sexes under normal incidence, one UV peak is located at UV-A (315–400 nm) and the other at germicidal UV-C (200–280 nm). With increasing incident angles, the UV-A peak of both sexes shows iridescence, shifting to short wavelengths. The UV-A peak shifts to UV-B (280–315 nm) at large incident angles.

The position and iridescence of UV peaks show distinct differences between sexes, namely, sexual dichromatic UV reflections. In males the UV-A peak at normal incidence is as intense as the visible one, while in females the UV-A peak has a smaller intensity than the visible one. The difference of the UV-A peaks between males and females resides in their positions: the UV-A peak of females lies at a shorter wavelength. As a result, the UV-A peak of females shifts faster towards the UV-B band than that of males with increasing observation angles.

UV vision and UV reflection are widespread in the animal kingdom and have important significance in signal communication and recognition [38,39]. Thus, the functionality and evolutionary significance of the UV reflections in *G. cacicus* is an interesting topic that needs in-depth studies.

As shown in Figure 3, all reflection peaks for both male and female shift to short wavelengths with increasing incident angles. As a result, male elytra appear a shallow iridescent greenish hue. For female the visible reflection peak is still broad at oblique observation angles such that we cannot observe iridescence. This is due to the strong diffused reflection by the random structure in the scale interior.

3.3 Polarization effects

For light scattering into backward directions by a surface consisting of an array of parallel tubes with their sizes larger than the wavelength, the specular reflection is dominant with a trend to preserve the linear polarization. If measured with two crossed polarizers, reflectance should be zero in the specular direction. For a rough surface, however, diffused reflection or scattering is expected, and the polarization of scattered light will be altered. As a result, with two crossed polarizers reflectance still exists even in the specular direction.

In both male and female beetles, tubular scales are filled with randomly distributed filaments. Thus, scattering should be different from hollow tubes. The random structure in the scale interior will play an important role in scattering. Consequently, there are two contributions to scattering, one from the cortex and the other from the interior random structure.

The reflectance spectra measured with two crossed polarizers stem from diffused reflection by the random structure in the scale interior. Those measured with two parallel

polarizers originate from specular reflection by the dorsal cortex of scale arrays together with the contribution of diffused reflection.

As can be seen from Figure 4, the UV reflection peaks for both sexes almost disappear with two crossed polarizers, suggesting that the random structure in the scale interior does not contribute much to UV scattering. UV reflection is thus caused mainly by the scale cortex. The visible reflection, on the other hand, is still noticeable with two crossed polarizers. It is especially true in female from the fact that the visible reflection intensity in female is much larger than that in male. This is because the filling fraction of the random structure in female is much larger than that in male, leading to a larger contribution to scattering in female than in male.

3.4 Luster

Luster is an important feature of a reflecting surface and dependent on viewing angles. It is, however, difficult to describe and measure in a quantitative way. Many formulae and methods have been suggested to quantify luster [34,40–43]. In general, reflection from a surface into backward directions consists of specular and diffused light. The larger the intensity ratio of specular to diffused light is, the higher the luster is. Luster is also strongly dependent on the angular distribution of reflected light [42,43]. The sharper the angular distribution of reflected light is, the higher the luster is.

In measurements of scattering spectra shown in Figures 5 and 6, two incident configurations were considered. Scattering patterns are distinctly different for two configurations. This implies that luster is different for different observation directions.

For the incident plane parallel to the scale orientation (Figure 5), it can be seen that at the zero incident angle the half-width angle (the range of angle at which the intensity of a peak drops to one half) of the visible peak is 19° for males and 36° for females. At the 30° incident angle, the visible peak has a half-width angle of 28° for males, much smaller than that of 47° for females. The small half-width angle of the visible peak for male gives rise to the silky luster for male elytra, consistent with the perception of the human eye. Female elytra do not possess luster since the half-width angle of the visible peak is too large. For the UV-A peak, the half-width angle for male is about 16° and 28° at the incident angles of 0° and 30°, respectively. For female it is similar, about 22° and 25° at the incident angles of 0° and 30°, respectively. These relatively small half-width angles imply that both male and female elytra possess UV luster, although it cannot be observed by the human eye. But it may be visualized instead by beetles.

For the incident plane perpendicular to the scale orientation (Figure 6), the corresponding half-width angles of both visible and UV-A reflection peaks for both males and fe-

males are much larger than those for the incident plane parallel to the scale orientation. This suggests that elytra of both sexes are lusterless when observing from the direction perpendicular to the scale orientation. In other words, elytral luster is highly direction dependent.

The presence of a random structure in the scale interior affects elytral luster considerably. As discussed in the above subsection, the visible reflection peak is influenced by the scattering from the random structure, while the UV-A peak is nearly unaffected. As is known, scattering by random structures will lead to the light emergence at other angles different from the specular reflection angle. Therefore, UV luster of elytra is nearly independent on the scattering by the random structure in the scale interior. On the contrary, visible luster depends strongly on the presence of the random structure. For the incident configuration with the incident plane parallel to the scale orientation, male elytra show silky luster and female ones are lusterless due to the fact that the filling fraction of the random structure in female scales is much larger than that in male ones. This implies that we can manipulate the elytral luster in the visible range by altering the filling fraction of the random structure in the scale interior.

3.5 Sexual dichromatism

The Beetle *G. cacicus* shows distinct sexual dichromatism, namely, differences in coloration and luster between males and females. In the visible spectrum, elytra of both males and females possess a broad reflection peak. The intensity of the visible peak of females is much larger than that of males, leading to bright appearance of elytra for females. Sexual dichromatism also exists in UV. Elytra of both sexes have a UV-A reflection peak positioned distinctly at different wavelengths.

In addition to coloration differences, elytra of male and female beetles display different luster, which is rarely found in the animal kingdom. In the visible range, male elytra show silky luster, while female ones are lusterless. In UV both sexes display UV luster. This sexual difference in luster may be one of important secondary male-female traits, which is of significance in intraspecific and interspecific communications.

4 Conclusions

We studied the structural and optical properties of tubular scales densely imbricated on the elytra of the beetle *G. cacicus*. Both male and female scales have a similar tubular shape filled with randomly distributed filaments in the interior. To our perception the silky luster in male elytra and bright whiteness in female elytra originate from the tubular scales. Elytra of both sexes display strong UV reflections and UV luster as well. Differences in scale sizes, cortex

thicknesses, and filling fractions of the random structure in the scale interior influences the coloration and luster of elytra in males and females, leading to sexual dichromatism in both the visible and UV ranges. Sexual dichromatism in both visible and UV bands may be of important significance in intraspecific and interspecific communications. The revealed tubular structures in scales and the mechanisms of regulating coloration and luster may inspire our design and fabrication of artificial materials for the future applications.

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