Scarab beetle iridescence

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The color of various insects, such as beetles and butterflies, in the natural world has attracted the attention of scientists since at least the time of Robert Hooke (1635–1703). Sir Isaac Newton (1642–1727) understood that the colors that are produced must be a result of the presence of “thin film structures.” It is now commonly recognized that the colors produced by insects and perceived by an observer are a result of the microstructures that are present on their bodies. In other words, the colors are produced by the interaction of light with the periodic structures on their bodies.

The present article deals with the iridescence of scarab beetles, particularly the color of*Chrysina gloriosa* or *Plusiotisgloriosa*, which possess a metallic green reflection that is circularly polarized. [Circularly polarized light consists of two perpendicular electromagnetic plane waves of equal amplitude but differing in phase by 90°; the resulting electric (or magnetic) field vector traces a circle as it approaches an observer.] It should be noted that linearly polarized light (that is, light in the form of a plane wave) is quite commonplace in nature, but circularly polarized light is quite rare. Among a number of species of beetles that have been examined, so far only the scarabs possess circularly polarized reflectance. Often, scarab beetles are referred to as jewel beetles, based on the fact that reproductions of them have been used as ornaments in many Asian countries. The term iridescence, as used in different fields of study, can refer to different characteristics; in this article, the term is used to mean a change in the hue of the object possessing the perceived color as the angle of vision is varied, which is a definition quite similar to what C. W. Mason used in 1927. The term metallic is often used to describe the saturation or the purity of color.

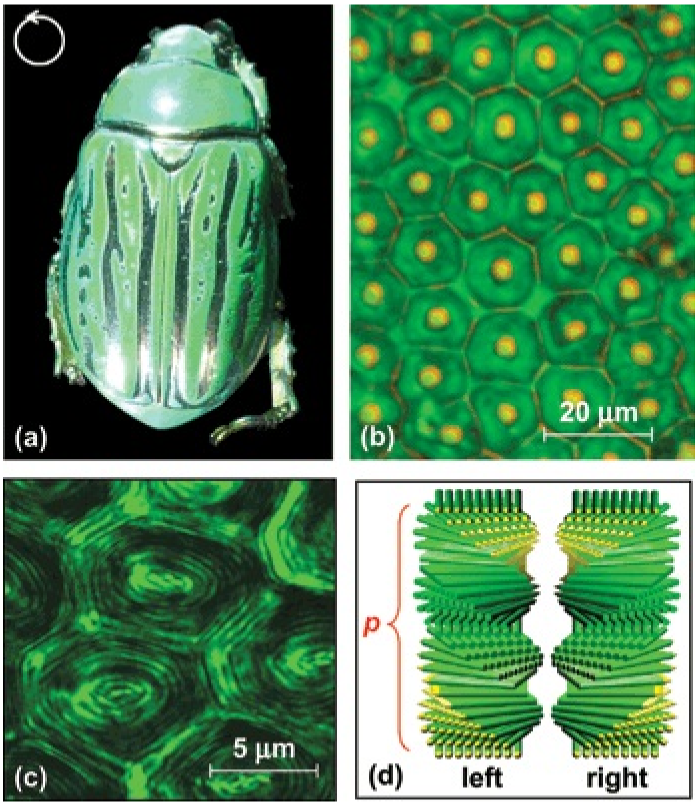
Color and reflectance

The color of beetles has been studied since the early 1900s, when Albert A. Michelson observed that some scarab beetles possessed a metallic reflection and that the reflection was circularly polarized. Michelson described the color of the beetle *P. resplendens* as follows: “[This] is a beetle whose whole covering appears as if coated with an electrolytic deposit of metal with a lustre resembling brass. Indeed, it would be difficult for even an experienced observer to distinguish between the metal and the specimen.” Although *C. gloriosa* is green in color, it does possess the metallic luster to which Michelson referred. Michelson noted that the reflection was circularly polarized, but he did not specify the handedness. However, he did mention that the handedness reverses if one looked at the reflectance from the blue part of the visible spectrum to the red; that is, the polarization was found to reverse near the red end of the spectrum and was completely reversed in the extreme red. He also postulated that “the effect must therefore be due to a screw structure of ultramicroscopic, probably of molecular dimension.” Although Michelson did not pursue this further, others (such as A. C. Neville and S. Caveney) investigated the origin of circularly polarized reflection in several scarab cuticles, using electron microscopy. It was found that a “helicoidal structure” is responsible for the color (selective reflection) and handedness of the circular polarization. Scarab beetle cuticles were seen to be analogous to cholesteric liquid crystals (a type of liquid-crystal material in which the elongated molecules are parallel to each other within the plane of a layer, but the direction of orientation is twisted slightly from layer to layer to form a helix through the layers).

Microstructure analysis of the exocuticle

In an effort to understand the microstructure responsible for these optical effects, examinations were undertaken to study the structure of the exocuticle of the *C. gloriosa* beetle, which selectively reflects left-circularly polarized light and possesses a brilliant metallic appearance (**illus.** *a*). If left-circularly polarized light is blocked by the use of a quarter-wave plate and a polarizer, the beetle “loses” its characteristic bright green reflection. The reflectance of the *C. gloriosa* beetle has a broad halo from 500 to 600 nm, with two peaks at 530 (green) and 580 nm (yellow).

Views of scarab beetle iridescence. (*a*) Photograph of the beetle *C. gloriosa* displaying the bright green metallic color with silver stripes as seen in unpolarized light or with left-circularly polarized light. (*b*) An image using a reflected-light microscope of the exoskeleton of the beetle *C. gloriosa* showing the bright yellow core surrounded by greenish reflection. (*c*) An *x–y* section using a confocal light microscope showing the concentric rings resolved at high magnification and present near the free surface. (*d*) A schematic representation of the cholesteric helix for right- and left-handedness (*p* = pitch of the helix).



When the beetle is observed under a reflected-light microscope, the body is seen to consist of a richly decorated mosaic of regularly spaced polygons that cover the entire cuticle of the beetle, where it looks green. Such structures have been observed by a number of researchers, but most notably by A. Pace in 1972. When viewed in bright-field microscopy (**illus.** *b*), the structure seems to consist of mostly hexagonal cells (approximately 8–10 µm in size), and each cell has a bright yellow core surrounded by green. The regular lattices of the cells contain not only hexagonal cells but also cells that are pentagonal and heptagonal. It was also noticed that, as the curvature of the beetle exocuticle increased, the number of heptagons decreased a bit and the number of hexagons decreased more, whereas the number of pentagons increased the most. In other words, the more curved the surface of the beetle was, the more pentagons were found, thus leading to higher disorder with increasing curvature. Although hexagonal packing affords the most efficient use of space on a plane, defects (pentagons and heptagons) are essential for tessellating (tiling) a curved surface, thus leading to higher disorder of the structures on the head, thorax, and abdomen of the beetle because of the curved nature of its body. Quantification of these structures found on the beetle cuticles has shown that it is energetically unfavorable to create a completely hexagonal packing on the exocuticle of the scarab beetles.

In an effort to better understand the structure of the beetle exocuticle, a laser scanning confocal microscope was employed to reconstruct a three-dimensional (3D) map of the underlying structure, using the autofluorescence of the beetle, where the fluorescence was excited by a 488-nm laser line of an argon-ion laser. The cells under the fluorescence microscope exhibited nearly concentric bands that are bright and dark (**illus.** *c*), which have been attributed to the underlying structure of the exocuticle. The 3D reconstruction suggests the existence of a nested arc that is similar to what would be observed for a cholesteric liquid crystal.

We have alluded to the fact that the color of the reflected light by the beetle is analogous to the selective reflection of cholesteric liquid crystals. Such liquid crystals possess long-range orientational order, described by a unit vector $\mathbf{n}$, known as the director; for a cholesteric liquid crystal, the equilibrium director structure is a helix (**illus.** *d*). The director advances uniformly, tracing a helix of pitch p. Pace noticed the polygonal structures in the transmission electron micrographs from the exoskeleton of *C. gloriosa*, collectively calling them a Bouligand structure (also known as focal conic defects). Extensive studies have been carried out on the similarity of textures observed in crabs and other organisms to cholesteric liquid crystals, and their role in morphogenesis has been explored. Such structures form when a cholesteric liquid crystal has a surface exposed to air (in other words, a free surface). The structure that is found by confocal microscopy (using nondestructive imaging techniques) on the beetle exocuticle is completely analogous to the structure found on the free surface of cholesteric liquid crystals. In fact, the 3D microstructure of the beetle elytra (forewings) shows unmistakable similarity to the cholesteric focal conic texture at a free surface.

Because of its helical structure, the cholesteric phase exhibits selective reflection when the pitch of the helix is comparable to the wavelength of visible light. Of course, the reflection has the same handedness as the cholesteric helix. Hence, when unpolarized light is incident on the cholesteric helix, with the helical axis oriented normal to the surface, it reflects 100% of the light with the same handedness. Unpolarized light can be thought of as a mixture of left- and right-circularly polarized light; therefore, light of the same handedness (approximately 50%) is reflected, whereas the rest is transmitted. It should be pointed out that there is very little absorption in a cholesteric fluid; however, this may not be the case for the beetle exocuticle. For helices oriented at some other angles or for light that is incident at some oblique angle, the optical properties are a bit more complicated (and beyond the scope of this article). Thus, the patterns found on scarab beetles are surmised to be largely a consequence of the array of focal conic defects formed at the free surface of a cholesteric liquid crystal formed from chitin, and the color is a result of the selective reflection mediated by the defect array on the surface.

Explanation and purpose

Insofar as the colors and circularly polarized reflection are created by an underlying cholesteric phase, one might wonder about the purpose of such colors and the resulting polarization. Can the beetles in fact sense the circular polarization? Questions of this sort are beginning to be answered. In a recent study, the response of *C. gloriosa* toward different light stimuli was studied. It was found that these beetles exhibit flight orientation that is dependent on the polarization of the light, thereby indicating that these beetles are sensitive to circular polarization of the light. It is possible that this sensitivity to circular polarization allows *C. gloriosa* to communicate in some fashion, because the signals are independent of their orientation.

A number of other beetles and butterflies also produce iridescent colors as a result of the periodic structures on their wing scales. The beetle *Calidea panaethiopica* exhibits a complex color pattern that contains blue-green iridescent stripes. In this case, the color is produced by a multilayer structure that has tiny cups, with the cups producing two different colors that are color-mixed to provide the perception of a single color. Such is the case with the butterfly *Papilio palinurus*; each wing scale is about 120 μm in length, with 5–10-μm-diameter bowls, and each is lined with a multilayer stack of alternating layers of chitin and air. The distinct green color of the wing results from an additive color mixing of yellow and blue reflections. The yellow-colored reflection is from the bottom of the bowl, and the blue results from two reflections at 45° at the edge of the bowl. It is remarkable that the natural world has a number of different but elegant solutions to producing iridescent colors for a variety of purposes.

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See also: Coleoptera; Color; Confocal microscopy; Insect physiology; Liquid crystals; Optics; Physiological ecology (animal); Polarized light; Reflection of electromagnetic radiation

Related Primary Literature

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- Scarabaeinae Dung Beetles