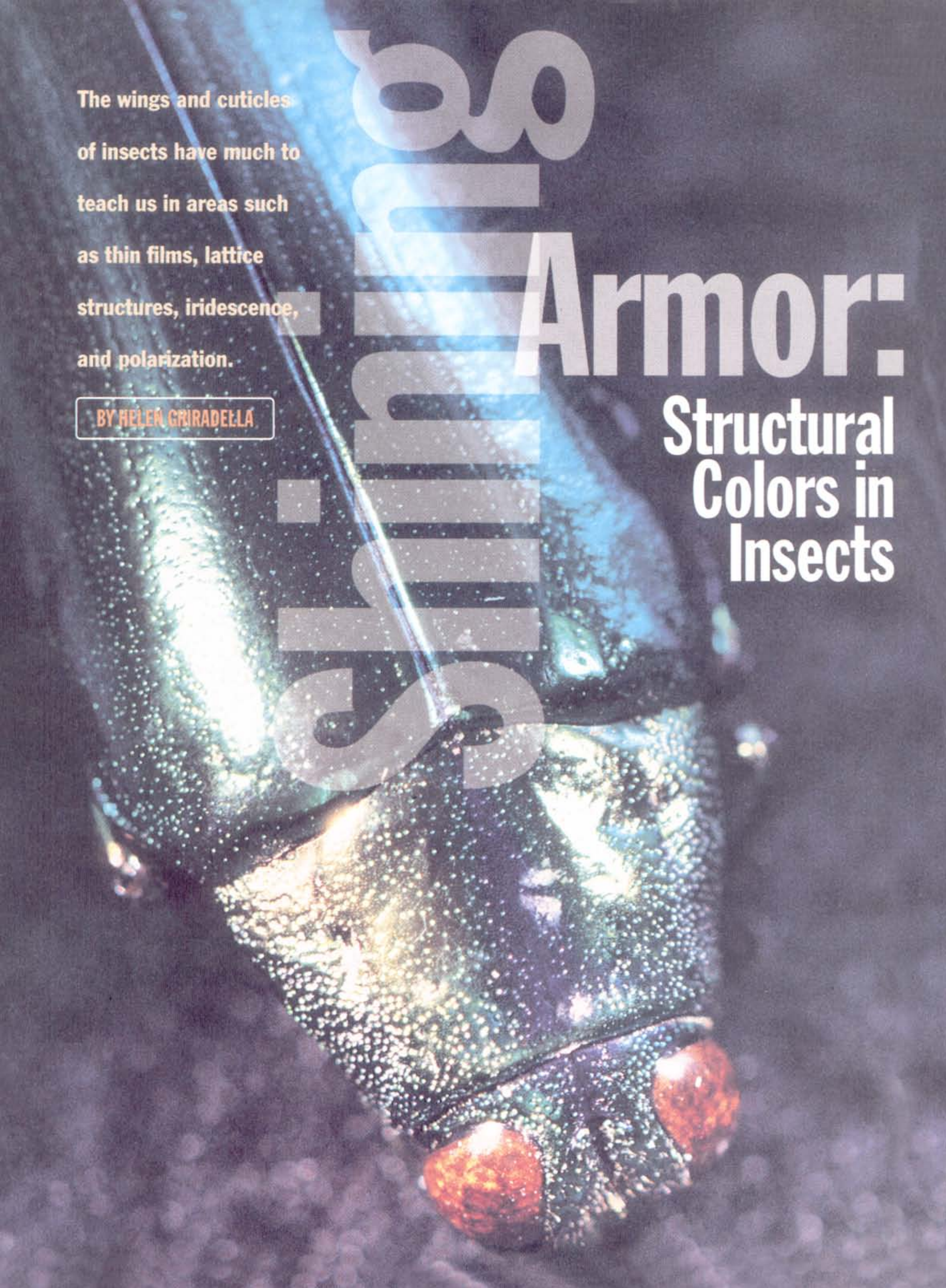

Shining Armor: Structural Colors in Insects

The wings and cuticles of insects have much to teach us in areas such as thin films, lattice structures, iridescence, and polarization.

BY HELEN GHIRADELLA

Insects are master materials scientists; their very existence is made possible by their external *cuticle*, a light, tough, strong, and extraordinarily versatile material. Insects are also master optical engineers; not only can they color the cuticle with various pigments, but they can fashion it into a variety of microarchitectures that produce a dazzling range of structural colors and other effects. A brief view of each of three systems—butterfly and moth scales,[1] transparent butterfly and moth wings, and iridescent beetle cuticles—illustrates the range of these accomplishments.

Butterfly and moth scales

The brilliant iridescent colors of butterflies and moths are usually carried in their *scales*, thin plates that plug into sockets on the wing (see Fig. 1). The scales are essentially flattened hollow sacs, but they can be filled with stacks of thin films (see Fig. 2) tuned to produce green, blue, violet, or perhaps ultra-violet (likely, but not yet reported). Alternatively, the scale interiors may contain crystallites of a lattice (see Fig. 3) that diffracts light to produce a muted green.[2, 3]

The visible surface of most scales is thrown into a reticular "superstructure" that consists of longitudinal *ridges* joined at intervals by transverse *crossribs* (see Figs. 3, below, and 4, page 48); by modifying these, structural colors can be produced. In some iridescent scales the ridges carry lateral flanges (see Fig. 4) that function as thin-film stacks,[1, 4] or the ridges, and sometimes the flat areas between them, may carry fine flutings that diffract light to produce iridescent color.[5] Alternatively, the surfaces between the ridges are sometimes elaborated into regularly spaced pores that scatter light to produce a Tyndall blue.[6]

Structural colors can be modulated by pigments. Many butterfly scales reflect simultaneously structural ultraviolet and pigmentary white or yellow.[4] The scales of some Morpho butterflies are deep iridescent blue while those of other Morphos are pale and pearlescent; the former scales, but not the latter, "back" the reflective elements of the scale with a layer of the dark pigment, melanin, that absorbs extraneous light that would otherwise "fog" the reflector.

The range of optical effects is even further extended when two or more scales work together to modify each other's performance. In some species, it is being shown that transparent surface scales modify the angle-spread of reflectance of the iridescent scales beneath them.[7] Other visibly interactive effects await study. For example, many clear scales turn blue when two or more are stacked together.

Transparent wings

Many "clear-wing" butterflies and moths show little or no specular reflection from the clear patches on their wings. These wing surfaces are covered with fine "nipples" (see Fig. 5, page 48) that serve as antireflection coatings.[8] First described on the corneal surfaces of insect eyes,[9, 10] these structures might generally be present wherever particular transparency is needed.

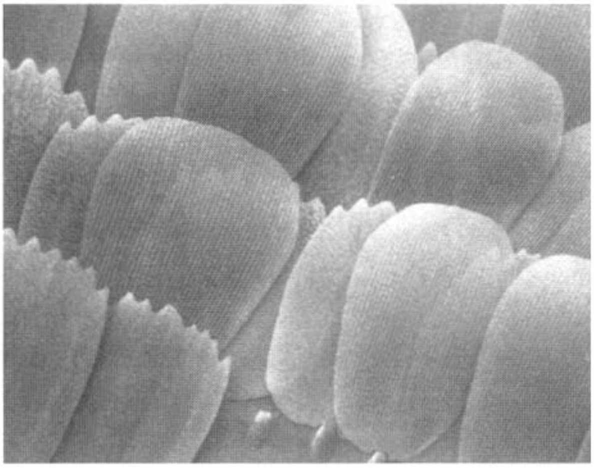

Figure 1. *Edenopsis taxila*, part of a wing with attached scales. Several scales have been removed to show the sockets (one empty) into which their neighbors are plugged. The larger scales show faintly the longitudinal ridges that are characteristic of most scales. Bar = 50 μm.

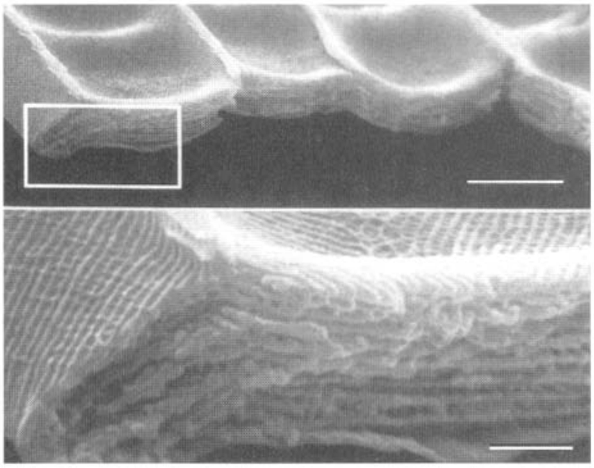

Figure 2. *Papilio palinurus*, part of a fractured scale. The boxed area (top) is enlarged at bottom to show the stack of internal lamellae that produce a green thin film interference color. Bar = 5 μm (top), 1 μm (bottom).

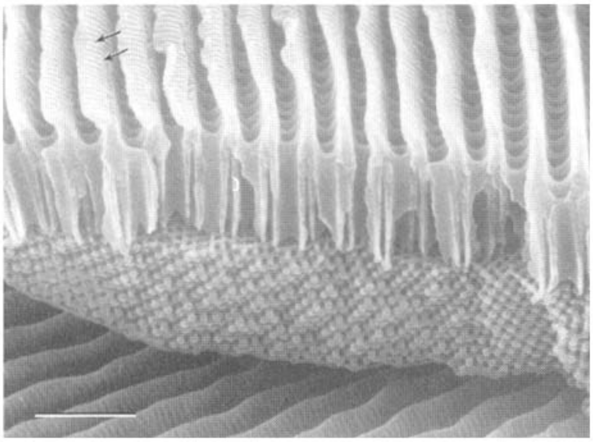

Figure 3. *Parides sesostris*, part of a scale fractured in cross section (and resting on another scale). The lattice in the scale interior produces a green diffraction color.[2] In other scale types, diffraction colors may be produced by elaboration of the faint striations (arrows) on the ridges of the scale "superstructure."[5] Bar = 2 μm.

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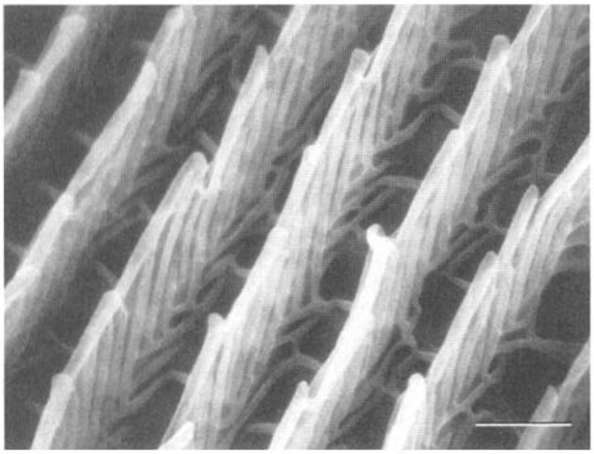

Figure 4. *Caligo ilioneus,* part of the surface of an iridescent scale. The ridges are high and have on them lateral flanges that act as thin-film stacks. The crossribs are visible in the "valleys" between the ridges. Bar = 1 μm.

Iridescent cuticles

The brilliantly metallic cuticles of many beetles result from yet a different mechanism. As a composite, cuticle generally consists of microfibrils of chitin—a tensile material found in insect cuticles—embedded in a complex matrix. During its assembly, the chitin microfibrils may be laid down in any of a great variety of orientations.[11] These include "cholesteric" (fibril direction rotated slightly in each subsequent layer, analogous to the form in cholesteric liquid crystals) and "preferred" (fibrils oriented in one direction only). In the beetle cuticles, the orientation is generally cholesteric and the pitch of the microfibril rotation is precisely controlled to produce the regularly spaced alternation of high and low refractive index needed for effective iridescence.[12] Some of these beetles reflect both left and right circularly polarized light, having inserted a preferred half-wave plate in the otherwise cholesteric array.[13] Those producing gold or silver colors can apparently modify the array so that it is "chirped" (pitch varying systematically with depth in the array), or otherwise varied in pitch.[14]

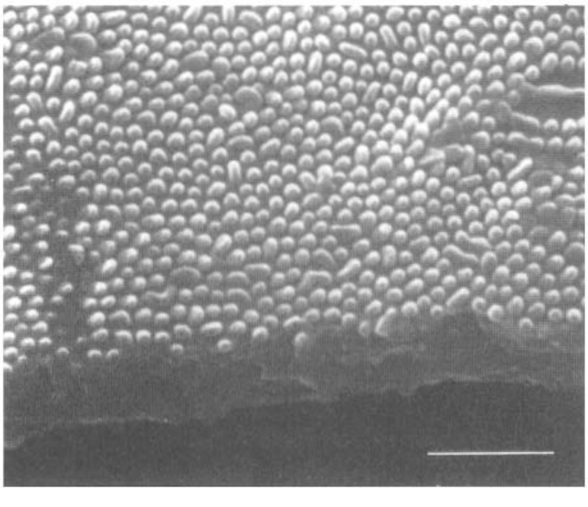

Figure 5. *Podosesia syringae,* part of a transparent patch of wing. The fine "nipples" function as an anti-reflection layer[8] and enhance the transparency of the wing. The fractured edge of the wing membrane appears at bottom. Bar = 2 μm.

It is clear that these systems can teach us much about how to handle light, but biologists have other questions as well. We would like to know how insects *make* these structures. Each wing scale, for example, is made by a single cell that somehow understands where it is on the wing, what kind of scale it must make, and how it will specify and produce the complex physical and chemical architecture of that scale. We also wonder about the nature of the evolutionary "intelligence" that has led to such an extraordinary material and such extraordinary shaping of it. Considering that most biological structures are designed to be multifunctional (for example, in some iridescent scales, the thin-film stacks also control IR transmissivity,[15, 16] thereby presumably influencing the heat budgets of their owners), we are currently almost certainly seeing just part of the complexity that is actually there. It's a rich source of questions, and as we study these systems, we are constantly reminded that our small six-legged colleagues are first-rate engineers . . . and potentially fine teachers as well.

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