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Article Addendum

Contributions of iridescence to floral patterning

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The *Hibiscus trionum* flower is distinctly patterned, with white petals each with a patch of red pigment at the base, producing a 'bull's-eye' pattern on the whole flower. The red pigmented patches are also iridescent, due to the presence of a series of overlying cuticular striations that act as a diffraction grating. We have previously reported that scanning electron microscopy revealed a sharply defined difference between the surface structure overlying the pigmented patch and that over the rest of the petal, with the diffraction grating only present over the pigmented region. Here we show that differences in petal surface structure overlie differences in pigment color in three other species, in a range of different patterns. Floral patterns have previously been shown to be advantageous in pollinator attraction, and we discuss whether emphasis of pigment patterns by structural color may increase floral recognition by pollinators.

The primary function of many floral traits appears to be to ensure that flowers are highly visible, recognizable and attractive to animal pollinators. One floral trait that has been shown to increase pollinator visitation to a flower is that of contrasting color patterns.¹⁻¹⁰ These patterns can act as guides to pollinators to aid foraging by highlighting the location of nutritional rewards, or can increase visibility by using strongly contrasting colors.¹⁻¹⁰ Patterns can occur in the range of wavelengths visible to the human eye, but are also common in the UV (ultraviolet) region of the spectrum.¹¹ Such UV patterns are invisible to humans but visible to many pollinating insects such as bumblebees, whose visual spectrum extends into the near UV region.¹

Hibiscus trionum (also known by the common names of 'flower-of-an-hour' and 'modesty' due to its very short flowering time) produces flowers with a distinct 'bull's-eye' pattern (Fig. 1A). The majority of this radially symmetrical (actinomorphic) flower is white, but it has a dark purple center. This dark center is due to a region of purple pigmentation produced at the base of each petal. However,

this pigmented region is particularly eye-catching due to the iridescent luster that overlies it. This luster does not extend into the rest of the white colored petal. Analysis of the surface structure of this flower by scanning electron microscopy (SEM) showed a distinct difference in surface structure between the two regions (Fig. 1B). While the white region of the petal, in common with around 79% of all other flowers, has an epidermis composed of conical cells,¹² the epidermis over the pigmented region is instead composed of flat (elongated) cells covered by a series of regular parallel striations. We have shown that these striations act as a diffraction grating, producing the visible iridescence.¹³ Iridescence is the change of hue in the color of a surface according to the angle from which it is being observed. This physical phenomenon results from periodical structured material surfaces or interfaces and can not be caused by pigments alone.

UV-vis spectroscopy measurements suggest that the petal surface of *H. trionum*, displaying elongated flat cells that are overlaid with continuous, periodically spaced striations, shows enhanced reflectance in the UV compared to non structured surfaces.¹³

Bull's-Eye Patterns

The bull's-eye image has been shown to increase the attractiveness of a flower from a distance, and may also help pollinators orientate themselves on the flower shortly before and after they have landed.² The pigment bull's-eye pattern in *H. trionum* is overlaid by a structural bull's-eye pattern. A similar, although in each case slightly different, situation is found in *Nolana paradoxa* and *Tulipa humilis* flowers. *N. paradoxa*, like *H. trionum*, produces radially symmetrical flowers, but in *N. paradoxa* the base of the petal is white while the rest of the petal is blue (Fig. 1D). As in *H. trionum*, the base of the petals has a flat-celled heavily striated surface that, when replicated in transparent, colorless epoxy¹³ produces iridescence that is visible to the human eye (Fig. 1E), while the rest of the petal is instead covered in conical cells (Fig. 1F). In direct contrast, *T. humilis*, which has flowers with a dark black center against a pink background, develops striations over the whole tepal except for the central bull's-eye (Fig. 1G-I).

Nectar Guides

Nectar guides have also been shown to increase the attractiveness of flowers to their pollinators, by helping to increase the efficiency with which pollinators can forage. These nectar guides are often found to contrast with the rest of the flower by absorbing strongly in the UV.¹¹ This is certainly the case in *Lathyrus pratensis*, where

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the flower appears yellow to human eyes, with black nectar guides that extend over the upper and middle part of the flag (Fig. 1J). However, with a UV sensitive camera, alternative, UV absorbing nectar guides which do not reach the base of the flag and do not correspond with the black pigment nectar guides are visible at the base of the flag of the flower (Fig 1K, indicated by arrows). As with the bulls-eye pattern of *H. trionum*, *N. paradoxa* and *T. humilis*, the pattern of the UV nectar guides can be seen on the surface structure of the petal. Over the majority of the UV-reflecting flag lie ordered striations similar to those found in *H. trionum*. Over the UV-absorbing nectar guides these striations are missing (Fig. 1L, base of flag indicated by arrow). To what extent the UV absorbing nectar guides in *L. pratensis* are caused by differences in surface structure or by the interplay of surface structure and underlying pigment is still to be determined.

Other Patterns

Many species of Ophrys orchids have been reported to have an iridescent patch, the speculum, on the elaborate labellum of the flower (Fig. 1C).¹⁴ These orchids use sexual deception of male wasps and solitary bees as their mechanism of pollination, and the shape and iridescence of the speculum is thought to mimic the closed wings of the female.

What are the Advantages of Floral Iridescence?

What would be the evolutionary advantage of producing structural colors when plants already have such a diverse repertoire of pigments available to them? In the case of Ophrys, the advantage appears straight forward. Iridescence can only be produced through structural mechanisms, not pigment-based ones. The floral iridescence mimics the iridescence displayed by insect wings, and increases the extent to which the Ophrys flowers act as convincing mimics. Similar mimicry may also be important in other flower-pollinator relationships. One potential area of interest is that many pollinating animals are themselves iridescent.

Iridescence on flowers that do not rely on mimicry for pollination may have a range of other advantages. One potential advantage is that the iridescent color is directional. Floral patterns have already been shown to help pollinators orientate themselves on flowers, and, in the same way that pilots use landing lights to land planes, insects could use the directionality of iridescent color to forage more efficiently.

It has previously been shown in both birds and butterflies that structural color can enhance pigment color either by an additive or a contrast effect, both in the human-visible and UV wavelengths.¹⁵⁻¹⁷ The combination of both structural and pigment can produce uniquely enhanced colors.¹⁸ As the attractive nature of the floral patterns that we have been considering relies on the color contrast between the two underlying pigments, an overlying surface that highlights or enhances the difference could increase the attractiveness of the whole flower.

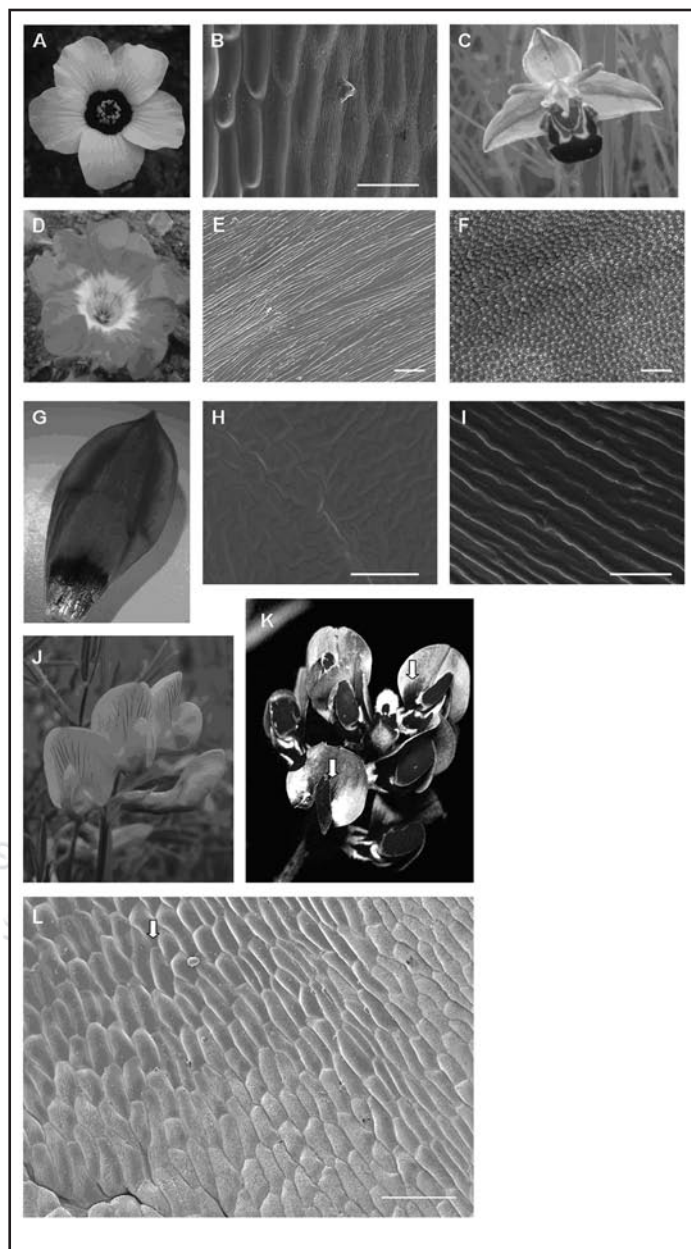


Figure 1. Photographic floral images (both in visible and UV light) and corresponding scanning electron micrographs. (A and B) *Hibiscus trionum* flower showing 'bull's-eye' pattern. (B) SEM of *Hibiscus trionum* petal image showing the boundary region (B, scale bar = 50 μm) between the pigmented (striated) region and the white (conical) on the petal. (C) *Ophrys apifera* flower. (D-F) *Nolana paradoxa* flowers. (E) striated center white region (E, scale bar = 20 μm). (F) The outer blue region with conical cells (F, scale bar = 100 μm). (G-I) *Tulipa humilis* petal. (H) The dark inner center with no cuticular striations (H, scale bar = 10 μm). (I) the rest of the petal which has ordered striations (I, scale bar = 5 μm). (J-L) *Lathyrus pratensis*. (J) *Lathyrus pratensis* flowers in visible light. (K) *Lathyrus pratensis* flowers showing UV reflection. The nectar guides at the base of the flag petal are indicated with arrows. (L) SEM of flag showing unstriated region corresponding to nectar guides (base of flag indicated by arrow) (L, scale bar = 100 μm).

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