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ULTRAVIOLET ABSORPTION BY FLOWERS OF THE ESCHSCHOLZIOIDEAE (PAPAVERACEAE)

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Abstract

Corollas of the subfamily Eschscholzioideae strongly absorb long-wave ultraviolet radiation, which likely makes them attractive as a source of food reward to foraging pollinators. Filled anthers are also absorptive, but they become reflective as they are emptied of pollen. The epidermis of both the corolla and the anthers is composed of elongated prismatic cells that may have a function in ultraviolet absorption.

The importance of ultraviolet patterns to the vision of pollinating insects has long been recognized (Lutz, 1924; Kugler, 1947, 1963, 1966; Daumer, 1958) and recently has been subjected to intensive scrutiny (Eisner et al., 1969; Ornduff and Mosquin, 1970; Horovitz and Cohen, 1972; Mulligan and Kevan, 1973; Jones and Buchmann, 1974; Guldberg and Atsatt, 1975; King and Krantz, 1975; Utech and Kawano, 1975). In summary, it has been found that food rewards in flowers are often marked by structures or patterns that absorb long-wave ultraviolet radiation, which is visible to bees and many other insects but not to humans, and at the same time reflect wavelengths of visible light. These patterns contrast in an insect's vision with other parts of the flower, or with the background (Frohlich, 1976), which reflect ultraviolet, often strongly.

In conjunction with my studies of the genus *Eschscholzia* of the Papaveraceae, I investigated the UV floral patterns of ten of the fourteen species of that genus, the monotypic *Hunnemannia fumariifolia,* and the two varieties of the monotypic *Dendromecon rigida,* which together constitute the subfamily Eschscholzioideae (Ernst, 1962). I sought to determine whether there were UV patterns that might provide visual clues to pollinating insects, and how these patterns varied within the tribe.

Methods

Flowers of 22 populations of the 12 species were photographed in the greenhouse, field, or lab using single-lens reflex cameras with glass lenses and Kodak Tri-X film. Visible-light pictures were made with no filtration, and UV photographs with a Wratten 18A filter, which transmits only long-wave ultraviolet. Exposures were determined with a through-the-lens meter.

After preparing the corollas by the technique of Lynch and Webster (1975) for fresh pollen and coating with gold in a Polaron sputter coater, I examined the surface features with a Cambridge Stereoscan S4 scanning electron microscope, taking photographs on Kodak 4127 film.

Species examined include *Dendromecon rigida* Bentham var. *rigi-*

da, D. rigida var. *harfordii* K. Brandegee, *Eschscholzia californica* Chamisso, *E. mexicana* Greene, *E. caespitosa* Bentham, *E. parishii* Greene, *E. covillei* Greene, *E. minutiflora* Watson, *E. glyptosperma* Greene, *E. lemmonii* Greene, *E. hypecoides* Bentham, *E. lobbii* Greene, and *Hunnemannia fumariifolia* Sweet.

Results

Examined corollas all strongly absorb long-wave ultraviolet radiation, appearing black in the photographs (Figs. 1–4). The species are indistinguishable on this character alone. The UV-absorbing corollas contrast strongly with backgrounds of annual grasses and forbs (Fig. 5) and reflective soils, although not so strongly with the chaparral habitats of *Dendromecon.*

Highlights on the flowers (arrow in Fig. 2) represent specular reflection from the ridged surface of the corolla, which consists of files of elongated prismatic cells (Figs. 6 and 7). This same reflection in visible light accounts for the "satiny sheen" that is a well-known feature of *Eschscholzia* flowers (Smith, 1902). Specular reflection is also apparent on the tips of the anthers in Figs. 3 and 4.

The anthers appearing reflective in Fig. 2 are empty. Anthers filled with pollen grains are hardly less absorptive than the corollas (Fig. 3). The locules of the anthers also possess a ridged epidermis.

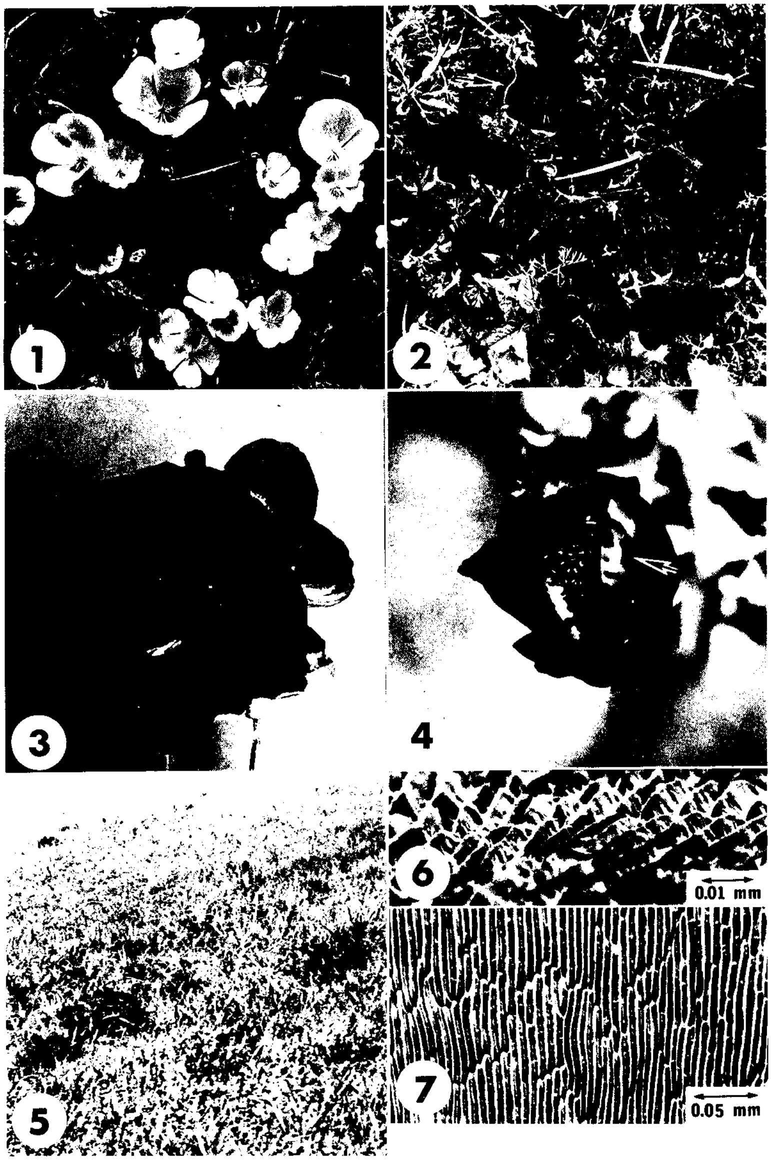
The yellow and orange pigments of the corollas are not responsible for the UV absorption. A mutant plant near Mariposa, California, with cream-colored corollas absorbed UV as strongly as the wild type.

Discussion

The corollas of the Eschscholzioideae, contrasting with their backgrounds in both visible and UV wavelengths, should be quite conspicuous to pollinating insects. The strong UV absorption is a signal of food rewards, i.e., pollen. Undehisced anthers are absorptive; foraging insects break these open to remove the pollen. As the anthers are emptied, they become more reflective and presumably less attractive, the insects' attention being drawn to the floral cup, where the pollen accumulates after it leaves the anthers. The pollen grains themselves appear to be absorptive.

The epidermal ridges of the corolla are suggestive of the papillae reported by Brehm and Krell (1975) on the UV-absorptive portions of composite ray flowers. Those papillae contain UV-absorbing pigments. I do not have any evidence of specific function of the epidermal ridges in UV absorption, but it is noteworthy that the absorptive anthers also have these ridges.

The ultraviolet floral pattern appears to be constant throughout the subfamily. This is not surprising, as the flowers are constant in most other respects. The only substantial differences even among the genera are in the form of the calyx, receptacle, and stigmas. Similarity of



FIGS. 1–7. 1. *Eschscholzia californica* photographed in visible light. 2. The same plant photographed in ultraviolet light; arrow, specular reflectance (see text). 3. Ultraviolet photograph of *Hunnemannia fumariifolia*. 4. Ultraviolet photograph of *Dendromecon rigida* var. *harfordii*; arrow, honeybee (*Apis mellifera*) visiting the flower for pollen. 5. *E. californica* on a hillside of grasses near Byron, California, photographed in ultraviolet light. 6. Oblique view of the prismatic epidermal cells of *E. lemmonii*. 7. Face view of the prismatic epidermal cells of *E. lemmonii*.

floral morphology might argue for similarity of pollination syndrome, and indeed all the species studied seem to be generalists, being pollinated by a variety of insects including bees, beetles, and flies. The autogamous *E. minutiflora,* which has undergone a diminution of flower size and reduction in stamen number, retains the UV pattern of the entomophilous species.

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