

FLORAL ULTRAVIOLET IN THE *ENCELIA* ALLIANCE (ASTERACEAE: HELIANTHEAE)

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ABSTRACT

The *Encelia* alliance is a monophyletic group comprising *Encelia*, *Geraea*, and *Enceliopsis*. Disk corollas, usually yellow, but dark brown in some species of *Encelia*, all absorb long-wave ultraviolet radiation. Ray corollas of *Enceliopsis* and *Geraea* are all yellow, and all absorb long-wave ultraviolet. One group of *Encelia* species (including the one white-rayed member) also has ultraviolet-absorbing rays; another group has rays that reflect ultraviolet. Outgroup comparison suggests that ultraviolet reflection is an apomorphy within the alliance that, along with other characters, marks the group of species possessing it as a clade.

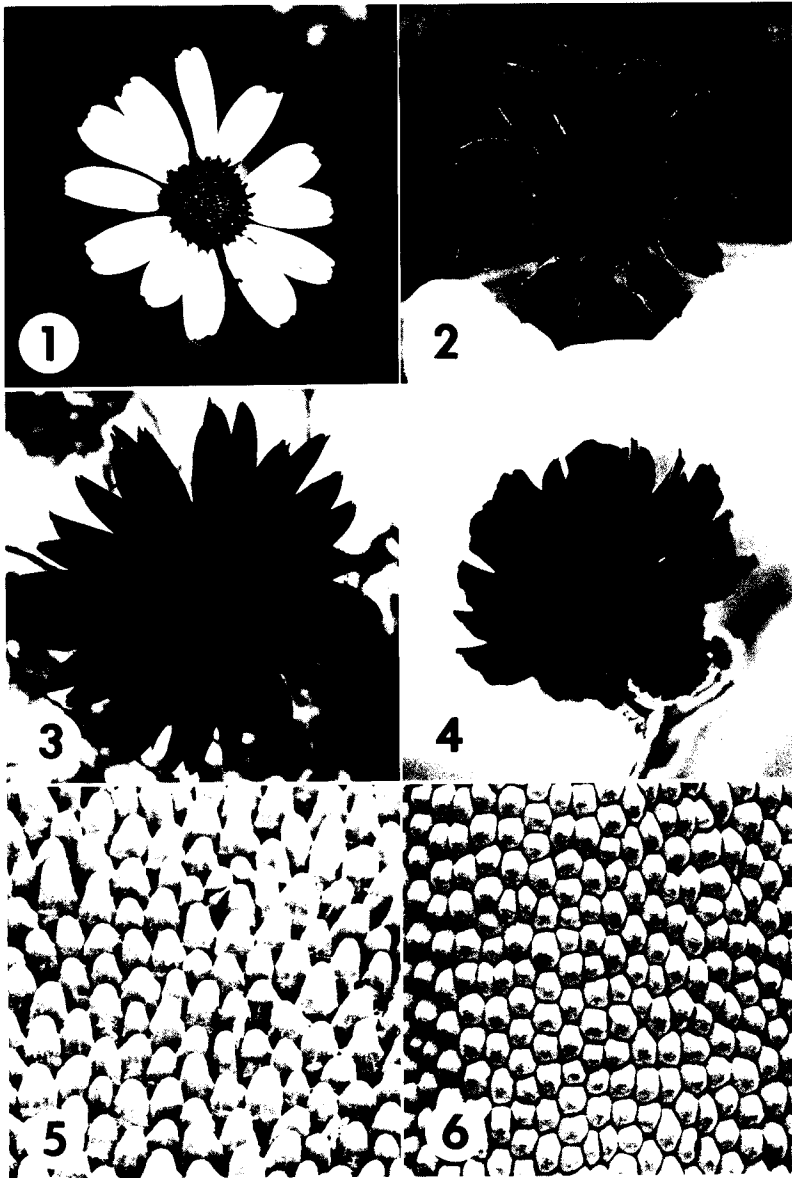
Over the last 15 years there has been a resurgence of interest in the role of floral ultraviolet (UV) in the vision of pollinating insects (Clark 1979 provides a brief summary), but comparatively few studies have addressed its usefulness as a taxonomic character. We maintain that ultraviolet is no less important a floral color, especially in insect-pollinated flowers, than those colors visible to humans, and that it is important for taxonomists to characterize floral UV in the groups they study, whether or not they address its importance in pollination.

The genera *Encelia*, *Geraea*, and *Enceliopsis* form a monophyletic group diagnosed by the presence of caducous paleae coupled with flattened, black achenes having a depigmented ciliate margin. *Encelia*, comprising 20 species of shrubs, is broadly distributed in arid southwestern North America. The five species of *Enceliopsis* are herbaceous rosette perennials, and are found in the region of the Colorado Plateau. *Geraea* consists of two species, a widespread desert annual and an herbaceous perennial of chaparral in eastern San Diego Co., California. As part of our investigations of these genera, we have examined the UV patterns and associated micromorphology of the corolla surfaces of all the species.

METHODS

As part of field and greenhouse studies of the species, we have made UV photographs of flower heads, and have accumulated data from several to many plants from every species.

Heads were photographed with a single-lens reflex camera having



FIGS. 1-6. Capitula photographed in long-wave ultraviolet light. 1. *Encelia californica*, south of El Rosario, Baja California. 2. *Encelia virginensis*, greenhouse-grown from cutting taken at St. George, UT. 3. *Enceliopsis argophylla*, near Lake Mead, NV. 4. *Geraea canescens*, near Indio, CA. FIGS. 5, 6. Scanning electron micrographs of adaxial ray corollas, $\times 200$. 5. *Enceliopsis covillei*. 6. *Encelia palmeri*.

TABLE 1. SPECIES WITH UV-ABSORBING RAY COROLLAS.

<i>Geraea canescens</i> T. & G.
<i>Enceliopsis argophylla</i> (D. C. Eaton) A. Nelson
<i>Enceliopsis covillei</i> (A. Nelson) S. F. Blake
<i>Enceliopsis nudicaulis</i> (A. Gray) A. Nelson var. <i>nudicaulis</i>
<i>Enceliopsis nudicaulis</i> var. <i>corrugata</i> Cronquist
<i>Encelia actoni</i> Elmer
<i>Encelia frutescens</i> (A. Gray) A. Gray var. <i>resinosa</i> Jones ex Blake
<i>Encelia ravenii</i> Wiggins
<i>Encelia virginensis</i> A. Nelson

automatic through-the-lens exposure (generally an Olympus OM-2) and a glass lens. UV photographs were taken on Kodak Tri-X film (exposed at ISO 125 in the OM-2 rather than its rated speed of ISO 400, and developed in Kodak Microdol-X diluted 1:3) through a Wratten 18-A filter or a Corning 7-60 filter, both of which transmit only long-wave UV in the neighborhood of 360–370 nm. Visible-light photographs were taken with no filtration.

Corollas were prepared for scanning electron microscopy by the techniques of Clark (1979), Kyhos et al. (1981), or Charest-Clark (1984), which reflect ongoing improvements.

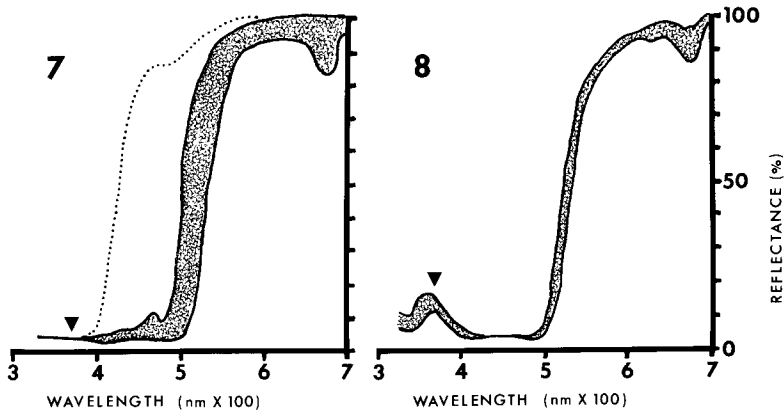
We prepared ray corollas for reflectance spectrophotometry by removing them from the heads, affixing them to cards with double-faced tape, adaxial side up, and placing the cards in the sample slot of a Shimadzu/B&L Spectronic 210 UV recording spectrophotometer. Magnesium oxide was used as a reference.

RESULTS

Disk corollas of all species absorb long-wave UV (e.g., Figs. 1–4). Three species [*Encelia frutescens* (A. Gray) A. Gray var. *frutescens*, *Enceliopsis nutans* (Eastwood) A. Nelson, and *Geraea viscida* (A. Gray) S. F. Blake] lack rays; the rest fall into two distinct groups,

TABLE 2. SPECIES WITH UV-REFLECTING RAY COROLLAS.

<i>Encelia asperifolia</i> (S. F. Blake) Clark & Kyhos
<i>Encelia californica</i> Nutt.
<i>Encelia canescens</i> Lam.
<i>Encelia conspersa</i> Benth.
<i>Encelia</i> sp. nov.
<i>Encelia farinosa</i> A. Gray var. <i>farinosa</i>
<i>Encelia farinosa</i> var. <i>phenicodonta</i> (S. F. Blake) I. M. Johnston
<i>Encelia farinosa</i> var. <i>radians</i> (T. S. Brandegeee) S. F. Blake
<i>Encelia halimifolia</i> Cav.
<i>Encelia palmeri</i> Vasey & Rose
<i>Encelia ventorum</i> T. S. Brandegeee



FIGS. 7, 8. Reflectance spectrograms. Shaded portion indicates variation among species, triangle marks 370 nm, the wavelength important in insect vision. 7. UV-absorbing species; dotted line corresponds to the white-rayed *Encelia ravenii*. 8. UV-reflecting species.

those with rays UV-absorbing over their entire length (Table 1, Figs. 2–4) and those with rays UV-reflecting over their entire length (Table 2, Fig. 1).

Because many of the photographs were taken without a gray scale as reference, we were concerned that different densities in the negatives might represent different absolute amounts of absorption or reflection. Reflectance spectrophotometry of the rays of UV-absorbing species showed no differences in the amount of UV absorption between species—all show a reflectance at 370 nm of about 3% of the reference (Fig. 7). UV-reflecting species showed slight differences at 370 nm, varying from 11% to 16% reflection (Fig. 8); however, they show a clear discontinuity from the absorbing species. Reflectance at other wavelengths was markedly uniform among the yellow-rayed species, confirming the visual similarity of their pigmentation.

The adaxial epidermes of both the ray and disk corollas of the species studied show “Helianthoid” papillae (Baagøe 1977). Such papillae have been implicated in UV absorption (Brehm and Krell 1975). Dimorphism has been noted in some species having rays with a “bullseye” pattern (reflecting distally and absorbing proximally), the papillae being taller and more conical in the absorbing region (Baagøe 1977, Scogin and Rogers 1980). In those species studied that have absorptive rays, and in the disk corollas of all species, the papillae are tall and conical (Fig. 5). In the species with reflecting rays, the papillae are generally lower, usually with a flattened or rounded apex (Fig. 6). Because the differences are not always con-

sistent, it is not always possible to identify UV-absorbing species by papilla height. In general, though, this group exhibits the same dimorphism between species as has been reported (Scogin and Rogers 1980) within the UV-bicolored rays of a single species.

DISCUSSION

Ultraviolet-reflecting rays are restricted to a group of species in *Encelia*. The other species of *Encelia*, as well as all the radiate species of *Geraea* and *Enceliopsis*, have absorbing rays. Using the outgroup comparison method (Watrous and Wheeler 1981), we conclude that, within *Encelia*, UV reflection is the apomorphic (derived) state and UV absorption is plesiomorphic (ancestral). This is evidence that the UV-reflecting *Encelia* species constitute a monophyletic group. Another character also supports this hypothesis of monophyly. Proksch and Clark (unpubl.) have found in this same group of *Encelia* species, with one exception, a unique secondary metabolite, a dimer of a benzopyran and a benzofuran. The exception, *E. asperifolia*, is instructive in two regards. First, Clark and Kyhos (1979) have proposed that it originated from hybrids between *E. californica* and a glandular form of *E. frutescens*; this new information is consistent with that hypothesis, because it has the UV reflectance of one parent and the absence of the unique chemical compound of the other. Second, it demonstrates that the chemical compound is not involved with UV reflectance.

It was suggested by an anonymous reviewer that UV absorption of the rays might not be homologous among the three genera, because it has been shown (Harborne and Smith 1978) that at least four different groups of flavonoid pigments provide UV absorption in different genera of the Asteraceae. We find this statement provocative for two reasons. First, although chemical differences among species have been used taxonomically for a number of years, it is still common for taxonomists to address flower color without reference to its chemical basis. This is not to say that the chemical basis should be ignored, just that it often has been. Second, there is more to UV absorption than absorptive pigments. These pigments are accumulated in the vacuoles of the epidermal cells of the corolla (Harborne and Smith 1978, Brehm and Krell 1975, Rieseberg and Schilling 1985), and the adaxial cells are often enlarged (Baagøe 1977). We suggest that, within groups of clearly related species, this syndrome associated with pigment accumulation may be the homology, and that the nature of the pigments themselves may be determined by the general biochemical pathways of the plant. Nevertheless, a preliminary assessment of the ray pigments suggests little variation among the UV-absorbing species, and demonstrates the absence of anthochlors, one of the four classes of pigments.

Although we have not intended specifically to address the function of floral UV in the pollination of this group, it is worth noting that spontaneous natural hybrids are common in areas of sympatry between the UV-absorbing *E. actoni* and the UV-reflecting *E. farinosa*, and between the latter and the rayless *E. frutescens*, suggesting that the differences are not important to the variety of insects that pollinate these species.

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ERRATA

p. 130, second paragraph — change "The five species of *Enceliopsis*" to "The five taxa of *Enceliopsis*" .

p. 131, legend for Fig. 3 should read "*Enceliopsis covillei*, Panamint Mountains, CA".