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PETAL EPIDERMAL DIMORPHISM AND UV ABSORPTION
IN ANTHOCHLOR-PIGMENTED FLOWERS

Ron Scogin and Patricia Rogers

Introduction

The floral parts of numerous plants exhibit patterns of absorption and reflection of ultraviolet (UV) wavelength light. The only floral pigments demonstrated to date to be involved in UV absorption have been flavonoids (Thompson et al. 1972; Scogin et al. 1977). Petal epidermal cell morphology has also been implicated in UV patterning by virtue of its effect on the efficiency of light absorption at the petal surface. An epidermal cell dimorphism which correlated with UV absorption and reflection was observed in the anthochlor-containing petals of *Lasthenia chrysostoma* (Fisch. & Mey.) Greene by Brehm and Krell (1975). The occurrence of anthochlor pigments and UV patterns correlated with their sequestering has also been demonstrated in numerous additional taxa of the Asteraceae (Scogin 1976; Scogin and Zakar 1976) and in the Fabaceae (Scogin, unpub. data). To investigate the generality of the dimorphism observed in *Lasthenia*, the present study was initiated, in which epidermal cell morphology was investigated by scanning electron microscopy in several genera of anthochlor-containing plants in which UV patterning was present and absent in different members of each genus.

Materials and Methods

Floral materials used in these studies were collected from plants in cultivation at the Rancho Santa Ana Botanic Garden. Entire floral heads were fixed for 72 hr in FAA and then transferred to 70% ethanol. Individual ligules were placed in small, lens-paper envelopes, rinsed in distilled water for 15 min, and dehydrated by passage through an ethanol solution series (50%, 70%, 95%, 100%, 100%; 20 min in each solution). Samples were prepared for critical-point drying by replacing ethanol with Freon TF (113) in a replacement series consisting of solutions of ethanol in Freon TF (113) in the following proportions: 3:1, 1:1, 1:3, 100% Freon TF (113). Samples remained in each solution for a period of 15 min. Samples were dried at the critical point using Freon 13 as the final replacement fluid. Specimens were mounted, coated with a thin layer of Au/Pd (60/40) by sputter coating, and examined in an AMR 1200 scanning electron microscope.

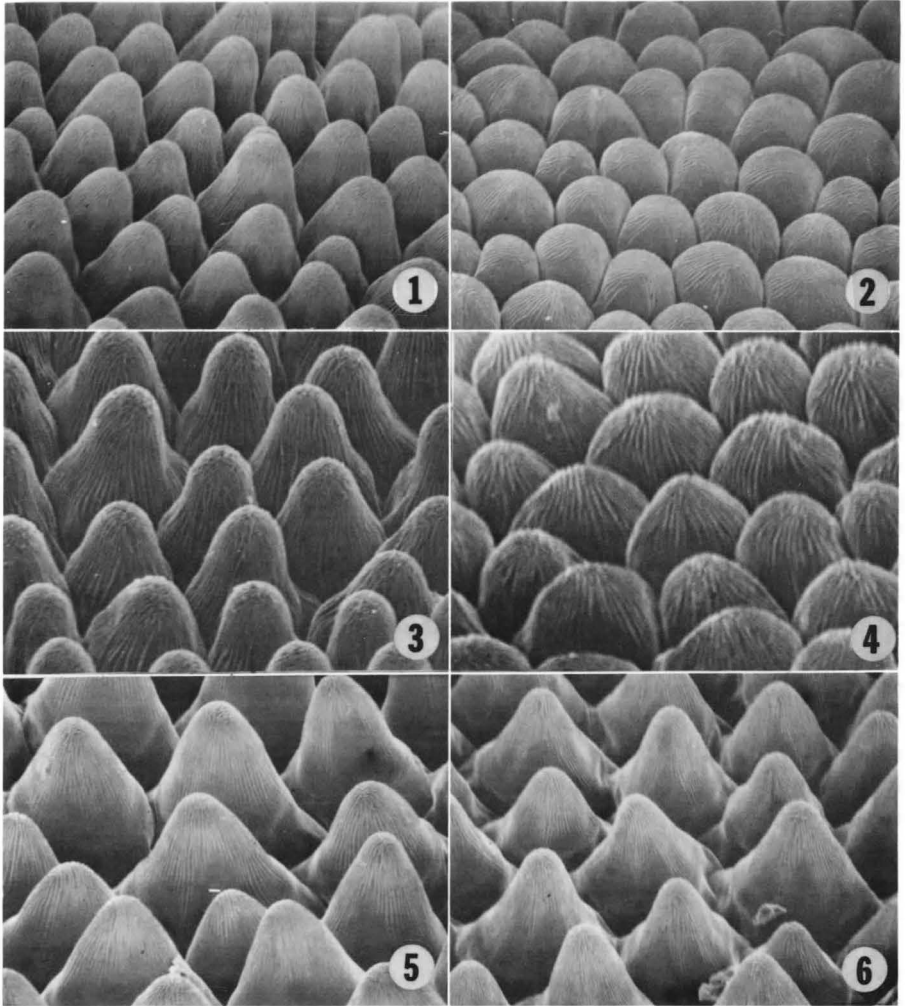


Fig. 1-6. Scanning electron micrographs of ligule surfaces.—1. *Bidens laevis* proximal.—2. *B. laevis* distal.—3. *Viguiera deltoidea* proximal.—4. *V. deltoidea* distal.—5. *Coreopsis grandiflora* proximal.—6. *C. grandiflora* distal. (All Figs. $\times 3685$.)

Results

Representative results from a survey examining epidermal cell morphologies by scanning electron microscopy in UV-absorbing, anthochlor-containing flowers are shown in Fig. 1-10.

Among those anthochlor-containing members of the Asteraceae exhibiting a "bull's-eye" UV absorption-reflection pattern, a dimorphism was consis-

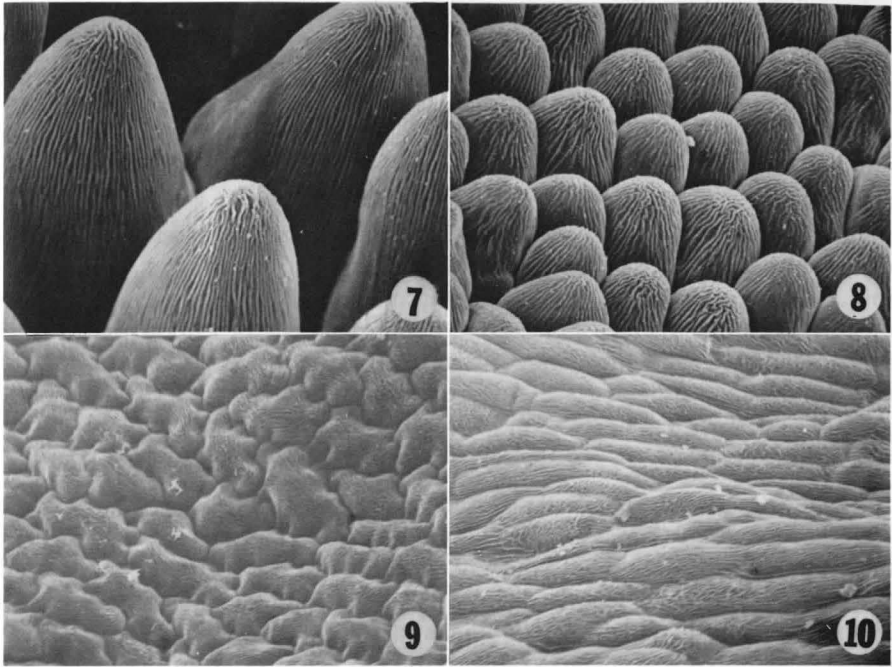


Fig. 7-10. Scanning electron micrographs of petal surfaces.—7. *Rudbeckia hirta* ligule.—8. *Helianthus annuus* ligule.—9. *Parkinsonia aculeata* banner.—10. *P. aculeata* wing. (All Figs. $\times 3685$.)

tently observed in the epidermal papillae between absorptive and reflective portions of the ligules. As shown in Fig. 1 and 2, the papillae of proximal, UV-absorptive epidermal cells in *Bidens laevis* L. have a generally conical shape, while the papillae of the distal, UV-reflective epidermal cells show a rounded, globose shape. In some taxa a well-defined projection is observed at the papillary tip in UV-absorptive cells as shown for *Viguiera deltoidea* A. Gray in Fig. 3. In addition to the species shown, this dimorphic pattern was also observed in *Viguiera multiflora* Blake, *Bidens ferulaefolia* (Jacq.) DC., and *Coreopsis gigantea* (Kellogg) H. M. Hall.

Other species of the same genera, but in which the ray flower is totally UV absorptive, were examined for comparison. A dimorphism in epidermal papillae is consistently absent in these taxa and all papillae of the ligule exhibit a morphology typical of the proximal (conical) papillae type in patterned flowers. The epidermal cells of the base and tip of a ligule from *Coreopsis grandiflora* Hogg. are shown in Fig. 5 and 6. In addition to the species shown, similar isomorphic, conical papillae were observed uniformly over the ligule length in *Viguiera reticulata* S. Wats., *Coreopsis pubes-*

cens Ell., and *C. stillmanii* (A. Gray) Blake, all of which possess totally UV-absorptive ray flowers.

For comparison, two nonanthochlor-containing helianthoid taxa which exhibit a bull's-eye UV pattern were also examined. *Rudbeckia hirta* L. and *Helianthus annuus* L. have isomorphic papillae along the entire ligule and are generally conical, although more rounded in the case of *Helianthus* (see Fig. 7–8).

In *Parkinsonia aculeata* L. an anthochlor-containing taxon of the Fabaceae, an epidermal cell dimorphism was observed between the UV-absorbing, anthochlor-containing banner petal and the UV-reflecting, anthochlor-lacking lateral petals (see Fig. 9–10). Epidermal cells of *Parkinsonia* petals are nonpapillate and the major difference between epidermal cells of the banner and lateral petals is the degree of convolution of the cell margins.

Discussion

Baagoe (1977) has noted that ligule epidermal morphologies within the Asteraceae fall into three main categories. All asteraceous taxa investigated in the present study belong to the "helianthoid type" which is characterized by papillose, nearly isodiametric epidermal cells and which is characteristic of the tribes Anthemideae, Heliantheae, and Tageteae (Baagoe 1977). Baagoe further noted that any UV-absorption pattern present in the ligule was often correlated with a dimorphism in epidermal cells; notably, UV-absorbing, proximal cells were approximately twice the height of UV-reflecting, distal cells. Difference in cell height, however, is not a sufficient condition for differential UV absorption as some ligules showing this dimorphism exhibit no UV pattern, while other ligules with uniform epidermal cell height show differential UV absorption (e.g. *Calendula* species). Baagoe's observations were confirmed among nonanthochlor-containing taxa in the present study. *Rudbeckia hirta* and *Helianthus annuus* (both anthochlor lacking) exhibit a strong bull's-eye UV pattern, but the papillose epidermal cells of their ligules are morphologically uniform along the entire ligule length. In contrast, all anthochlor-containing taxa which exhibited a UV pattern showed a strongly correlated dimorphism in their epidermal cell shapes. Epidermal dimorphism associated with UV patterning is not distributed along taxonomic lines. In the single subtribe Helianthinae (tribe Heliantheae) (Steussey 1977) epidermal dimorphism is present in *Viguiera* species, but absent in *Rudbeckia* and *Helianthus*, all of which have strong bull's-eye UV patterns. Thus, at least within the Asteraceae, epidermal dimorphism in cell outline appears only in those taxa containing anthochlor pigments. The selective value for this difference in shape is postulated to be to allow the more efficient presentation of anthochlor pigments in a favorable geometry to effect maximum absorption and thereby yield a strongly patterned flower to the eye of insect visitors.

Epidermal cells of *Parkinsonia* petals are not papillate. In addition, the banner petal of *Parkinsonia aculeata* does not absorb incident UV wavelengths as effectively as the proximal portion of appropriate helanthoid ligules. This observation supports the postulate that a papillate epidermis of conical cells is necessary for highly efficient UV absorption by anthochlor pigments in petals.

Acknowledgment

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