Proc. Nat. Acad. Sci. USA
Vol. 70, No. 4, pp. 1002–1004, April 1973

Ultraviolet Patterns on Rear of Flowers: Basis of Disparity of Buds and Blossoms

(ontogeny/pollination/biocommunication)

THOMAS EISNER*, MARIA EISNER*, AND D. ANESHANSLEY†

* Section of Neurobiology and † Department of Electrical Engineering, Cornell University, Ithaca, New York 14850

Contributed by Thomas Eisner, January 24, 1973

ABSTRACT **Flowers of *Jasminium primulinum* and *Hypericum* spp. have ultraviolet patterns on the reverse surface of the corolla. Those areas of the surface that are exposed to the outside in the bud are ultraviolet absorbent, whereas the portions that come into view at maturity in the open blossom are ultraviolet reflectant. Buds and blossoms, as a result, appear different in color to insects sensitive to ultraviolet light. Experimental evidence indicates that the ultraviolet-absorbent quality of the outer surface of the bud is a consequence of exposure itself, attributable possibly to a "sun tanning" effect.**

Many flowers have ultraviolet patterns, invisible to man, but visible to insects such as honeybees, whose visual sensitivity extends into the near-ultraviolet region of the solar spectrum (1, 2). Ordinarily these patterns, which are meaningful to the pollinator (1), are displayed on the exposed "facial" surface of the flower only. We have found flowers that have ultraviolet patterns on the rear as well as on the front surface. The phenomenon is anomalous, but readily explicable.

The species studied were *Hypericum* (*Ascyrum*) *peltatum* (Guttiferae) and *Jasminium primulinum* (Oleaceae) (Fig. 1). Their flowers are all evenly yellow to the human eye, on both the front and rear surface of the corolla (Fig. 1, *A*, *C*, and *E*). The ultraviolet pattern (3, ‡) on their frontal surface is conventional (Fig. 1, *B* and *D*). The center of each flower, including the reproductive parts, is absorbent, and the periphery, comprising most of the petal surface, is reflectant. Insects such as honeybees, which are visually sensitive to yellow as well as ultraviolet light, see such flowers as "bull's eyes," with yellow centers and surrounds of "bee purple" (the sum, in the color circle of the bee, of yellow and ultraviolet) (2). The ultraviolet pattern on the rear of the flowers, superimposed on the evenly yellow reverse surface of the petals, differs in the two genera. In *Hypericum* the pattern is consistent and symmetrical, each petal being divided diagonally into absorbent and reflectant halves (Fig. 1*B*, *right*). In *Jasminium* there is greater irregularity (Fig. 1*F*). Some petals are evenly absorbent, others are reflectant, and still others show variable lengthwise delineation into absorbent and reflectant zones. Additional observations were made on several other species of *Hypericum* [*H. fasciculatum; H. opacum; H. perforatum; H.* (*Ascyrum*) *cuneifolium*]. All showed essentially identical visible and ultraviolet features as *H. peltatum*.

‡ Ultraviolet patterns were recorded in live flowers by photography (Zeiss-Jena ultraviolet lens, Zeiss U5 filter) and by the video-taping technique described by Eisner *et al.* (3).

Reflection spectra were taken of the ultraviolet absorbent and reflectant zones on the rear of petals of two species of *Hypericum: H. peltatum*, and an horticultural hybrid ("Hypericum Sungold," Wayside Gardens, Mentor, Ohio). The results were identical for both flowers and are shown for *H. peltatum* in Fig. 2. As is apparent from the curves, the two petal zones show virtually no difference in reflectance in the visible spectrum but do show a distinct difference in the ultraviolet spectrum. The ultraviolet spectra of these two petal zones are practically equivalent to those of the reflectant and absorbent areas found in *Rudbeckia hirta*, where the ultraviolet pattern is on the front of the petals (4).

Offhand it would seem that ultraviolet designs borne inconspicuously on the least exposed surface of the corolla should be of no visual significance to a pollinator. This is true, but only as it applies to the mature flower in open bloom. In the bud, the corolla is as yet unsplayed, and only its reverse is exposed to view. But the petals are folded with overlap and hence are exposed only in part. Closeup examination of live buds, and of the blossoms into which they developed, showed that the ultraviolet pattern on the floral rear is a precise indication of the petal folding pattern of the bud. In *Hypericum* the folding is regular, so that each petal overlaps roughly half of a neighbor. In *Jasminium*, petal number and arrangement are variable, and the pattern of overlap is inconsistent. In either case, there is an exact correspondence between those regions that are ultraviolet absorbent on the rear surface of the petals, and the portions of the corolla that are exposed to view in the bud. This points up the significance of the phenomenon. The buds, for as long as they are closed, are ultraviolet absorbent and unpatterned (Fig. 1, *B* and *D*). Revealing themselves in yellow only, they retain in concealment all parts that are ultraviolet reflectant and that could on exposure impart upon them an image prematurely imitative of the adult flower in bloom. Buds and blossoms, although indistinguishably yellow to us, are in fact recognizably different to any insect visually sensitive to ultraviolet light. The blossoms, with their fringe of "purple" petals, stand in sharp distinction to the yellow buds. To the plant, the difference, like any between bud and blossom, must be adaptive. Open flowers, in their bid for a pollinator's persistent visitation, profit if they advertise themselves unequivocably, without competition from the potentially distracting buds. In both *Jasminium* and *Hypericum*, buds already differ from blossoms in both size and form. The difference in ultraviolet brightness merely accentuates the

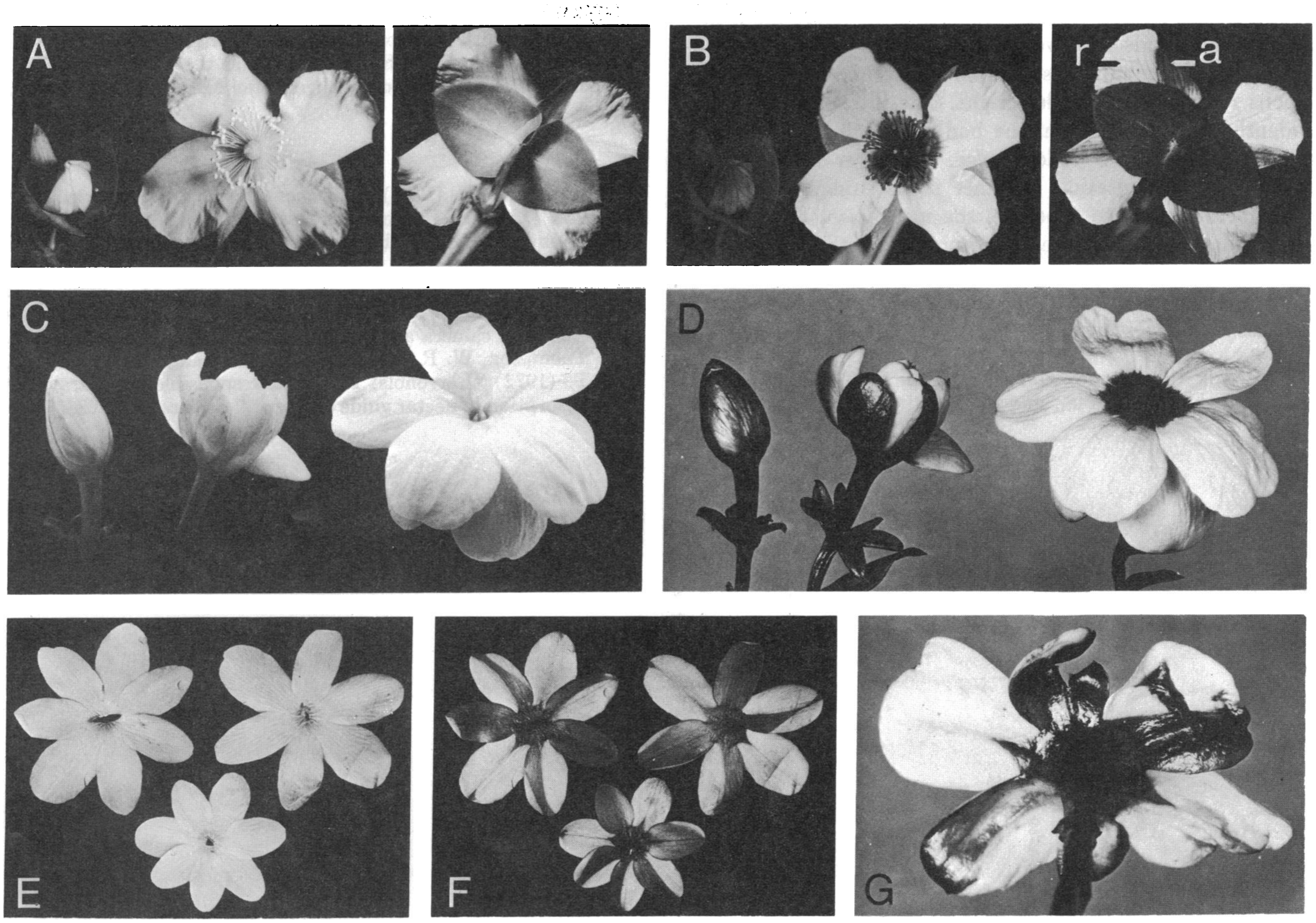

FIG. 1. (*A, B*) *Hypericum peltatum*, photographed in visible (*A*) and in ultraviolet light (*B*). In visible light, the bud and the flower in frontal view (*A, left*), as well as the petals in rear view (*A, right*), appear evenly yellow. In ultraviolet light, the absorbent bud contrasts sharply with the reflctant open flower (*B, left*). In rear view (*B, right*) the portions of the petals that constitute the outside of the bud and give it its absorbent appearance are noticeable as dark marginal triangles (*a*) on the otherwise reflectant (*r*) petals. (*C, D, E, F, G*) *Jasminium primulinum*. (*C*) Bud, opening bud, and blossom, all evenly yellow in appearance, photographed in visible light. (*D*) Same, photographed in ultraviolet light; the bud is evenly absorbent when closed, but as it opens, the ultraviolet-reflectant, previously covered areas of the rear petal surface come into view. (*E*) Three freshly pressed corollas, in rear view, evenly yellow, photographed in visible light. (*F*) Same, in ultraviolet light; the portions of the corollas exposed to the outside in the bud are ultraviolet absorbent. (*G*) Rear view of flower (photographed in ultraviolet light) that has had a piece clipped away from an outer petal in the bud (petal in upper center of blossom). The bar-shaped area thus exposed in the underlying petal (right neighbor in blossom) has become "tanned."

disparity. Neither flower "lingers" long in the potentially ambiguous transitional stage between bud and blossom: petal unfolding takes place within hours, usually in the early morning before pollination reaches its peak§.

Nothing definite is known about the mechanism whereby the ultraviolet pattern on the rear of the flower is laid down. Preliminary evidence suggests that ultraviolet absorption in the exposed portion of the bud is a consequence of differential deposition of absorbent pigment [perhaps flavonols, or related pigments (4)], produced *in situ* under influence of sunlight. Clipping away pieces from the outermost petals of *Jasminium* buds caused the exposed regions on the petals beneath to lose their ultraviolet brightness and to become darkly absorbent (Fig. 1*G*). This presumed "sun tanning" effect was demonstrable only when petal clipping was per-

§ The buds are distinctly visible as colored entities, and hence potentially competitive with the open flower, for 2 days before blossoming in *H. peltatum*, and for usually no less than 4 days in *J. primulinum*. Petal unfolding takes place in the early morning in *H. peltatum* and usually also in *J. primulinum*. The blossom lasts one day in *H. peltatum* (petals have usually fallen by evening) and several days in *J. primulinum* (the petals eventually shrivel and bleach to white).

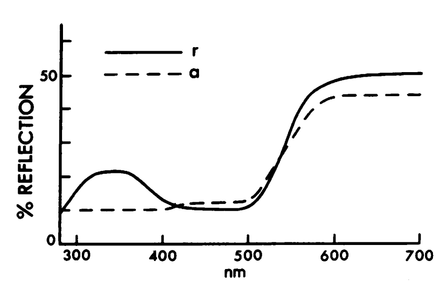

FIG. 2. Reflection spectra of absorbent region (*a*) and reflectant region (*r*) of the rear surface of a petal of *Hypericum peltatum*. The regions are shown and lettered in Fig. 1*B*.

formed in young, still greenish buds (7 days before blossoming). In older buds that were already yellow (3 days before blossoming), the clippings had no effect and the exposed regions remained ultraviolet-bright. The ultraviolet pattern evidently develops early in the bud, in synchrony with the differentiation of the yellow color. Whatever controls the ultraviolet differentiation, whether it be sunlight or some other factor linked to exposure, the mechanism must differ from that controlling the development of the ultraviolet pattern on the frontal surface of the corolla, which is laid down within the inner (and presumably uniformly dark) confines of the closed bud.

We thank the director and staff of the Archbold Biological Station, Lake Placid, Fla., and of the Division of Entomology, CSIRO, Canberra, Australia, for kindness and hospitality while some of this work was done at these institutions. The study was supported by the USPHS (AI-02908) and the CSIRO while T. Eisner was a John Simon Guggenheim Memorial Foundation fellow.

1. Von Frisch, K. (1967) *The Dance Language and Orientation of Bees* (Harvard University Press, Cambridge, Mass.).
2. Daumer, K. (1958) "Blumenfarben wie sie die Bienen sehen," *Z. Vergl. Physiol.* **41**, 49–110.
3. Eisner, T., Silberglied, R. E., Aneshansley, D., Carrel, J. & Howland, H. C. (1969) "Ultraviolet video-viewing: the television camera as an insect eye," *Science* **166**, 1172–1174.
4. Thompson, W. R., Meinwald, J., Aneshansley, D. & Eisner, T. (1972) "Flavonols: Pigments responsible for ultraviolet absorption in nectar guide of flower," *Science* **177**, 528–530.