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FLORAL COLOR CHANGE: A WIDESPREAD FUNCTIONAL CONVERGENCE[1]

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Ontogenetic color changes in fully turgid flowers are widespread throughout the angiosperms, and in many cases are known to provide signals for pollinators. A broad survey of flowering plants demonstrates that such color changes appear in at least 77 diverse families. Color-changing taxa occur commonly within what are considered derived lineages, and only rarely in early or primitive groups. The pattern of distribution of floral color change across orders, families, genera, and species demonstrates that the occurrence of the phenomenon within a group is not simply a result of phylogenetic history. Color changes can affect the whole flower or they can be localized, affecting at least nine floral parts or regions. The scale of color change (localized or whole-flower) is broadly correlated with the type of pollinator that characteristically visits the plant. Color changes can come about through seven distinct physiological mechanisms, involving anthocyanins, carotenoids, and betalains. Color changes due to appearance of anthocyanin are the most common, occurring in 68 families. Floral color change has clearly evolved independently many times, most likely in response to selection by visually oriented pollinators, and reflects a widespread functional convergence within the angiosperms.

Dramatic ontogenetic changes in flower color occur throughout the angiosperms. Such color changes occur in fully turgid flowers, and are distinct from the darkening or fading often associated with floral senescence. Despite the dramatic nature of some color changes, and their early appearance in the literature (e.g., Rumpf, 1743; Sprengel, 1793), floral color change has received surprisingly little study. Color change has been reported in a limited number of species (see references in Weiss, 1992), and only a few studies have investigated its occurrence in more than a single taxon (Delpino, 1873; Ludwig, 1885; Vogel, 1950; Gori, 1983; Lamont, 1985; Weiss, 1991). Several recent studies have investigated the factors underlying the maintenance of color change in particular species (Cruzan, Neal, and Willson, 1988; Delph and Lively, 1989; Gori, 1989); however, the prevalence of the phenomenon has gone largely unrecognized.

Floral color phase can provide important information for pollinators at close range. Prechange flowers reliably provide a nectar reward, offer pollen, and have receptive stigmas, while postchange flowers are generally unrewarding and sexually inviable (Weiss, 1992). Visitors to plants with color-changing flowers, including insects in 15 families and birds in four families (Weiss, 1992), discriminate between flowers in different color phases, visiting prechange flowers significantly more than would be expected (Schaal and Leverich, 1980; Jones and Cruzan, 1982; Gori, 1983; Casper and La Pine, 1984; Delph and Lively, 1985; Lamont, 1985; Cruzan, Neal, and Willson 1988; Gori, 1989; Weiss, 1991). For some butterflies (Weiss, 1991; Weiss, unpublished data) and birds (Lamont and Collins, 1988), preference for a given color phase is learned.

The retention and maintenance of older, postchange flowers on a plant increases the size of its floral display, and may thereby provide a long-distance attractant for pollinators. Experimental investigations of a variety of color-changing species demonstrate that in some cases, plants that retain flowers receive more pollinator visits than do those from which the older flowers have been removed (Jones and Cruzan, 1982; Cruzan, Neal, and Willson, 1988; Gori, 1989; Weiss, 1991), while in other cases floral retention does not contribute to increased visitation (Casper and La Pine, 1984; Delph and Lively, 1989).

Floral retention and color change may increase the efficiency of the pollination interaction for both plant and pollinator. Plants receive efficient pollination service that may result in greater fitness, through either male function, female function, or both (Casper and La Pine, 1984; Cruzan, Neal, and Willson, 1988; Gori, 1989). Pollinators, for their part, are accurately directed to rewarding flowers, and so may save time and energy while foraging.

Interactions between color-changing flowers and their pollinators are important components of many diverse pollination systems. To determine the taxonomic distribution of floral color change and to characterize the phenomenon, I conducted a broad survey of flowering plants, based mainly on personal field observations, but also involving field guides, color-illustrated floras, and the literature. Here I report on the taxonomic extent and distribution of floral color change, the range of floral parts and pigments involved, and the physiological mechanisms or processes by which the color change is mediated.

MATERIALS AND METHODS

Survey—I surveyed natural field sites, botanical gardens, arboreta, and parks for color-changing taxa, ex-

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amining virtually every flowering plant species encountered over a 5-year period. For each color-changing plant, I noted floral part affected, pre- and postchange colors, growth form, and life history status. Field sites were concentrated in California, but were also located in other parts of the United States, and in Costa Rica, Europe, and the Virgin Islands. Native and alien wild species, as well as horticulturally selected plants, were included. A study of more than 50 field guides and floras illustrated with color photographs extended the geographical range of the survey. In photographs, I looked for such details as the condition of the anthers and the appearance of opening buds and of wilting flowers to establish the direction of the color change. I included only plants with clear and obvious color changes, the nature of which I could assess unequivocally.

I established, either through direct observation or by reference to the literature (including Knuth, 1906–1909), the type of pollinators that visited color-changing species in 66 genera. I focused my efforts on plants that were adapted to particular groups of pollinators: bees, butterflies, flies, birds (including hummingbirds and passerine birds), night-flying moths, and bats. I then looked for associations between pollinator type and scale of color change (i.e., whether the change affected a localized part of the flower or the whole flower). I also established, through reference to the literature, the geographic distribution of color-changing plants in 211 genera, in order to determine whether native habitat was associated with presence of color change.

Although it is impossible to assess the total number of species surveyed in the course of my study, I estimate that I examined plants in approximately 50% of all angiosperm families. (Here, and throughout my study, I follow Cronquist's 1988 classification of the flowering plants). Thus, although the sample is quite large, my results underrepresent the true extent of floral color change within the angiosperms.

Physiological mechanisms of color change—It is possible in microscopic examinations of hand sections of floral tissue to distinguish between anthocyanins and carotenoids (Goodwin, 1976; Scogin, 1983). Anthocyanins are water-soluble, located in vacuoles, and generally red, blue, or purple in color, while carotenoids are lipid-soluble, localized in plastids, and usually yellow or orange in color. Further, it is also possible to identify betalains, as these pigments look like anthocyanins but occur uniquely in many of the families in Caryophyllales (Piatelli, 1976; Scogin, 1983). I hand-sectioned pre- and postchange flowers of 40 species in 26 families to identify at a gross level the class of pigment involved in the color change.

As anthocyanins were the most common type of pigment involved in floral color changes, I used spectrophotometric analyses to confirm the identify of these compounds. I extracted pigments from flowers of 28 color-changing species in 20 families, and compared the absorption spectra of the pre- and postchange flowers over visible and ultraviolet wavelengths. The parts of the flower that changed color were dissected out of prechange and postchange flowers; comparable samples for a given species were produced by using parts from equivalent numbers of flowers in each phase. Samples were extracted in 2–3 ml of methanol containing 1% concentrated hydrochloric acid, by volume (Harborne, 1973), and were maintained at 4 C, in the dark, in airtight tubes. Analyses were performed not less than 3 hours and not more than a week after extraction. Absorption spectra were obtained with a Perkin-Elmer Lambda-6 UV-Visible spectrophotometer. Scans were conducted at 300 nm/minute, with a slit width of 4 nm. The extracts read over the visible range, from 400 to 750 nm, were generally not further diluted. For the UV readings, in the 225–400 nm range, all extracts were diluted an additional 100-fold. This dilution was necessary because flavonoid compounds are highly UV absorbent (Harborne, 1988), and undiluted samples absorbed too strongly across the UV range to permit an accurate reading.

I investigated the pigment types involved in color changes directly, using microscopic examination or spectrophotometry, for taxa in 26 families; all three pigment types were represented in these taxa. For the remaining taxa, I predicted the pigments involved in the color changes based on color pattern and taxonomic affiliation. Excepting betalain-containing taxa in the Caryophyllales, I assumed that color changes in which white, yellow, green, or pink tissue turned to orange, red, or purple were due to appearance of anthocyanins, and that the converse resulted from loss of anthocyanins. Based on microscopic observations of yellow chromoplasts in postchange flowers of *Lonicera hildebrandiana* (Caprifoliaceae) and *Pittosporum* sp. (Pittosporaceae), I assumed that white to yellow changes involving whole flowers were due to appearance of carotenoids. While my assumptions may be incorrect in some cases, these predictions serve as a basis for a first approximation of the relative frequency of different pigment types involved in floral color changes.

In this paper I summarize the results of my survey of color-changing taxa. For each family that contains color-changing species, I report the number of genera in which I observed color change, the parts that change, and the pigments and/or physiological processes likely to be responsible for the change. I also report the frequency of different mechanisms of change among the color-changing families, and examine associations between type of pollinator and part of the flower that changes. To illustrate the distribution of the phenomenon, I have mapped the occurrence of color-changing taxa onto representative phylogenies at two different taxonomic levels. A tabulation of color-changing species is included as Appendix 1.

RESULTS

Taxonomic distribution of floral color change—Floral color change is surprisingly common and widespread within the angiosperms, appearing in both monocots (Liliopsida) and dicots (Magnoliopsida). Changes occur in at least 38% (33/86) of angiosperm orders, and at least 20% (77/387) of angiosperm families (Table 1). Although I cannot accurately estimate the prevalence of color change at the generic or specific level, it occurs in flowers in at least 241 genera and 393 species.

Following any one of the several recent schemes of higher-level relationships among the angiosperms (e.g., Cronquist, 1988; Thorne, 1992; Chase et al., 1993), color-changing taxa occur commonly within what are considered derived lineages or subclasses, and only rarely if at all in early or primitive groups. Using Cronquist's 1988 classification of angiosperms, for example, floral color changes occur commonly in his advanced dicot subclasses Dilleniidae, Rosidae, and Asteridae, while they are rare to absent in the more primitive Caryophyllidae, Magnoliidae, and Hamamelidae. Within the monocots, most color changes occur in Liliidae and Zingiberidae, groups considered advanced by Cronquist.

Within the more derived angiosperm lineages, floral color change is not consistently distributed among families, genera, or even species. For example, color-changing taxa appear in approximately half of the families in the Lamiidae (Fig. 1). Within families, color changes occur in some genera and not in others (e.g., Solanaceae, Fig. 2), and within genera, color changes occur in only certain species. Finally, color change may occur in some individuals of a given species, while it is absent in others. In some individual plants of *Lobularia maritima* (Cruciferae), for example, the filaments turn from green to deep purple, while in others they remain green throughout the life of the flower. Similarly, the center of the flower changes from whitish to pink in some individuals of *Armeria maritima* (Plumbaginaceae), and not in others.

Biogeography and life history of color-changing taxa—Color-changing taxa are diverse in geographic distribution (see Appendix 1). Of the taxa for which I could determine range information, 68 genera are from the New World and 137 are from the Old World; 74 are temperate and 42 are tropical in distribution. In these widespread regions, color-changing taxa occupy a diverse range of habitats, including the Saudi Arabian desert, Brazilian rain forest, Alaskan tundra, California grassland, Australian dry forest, and alpine China.

Color-changing plants exhibit a diversity of life history strategies and growth forms. My sample includes 19 annual and 150 perennial genera, 69 herbaceous and 105 woody genera. Further, color-changing species may be forbs, trees, vines, or shrubs. They may be terrestrial or epiphytic, autotrophic or heterotrophic. Among the heterotrophs, there are hemiparasites, and even an aquatic

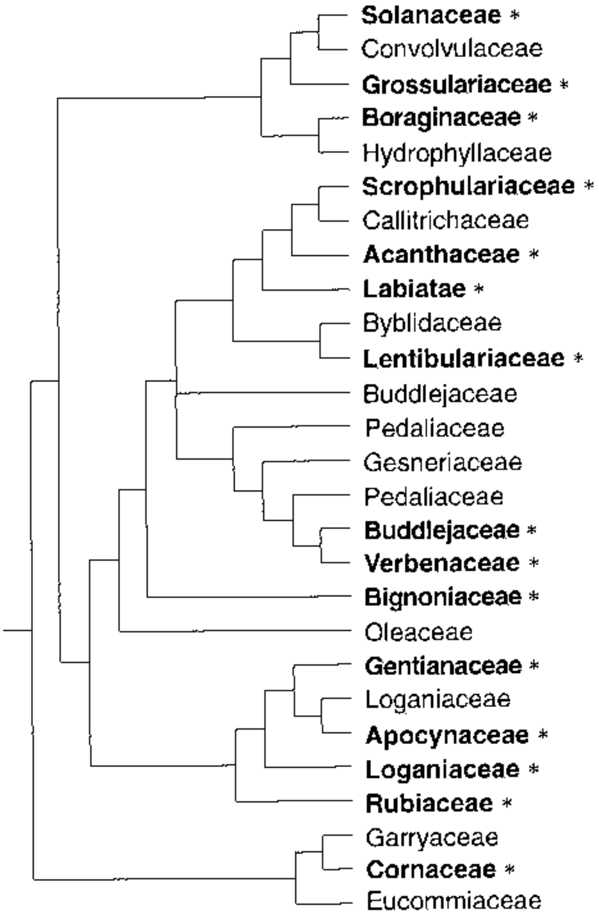

Fig. 1. Occurrence of color-changing taxa within families in the Lamiidae. Families indicated in bold and marked with an asterisk contain color-changing taxa. Tree drawn after Olmstead et al., 1993, fig. 5.

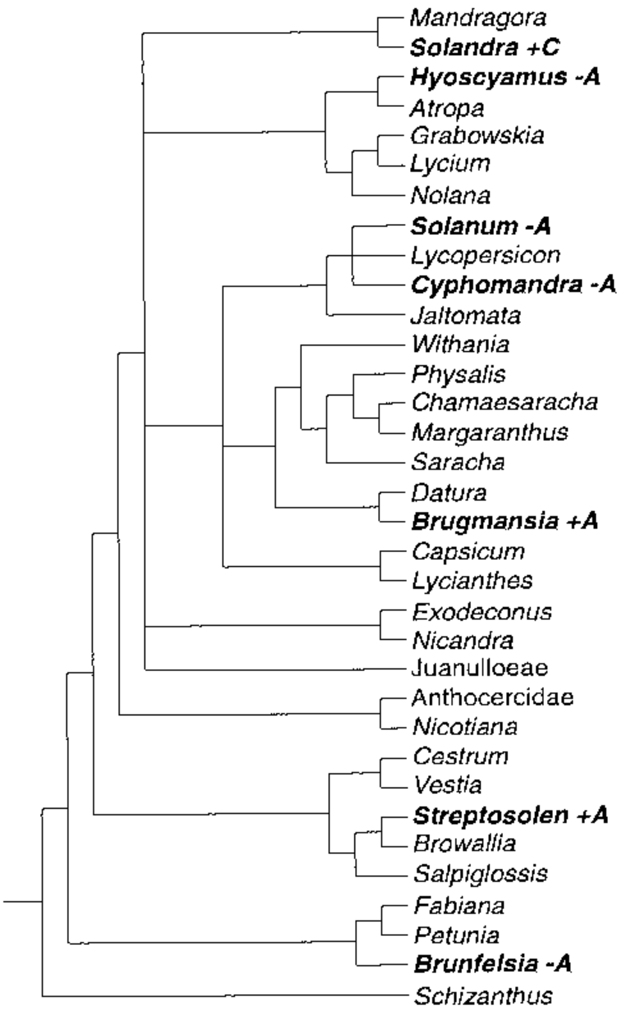

Fig. 2. Occurrence of color-changing taxa within genera in the Solanaceae. Genera indicated in bold contain color-changing species. Mechanism of change is also shown; see legend to Table 1 for explanation of abbreviations. Tree drawn after Olmstead and Palmer, 1992, fig. 2.

TABLE 1. Summary of known occurrence of floral color change, by family.

Order	Family	Number of color-changing genera	Probable mechanism of change[a]	Parts that change
Asterales	Compositae	4	+A*	2; 7
Bromeliales	Bromeliaceae	1	pH	1
Campanulales	Campanulaceae	1	+A	1; 3
	Goodeniaceae	2	+A	2
	Stylidiaceae	1	−A	5
Capparales	Capparidaceae	3	+A	2; 5
	Cruciferae	23	+A*; −C	1; 2; 5; 6; 9; 10
Caryophyllales	Aizoaceae	1	+B	1
	Cactaceae	1	+B	1
	Caryophyllaceae	2	+A	2; 10
Cornales	Cornaceae	1	+A	4
Dipsacales	Caprifoliaceae	3	+A*; +C*	1; 5
	Dipsacaceae	1	+A	3
	Valerianaceae	2	+A; −C	1; 2
Ericales	Epacridaceae	2	+A	1; 9
	Ericaceae	1	+A*	5
Euphorbiales	Euphorbiaceae	1	+A	4
Fabales	Caesalpiniaceae	7	+A*; +C; mvt	1; 7
	Mimosaceae	2	−A	1
	Papilionaceae	14	+A*; −A	1; 5
Gentianales	Apocynaceae	2	+A	2
	Asclepiadaceae	3	+C; pH	1; 8
	Loganiaceae	1	+A	3
	Geraniaceae	1	+A	2
Lamiales	Boraginaceae	11	+A*; −A; +C; −C*; pH	1; 2; 5; 6; 9
	Labiatae	2	+A	5
	Verbenaceae	6	+A*, −C*	1; 2; 5; 6; 10
Liliales	Agavaceae	1	+A*	1
	Liliaceae	7	+A; −A; −C	1; 2; 4
Linales	Linaceae	1	+A	6; 9
Malvales	Elaeocarpaceae	1	+A*	1
	Malvaceae	4	+A*; −A	1
	Sterculiaceae	2	+A	1
Myrtales	Combretaceae	2	+A	1
	Lythraceae	1	+A	2
	Melastomataceae	4	+A	1; 2; 9
	Myrtaceae	12	+A*	1; 4; 9
	Onagraceae	5	+A*	1; 2
	Penaeaceae	2	+A	2
	Thymelaeaceae	3	−A; −C	1; 2
Nymphaeales	Nymphaeaceae	1	+A	1
Orchidales	Orchidaceae	8	+A*; −A*; +C	1; 7; 8
Plumbaginales	Plumbaginaceae	1	+A	2
Polygalales	Malpighiaceae	4	+A	1; 9
	Polygalaceae	3	+A	1; 5; 8
	Vochysiaceae	1	+C	1
Polygonales	Polygonaceae	1	+A	1
Primulales	Primulaceae	2	+A*	6
Proteales	Proteaceae	5	+A	1; 9
Rhamnales	Rhamnaceae	1	+A	1
Rhizophorales	Rhizophoraceae	1	+A	1
Rosales	Crassulaceae	2	+A	10
	Grossulariaceae	1	+A*	6
	Pittosporaceae	4	+A; +C	1; 2; 10
	Rosaceae	6	+A*	1; 4; 9; 10
	Saxifragaceae	3	+A*	1; 9; 10
Rubiales	Rubiaceae	4	+A; +C	1
Santalales	Loranthaceae	2	+A	1; 3
	Santalaceae	3	+A	1; 2
Sapindales	Anacardiaceae	2	+A	1; 4
	Hippocastanaceae	2	+A*	5
	Rutaceae	2	+A	1; 2
	Sapindaceae	4	+A*	2; 8
Scrophulariales	Acanthaceae	2	+A	1
	Bignoniaceae	4	+A*; −A	1; 2; 5
	Buddlejaceae	1	+C*	1; 2
	Lentibulariaceae	1	+A	5
	Myoporaceae	2	+A*	3; 10

TABLE 1. Continued.

Order	Family	Number of color-changing genera	Probable mechanism of change[a]	Parts that change
	Scrophulariaceae	7	+A	1; 2; 3; 6; 7
Solanales	Polemoniaceae	4	+A*	1; 2; 6
	Solanaceae	7	+A*; −A*; +C	1; 5
Theales	Ochnaceae	1	+A	9
	Theaceae	1	+A	5
Violales	Begoniaceae	1	+A	10
	Frankeniaceae	1	+A	2
	Passifloraceae	1	+C	1
	Violaceae	1	+A*	7

[a] Abbreviations for probable mechanisms of change are as follows: A = anthocyanin; B = betalain; C = carotenoid; "+" = appearance of pigment; "−" = loss of pigment; mvt = movement of a floral part. * Identifies taxa for which mechanism of color change has been investigated directly; in all other cases, mechanism is inferred (see text for details). Parts that change are illustrated in Fig. 3; numbers refer to that figure. See Appendix 1 for species list.

insectivore. In short, the diversity of color-changing species reflects the diversity of animal-pollinated angiosperms.

Floral parts that undergo color change—Floral color changes may affect either whole flowers or localized parts of flowers (Fig. 3). They may take place in any of the four floral whorls, i.e., in the calyx, corolla, androecium, or gynoecium, and may affect a part of a whorl, an entire whorl, or several whorls or parts of whorls in combination. The category 'whole flower' is broadly defined; it may involve all of the parts of the flower, or may represent a color change of a highly visible part, such as a corolla or calyx. Localized changes may affect at least nine parts or regions of a flower, including the center of the flower, outside of the corolla tube, nectary or hypanthium, nectar guide or banner petal spot, eye or corona, specialized petal, petal appendage, androecium, or gynoecium.

Certain floral parts undergo color change more commonly than others. Whole-flower color changes appear in 48 families, while localized changes, taken together, occur in 61 families. Some localized changes, such as those affecting the center of the flower or the nectar guide/banner petal spot, are relatively common, occurring in 27 and 14 families, respectively, while others, such as changes in petal appendages or specialized petals, are relatively uncommon, occurring in only four families each.

The distribution of floral parts that change color is not necessarily consistent within either families or genera. In 41 families only a single floral part changes color, while in five families (Boraginaceae, Cruciferae, Rosaceae, Scrophulariaceae, and Verbenaceae), four or more floral parts change color in different genera (see Table 1). The floral part that changes color may also vary among species or varieties within a genus. In *Lantana camara* (Verbenaceae), the entire corolla undergoes a color change, while only a central ring changes color in *L. hirta* and *L. montevidense.* (These three species also differ in the physiology of their changes; see below). In the white form of *Lobularia maritima* (Cruciferae), the filaments alone change color, while in the purple form, the entire flower undergoes the change.

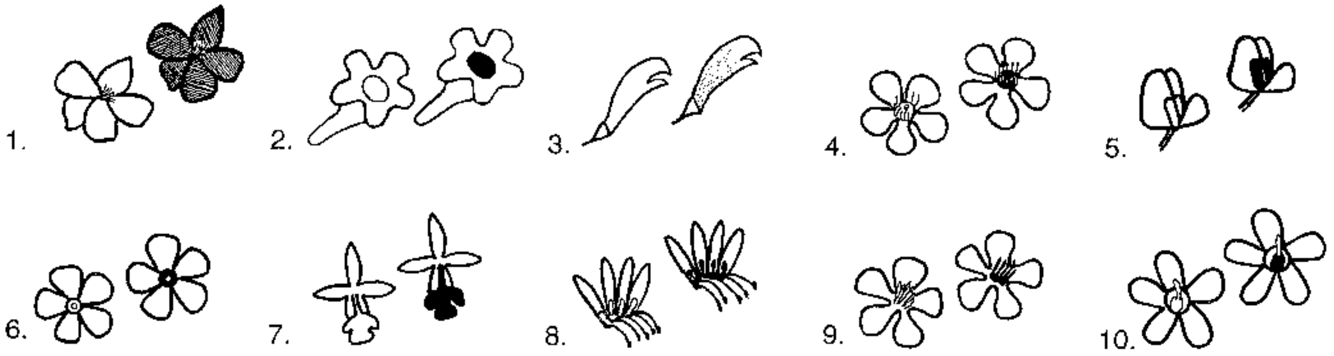

Fig. 3. Floral parts that change color. In each case, prechange flower is on left, with changing part or region indicated in white; postchange flower is on right, with changed part dark. 1. *Whole Flower* includes whole perianth; sepals alone if no petals are present; petals alone if petals form the major component of the floral display; also flowers in which the inside of the corolla changes color while the outside does not change. 2. *Center of Flower* includes center of open flowers; inside of corolla throat; bases of petals, filaments and/or style; also disk florets in the Compositae. 3. *Corolla Tube* includes all or part of the outside of the corolla tube. 4. *Nectary/Hypanthium* includes nectary; whole hypanthium or outer ring of hypanthium. 5. *Nectar Guide/Banner Petal Spot* includes nectar guides and banner petal spots. 6. *Eye/Corona* includes central eyes or raised coronas; also color-changes in corona-like petals of *Ribes.* 7. *Selected Petals* includes one or more petals that change apart from the rest of the petals; also ray florets in the Compositae; movement of the banner petal in Caesalpiniaceae. 8. *Petal Appendages* includes miscellaneous small petal appendages; e.g., flaps at base of petals in Sapindaceae; bumps on petals in Orchidaceae; fringed keels in Polygalaceae. 9. *Androecium* includes whole filaments or bases of filaments; also landing knobs or pollen presenters in Proteaceae. 10. *Gynoecium* includes all or part of ovary and/or style; also stigma alone.

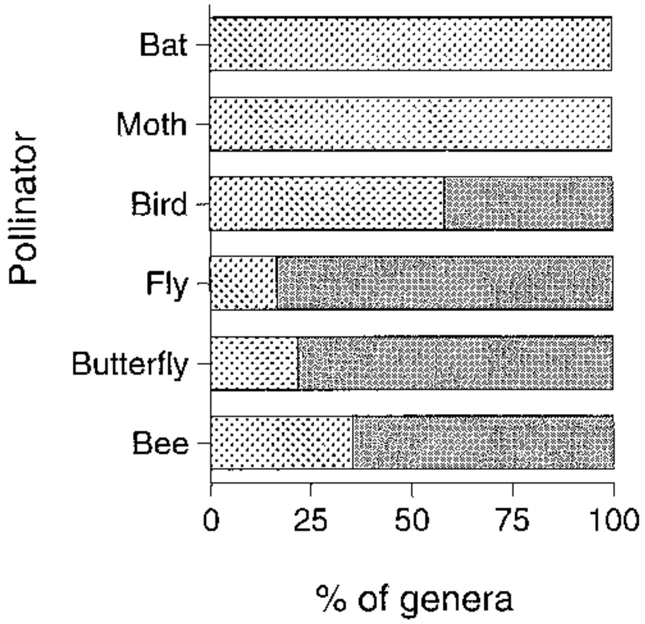

Fig. 4. Frequency of whole-flower (stippled) and localized (grey) changes by pollinator type. Localized changes include all nine floral parts or regions illustrated in Fig. 3. Number of genera included in each category: bat: 3; moth: 5; bird: 12; fly: 6; butterfly: 9; bee: 31.

The floral part or region that changes color is correlated with its visibility. Within a given family, structures or parts that are clearly visible in some floral forms, and are thus good candidates for color change, may be hidden, reduced, or absent in others. In the Myrtaceae, for example, color changes affect different parts in four genera: in *Leptospermum*, the prominent central hypanthium undergoes a color change; *Calytrix* lacks a hypanthium, but its showy filaments undergo a change; *Darwinia* has no hypanthium and its reduced filaments are adnate to a tubular corolla, and in this case it is the corolla that changes; finally, in *Myrtella* the entire flower undergoes a color change. A similar situation is apparent in Rosaceae: in *Physocarpus* the prominent carpels change color; in *Crataegus*, the large hypanthium undergoes the change; in *Raphiolepis* the exserted filaments change color; and in *Rosa* the petals change. In each case, the color change affects a visually prominent part of the flower.

Correlations between part that changes and pollinator type—The scale of color change (localized or whole-flower) is broadly correlated with the type of pollinator that characteristically visits the plant (Fig. 4). Color changes in flowers typically pollinated by moths or bats affect whole flowers, while those in flowers pollinated by bees, butterflies, and flies are likely to affect a localized floral part. Color changes in bird-pollinated taxa often affect whole flowers; however, those that involve localized changes generally affect the outside of the corolla tube.

Physiological mechanisms of floral color change—At least seven different physiological processes, including all three of the major classes of floral pigments, flavonoids, carotenoids, and betalains, are involved in producing floral color changes. Color changes may come about through appearance or loss of anthocyanin, appearance or loss of carotenoid, or appearance of betalain; I have not observed color changes involving loss of betalains. Additionally, color change may result from a change in pH, or a floral part may move, producing an apparent color change.

Changes in pH can affect anthocyanin pigments, altering red, purple, or blue colors, while the flowers remain turgid. *Aechmea* (Bromeliaceae) flowers turn from pink to blue, and those of *Pulmonaria* (Boraginaceae) from red to blue, while *Oxypetalum* (Asclepiadaceae) flowers turn from blue to pink.

An uncommon and visually striking mechanism of floral color change involves movement of a particular flower part, rather than a change in pigment. I found such changes in only two genera, *Bauhinia* and *Delonix*, both in the Caesalpiniaceae. A young flower of *Bauhinia monandra* is initially white, with a large red spot in the middle of the central petal. In the older flower, the central petal curls back on itself and away from the center of the flower, so that the red spot is hidden from view; meanwhile, the four white side petals change to a pale pink. Thus, the young flowers are white, with a bright red banner petal spot, while the older flowers appear to be a uniform pink. In *Delonix regia*, a different kind of movement, i.e., an in-rolling of the central petal, produces the same end result.

Some of the mechanisms of color change described above can account for both whole-flower and localized color changes, while others produce only one or the other. Both appearance and loss of anthocyanins, for example, can produce either whole-flower or localized changes. Appearance of carotenoids can also produce either type, while loss of carotenoids seems to be involved in only localized changes. Movement of particular floral parts results in localized changes, while pH changes and appearance of betalains affect whole flowers.

Absorption spectra of pigment extracts support the identification of anthocyanins for 27 of the 28 species examined. Representative spectra are presented in Fig. 5; spectra of all 28 species appear in Weiss, 1992. For flowers in which color appears in the postchange phase, extracts from prechange floral tissues yield virtually clear solutions, and show little or no absorption between 515 and 545 nm, a region in which anthocyanins are characteristically strongly absorbent (Harborne, 1973). Extracts from purple or red postchange tissues, on the other hand, yield deeply colored solutions and show strong absorption peaks around 535–540 nm (Fig. 5, above left). For color changes that proceed in the other direction, i.e., in which the prechange flowers contain pigment which is absent in the postchange flowers, the reverse pattern is found (Fig. 5, above right).

One postchange absorption spectrum, that of *Buddleja davidii* (Buddlejaceae), differs from the typical anthocyanin profile. Its two peaks, at approximately 435 and 460 nm, resemble a typical spectrum for crocin, a water-soluble carotenoid (Harborne, 1973). Based on microscopic observations of deep orange chromoplasts in postchange *Buddleja* flowers, and on the carotenoid-like absorption spectrum, I presume that the color change in *Buddleja* is due to production of carotenoid.

While all of the pre- and postchange flowers examined show marked differences in absorbance in the visible region of the spectrum, they show little or no difference in

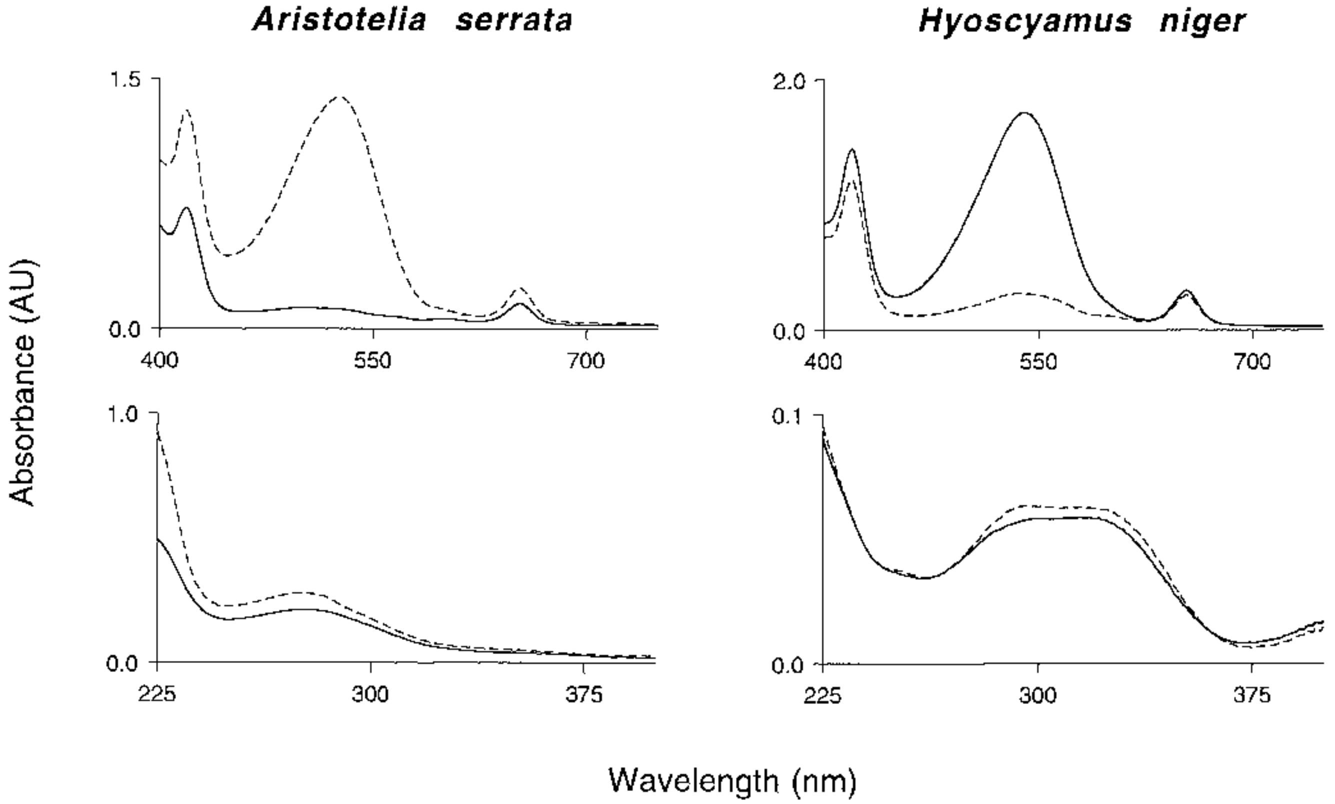

Fig. 5. Representative absorption spectra from pigment extracts of prechange (solid line) and postchange (dashed line) flowers. Upper graphs show visible spectra (400–750 nm); lower graphs show UV spectra (225–400 nm). Left, *Aristotelia serrata* (Elaeocarpaceae) shows appearance of anthocyanin in visible; no change in absorption in UV. Right, *Hyoscyamus niger* (Solanaceae) shows loss of anthocyanin in visible; no change in absorption in UV.

the UV region (Fig. 5, below). For all species, paired absorption curves for pre- and postchange extracts over the range from 225 to 400 nm are strictly congruent, rising and falling in parallel.

Mechanisms of floral color change do not occur with equal frequency (Fig. 6). Appearance of anthocyanin is by far the most common: I have determined through microscopic examination and/or spectrophotometry that it is responsible for color changes in 25 families, and have estimated that it occurs in 68 out of 77 color-changing families. The other six mechanisms of color change are all less common, appearing in one to 11 families.

In 61 families, color changes come about as a result of only one physiological mechanism, while in 16 families two or more different mechanisms result in color changes (see Table 1). In the Boraginaceae, color changes come about through five different mechanisms: appearance or loss of anthocyanins, appearance or loss of carotenoids, and change in pH. In the Myrtaceae, on the other hand, color changes in 12 different genera all involve appearance of anthocyanin.

The distribution of mechanisms of color change within a family is not simply a consequence of phylogenetic history, because all taxa in which changes occur as a result of a particular mechanism do not necessarily belong to the same lineage; nor do all taxa within a lineage undergo color changes. In the Solanaceae, for example, color changes in seven genera come about through a total of three different mechanisms (Fig. 2). Color changes due to loss of anthocyanin occur in three subfamilies; those due to appearance of anthocyanin occur in two subfamilies, one of which also contains a loss-of-anthocyanin change; appearance of carotenoid produces color change in a fifth subfamily. Further, not all of the species within these color-changing genera undergo color changes. In *Cyphomandra*, for example, flowers of *C. sciadostylis*, *C. diploconos*, and *C. endopogon* (Gracie, 1993; Sazima et al., 1993) change from violet to cream or greenish-white, while flowers in some other species in the genus do not undergo color changes (Sazima et al., 1993; L. Bohs, University of Utah, Salt Lake City, UT, personal communication).

Within a single genus and/or species, more than one mechanism may produce color changes. In *Bauhinia* (Caesalpiniaceae), for example, two different mechanisms are involved: in *B. bidentata*, the entire flower changes from yellow to red, presumably as a result of appearance of anthocyanin, while in *B. monandra*, both movement of the middle petal and appearance of anthocyanin in the side petals dramatically alter the appearance of the flower. Two mechanisms of change produce three different patterns in three species of *Lantana* (Verbenaceae). In *L. camara*, entire yellow flowers turn a bright red due to appearance of anthocyanin. By contrast, in *L. hirta*, loss of a ring of yellow carotenoid around the entrance to the corolla throat leaves the postchange flower entirely white. In *L. montevidense*, a combination of the above two mechanisms produces the color change: a yellow ring circling the throat of the lavender flowers disappears, and purple anthocyanin pigment fills in the center of the flower.

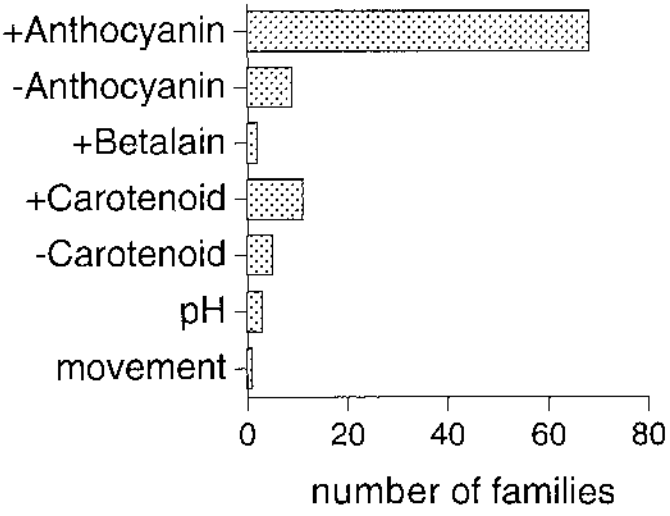

Fig. 6. Frequency distribution of mechanisms of color change across families.

DISCUSSION

Taxonomic distribution of color change—The pattern of distribution of floral color change across orders, families, genera, and species demonstrates that the occurrence of the phenomenon within a group is not simply a result of phylogenetic history. The distribution of color-changing taxa is patchy irrespective of the phylogenetic or taxonomic framework under which it is examined. Floral color change could not have come about from a single or even several evolutionary events; it must have originated or been lost many times, in many different lineages. The lack of correlation between the occurrence of color change and plant life history, habitat, geographic range, or growth habit implies that these factors are not primary determinants of the evolution of color change. Floral color change has most likely evolved in response to selection by pollinators, and reflects a widespread functional convergence within the angiosperms.

The apparent absence of floral color change within the early angiosperm lineages or groups, many of which are pollinated by relatively unspecialized pollen-eating insects, including beetles and flies (Stebbins, 1970; Kevan and Baker, 1983; Crepet and Friis, 1987), suggests that the trait may have become important as more specialized visually oriented lepidopteran, dipteran, and hymenopteran insects evolved as the primary angiosperm pollinators. It is not likely that the absence of color change in the primitive angiosperms is an artifact of insufficient sampling within those groups, as I estimate that I examined roughly comparable numbers of taxa within primitive and derived angiosperm subclasses. I looked for presence or absence of color change, for example, in plants from at least 16 out of 39 magnoliid families (41%) and 13 out of 26 hamamelid families (50%), vs. 34 out of 78 families in Dilleniidae (44%) and 49 of 116 families in Rosidae (42%).

Floral parts and pollinator types—Color changes affect features of the flower that are apparent to pollinators. If a flower in its prechange condition has a color pattern, such as a nectar guide or corona, that directs pollinators toward reward and sexual structures, then almost invariably that will be the part of the flower that changes color. If flowers initially lack an explicit color pattern, then the center of the flower, the reproductive parts themselves, or the whole flower is likely to change color. Localized color changes do not affect floral parts that are distant from the reproductive or reward structures, such as the distal end of a petal or the underside of a sepal.

Several factors, involving pollinator type and floral morphology, contribute to the diversity and distribution of floral parts that change color within a given group. Floral morphology is to a certain extent a reflection of pollinator morphology, so it is not surprising that flowers characterized by a particular type of pollinator would be likely to have certain types of color change. In addition, the pollinator's visual acuity and the ambient light conditions under which it ordinarily visits flowers must affect its ability to perceive and interpret color cues (Gori, 1983).

Color changes in moth- and bat-pollinated plants affect whole flowers. Both moths and bats ordinarily feed at dusk or at night, and flowers pollinated by these animals are generally light in color, contrasting with a dark background. While a subtle localized change might not be perceptible to a moth or a bat, a change in overall brightness that affected the whole flower would likely be discernible (Gori, 1983). The six genera of moth-pollinated flowers in my sample all change from white or cream to a darker color. For example, flowers of *Quisqualis indica* (Combretaceae), *Lonicera hildebrandiana* (Caprifoliaceae), and *Morina* sp. (Dipsacaceae) all open white at dusk, and by the following evening are dark red, deep gold, and purple, respectively. I have observed hawkmoths visiting yellow and ignoring red flowers of *Lantana camara* (ordinarily pollinated by day-flying butterflies) at dusk, and Eisikowitch and Rotem (1987) report that two species of hawkmoths visit only the white-phase flowers of *Q. indica*.

The three bat-pollinated species in my survey follow the same pattern: flowers of *Cobaea scandens* (Polemoniaceae), *Brugmansia* sp., and *Solandra* sp. (both Solanaceae) open a creamy white; *Cobaea* flowers turn a dusky purple color, *Brugmansia* flowers turn reddish-orange, and *Solandra* flowers turn a deep yellow-gold. In each case the prechange color contrasts strongly with the background, while the postchange color tends to blend in.

For both moth- and bat-pollinated species, retention of older flowers is unlikely to contribute to a showy visual display that will attract pollinators from a distance, as dark-colored postchange flowers will not stand out against a foliage background. However, if the postchange flowers continue to produce odors, they may increase the plant's olfactory attractiveness.

Flowers adapted for pollination by bees, butterflies, or flies often have a color pattern that functions as a nectar or pollen guide, and it is these parts that commonly change color. Thus, the banner petal spot changes color in bee-pollinated *Lupinus* (Papilionaceae) flowers; the modified petal that contains nectar changes color in butterfly-pollinated *Caesalpinia pulcherrima* (Caesalpiniaceae) flowers, and the eye changes color in fly-pollinated *Androsace lanuginosa* (Primulaceae) flowers. The common occurrence of such localized color patterns indicates that these visually oriented, day-flying visitors are able to resolve patterns on a relatively small scale.

Because flowers adapted to pollination by birds (and in particular hummingbirds) tend to have long tubular corollas, the part of the flower that can change color and provide a signal to pollinators is constrained by floral morphology. Changes in an external feature of the flower would likely be apparent to an approaching pollinator, while changes in structures hidden inside the floral tube would not be visible. Indeed, color changes in bird-pollinated flowers, such as *Lobelia laxiflora* (Campanulaceae), *Fuchsia excorticata* (Onagraceae), or *Kniphofia* sp. (Liliaceae), affect either the whole flower or an externally visible portion of the corolla tube. Birds have excellent visual acuity, and I have observed hummingbirds selectively visit the prechange flowers of *Ribes sanguineum* (Grossulariaceae), in which the small, corona-like petals change color. However, the tubular morphology of most hummingbird-pollinated flowers makes such localized changes uncommon.

Beetle pollination is almost entirely absent among color-changing flowers; this may be because coleopterans seem to rely largely on scent cues to locate flowers (Faegri and van der Pijl, 1966; Meeuse and Morris, 1984). In flowers of the two color-changing species for which beetle pollination or visitation has been reported, *Hypocalymma angustifolium* (Myrtaceae) (Lamont, 1985) and *Victoria amazonica* (Nymphaeaceae) (Meeuse and Morris, 1984), a change in floral odor accompanies the color change.

Physiology of color change—The various physiological mechanisms of floral color change (appearance and loss of different pigments, changes in pH, and movement of floral parts) involve very different biochemical pathways, regulatory processes, and perhaps metabolic costs. The diversity of mechanisms that result in floral color changes underscores the strength of selection for the phenomenon, as color changes resulting from these physiologically distinct processes must have had separate evolutionary origins. Furthermore, some of these color changes must have occurred relatively recently, as evidenced by the diversity of mechanisms within derived families such as the Solanaceae.

Of the seven mechanisms of color change I characterize, appearance of anthocyanin is by far the most common. Anthocyanins are ubiquitous in higher plant tissues and probably can be synthesized in all plant cells, given the right environment, and provided that genetic factors inhibiting synthesis are absent (Harborne, 1965). This idea is supported by the recent finding that transcriptional activators of anthocyanin synthesis from maize are able to cause anthocyanin production in *Nicotiana* (Lloyd, Walbot, and Davis, 1992). Investigations of color change in *Hibiscus mutabilis* (Amrhein and Frank, 1989) and *Cymbidium* sp. (Woltering and Somhorst, 1990), both of which have flowers that turn red after anthesis, suggest that the change is due to de novo synthesis of anthocyanin, and that ethylene is involved in regulation of the process. It is yet unknown whether the prevalence of anthocyanin-mediated color change is due to economy of production, or because the resultant colors (reds, purples, blues) may be particularly suitable as signals for pollinators.

Many flowers have been shown to possess UV nectar guides and floral patterns that are invisible to humans but visible to most insects (Eisner et al., 1973; Rosen and Barthlott, 1991). It is possible that changes in UV patterns might also play a role in providing signals to pollinators. Such changes could occur either in the UV alone or in addition to visible changes. However, I have found no evidence for ontogenetic changes in the UV portion of the spectrum. Neither spectrophotometric analyses of pigment extracts nor direct UV imaging of color-changing and non-color-changing flowers revealed any evidence of UV changes (Weiss, 1992). A wider survey of young and old flowers in the UV would be informative.

Changes in floral characteristics such as odor, size, shape, and position may occur in conjunction with color changes. For example, in *Aesculus hippocastanum* (Hippocastanaceae), a change in floral odor is reported to correlate with a change from yellow to red in the nectar guide (Lex, 1954); in two species of *Cyphomandra*, cessation of odor production and a marked increase in corolla size accompany the change in flower color from violet to cream (Sazima et al., 1993); in *Quisqualis indica*, flowers change their angle of orientation at the same time as they change color from white to deep red (Eisikowitch and Rotem, 1987). In the absence of floral color changes, changes in other floral characteristics may also provide cues for pollinators. More attention to the ontogeny of individual flowers is likely to reveal many such changes.

Until now, the extent and diversity of floral color change has been little appreciated. My survey demonstrates that this phenomenon is extremely widespread throughout the angiosperms, occurring in at least 77 taxonomically, morphologically, and geographically diverse families, and involving at least ten flower parts and seven physiological mechanisms of change. In all cases, regardless of the part that changes or the process involved, the end result is the same: young and old flowers are visually discriminable by the appropriate pollinator on a scale relevant to its foraging strategy. Selection by visually oriented pollinators has acted across a broad spectrum of flowering plants to produce this striking functional convergence.

LITERATURE CITED

AMRHEIN, N., AND G. FRANK. 1989. Anthocyanin formation in the petals of *Hibiscus mutabilis* L. *Zeitschrift fur Naturforschung C* 44: 357–360.

CASPER, B. B., AND T. R. LA PINE. 1984. Changes in corolla color and other floral characteristics in *Cryptantha humilis* (Boraginaceae): cues to discourage pollinators? *Evolution* 38: 128–141.

CHASE, M. W., D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVALL, R. A. PRICE, H. G. HILLS, Y-L QIU, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDRÉN, B. S. GAUT, R. K. JANSEN, K-J KIM, C. F. WIMPEE, J. F. SMITH, G. R. FURNIER, S. H. STRAUSS, Q-Y XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSEN, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, JR., S. W. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN, AND V. A. ALBERT. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. *Annals of the Missouri Botanical Garden* 80: 528–580.

CREPET, W. L., AND E. M. FRIIS. 1987. The evolution of insect pollination in angiosperms. *In* E. M. Friis, W. G. Chaloner, and P. R. Crane [eds.], The origins of angiosperms and their biological consequences, 181–201. Cambridge University Press, Cambridge.

CRONQUIST, A. 1988. The evolution and classification of flowering plants. The New York Botanical Garden, Bronx, NY.

CRUZAN, M. B., P. R. NEAL, AND M. F. WILLSON. 1988. Floral display in *Phyla incisa*: consequences for male and female reproductive success. *Evolution* 42: 505–515.

DELPH, L. F., AND C. M. LIVELY. 1985. Pollinator visits to floral colour phases of *Fuchsia excorticata*. *New Zealand Journal of Zoology* 12: 599–603.

———, AND ———. 1989. The evolution of floral color change: pollinator attraction versus physiological constraints in *Fuchsia excorticata*. *Evolution* 43: 1252–1262.

DELPINO, F. 1873. Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. *Atti della Societa Italiana di Scienze Naturali* 16: 151–349.

EISIKOWITCH, D., AND R. ROTEM. 1987. Flower orientation and color change in *Quisqualis indica* and their possible role in pollinator partitioning. *Botanical Gazette* 148: 175–179.

EISNER, T., M. EISNER, P. A. HYYPIO, D. ANESHANSLEY, AND R. E. SILBERGLIED. 1973. Plant taxonomy: ultraviolet patterns of flowers visible as fluorescent patterns in pressed herbarium specimens. *Science* 179: 486–487.

FAEGRI, K., AND L. VAN DER PIJL. 1966. The principles of pollination ecology. Pergamon Press, Oxford.

GOODWIN, T. W. [ED.]. 1976. The chemistry and biochemistry of plant pigments. Academic Press, London.

GORI, D. F. 1983. Post-pollination phenomena and adaptive floral changes. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 31–49. Scientific and Academic Edition, New York, NY.

———. 1989. Floral color change in *Lupinus argenteus* (Fabaceae): why should plants advertise the location of unrewarding flowers to pollinators? *Evolution* 43: 870–881.

GRACIE, C. 1993. Pollination of *Cyphomandra endopogon* var. *endopogon* (Solanaceae) by *Eufriesea* spp. (Euglossini) in French Guiana. *Brittonia* 45: 39–46.

HARBORNE, J. B. 1965. Flavonoids: distribution and contribution to plant colour. *In* T. W. Goodwin [ed.], Chemistry and biochemistry of plant pigments, 247–308. Academic Press, London.

———. 1973. Phytochemical methods. Chapman and Hall, London.

———. 1988. The flavonoids: recent advances. *In* T. W. Goodwin [ed.], Plant pigments, 299–343. Academic Press, London.

JONES, C. E., AND M. CRUZAN. 1982. Floral color changes in deerweed (*Lotus scoparius*): possible function. *Crossosoma* 8: 1–6.

KEVAN, P. G., AND H. G. BAKER. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28: 407–453.

KNUTH, P. 1906–09. Handbook of flower pollination. Oxford University Press, Oxford.

LAMONT, B. B. 1985. The significance of flower colour change in eight co-occurring shrub species. *Botanical Journal of the Linnean Society* 90: 145–155.

———, AND B. G. COLLINS. 1988. Flower colour change in *Banksia ilicifolia*: a signal for pollinators. *Australian Journal of Ecology* 13: 129–135.

LEX, T. 1954. Duftmale an Blüten. *Zeitschrift für Vergleichende Physiologie* 36: 212–234.

LLOYD, A. M., V. WALBOT, AND R. W. DAVIS. 1992. *Arabidopsis* and *Nicotiana* anthocyanin production activated by maize regulators R and C1. *Science* 258: 1773–1775.

LUDWIG, F. 1885. Die biologische Bedeutung des Farbenwechsels mancher Blumen. *Biologisches Centralblatt* 4: 196–197.

MEEUSE, B. J. D., AND S. MORRIS. 1984. The sex life of flowers. Facts on File Publications, New York, NY.

OLMSTEAD, R. G., AND J. D. PALMER. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. *Annals of the Missouri Botanical Garden* 79: 346–360.

———, B. BREMER, K. M. SCOTT, AND J. D. PALMER. 1993. A parsimony analysis of the Asteridae sensu lato based on rbcL sequences. *Annals of the Missouri Botanical Garden* 80: 700–722.

PIATTELLI, M. 1976. Betalains. *In* T. W. Goodwin [ed.], Chemistry and biochemistry of plant pigments, vol. 1, 560–596. Academic Press, New York, NY.

ROSEN, D., AND W. BARTHLOTT. 1991. Ökologische Aspekte der Ultraviolett-Reflexion von Blumen in Mitteleuropa, besonders in der Eifel. *Decheniana (Bonn)* 144: 72–112.

RUMPF, G. E. 1743. Herbarium amboinense. Meinardum Uytwerf, Amsterdam.

SAZIMA, M., S. VOGEL, A. COCUCCI, AND G. HAUSNER. 1993. The perfume flowers of *Cyphomandra* (Solanaceae): pollination by euglossine bees, bellows mechanism, osmophores, and volatiles. *Plant Systematics and Evolution* 187: 51–88.

SCHAAL, B. A., AND W. J. LEVERICH. 1980. Pollination and banner markings in *Lupinus texensis* (Leguminosae). *Southwestern Naturalist* 25: 280–282.

SCOGIN, R. 1983. Visible floral pigments and pollinators. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 169–172. Scientific and Academic Editions, New York, NY.

SPRENGEL, C. K. 1793. Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Friedrich Vieweg, Berlin.

STEBBINS, G. L. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual Review of Ecology and Systematics* 307–326.

THORNE, R. F. 1992. An updated phylogenetic classification of the flowering plants. *Aliso* 13: 365–389.

VOGEL, S. 1950. Farbwechsel und Zeichnungsmuster bei Blüten. *Österreichische Botanische Zeitschrift* 97: 44–100.

WEISS, M. R. 1991. Floral colour changes as cues for pollinators. *Nature* 354: 227–229.

———. 1992. Ecological and evolutionary significance of floral color change. Ph.D. dissertation, University of California, Berkeley, CA.

WOLTERING, E. J., AND D. SOMHORST. 1990. Regulation of anthocyanin synthesis in *Cymbidium* flowers: effects of emasculation and ethylene. *Journal of Plant Physiology* 136: 295–299.

LITERATURE CITED—APPENDIX 1

1. ALMEDA, F. California Academy of Sciences, San Francisco, CA. Personal communication.
2. AMES, O. 1947. Color changes in *Epidendrum tampense*. *American Orchid Society Bulletin* 16: 442–443.
3. ARDITTI, J., N. M. HOGAN, AND A. V. CHADWICK. 1973. Post-pollination phenomena in orchid flowers. IV. Effects of ethylene. *American Journal of Botany* 69: 883–888.
4. BAILEY, L. H. 1949. Manual of cultivated plants. Macmillan, New York, NY.
5. BARROWS, E. M. 1977. Floral maturation and insect visitors of *Pachyptera hymenaea* (Bignoniaceae). *Biotropica* 9: 133–134.
6. BLUNDELL, M. 1987. Collins guide to the wild flowers of East Africa. Collins, London.
7. BRAMWELL, D., AND Z. BRAMWELL. 1984. Wildflowers of the Canary Islands. Stanley Thornes Ltd., Cheltenham.
8. BROCK, J. 1988. Top End native plants. John Brock, Darwin.
9. BUCK, R. 1989. University of California, Berkeley, CA. Personal communication.
10. BURG, S. D., AND M. J. DIJKMAN. 1967. Ethylene and auxin participation in pollen induced fading of *Vanda* orchid blossoms. *Plant Physiology* 42: 1648–1650.
11. CASPER, B. B., AND T. R. LA PINE. 1984. Changes in corolla color and other floral characteristics in *Cryptantha humilis* (Boraginaceae): cues to discourage pollinators? *Evolution* 38: 128–141.
12. CHIN, H. F. 1977. Malaysian flowers in color. Tropical Press, Kuala Lumpur, Malaysia.
13. COCHRANE, G. R., B. A. FUHRER, E. R. ROTHERHAM, AND J. H. WILLIS [EDS.]. 1973. Flowers and plants of Victoria. A. H. and A. W. Reed, Sydney.
14. COLLENETTE, S. 1985. An illustrated guide to the flowers of Saudi Arabia. Scorpion Flora publication (Saudi Arabia Meteorology and Environmental Protection Administration), no. 1, London.
15. COSTERMANS, L. F. 1981. Native trees and shrubs of southeastern Australia. Rigby, Adelaide.
16. CRAVEN, L. A. 1987. A taxonomic revision of *Calytrix* Labill. (Myrtaceae). *Brunonia* 10: 1–138.
17. CRUZAN, M. B., P. R. NEAL, AND M. F. WILLSON. 1988. Floral display in *Phyla incisa*: consequences for male and female reproductive success. *Evolution* 42: 505–515.
18. DELPH, L. 1993. Indiana University, Bloomington, IN. Personal communication.
19. DELPH, L. F., AND C. M. LIVELY. 1989. The evolution of floral

color change: pollinator attraction versus physiological constraints in *Fuchsia excorticata*. *Evolution* 43: 1252–1262.

20. DELPINO, F. 1873. Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. *Atti della Societa Italiana di Scienze Naturali* 16: 151–349.
21. DUNCAN, W. H., AND M. B. DUNCAN. 1987. The Smithsonian guide to seaside plants of the Gulf and Atlantic coasts. Smithsonian Institution Press, Washington DC.
22. ———, AND L. E. FOOTE. 1975. Wildflowers of the southeastern United States. University of Georgia Press, Athens, GA.
23. ERICKSON, R., A. S. GEORGE, N. G. MARCHANT, AND M. K. MORCOMBE. 1973. Flowers and plants of western Australia. Reed, Sydney.
24. ESTES, J. R., AND L. S. BROWN. 1973. Entomophilous, intrafloral pollination in *Phyla incisa*. *American Journal of Botany* 60: 228–230.
25. FRANKIE, G. 1989. University of California, Berkeley, CA. Personal communication.
26. FREEMAN, C. C., AND E. K. SCHOFIELD. 1991. Roadside wildflowers of the southern Great Plains. University Press of Kansas, Lawrence, KS.
27. FRIEDMANN, F. 1986. Fleurs et arbres des Seychelles. Office de la Recherche Scientifique et Technique Outre-Mer, Paris.
28. GILL, F. B., AND L. L. WOLF. 1975. Foraging strategies and energetics of east African sunbirds at mistletoe flowers. *American Naturalist* 109: 491–510.
29. GORI, D. F. 1983. Post-pollination phenomena and adaptive floral changes. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 31–49. Scientific and Academic Editions, New York, NY.
30. ———. 1989. Floral color change in *Lupinus argenteus* (Fabaceae): why should plants advertise the location of unrewarding flowers to pollinators? *Evolution* 43: 870–881.
31. GOTTSBERGER, G. 1971. Colour change of petals in *Malvaviscus arboreus* flowers. *Acta Botanica Neerlandica* 20: 381–388.
32. GRACIE, C. 1993. Pollination of *Cyphomandra endopogon* var *endopogon* (Solanaceae) by *Eufriesea* spp. (Euglossini) in French Guiana. *Brittonia* 45: 39–46.
33. HEYWOOD, V. H. [ED.]. 1978. Flowering plants of the world. Mayflower Books, New York, NY.
34. HILLIARD, O. 1992. Royal Botanic Garden, Edinburgh, Scotland. Personal communication.
35. HOBBIE, S. 1991. University of California, Berkeley, CA. Personal communication.
36. JONES, C. E., AND S. L. BUCHMANN. 1974. Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. *Animal Behaviour* 22: 481–485.
37. JONES, C. E., AND M. CRUZAN. 1982. Floral color changes in deerweed (*Lotus scoparius*): possible function. *Crossosoma* 8: 1–6.
38. KINGSBURY, J. M. 1988. 200 conspicuous, unusual, or economically important tropical plants of the Caribbean. Bullbrier Press, Ithaca, NY.
39. KOPTUR, S. 1990. Florida International University, Miami, FL. Personal communication.
40. KUCK, L., AND R. C. TONGG. 1958. Hawaiian flowers and flowering trees: a guide to tropical and semi-tropical flora. C. E. Tuttle, Rutland, VT.
41. KUGLER, H. 1943. Hummeln als Blütenbesucher, ein Beitrag zur experimentellen Blütenbiologie. *Ergebnisse der Biologie* 19: 143–323.
42. KUNIN, W. 1988. University of Washington, Seattle, WA. Personal communication.
43. LACKIE, P. M., C. D. THOMAS, M. J. BRISCO, AND D. N. HEPPER. 1986. On the pollination ecology of *Hamelia patens* (Rubiaceae) at Monteverde, Costa Rica. *Brenesia* 25–26: 203–213.
44. LAMONT, B. B. 1985. The significance of flower colour change in eight co-occurring shrub species. *Botanical Journal of the Linnean Society* 90: 145–155.
45. ———. 1990. Curtin University, Perth, Australia. Personal communication.
46. ———, AND B. G. COLLINS. 1988. Flower colour change in *Banksia ilicifolia*: a signal for pollinators. *Australian Journal of Ecology* 13: 129–135.
47. LLOYD, D. G. 1990. University of Canterbury, Christchurch, New Zealand. Personal communication.
48. LUDWIG, F. 1886. Einige neue Fälle von Farbenwechsel in verblühenden Blütenständen. *Biologisches Centralblatt* 6: 1–3.
49. MABBERLEY, D. J. 1987. The plant-book. Cambridge University Press, Cambridge.
50. MACOBOY, S. 1979. What tree is that? Tiger Books, London.
51. ———. 1982. Trees for flower and fragrance. Lansdowne Press, Sydney.
52. ———. 1984. Flowering shrubs. Lansdowne Press, Sydney.
53. ———. 1989. What shrub is that? Outlet Book, Avenal, NJ.
54. MARQUIS, R. 1988. University of Missouri, St. Louis, MO. Personal communication.
55. MATHUR, G., AND H. Y. MOHAN RAM. 1978. Significance of petal colour in thrips-pollinated *Lantana camara* L. *Annals of Botany* 42: 1473–1476.
56. MEEUSE, B. J. D. 1989. University of Washington, Seattle, WA. Personal communication.
57. MORCOMBE, M. K. 1968. Australia's western wildflowers. Landfall Press, Perth.
58. MÜLLER, F. 1877. (Letter to the editor). *Nature* 17: 78–79.
59. MÜLLER, H. 1883. The effect of the change of colour in the flowers of *Pulmonaria officinalis* upon its pollinators. *Nature* 28: 81.
60. NATIONAL BOTANIC GARDENS OF SOUTH AFRICA, KIRSTENBOSCH. 1980. Wildflowers of South Africa. C. Struik, Cape Town.
61. NIERING, W. A., AND N. C. OLMSTEAD. 1979. The Audubon society field guide to North American wildflowers—eastern. Alfred A. Knopf, New York, NY.
62. OKUDA, S. 1985. Grassland plants of Japan. Tokai Daigaku Shuppankai, Tokyo.
63. ———. 1985. Montane forest plants of Japan. Tokai Daigaku Shuppankai, Tokyo.
64. ORR, R. T., AND M. C. ORR. 1974. Wildflowers of western America. Alfred A. Knopf, Chanticleer Press, New York, NY.
65. PERRY, F., AND R. HAY. 1982. A field guide to tropical and subtropical plants. Van Nostrand Reinhold, New York, NY.
66. PHILLIPS, R., AND M. RIX. 1989. The Random House book of shrubs. Random House, New York, NY.
67. POLUNIN, I. 1987. Plants and flowers of Singapore. Times editions, Singapore.
68. POLUNIN, O. 1969. Flowers of Europe—a field guide. Oxford University Press, London.
69. ———, AND A. HUXLEY. 1966. Flowers of the Mediterranean. Houghton Mifflin, Boston, MA.
70. ———, AND A. STAINTON. 1984. Flowers of the Himalaya. Oxford University Press, Delhi.
71. ———, AND ———. 1987. Concise flowers of the Himalaya. Oxford University Press, Delhi.
72. PROCTOR, J., AND S. PROCTOR. 1978. Nature's use of colour in plants and their flowers. Peter Lowe, Eurobook Ltd., London.
73. RENNER, S. 1991. Universität Mainz, Mainz, Germany. Personal communication.
74. RICHARDS, A. J. 1986. Plant breeding systems. George Allen and Unwin, London.
75. ROSS, R. A., AND H. L. CHAMBERS. 1988. Wildflowers of the western Cascades. Timber Press, Portland, OR.
76. ROTHERHAM, E. R. [ED.]. 1975. Flowers and plants of New South Wales and southern Queensland. Reed, Terrey Hills, NSW.
77. RUMPF, G. E. 1743. Herbarium amboinense. Meinardum Uytwerf, Amsterdam.
78. SALMON, J. 1968. Collins guide to the alpine plants of New Zealand. Collins, Auckland.
79. SAZIMA, M., S. VOGEL, A. COCUCCI, AND G. HAUSNER. 1993. The perfume flowers of *Cyphomandra* (Solanaceae): pollination by euglossine bees, bellows mechanism, osmophores, and volatiles. *Plant Systematics and Evolution* 187: 51–88.
80. SCHAAL, B. A., AND W. J. LEVERICH. 1980. Pollination and banner markings in *Lupinus texensis* (Leguminosae). *Southwestern Naturalist* 25: 280–282.
81. SCHEMSKE, D. W. 1976. Pollinator specificity in *Lantana camara* and *L. trifolia* (Verbenaceae). *Biotropica* 8: 260–264.
82. ———. 1980. Floral ecology and hummingbird pollination of *Combretum farinosum* in Costa Rica. *Biotropica* 12: 169–181.

83. SCHOEN, D. J. 1977. Floral biology of *Diervilla lonicera* (Caprifoliaceae). *Bulletin of the Torrey Botanical Club* 104: 234–240.

84. SMITINANA, T. 1985. Wildflowers of Thailand. Forestry Association of Thailand, Bangkok.

85. ———, AND K. LARSEN [EDS.]. 1984. Flora of Thailand, vol. 4, part 1, Leguminosae—Caesalpinoideae. The Forest Herbarium, Royal Forest Department, Bangkok.

86. SOHMER, S. H., AND R. GUSTAFSON. 1987. Plants and flowers of Hawai'i. University of Hawaii Press, Honolulu, HI.

87. STAINTON, A. 1988. Flowers of the Himalayas—A supplement. Oxford University Press, Dehli.

88. STRICKLER, D., AND Z. STRICKLER-WILSON. 1989. Prairie wildflowers. The Flower Press, Columbia Falls, MT.

89. SUN, I. 1991. University of California, Berkeley, CA. Personal communication.

90. TIMME, S. L. 1989. Wildflowers of Mississippi. University Press of Mississippi, Jackson, MS.

91. VAN DER SPUY, U. 1971. South African trees and shrubs for the garden. Hugh Keartland, Johannesberg.

92. VAN WYK, B., AND S. MALAN. 1988. Field guide to the wild flowers of the Witwatersrand and Pretoria region. Struik, Cape Town.

93. VILLA, J. D. 1991. University of Louisiana, Baton Rouge, LA. Personal communication.

94. WAINWRIGHT, C. M. 1978. The floral biology and pollination ecology of two desert lupines. *Bulletin of the Torrey Botanical Club* 105: 24–38.

95. WEISS, M. R. Personal observation.

96. WELSH, S. L., AND B. RATCLIFFE. 1986. Flowers of the Canyon Country. Canyonlands Natural History Association, Moab, UT.

97. WHITE, H. [ED.]. 1974. The Alaska-Yukon wildflowers guide. Alaska Northwest Publishing, Anchorage, AK.

98. WILLIAMS, K. A. W. 1979. Native plants—Queensland. Keith A. W. Williams, North Ipswich.

99. WOLTERING, E. J., AND D. SOMHORST. 1990. Regulation of anthocyanin synthesis in *Cymbidium* flowers: effects of emasculation and ethylene. *Journal of Plant Physiology* 136: 295–299.

100. ZHANG, J. [ED.]. 1982. The Alpine plants of China. Science Press, Beijing.

APPENDIX 1. Color-changing taxa. Abbreviations for parts that change are explained in legend to Fig. 3; reference numbers refer to a literature cited section.

Taxon	Part that changes	Color change	Native habitat	Reference
Acanthaceae				
Asystasia gangetica	WF	Pale yellow to lavender	India	38
Crossandra wissmannii	WF	White to lavender	Saudi Arabia	14
Agavaceae				
Beschorneria yuccoides	WF	Green to pink	Chiapas, Mexico	95
Aizoaceae				
Carpobrotus edulis	WF	Pale yellow to pink	S. Africa	45, 95
Anacardiaceae				
Anacardium occidentale	WF	White to pink	Tropical America	95
Rhus ovata	N/H	Yellow to deep orange	S. Calif., Arizona	95
Apocynaceae				
Adenium obesum	CF	Yellow to orange-red	E. Africa	52
Plumeria acuminata	CF	Yellow to orange	Tropical America	95
Asclepiadaceae				
Asclepias nyctaginifolia	PA	Pinkish white to pale yellow	Arizona, S. Calif.	95
Glossonema revoilii	WF	White to yellow-bronze	East Africa	6
Oxypetalum caerulea	WF	Pale blue to pink	Brazil, Uruguay	95
Begoniaceae				
Hillebrandia sandwicensis	GYN	Yellow to red	Hawaii	86
Bignoniaceae				
Catalpa bignonioides	NG/BPS	Yellow to deep red	SE. U.S.	95
Distictis buccinatoria	CF	Yellow to deep orange	Mexico	95
Pachyptera hymenaea	WF	Purple to white	Central America	5
Tabebuia impetuginosa	CF	Yellow to orange-pink	Costa Rica	25
Boraginaceae				
Anchusa capensis	E/C	White to rusty red	Europe	95
Arnebia echioides	NG/BPS	Deep red to white	Armenia	74
Arnebia euchroma	WF	Pink to deep purple	Himalayas	71
Cordia boissieri	CF	Yellow to orange	Mexico	95
Cryptantha flava	WF	White to yellow	SW. U.S.	96
Cryptantha humilis	E/C	Yellow to white	W. U.S.	11
Echium decaisnei	AND	Red to white	Canary Islands	95
Eritrichium aretioides	E/C	Yellow to white	Alaska	97
Heliotropium anchusaefolium	CF	Yellow to purple	S. America	95
Heliotropium arbainense	WF	Pale cream to deep yellow	Saudi Arabia	14
Heliotropium curassavicum	CF	Yellow to dark purple	U.S.	95
Moltkiopsis ciliata	CF	Pale yellow to purple	Saudi Arabia	14
Myosotis alpestris	E/C	Yellow to white	Europe	95
Myosotis alpestris ssp. *asiatica*	CF	Yellow/blue to white/red	N. Alaska	35
Myosotis australis	E/C	Yellow to pink	Australia, NZ	13

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Myosotis suaveolens	E/C	Yellow to white	Victoria, Aust.	13
Myosotis sylvatica	E/C	Yellow to red	Europe, Asia	96
Oreocarya glomerata	E/C	Yellow to white	W. N. America	95
Pulmonaria officinalis	WF	Red to blue	Europe	59
Bromeliaceae				
Aechmea sp.	WF	Pink to blue	Tropical America	95
Buddlejaceae				
Buddleja davidii	CF	Yellow to deep orange	China	95
Buddleja marrubifolia	WF	Yellow to red	Chihuahuan desert	95
Cactaceae				
Opuntia phaeacantha	WF	Yellow to orange	Arizona	95
Caesalpiniaceae				
Bauhinia bidentata	WF	Yellow to red	Thailand	85
Bauhinia monandra	SP	Red spot hidden	Guyana, W. Indies	95
Caesalpinia pulcherrima	SP	Yellow to deep orange	Tropical Asia	95
Cercidium microphyllum	SP	White to pale yellow	SW. U.S., Mexico	95
Delonix regia	SP	White spot hidden	Madagascar	95
Intsia bijuga	WF	White to pink	Seychelles	27
Parkinsonia aculeata	SP	Yellow to orange	SW. U.S., Mexico	36, 95
Saraca declinata	WF	Pale yellow to red	Thailand	85
Saraca indica	WF	Pale orange to red	India, Malaysia	51
Saraca thaipingensis	WF	Yellow to deep orange-red	Malaysia	67
Campanulaceae				
Lobelia excelsa	WF	Orange to red	Chile	95
Lobelia laxiflora	CT	Yellow to orange	Mexico	95
Capparidaceae				
Capparis javanica	NG/BPS	Yellow to maroon	Old World	
Capparis micrantha	NG/BPS	Yellow to red	Old World	51
Cleome maculata	NG/BPS	Yellow/black to orange	S. Africa	92
Cleome parvipetala	NG/BPS	Bright yellow to dull red	East Africa	6
Maerua kirkii	CF	Yellow to black	East Africa	6
Caprifoliaceae				
Diervilla lonicera	WF	Yellow to orange	E. N. America	83, 95
Diervilla sessilifolia	NG/BPS	Yellow to red	SE. U.S.	95
Lonicera hildebrandiana	WF	White to yellow-orange	Burma	95
Lonicera japonica	WF	White to yellow	Japan	95
Lonicera morrowi	WF	White to yellow	Japan	61
Lonicera periclymenum	WF	White to yellow	Europe and Medit.	95
Lonicera tatarica	WF	White to yellow	Europe	61
Weigela decora	WF	Pale yellow to pink	Japan	63
Weigela florida	NG/BPS	Yellow to pink	N. China, Korea	95
Caryophyllaceae				
Gypsophila cerastioides	GYN	Green to red	Himalayas	95
Gypsophila oldhamianana	GYN	Green to red	Korea, China	95
Gypsophila repens	GYN	White to red	Spain	95
Silene alpestris	GYN	Green to red	Europe	95
Silene fruticosa	CF	White to lavender	Italy	95
Combretaceae				
Combretum farinosum	WF	Green to orange	S. and C. America	82, 95
Quisqualis indica	WF	White to deep red	Burma	95
Compositae				
Aster divaricatus	CF	Yellow to purple	E. U.S.	61
Aster dumosus	CF	Yellow to red	E. U.S.	95
Aster laevis	CF	Yellow to orange-red	U.S.	61
Aster lateriflorus	CF	Yellow to pink-red	U.S.	61
Aster linariifolius	CF	Yellow to orange-red	E. U.S.	95
Aster nova-angliae	CF	Yellow to red	E. U.S.	61
Aster novi-belgii	CF	Yellow to red	E. U.S.	61
Aster puniceus	CF	Yellow to red	SE. U.S.	22
Aster sikkimensis	CF	Yellow to red-purple	Himalayas	87
Aster tardiflorus	CF	Yellow to red	N. America	95
Aster tripolium	CF	Yellow to orange-red	Europe	68

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Aster undulatus	CF	Yellow to purple	U.S.	95
Aster vimineus	CF	Yellow to pink	U.S.	61
Calycadenia multiglandulosa	CF	White to pink	California	95
Erigeron glaucus	CF	Yellow to purple	California	95
Erigeron karvinskianus	SP	White to pink	C. America	95
Felicia filifolia	CF	Yellow to orange	S. Africa	92
Cornaceae				
Cornus paucinervis	N/H	Pink to purple	Asia	95
Crassulaceae				
Kalanchoe pumila	GYN	Green to red	Old World tropics	95
Sedum villosum	GYN	Yellow to red	Europe	68
Cruciferae				
Aethionema saxatile	AND	Yellow to red	Europe	68
Arabis alpina	GYN	Yellow to purple	Europe	95
Aubrieta intermedia	CF	Yellow to red	Medit.	67
Aubrieta superbissima	E/C	Yellow to purple	Europe	95
Berteroa incana	NG/BPS	Yellow to white	Europe and Asia	89
Cakile maritima	AND	Yellow to purple	Medit.	95
Cardaminopsis arenosa	CF	Yellow to pink	Europe	68
Cheiranthus mutabilis	WF	White to purple	Canary Islands	95
Cheiranthus scoparius	WF	White to purple	Canary Islands	95
Cheiranthus virescens	WF	White to lavender	Canary Islands	7
Chorispora purpurascens	CF	Yellow to deep purple	Saudi Arabia	14
Crambe maritima	CF	Yellow to red	Medit.	68
Dithyrea wislizenii	AND	Yellow to red	SW. U.S.	95
Farsetia burtonae	CF	Pale yellow to pale rose	Saudi Arabia	14
Horwoodia dicksoniae	CF	Yellow to deep red	Saudi Arabia	14
Iberis amara	AND	Yellow to red	Medit.	68
Iberis linifolia	WF	White to lavender	Spain	95
Iberis perennis	AND	Yellow to red	Medit.	95
Iberis sempervirens	AND	Yellow/green to purple	S. Europe	95
Lobularia maritima	WF	White to purple	Medit.	95
Lobularia maritima	AND	Yellow/green to purple	Medit.	95
Malcolmia maritima	E/C	Yellow to dark pink	S. Europe	69
Malcolmia littorea	CF	Yellow/white to red	Spain	95
Matthiola fruticulosa	E/C	Yellow-green to deep red	S. Europe	68
Matthiola incana	E/C	White to magenta	S. Europe	95
Morettia canescens	CF	Pale yellow to purple	Saudi Arabia	14
Nasturtium officinale	AND	Green to purple	Europe	95
Phaeonychium parroides	CF	Yellow to orange-red	China	100
Ptilotrichum halimifolium	GYN	Yellow/green to red	S. Europe	95
Ricotia lunaria	E/C	White to dark pink	N. Israel	42
Rorippa gambellii	AND	Yellow to purple		95
Smelowskia calycina	AND	Yellow to red	W. N. America, E. Asia	95
Dipsacaceae				
Morina longifolia	CT	White to pink	Himalayas	71
Elaeocarpaceae				
Aristotelia fruticosa	WF	White to red	New Zealand	78
Aristotelia racemosa	WF	White to red	New Zealand	33
Aristotelia serrata	WF	White to red	New Zealand	95
Epacridaceae				
Brachyloma preissii	WF	White to red	Australia	23
Epacris impressa	AND	Bright red to black	Victoria, Aust.	13
Ericaceae				
Rhododendron ponticum	NG/BPS	Yellow to red	Europe, Asia Minor	95
Euphorbiaceae				
Euphorbia florida	N/H	White to pink	SW. U.S.	95
Frankeniaceae				
Frankenia ericifolia	CF	Pale yellow to pink	Canary Islands	95
Geraniaceae				
Geranium dalmaticum	CF	Pale pink to deep pink	Europe	95

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Goodeniaceae				
Dampiera eriocephala	CF	White to pink	W. Australia	23
Dampiera linearis	CF	White to blue	W. Australia	23
Leschenaultia macrantha	CF	Yellow to orange	W. Australia	23
Grossulariaceae				
Ribes aureum	E/C	Yellow to red	California	20, 95
Ribes odoratum	E/C	Yellow to red	E. U.S.	95
Ribes sanguineum	E/C	White to pink	California	95
Hippocastanaceae				
Aesculus californica	NG/BPS	Yellow to pink	California	95
Aesculus carnea	NG/BPS	Yellow to red		95
Aesculus hippocastanum	NG/BPS	Yellow to red	Europe	41, 95
Aesculus pavia	NG/BPS	Yellow to red	SE. U.S.	93
Billia hippocastanum	NG/BPS	Yellow to red	Costa Rica	39
Labiatae				
Salvia columbariae	NG/BPS	White to blue	California	95
Thymus pannonicus	NG/BPS	White to lavender	Medit.	95
Lentibulariaceae				
Utricularia menziesii	NG/BPS	Yellow to red	Australia	57
Liliaceae				
Colchicum agrippinum	CF	Pale yellow to pink	Europe	95
Cybistetes longifolia	CF	Pale yellow to deep pink	S. Africa	60
Gloriosa superba	CF	Yellow to red	Trop. Afr. and Asia	95
Kniphofia sp.	CT	Red to yellow	S. Africa	95
Lilium washingtonianum	CF	White to pink	W. U.S.	95
Trillium ovatum	WF	White to deep pink	W. U.S.	95
Zigadenus glaberrimus	WF	White to pale yellow	Mississippi	90
Zigadenus fremontii	N/H	Yellow to pale green	California	95
Linaceae				
Linum pubescens	E/C	Yellow to dark pink	Medit.	69
Linum suffruticosum	AND	White to dark red	Europe	68
Loganiaceae				
Desfontainia spinosa	CT	Yellow to red	Peru, Chile	66
Loranthaceae				
Phragmanthera dshallensis	WF	Yellow to red	East Africa	28
Phragmanthera regularis	WF	Yellow to red	East Africa	6
Plicosepalus acaciae	CT	Green to red	Saudi Arabia	14
Lythraceae				
Lythrum junceum	CF	White to red	Europe	95
Malpighiaceae				
Byrsonima crassifolia	WF	Yellow to orange	Costa Rica	95
Galphimia glauca	AND	Yellow to red	Mexico	65
Tetrapterys phlomoides	WF	Yellow to orange	Brazil	95
Tristellateia australasiae	AND	Yellow to red	Africa	40
Malvaceae				
Gossypium hirsutum	WF	Cream to pink		95
Hibiscus mutabilis	WF	Yellow to orange-red	China	12, 77
Hibiscus tiliaceous	WF	Yellow to orange-red	Pantropical	95
Malvaviscus arboreus	WF	Red to pink	S. America	31
Thespesia populnea	WF	Yellow to purple	Pantropical	49
Melastomataceae				
Miconia stenostachya	AND	Yellow to red	Tropical America	73
Miconia dodecandra	AND	Yellow to red	Costa Rica	1, 95
Pleroma sellowiana	WF	White to red	Brazil	48
Rhexia virginica	AND	Yellow to orange-red	SE. U.S.	21
Tibouchina grandifolia	CF	White to red	Brazil	1, 95
Tibouchina heteromala	CF	White to red	Tropical America	1
Tibouchina lepidota	WF	Magenta to purple	Ecuador	1
Tibouchina multiflora	CF	White to red	Brazil	1

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Mimosaceae				
Dichrostachys cinerea	WF	Pink to white	South Africa	92
Mimosa rubicaulis	WF	Pink to white	Himalayas	70
Myoporaceae				
Eremophila duttonii	CT	Yellow-orange to red	Australia	15
Myoporum parvifolium	GYN	Green to red	Australia	95
Myrtaceae				
Agonis flexuosa	N/H	Green to red	Australia	23
Baeckea gunniana	N/H	Green to red	Australia	13
Baeckea utilis	N/H	Green to red	Australia	15
Baeckea virgata	N/H	Green to red	Australia	95
Baeckea fascicularis	N/H	Green to red	Australia	52
Calytrix brevifolia	AND	Yellow to red	Australia	57
Calytrix exstipulata	AND	Yellow to red	Australia	98
Calytrix fraseri	AND	Yellow to red	Australia	57
Calytrix glutinosa	AND	White to red	Australia	16, 44
Calytrix leptophylla	AND	Yellow to red	Australia	98
Calytrix longiflora	AND	Yellow to red	Australia	98
Calytrix microphylla	AND	Yellow to red	Australia	57
Calytrix strigosa	AND	Yellow to red	Australia	53
Chamelaucium megalopetalum	WF	White to red	Australia	23
Darwinia citriodora	WF	Yellow to red	Australia	44
Darwinia fasciculata	WF	White to red	Australia	44, 95
Hypocalymma angustifolium	WF	White to deep pink	Australia	44
Hypocalymma robustum	N/H	Yellow to red	Australia	57
Kunzea pomifera	N/H	Green to red	Australia	95
Leptospermum laevigatum	N/H	Green to red	Australia	95
Leptospermum phylicoides	N/H	Green to red	Australia	76
Leptospermum speciosum	N/H	Green to red	Australia	76
Leptospermum whitei	N/H	Green to red	Australia	98
Micromyrtus ciliata	N/H	Green to red	Australia	15
Micromyrtus hexamara	N/H	Greenish-yellow to red	Australia	98
Myrtella sp.	WF	White to pink	Australia	8
Thryptomene calycina	N/H	Yellow to red	Australia	15
Verticordia acerosa	WF	Yellow to orange-red	Australia	44, 95
Verticordia chrysantha	WF	Yellow to red	Australia	44
Verticordia grandiflora	WF	Yellow to orange	Australia	23
Verticordia huegelii	WF	White to red	Australia	44
Nymphaeaceae				
Victoria amazonica	WF	White to pale purple	S. America	95
Ochnaceae				
Ochna integerrina	AND	Yellow to orange-red	Old World tropics	84
Onagraceae				
Cammisonia claviformis	CF	Yellow-green to red-brown	S. California	95
Fuchsia excorticata	WF	Green and black to deep red	New Zealand	19, 95
Gaura coccinia	WF	White to maroon	SW. U.S.	96
Hauya sp.	WF	White to deep pink	C. America	53
Oenothera cuprea	WF	Green to orange-red	Venezuela	95
Orchidaceae				
Brassia verrucosa	PA	Green to red	Tropical America	95
Cymbidium sp.	SP	White to red	Old World tropics	3, 99
Cyrtorchis arcuata	WF	White to yellow	East Africa	6
Epidendrum ciliare	WF	White to pale yellow	Tropical America	95
Epidendrum paniculatum	WF	White to yellow	Tropical America	95
Epidendrum pseudoepidendrum	SP	Pink/white to orange/pink	Tropical America	95
Epidendrum radicans	SP	Yellow to red	C., S. America	95
Epidendrum stamfordianum	WF	White to pale yellow	Tropical America	95
Epidendrum tampense	SP	White to yellow	SE. U.S.	2
Malaxis sechellarum	WF	Green to maroon	Seychelles	27
Oerstedella pseudoshumanniana	SP	Lavender to red-brown	Tropical America	95
Vanda sp.	WF	Lavender to white	Old World	10
Ypsilopus longifolia	WF	White to yellow-green	East Africa	6
Papilionaceae				
Argyrolobium fischeri	WF	Bright yellow to red	East Africa	6

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Cadia purpurea	WF	White to dark pink	Saudi Arabia	14
Castanospermum australe	WF	Yellow to red	Australia	50
Chamaecytisus hirsutus	NG/BPS	Yellow to red	Europe	68
Chesneya nubigena	NG/BPS	Yellow to orange	W. Nepal	70
Colutea multiflora	WF	Yellow to pink-red	E. Nepal	70
Dalea pulchra	NG/BPS	Pale yellow to magenta	SW. U.S.	95
Daviesia pectinata	NG/BPS	Yellow-green to dark red	Australia	23
Lotononis eriantha	WF	Yellow to orange-red	South Africa	92
Lotononis laxa	WF	Yellow to orange	South Africa	92
Lotus corniculatus	WF	Yellow to deep orange	Europe, Asia	37, 95
Lotus heermannii	WF	Yellow to red-orange	California	95
Lotus scoparius	WF	Yellow to deep orange	California	95
Lotus uliginosus	WF	Yellow to red	California	95
Lupinus albifrons	NG/BPS	White to purple	California	95
Lupinus angustifolius	NG/BPS	White to deep pink	Medit.	68
Lupinus argenteus	NG/BPS	Yellow to purple	W. U.S.	29, 30
Lupinus arizonicus	NG/BPS	Cream to magenta	W. U.S.	94, 95
Lupinus bicolor	NG/BPS	White to purple	W. U.S.	95
Lupinus blumeri	NG/BPS	White to purple	Arizona	95
Lupinus excubitus	NG/BPS	Yellow to purple	S. Calif.	95
Lupinus latifolius	NG/BPS	White to magenta	W. U.S.	64
Lupinus longifolius	NG/BPS	Yellow to purple	Baja, Calif.	95
Lupinus nanus	NG/BPS	White to purple	California	95
Lupinus propinquus	NG/BPS	White to purple	California	95
Lupinus pusillus	NG/BPS	White to deep purple	SW. U.S.	96
Lupinus sparsiflorus	NG/BPS	White to deep purple	SW. U.S.	94
Lupinus stiversii	NG/BPS	Yellow to orange	California	95
Lupinus succulentus	NG/BPS	White to deep pink	California	95
Lupinus texensis	NG/BPS	White to purple	Texas	80, 95
Lupinus vallicola	NG/BPS	White to purple	California	95
Lupinus varius	NG/BPS	White to purple	Medit.	67
Pearsonia sessilifolia	WF	Yellow to red	S. Africa	92
Psoralea esculenta	WF	Lavender to pale yellow	S. Africa	26
Trifolium stellatum	WF	White to deep pink		95
Passifloraceae				
Passiflora novae-zelandiae	WF	White to yellow	New Zealand	47
Penaeaceae				
Glischrocolla formosa	CF	White to red	S. Africa	60
Sonderothamnus petraens	CF	Pale pink to dark pink	S. Africa	60
Pittosporaceae				
Billardiera cymosa	CF	Yellow-green to deep pink	Australia	13
Billardiera procumbens	GYN	Green to red	Australia	98
Billardiera ringens	WF	Yellow-orange to red	Australia	23
Hymenosporum flavum	CF	white to yellow and red	Australia	76
Marianthus procumbens	GYN	Green to red	Australia	76
Pittosporum rhombifolium	WF	White to orange-yellow	Australia	4
Pittosporum undulatum	WF	White to yellow	Australia	95
Plumbaginaceae				
Armeria maritima	CF	Whitish to pink	California	95
Polemoniaceae				
Cobaea scandens	WF	Whitish to purple	Tropical America	72, 95
Leptodactylon californicum	E/C	White to purple	S. California	95
Linanthus montanus	CF	White to purple	California	95
Phlox longifolia	E/C	White to deep pink	SW. U.S.	96
Polygalaceae				
Monnina sp.	NG/BPS	Yellow to deep blue	Costa Rica	95
Nylandtia spinosa	PA	White to rose	S. Africa	60
Polygala arillata	PA	Yellow to orange-red	Himalayas	87
Polygala chamaebuxus	PA	Yellow to red	Central Europe	68
Polygala cruciata	WF	White to pink	SE. U.S.	22
Polygala curtissii	WF	White and yellow to pink	SE. U.S.	22
Polygala dalmasiana	PA	White to lavender	S. Africa	95
Polygonaceae				
Polygonum emondii	WF	Red to whitish	Himalayas	95

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Primulaceae				
Androsace carnea	E/C	Yellow to red	Europe	68
Androsace hookeriana	E/C	Yellow to red	Himalayas	100
Androsace lanuginosa	E/C	Yellow to red	Himalayas	87, 95
Androsace lehmannii	E/C	Yellow to red	Himalayas	87
Androsace muscoidea	E/C	Yellow to orange	Himalayas	87
Androsace primuloides	E/C	Yellow to red	Kashmir	70
Androsace robusta	E/C	Yellow to red	China	100
Androsace rotundifolia	E/C	Yellow to red	Kashmir	70
Androsace tapete	E/C	Yellow to red	S. Tibet	100
Androsace zambalensis	E/C	Yellow to red	W. Nepal	70
Primula farinosa	E/C	Yellow to orange	Old World	95
Proteaceae				
Banksia ilicifolia	WF	Yellow to red	Australia	46
Grevillea pilulifera	AND	Yellow to red	Australia	44
Isopogon dubius	AND	Yellow to orange-red	Australia	95
Isopogon formosuus	AND	Yellow to orange-red	Australia	23
Leucospermum conocarpodendron	AND	Yellow to orange	S. Africa	91
Leucospermum oleaefolium	WF	Yellow to orange-red	S. Africa	91
Petrophile biloba	AND	Yellow to orange-red	Australia	44
Rhamnaceae				
Cryptandra amara	WF	White to red	Australia	76, 98
Rhizophoraceae				
Ceriops tagal v. *australis*	WF	White to orange	N. Australia	8
Rosaceae				
Chaenomeles sp.	AND	White to red	E. Asia	95
Crataegus pubescens	N/H	Green to dark red	Mexico	95
Physocarpus capitatus	GYN	Green to red	W. U.S.	95
Physocarpus opulifolius	GYN	Green to red	E. U.S.	95
Prunus cerasifera	N/H	White to deep pink	SW. Asia	68
Prunus sargentii	AND	White to red	N. Japan, Korea	95
Raphiolepis indica	AND	White to red	S. China	95
Raphiolepis umbellata	AND	White to red	Japan	95
Rosa chinensis v. *mutabilis*	WF	Yellow to deep pink	China	95
Rubiaceae				
Canthium lucidum	WF	White to yellow	N. Australia	8
Glionnetia sericea	WF	White to dark red	Seychelles	27
Hamelia patens	WF	Orange to red	Costa Rica	43
Ixora javanica	WF	Yellow-orange to red	SE. Asia	67
Rutaceae				
Boronia elatior	WF	Magenta to deep red	Old World	95
Boronia polygalifolia	WF	Pale yellow to pinkish	Australia	98
Phebalium whitei	CF	Yellow-green to red	Australia	76
Phebalium woombye	CF	Yellow to red	Australia	98
Santalaceae				
Choretrum pauciflorum	CF	Green to red	Australia	76
Quinchamalium chilense	WF	Yellow to orange	Andes	
Santalum freycinetianum	WF	Greenish-yellow to red	Hawaii	86
Santalum haleakalae	WF	White to red	Hawaii	86
Santalum spicatum	WF	White to red	Australia	23
Sapindaceae				
Diplopeltis stuartii	CF	Yellow to orange-red	Australia	23
Koelreuteria paniculata	PA	Yellow to red	Asia	95
Ungnadia speciosa	PA	Pale yellow to pink-red	Mexico	95
Xanthoceras sorbifolium	CF	Yellow to red	China	66
Saxifragaceae				
Bergenia crassifolia	AND, GYN	Green to red	Siberia	95
Saxifraga integrifolia	GYN	Green to red	W. U.S.	75
Tellima grandiflora	WF	White to red	W. U.S.	95
Scrophulariaceae				
Castilleja sessiliflora	SP	White to pink	Great Plains, U.S.	88
Erinus alpinus	CF	White to lavender	Spain	95

APPENDIX 1. Continued.

Taxon	Part that changes	Color change	Native habitat	Reference
Euphrasia glacialis	CF	Yellow to orange-red	Australia	13
Hebe townsonii	WF	Purple to white	New Zealand	18
Melampyrum arvense	CT	Yellow/pink to white/pink	Europe	68
Melampyrum cristatum	CT	White/yellow to purple/orange	Europe	68
Melampyrum laxum	CT	White to pink	Japan	62
Melampyrum nemorosum	CT	Yellow to orange	Europe	68
Orthocarpus erianthus v. *roseus*	SP	White to pink	W. N. America	9
Orthocarpus faucibarbatus	SP	White to pink	W. N. America	9
Orthocarpus lithospermoides	SP	White to pink	W. N. America	
Orthocarpus purpurascens	SP	White to pink	W. N. America	95
Zaluzianskia affinis	E/C	Yellow to red	S. Africa	34
Zaluzianskia crocea	E/C	Yellow to red	S. Africa	34
Zaluzianskia villosa	E/C	Yellow to red	S. Africa	34
Solanaceae				
Brugmansia versicolor	WF	Cream to pink	S. America	95
Brunfelsia calycina	WF	Purple to white	Tropical America	95
Cyphomandra diploconos	WF	Violet to yellow-ochre	Tropical America	79
Cyphomandra endopogon	WF	Lavender to greenish-white	Tropical America	32
Cyphomandra sciadostylis	WF	Violet to yellow-ochre	Tropical America	79
Dunalia lorentzii	NG/BPS	Lavender to white	Argentina	95
Hyoscyamus niger	NG/BPS	Dark purple to light green	Mediterranean	95
Solandra sp.	WF	White to yellow	Tropical America	91
Streptosolen jamesonii	WF	Yellow to deep orange	Peru	95
Sterculiaceae				
Brachychiton discolor	WF	White to purple	Australia	51
Lasiopetalum behrii	WF	Pale yellow to pink	Australia	15
Stylidiaceae				
Stylidium pilosum	NG/BPS	Pink to white	Australia	23
Theaceae				
Stewartia pseudo-camellia	NG/BPS	White to red	Japan	56
Thymelaeaceae				
Dais cotinifolia	CF	Pink to white	S. Africa	51
Edgworthia papyrifera	WF	Yellow to white	China	52
Pimelea ferruginea	WF	Pink to white	W. Australia	95
Valerianaceae				
Patrinia villosa	WF	Yellow to white	Old World	95
Plectritis macrocera	CF	White to dark pink	California	95
Verbenaceae				
Avicennia marina	WF	Yellow to orange	N. Australia	8
Lantana camara	WF	Yellow to red	West Indies	55, 58, 95
Lantana hirta	E/C	Yellow to white	Mexico	95
Lantana montevidense	E/C	White and yellow to purple	S. America	95
Lantana sellowiana	E/C	Blue to white		12
Lantana trifolia	E/C	Yellow to lavender	Tropical America	81
Lantana viburnoides	WF	Yellow to deep pink	Saudi Arabia	14
Lippia javanica	CF	Yellow to white	East Africa	6
Lippia ukambensis	CF	Yellow to white	East Africa	6
Phyla incisa	NG/BPS	Yellow to purple		17, 24, 95
Phyla nodiflora	NG/BPS	Yellow to purple	Tropics, subtropics	95
Verbena gooddingii	E/C	White to purple	W. U.S.	64
Verbena lilacina	E/C	White to lavender	Mexico	95
Verbena tenuisecta	E/C	White to purple	U.S.	95
Vitex agnus-castus	GYN	White to lavender	S. Europe	95
Violaceae				
Viola tricolor	SP	White to purple	Europe	95
Vochysiaceae				
Qualea multiflora	WF	White to pale yellow	Brazil	54