

RELATIONSHIPS AND FLORAL BIOLOGY OF *BIDENS COSMOIDES* (ASTERACEAE)¹

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ABSTRACT. *Bidens cosmoides*, in the monotypic section *Degeneria*, is a morphologically unique species endemic to Kaua'i. Contrary to previous reports it will hybridize successfully with other Hawaiian species of *Bidens*, all in section *Campylotheca*. All Hawaiian species of *Bidens* are interfertile, suggesting that they are the products of adaptive radiation from a single ancestral introduction rather than two separate introductions and lineages as previously postulated. The elongated styles of *B. cosmoides*, exerted 20-30 mm beyond the corollas, that present pollen on the style tips, are unique in the genus. Flowers produce more than 30 times as much nectar by volume than do other Hawaiian species of *Bidens*, but the sugar concentration of the nectar is only half that of other species (30% vs. 60%). These unique floral features appear to represent adaptations to pollination by birds, although pollination of *B. cosmoides* has not yet been observed in nature.

Bidens, with over 200 species, is the largest genus in subtribe Coreopsideinae, tribe Heliantheae of the Asteraceae (Stuessy, 1977). Sherff (1937) recognized 14 sections in *Bidens*, two of which occur in the Hawaiian Islands. *Bidens cosmoides* (A. Gray) Sherff, endemic to the mountains of Kaua'i, is the sole member of section *Degeneria*. Sherff (1937, 1941a, 1941b, 1944a, 1944b, 1949, 1951a, 1951b, 1953, 1960, 1962, 1964) recognized a total of 42 other species and about 20 varieties of *Bidens* native to the Hawaiian Islands, all members of section *Campylotheca*. Section *Campylotheca* also includes some additional species native to southeastern

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Polynesia. Gillett (1975) suggested lumping all Hawaiian taxa of section *Campylotheca* into a single species with perhaps seven subspecies, although he made no formal nomenclatural changes in the taxonomy of the genus. However, it should be noted that Gillett did not investigate several of the more distinctive taxa of Hawaiian *Bidens*. Most of Sherff's taxa are unworthy of taxonomic recognition, but we think Gillett's suggested treatment is a bit extreme. We currently recognize 19 species and 8 additional subspecies of *Bidens* native to the Hawaiian Islands (Table 1). All except *B. cosmoides* are members of section *Campylotheca*.

Morphologically, *Bidens cosmoides* is the most distinctive species in the genus. Sherff (1937) called it "a strange and anomalous species," primarily because of its large flower heads and its enormously exerted styles which commonly extend 20-25 mm beyond the exerted anthers (Fig. 1). Mature achenes of this species were unknown to Sherff and first described by Gillett and Lim (1970); they too are anomalous in the genus. They are irregularly curved or twisted (not that unusual in Hawaiian *Bidens*), but in addition each one is permanently enveloped by its subtending chaffy receptacular bract. The bract grows with the ripening achene and is also stretched by it. This is apparently a unique condition in subtribe Coreopsidinae. Vegetatively the species is distinctive but not particularly unusual for Hawaiian *Bidens*. It has the same chromosome number as the species of section *Campylotheca* that have been counted (Gillett and Lim, 1970; Gillett, 1975).

The numerous species of *Bidens* in the Hawaiian Islands are an excellent example of evolutionary radiation on an isolated oceanic archipelago (Gillett and Lim, 1970; Gillett, 1975). They exhibit far more diversity in morphology and ecology than do all the species in North America, from which their ancestor(s) probably came (Carlquist 1966; Gillett 1975), as well as more diversity than the *Bidens* of any other continent. Even more remarkable, genetic barriers among the species of section *Campylotheca* in the Hawaiian Islands are nonexistent or very weak (Gillett and Lim, 1970; Mensch and Gillett, 1972; Gillett, 1972a, 1972b, 1973, 1975). In all, Gillett obtained fertile hybrids among 11 of the 18 species and 2 of the 8 subspecies we recognize in section *Campylotheca* in the Hawaiian Islands. We have extended this in our program of experimental hybridizations to include all of the taxa we recognize except *B. campylotheca* ssp. *waihoiensis*, *B. hillebrandiana* ssp. *hillebrandiana*, and *B. micrantha* ssp. *kalealaha* (Ganders and Nagata, in press). Our attempts to cross Hawaiian species with American species have failed thus far. This is extremely strong evidence that the diverse Hawaiian species of section *Campylotheca* evolved from a single ancestral immigrant species (Gillett and Lim, 1970; Gillett, 1975).

In contrast, Gillett and Lim (1970) attempted crosses between *Bidens cosmoides* and 10 populations of 9 taxa (as we classify them) and all failed to produce achenes. The taxa of section *Campylotheca* used in their crosses were (with the names they used in parentheses): *B. hillebrandiana* ssp. *polycephala* (*B. hillebrandiana*), *B. mauiensis*, *B. menziesii* ssp. *filiformis*, *B. micrantha* ssp. *ctenophylla* (*B. ctenophylla*), *B. molokaiensis*, *B. sandvicensis*

ssp. *sandvicensis* (*B. coartata*), *B. sandvicensis* ssp. *confusa* (Gillett 1888, from Kaua'i, a putative hybrid according to Gillett), *B. torta* (*B. fulvescens*), and *B. wiebkei*. The morphological distinctness of *B. cosmoides* appeared to be correlated with crossability barriers, suggesting that the isolation between the two Hawaiian sections of *Bidens* had a long history. Gillett (1975) concluded that there had been two separate introductions of *Bidens* into the Pacific, the earlier one bringing the line from which *B. cosmoides* evolved. This lineage specialized and did not undergo extensive adaptive radiation. A second introduction underwent extreme adaptive radiation giving rise to the diversity of species in section *Campylotheca*, which from Hawai'i dispersed to southeastern Polynesia.

If this is true, two interesting points are raised. One is why did one lineage undergo adaptive radiation and the other (and according to Gillett, earlier one) not? Second, should not *Bidens* section *Degerneria* be recognized as a separate genus? Morphologically it is more different from the rest of *Bidens* than the universally recognized genus *Coreopsis* or the often segregated *Megalodonta*. *Megalodonta* is segregated on the basis of subterete achenes and dimorphic leaves associated with its aquatic habit. There are, in fact, no constant characters separating *Bidens* and *Coreopsis*. They are separated on the basis of ill-defined differences in habit, and achenes of *Coreopsis* are usually winged, and awns, if present, have antrorse barbs or none, while achenes of *Bidens* are usually not winged, and awns, if present, may have retrorse, antrorse, or no barbs (Sherff, 1937).

All of Gillett's experimental hybridizations between *Bidens* were performed on plants growing in greenhouses. However, *B. cosmoides* grew poorly for him and never flowered in cultivation. (It has grown well for us in greenhouses in British Columbia, although plants from cuttings have taken more than two years to flower.) Therefore, all of Gillett's crosses using *B. cosmoides* involved flowers collected in nature on Kaua'i, flown back to Honolulu, and used as pollen parents in crosses with other plants in the greenhouse (Gillett and Lim, 1970). Pollen of Asteraceae is trinucleate and this is correlated with a relatively short period of viability (Brewbaker, 1967). As far as we are aware, no one has studied the effect of reduced air pressure in commercial aircraft on pollen viability. Therefore, we were interested in reattempting hybridizations between *B. cosmoides* and species of section *Campylotheca*. Our results are completely opposite to those reported by Gillett and Lim (1970), and together with observations on the floral biology of *B. cosmoides* suggest a completely different interpretation of the evolutionary significance of *B. cosmoides*.

MATERIALS AND METHODS

All crosses between *Bidens cosmoides* and other species were made in February and March 1982 with plants flowering in a greenhouse at the University of British Columbia. Although the greenhouse was not insectproof, during these months pollinators are not a problem so plants did not need to be caged or bagged. Whenever possible, male-sterile plants were

used as pistillate parents. Gillett (1975) reported four species to be gynodioecious and we have found five more taxa to have at least some gynodioecious populations. All species are strongly protandrous so pollen was blown or washed off flower heads and pollinations made two or three days later when using hermaphrodites as pistillate parents. Subsequent observation of progenies from crosses revealed that there had been little accidental self pollination.

Nectar production and sugar concentration of nectar are technically difficult to measure in absolute terms, since evaporation can concentrate nectar and sugar in nectar can be reabsorbed by the flower (Shuel, 1961). In order to get comparable measurements, nectar volume and sugar concentration were measured in unpollinated flowers with receptive stigmas. The flowers had been open several days in the greenhouse under uniformly cloudy conditions, so presumably sugar concentration and nectar volume had reached equilibrium. Nectar was extracted with 1 μ l or 5 μ l pipettes, diluted as necessary with distilled water and sugar concentration measured as sucrose equivalents with a temperature compensated hand refractometer.

RESULTS OF CROSSING EXPERIMENTS

All attempted experimental hybridizations between *Bidens cosmoides* and 14 species and seven subspecies of *Bidens* section *Campylotheca* were successful (Table 1). In addition, hybridizations were successful between *B. cosmoides* and the F1 hybrid of *B. valida* and *B. molokaiensis*. Experimental crosses were successful with *B. cosmoides* as both pollen and pistillate parent, even though the styles of *B. cosmoides* are more than five times longer than those of the species of section *Campylotheca*. The F1 hybrids plants are viable and vigorous although none have yet flowered. *Bidens cosmoides* is not genetically isolated prezygotically from the other species of *Bidens* in Hawai'i, and because its chromosome number is the same as other species, we predict the hybrids will be fertile.

FLORAL BIOLOGY OF *BIDENS COSMOIDES*

Bidens cosmoides is protandrous and self-compatible, as are all other Hawaiian species of *Bidens*. Pollen is presented 3-4 days before the style tips diverge and expose the stigmatic surface. If pollen is not removed, the style branches ultimately recurve in a complete circle and self pollination can take place. Undisturbed flower heads set a full complement of seed. Many other Hawaiian species also exhibit full seed set by automatic self-pollination, but in some species, such as *B. mauiensis* and *B. molokaiensis*, the style tips do not recurve as completely and thus unassisted self-pollination only infrequently occurs.

Bidens cosmoides is distinctive in the morphological and mechanical aspects of its floral biology. The floral heads are campanulate in shape and pendant. The ray flowers are yellow, as in all Hawaiian *Bidens*, but corollas of disk flowers have a red orange tube and deep yellow lobes. All other Hawaiian *Bidens* have yellow disk corollas, although corolla lobes in *B. macrocarpa* are often partially black. The heads terminate lateral branches

on rather thick peduncles. Pollen presentation in *B. cosmoides* is unique. In other Hawaiian species the growing style acts as a piston to push the pollen mass above the anther tube, where the pollen rests until it is removed or pushed off as the style continues growing. Some pollen adheres to the tips of the papillose style branches as they diverge to expose the stigmatic region. The pollen is powdery and the individual grains separate readily. This is the typical mechanism of pollen presentation in the Asteraceae. In *B. cosmoides* the style branches have large papillae and the pollen is very sticky. As the styles elongate the pollen mass adheres to the closed style branches and is carried 20 mm or more above the anthers. Virtually no pollen is left on the anthers, but all of the elongated styles have pollen masses at their tips. Consequently, the pollen is presented to pollinators more than 20 mm above the throats of the disk flowers, which ultimately are nearly full of nectar. Functionally, the flower heads fits the "brush flower" type of Faegri and van der Pijl (1971). Three or four days later the style branches diverge and the stigmatic surfaces are exposed. Anthesis of all disk flowers in a single head usually occurs within one or two days, so that the pollen presentation phase and receptive stigma phase of all the disk flowers are nearly synchronous. Stigmas remain receptive for several days, and if pollen is not removed the style branches recurve and the adhering pollen brings about self-fertilization.

Individual disk flowers contain 12-15 μ l of nectar with an average sugar concentration of 30% (standard deviation 4.5%), measured as sucrose. Disk flowers of species of section *Campylotheca* contain 0.3-0.5 μ l of nectar. Sugar concentration measured for *Bidens amplexens*, *B. cervicata*, *B. populifolia*, *B. sandvicensis*, and *B. torta* averaged 62% (standard deviation 6.4%). Flowers of *B. cosmoides* secrete about 35 times as much nectar as those of other species, but the sugar in the nectar is only about half as concentrated.

DISCUSSION

All attempted hybridizations between *Bidens cosmoides* and other Hawaiian species of *Bidens* succeeded in producing normal seeds, and the hybrids grown so far are vigorous. Most of the possible interspecific hybridizations were made. This, combined with the demonstrated absence of interspecific genetic isolating mechanisms among the Hawaiian species assigned to section *Campylotheca* (Gillett and Lim, 1970; Gillett, 1975) is convincing evidence that all Hawaiian species of *Bidens* evolved from a single ancestral species. Although there has been remarkable adaptive radiation in morphology and ecological tolerance, prezygotic genetic isolating mechanisms have not evolved within this group. We conclude that there was only one lineage successfully established in the Hawaiian Islands, rather than two as suggested by Gillett (1975), and *B. cosmoides* just represents the most extreme divergence in floral morphology in the adaptive radiation of this lineage.

The first question raised about Gillett's hypothesis, why did one lineage undergo adaptive radiation and the other not, disappears, since the evi-

dence indicates that Hawaiian *Bidens* represent adaptive radiation of only a single lineage. The absence of crossability barriers between *B. cosmoides* and the other Hawaiian *Bidens* indicates a close genetic relationship and precludes recognizing *B. cosmoides* as a separate monotypic genus in the Asteraceae. Whether it still deserves separate sectional status depends on whether the hybrids prove to be fertile as we predict, whether one adopts a phenetic, evolutionary, or cladistic classification of the genus, and whether *B. cosmoides* is the end point of an early phylogenetic dichotomy separating it from the rest of Hawaiian *Bidens*. Resolution of this question awaits further evidence.

Our conclusion that all Hawaiian *Bidens*, including *B. cosmoides*, resulted from adaptive radiation in one lineage means that the extent of adaptive radiation is even greater than previously thought. Our observations indicate that the unique floral characters of *B. cosmoides* represent adaptations for pollination by birds, perhaps some species of Hawaiian honeycreepers.

Pollination of *Bidens cosmoides* in nature has not yet been observed. Our hypothesis that it is adapted to bird pollination is based on several circumstantial although convincing arguments. The first is the unique secondary pollen presentation mechanism whereby pollen is presented on the style tips more than 20 mm above the anthers and mouth of the corolla.

Native Hawaiian insects which might feed on nectar of *Bidens cosmoides* would be unlikely to regularly come in contact with either pollen or stigmas but would crawl between the styles on the disk corollas. A possible exception might be hovering hawk moths, but the yellow ray flowers and orange disk flowers are nearly scentless, and thus exhibit few of the characteristics of the moth pollination syndrome (Faegri and van der Pijl, 1971). The pollen and stigma are, however, presented in a position where they would be likely to contact the head of a bird feeding on the flowers. The "brush flower" form of the inflorescences is similar functionally to other bird pollinated flowers or inflorescences which have long exerted stamens and styles (Faegri and van der Pijl, 1971). The brush flower shape can also be adapted to pollen gathering bees, but in such cases the flowers produce little or no nectar, so it is unlikely that *B. cosmoides* is adapted to pollination by pollen gathering bees. The enormous nectar production of the flowers of *B. cosmoides*, over 30 times as much as other Hawaiian *Bidens* species, supports the hypothesis that it is adapted to bird pollination. Large volumes of nectar are typical of bird pollinated flowers and are necessary to attract such large pollinators. Finally, the relatively low sugar concentration of the nectar also suggests bird pollination. Hummingbird pollinated flowers in California and Costa Rica have nectars with significantly lower sugar concentrations than bee pollinated flowers (Baker, 1975). Although sugar concentrations in nectar of flowers pollinated by other families of birds have not been thoroughly studied, the concentrations in some, such as *Aloe graminicola* Reynolds, pollinated by sunbirds in Africa, is in the same range characteristic of hummingbird flowers (Wolf, 1975).

We conclude that *Bidens cosmoides* evolved from the same common ancestor as the other Hawaiian species of *Bidens* and therefore represents

the most extreme product of adaptive radiation in this monophyletic lineage. Circumstantial evidence suggests the unusual floral features of *B. cosmoides* are the result of adaptation to bird pollination.

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Table 1. Native Hawaiian taxa of *Bidens*. Taxa preceded by an asterisk have been successfully crossed with *B. cosmoides*.

<i>Taxon</i>	<i>Distribution</i>
* <i>B. amplexans</i> Sherff	O'ahu
* <i>B. asymmetrica</i> (H. Lev.) Sherff	O'ahu
<i>B. campylotheca</i> Schz. Bip. ssp. <i>campylotheca</i>	Hawai'i, Lana'i, O'ahu
<i>B. campylotheca</i> ssp. <i>pentamera</i> (Sherff)	
Ganders & Nagata	Maui
<i>B. campylotheca</i> ssp. <i>waihoiensis</i> St. John	Maui
* <i>B. cervicata</i> Sherff	Kaua'i, O'ahu, Ni'ihau
<i>B. conjuncta</i> Sherff	Maui
<i>B. cosmoides</i> (A. Gray) Sherff	Kaua'i
* <i>B. forbesii</i> Sherff ssp. <i>forbesii</i>	Kaua'i
* <i>B. forbesii</i> ssp. <i>kahiliensis</i> Ganders & Nagata	Kaua'i
* <i>B. hawaiiensis</i> A. Gray	Hawai'i
<i>B. hillebrandiana</i> (Drake) Deg. ex Sherff ssp. <i>hillebrandiana</i>	Hawai'i
* <i>B. hillebrandiana</i> ssp. <i>polycephala</i> Nagata & Ganders	Maui, Moloka'i
* <i>B. macrocarpa</i> (A. Gray) Sherff	O'ahu
* <i>B. mauiensis</i> (A. Gray) Sherff	Lana'i, Maui
* <i>B. menziesii</i> (A. Gray) Sherff ssp. <i>menziesii</i>	Maui, Moloka'i
* <i>B. menziesii</i> ssp. <i>filiformis</i> (Sherff) Ganders & Nagata	Hawai'i
* <i>B. micrantha</i> Gaud. ssp. <i>micrantha</i> <i>B. micrantha</i> ssp. <i>ctenophylla</i> (Sherff) Nagata & Ganders	Maui Hawai'i
<i>B. micrantha</i> ssp. <i>kalealaha</i> Nagata & Ganders	Lana'i, Maui
* <i>B. molokaiensis</i> (Hillebr.) Sherff	Moloka'i, O'ahu
* <i>B. populifolia</i> Sherff	O'ahu
* <i>B. sandvicensis</i> Less. ssp. <i>sandvicensis</i> <i>B. sandvicensis</i> ssp. <i>confusa</i> Nagata & Ganders	Kaua'i, O'ahu Kaua'i
* <i>B. torta</i> Sherff	O'ahu
<i>B. valida</i> Sherff	Kaua'i
<i>B. wiebkei</i> Sherff	Moloka'i

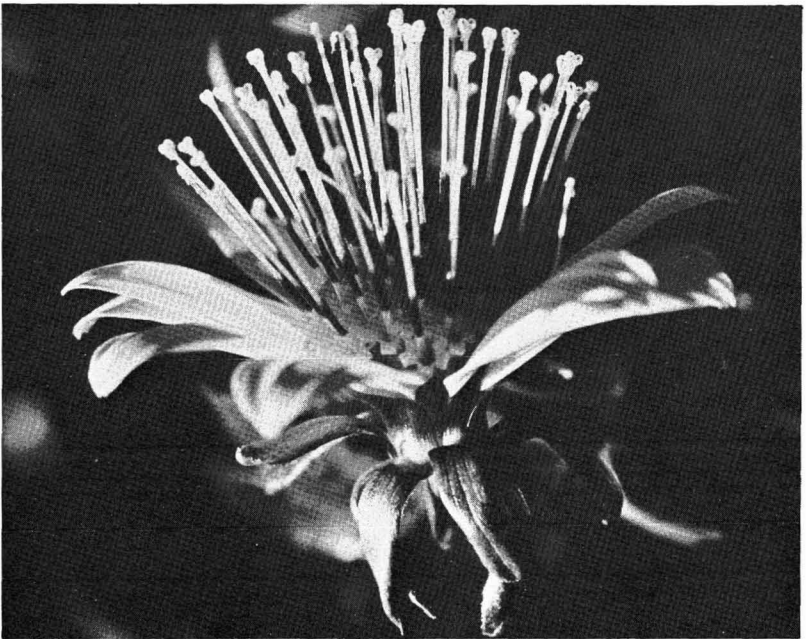
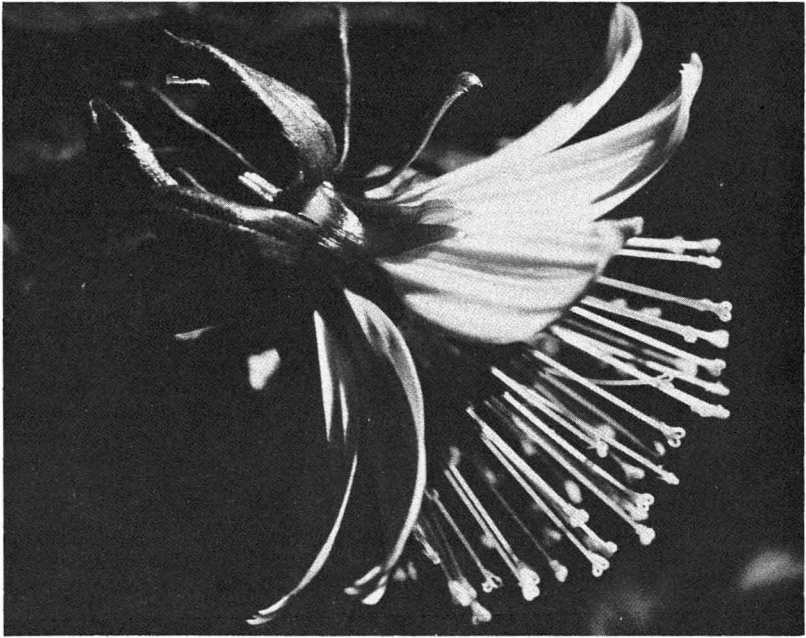


FIGURE 1. Flowering head of *Bidens cosmoides*, showing long exserted styles of the disk flowers.

