BLOOMING "BEHAVIOR" IN FIVE SPECIES OF *BOERHAVIA* (NYCTAGINACEAE)

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ABSTRACT

Observations are reported on anthesis, stamen and style movement, and insect visitation in five taxa of *Boerhavia*, one a pantropical perennial (*B. coccinea* Mill.), and five that are North American annuals (*B. intermedia* M.E. Jones, *B. spicata* Choisy, *B. torreyana* S.Wats., and *B. wrightii* A.Gray). Observations were made in natural situations in Las Cruces, New Mexico. Individual flowers are open for only a portion of one day. Insect visitors were Hymenoptera, Diptera, and Coleoptera. All species received insect visitation; the larger-flowered species had more visitors. Autogamy is believed to be the usual method of reproduction, either through insect pollination or self-pollination of the flower as stamens contact the stigma as the flowers close. There is no evidence of wind pollination even in crowded populations. Chromosome numbers are fairly high, especially for annuals. New chromosome number reports are made for *B. coccinea* (*n* = 26), *B. diffusa* L. (*n* = 27), *B. intermedia* (*n* = 26, ca. 27), *B. linearifolia* (*n* = ca. 26), *B. mathisiana* F.B. Jones (*n* = ca. 26), *B. spicata* (*n* = 26), and *B. wrightii* (*n* = 27). It is suggested that high chromosome number, prevalent autogamy, but occasional outcrossing or hybridization, produce a population structure of locally uniform populations that differ slightly to greatly from other populations, a pattern that can lead to difficulty in classification.

RESUMEN

Se informa de las observaciones del movimiento de los estambres y el estilo durante la antesis, así como de la visita de insectos en cinco taxa de *Boerhavia*, uno pantropical perenne (*B. coccinea* Mill.), y cinco anuales norteamericanos (*B. intermedia* M.E. Jones, *B. spicata* Choisy, *B. torreyana* S. Wats., and *B. wrightii* A. Gray). Las observaciones se hicieron en situaciones naturales en Las Cruces, New Mexico. Las flores individuales se abren sólo una parte de un día. Los insectos visitantes fueron Hymenoptera, Diptera, y Coleoptera. Todas las especies recibieron visitas de insectos; las especies de flores grandes tuvieron más visitantes. Se cree que la autogamia es el método normal de reproducción, tanto por entomogamia como por autopolinización de la flor mediante contacto de los estambres con el estigma cuando la flor se cierra. No hay evidencia de anemogamia ni siquiera en poblaciones densas. Los números cromosómicos son bastante altos, especialmente en las anuales. Se citan nuevos números cromosomáticos para *B. coccinea* (*n* = 26), *B. diffusa* L. (*n* = 27), *B. intermedia* (*n* = 26, ca. 27), *B. linearifolia* (*n* = ca. 26), *B. mathisiana* F.B. Jones (*n* = ca. 26), *B. spicata* (*n* = 26), y *B. wrightii* (*n* = 27). Se sugiere que el alto número cromosomático, la autogamia predominante, con reproducción cruzada ocasional o hibridación, producen una estruchura poblacional de poblaciones localmente uniformes que difieren de ligeramente a mucho de otras poblaciones, un patrón que puede llevar a dificultades en la clasificación.

INTRODUCTION

Nyctaginaceae comprise a small family of approximately 30 genera and 390 species (Mabberly 1997) consisting mostly of American genera, several of which are noted for

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their taxonomic problems. Among those genera is *Boerhavia* (ca. 20 species) which, in addition to being highly developed in North America, contains some rather difficult groups, for example, a pan-tropical complex of perennial forms (*B. diffusa* L., *B. coccinea* Mill., etc.) and at least two North American groups of annuals (*B. spicata* Choisy complex; *B. erecta* L. complex). As discussed by Ornduff (1969), insights into reproductive aspects may help to understand variation seen within and between populations and this, then, may be useful in taxonomic interpretations.

In the case of *Boerhavia*, populations in the field often appear homogenous within, but differ to a greater or lesser extent with neighboring populations. This population structure is conspicuous in the perennial *B. coccinea* where there are numerous races of maroon-flowered populations that differ in general robustness of plants, in nature and distribution of pubescence, or in number of fruits in the terminal clusters of the inflorescence. In addition, a few populations in this species vary markedly with respect to flower color and other characteristics. For example, an isolated consistently white-flowered population with bright green, lightly pubescent foliage occurs on a rock outcrop on the plains of southern New Mexico. Elsewhere in the region a yellow-flowered race with dull green more heavily pubescent foliage has been discovered adjacent to maroon-flowered less densely pubescent plants (white: New Mexico, Doña Ana Co., ca. 3 mi S of Cambray on Providence Cone, 25 Aug 1985, *Spellenberg and Zucker 8244* [NMC, NY]; yellow: New Mexico, Doña Ana Co., Doña Ana Mts., S slopes Summerford Mountain, 14 Sep 1969, *Spellenberg 2141* [NMC]). Within the annual species there are also a number of examples. *Boerhavia alata* S. Wats. (in the *B. erecta* L. complex) grows on the rocky coast in and near Guaymas in southern Sonora, Mexico. Without conspicuous habitat differences it contacts and intergrades very locally with *B. intermedia* M. E. Jones, common on the hillsides in the immediate vicinity (Mexico, Sonora, Guaymas, 26 Aug 1973, *Spellenberg and Willson 3627, 3629* [*B. alata*], *3630, 3631* [intermediates], *3628, 3632* [*B. intermedia*] [all at NMC, variously distributed to CIIDIR, MEXU, IBUG, RSA, NY, UC, etc.]) (herbaria acronyms from Holmgren et al. 1990).

Perhaps because of the curiosity of nocturnal flowering in a number of species of Nyctaginaceae and/or the presence of chasmogamic and cleistogamic flowers on different plants within populations of a species or, commonly, on the same plant, a number of authors have reported on floral reproductive features and insect visitation in several genera. Several papers report that Nyctaginaceae have flowers that attract insects but often self-pollinate by anthers contacting the stigma as the flower closes (*Boerhavia*, Chaturvedi 1989; *Mirabilis*, section *Mirabilis*, Hernández 1990) and/or through cleistogamy in plants that are also chasmogamous (*Acleisanthes*, *Ammocodon*, *Selinocarpus*, Spellenberg and Delson 1977; *Cyphomeris*, Mahrt and Spellenberg 1995; *Mirabilis*, section *Oxybaphus*, Cruden 1973). Self-incompatibility is known also in *Abronia* (Tillet 1967; Williamson & Bazeer 1997) and *Mirabilis*, section *Quamoclidion*, (Baker 1964; Pilz 1978).

Identification of specimens of *Boerhavia* is often equivocal; species are variable and often are differentiated by minute and subjective characteristics of the fruit. Differences in taxonomic treatments in floras during the past 50 years attests to the difficulty of satisfactorily circumscribing species in some groups of *Boerhavia*. Often in such groups of plants (in general and not just in *Boerhavia*) a combination of biological characteristics contribute to the source of the difficulties faced by the taxonomist. Here I make a comparison of pollination and floral action of five New World taxa, one perennial and four annuals, and relate these observations in a general sense to the variation seen in the genus.

METHODS

Taxa observed were *Boerhavia coccinea, B. intermedia, B. spicata*, a small-flowered form called *B. torreyana* (S. Wats.) Standl. (considered a synonym of *B. spicata*), and *B. wrightii* A. Gray. All were observed in Las Cruces, New Mexico, and are vouchered under my collection numbers in the New Mexico State University herbarium (NMC). Among these, *B. coccinea* (*7867*), the only perennial in this study, is a pan-tropical species similar to *B. diffusa*, the former often considered a synonym of the latter (compare, for example, Whitehouse [1996], both species recognized, and Wunderlin [1998] or Diggs et al. [1999], one species recognized). *Boerhavia spicata* Choisy (*7866*) is an annual which, in its inclusive sense, includes several synonyms referring to phases more or less different from one another (e.g., *B. torreyana - 7868*) but linked by various intermediate forms (Reed 1969). *Boerhavia intermedia* (*7869*), an annual of arid and semi-arid regions in southern North America, is sometimes considered as a variant of the widespread, weedy, *B. erecta* L. [*B. erecta* var. *intermedia* (M. E. Jones) Kearney & Peebles]. *Boerhavia wrightii* (*7870*) is part of a small complex of species from North and South America that are fairly distinct from one another.

Boerhavia plants respond to summer rains, flowering primarily in August and September in southern New Mexico. In 1984 summer rains in the region were "good," resulting in ample late season growth for both perennials and annuals. Observations on pollination mechanisms were made daily during an eight day period (31 Aug – 7 Sep). The positions of stamens and stigma during the period of anthesis were observed with a 10× hand lens. *Boerhavia coccinea* and *B. spicata* were studied in a small weedy area on the NMSU campus where the species were intermixed. The three other annuals were studied ca. 5 km E of the NMSU campus in Chihuahuan Desert vegetation dominated by *Larrea*, where they were also intermixed but plants were much more sparsely distributed.

Periods of observation.—Plants were observed daily, with observation of each taxon lasting for 10 minutes. The observation periods were rotated from one species to the next, with a few minutes allowed in between for relocation. The first period each morning began with a different species. Observations were made at each location (on or off campus) on alternate days.

Insect visitation.—Records were kept of insect visitors, the duration of visits, insofar as possible where the insect next visited, and general identity. Records were kept for visits to individual flower clusters (terminal spikes in *B. spicata*, *B. torreyana*, and *B. wrightii*, individual subumbellate clusters in *B. coccinea* and *B. intermedia*) and visits to entire plants under observation. The latter data were not corrected for number of visitors relative to the number of total terminal inflorescences. In addition to observations, insects were also collected either with a net or by aspiration, were killed, and later identified to taxon as precisely as possible. Number of insect visits per taxon were analyzed using JMP 3.0 (SAS Institute, Cary, North Carolina) to determine if insect visitation differed among species. An α level of 0.1 was considered significant.

Wind pollination.—To estimate the role of wind pollination, four glycerin-coated microscope slides were oriented horizontally on tops of stakes that were located within 10 cm of inflorescences of a single plant of each species. Slides, each having a surface area of 12.5 cm^2 were approximately aligned with cardinal directions. Slides were placed in populations one day during the entire period from immediately prior to perianth opening to closure.

Exclusion of pollinators.—Cross pollination was prevented by loosely wrapping an inflorescence in several layers of fine nylon stocking mesh immediately prior to anthesis. This effectively prevents passage of the large and spinulose *Boerhavia* pollen (pollen described in Nowicke 1970). The netting remained on the plant until seed maturation, typically 9–10 days. The netting prevented loss if fruits were shed prior to removal of the net. At the same time, other inflorescences were marked, exposed to open pollination, then bagged in a similar manner the following morning, after the flowers closed. Fruits were then collected from both treatments and opened to determine whether each contained a seed.

Pollen / ovule ratios.—Since *Boerhavia* species produce one ovule per fruit, pollen / ovule ratios were calculated simply by counting the pollen grains produced by a flower. Anthers from a single flower were crushed in cotton blue and lactophenol on a microscope slide and the pollen grains were counted using a compound microscope at 100× magnification. Ten flowers for each species were examined.

Hybridization.—As a generalization, breeding barriers may be weak within autogamous species beyond the barrier provided by the breeding system itself (e.g., Lewis 1963; Stebbins 1957), which might account for some of the variation patterns with the *B. spicata* or *B. erecta* complexes. Woodson and Kidd (1961) suggested that hybridization occurs within mixed populations of *B. diffusa* (perennial) and *B. erecta* (annual), the putative hybrids representing *B. coccinea* in the sense of Standley (1918). To attempt to gain some perspective on the potential for hybridization, an interspecific cross was made in early September, 1984. In the mixed population on the New Mexico State University campus, *B. coccinea* was used as the pollen-receiving plant, *B. spicata* was the pollen donor. Eleven flowers within a single umbellate cluster were emasculated very early in the onset of anther dehiscence with fine forceps under a dissecting microscope. Stigmas were thoroughly inspected with the dissecting microscope and the few pollen grains already on the stigmas were removed by "sweeping" them off with a moistened dissecting needle.

The stigmas were then saturated with many grains of the donor pollen by bringing an inflorescence of *B. spicata* to *B. coccinea* and brushing the dehisced anthers against the recipient stigmas. The flower cluster was bagged in double layers of nylon mesh and mature fruits were collected in 10 days.

RESULTS AND DISCUSSION

Floral "behavior."—In each of the species of *Boerhavia* an individual flower is open for only a portion of a day (Fig. 1). Anthesis begins near dawn, usually for all or most of the flowers in a single flower cluster. In *B. spicata* and *B. coccinea* anthesis began 1-2 hours before it began in the other three (the perhaps warmer and more mesic campus environment may have influenced timing and duration of anthesis). In all, anthesis begins with the opening of the corolla-like perianth, stamens and styles uncoil and, in the larger-flowered species, the final stigma position is slightly beyond the anthers. In the smaller-flowered species stigma and anthers are not as well separated initially (Fig. 1). As the morning progresses, the filaments and style curl and the anthers haphazardly contact the stigma. Self-pollination may occur at this time. Perianth closure begins in late morning and progresses rapidly, so that by mid-afternoon the perianth is crumpled, the stamens and style usually contained within. Only rarely do flowers weakly open a second day. These observations fully support those of Chaturvedi (1989), who reported that the widespread perennial, *B. diffusa*, is autogamous (as known from plants studied in the botanic garden, Allahabad University, India).

Insect visitation.—Insect visitors varied in kind, frequency and duration (Table 1), with various bees and flies frequent visitors. This is concordant with Bittrich and Kühn's (1993) review that *Boerhavia* flowers fit the profile of bee and fly pollination. In a previous observation, however, ants covered with pollen grains were noted entering flowers of *B. coccinea*. On such occasions, ants may also serve as pollen vectors (observation and comment on specimen, Mexico, Colima, 10 km SW of Tecoman, El Real, *Spellenberg 2955*, NMC). The total number of insect visits varied considerably for the five taxa of *Boerhavia* studied (Table 2). Small sample size and considerable variation must be considered when viewing data in these tables. Raw data of total insect visit per species per day, summarized in Table 2, is not normally distributed (Shapiro-Wilk W Test, prob $< W < 0.0001$). The Wilcoxon / Kruskal-Wallis Ranked Sums Test indicated significant differences in the data ($\chi^2 = 9.196$, $df = 4$, $p = 0.0564$). The Tukey-Kramer comparison of all pairs indicated that *Boerhavia spicata* differed most from all other species, significantly from from *B. wrightii*, *B. intermedia* and *B. torreyana*.

Based on these preliminary observations, no conspicuously strong floral fidelity was observed by visiting insects. An insect initiating visits on one species might fly to several inflorescences on the same plant, then move to another plant of the same or different species, then return to the original plant, and so forth. Therefore, insect movement would allow both for autogamy, xenogamy, and hybridization.

Wind pollination.—Very little *Boerhavia* pollen was trapped on the glycerin-coated

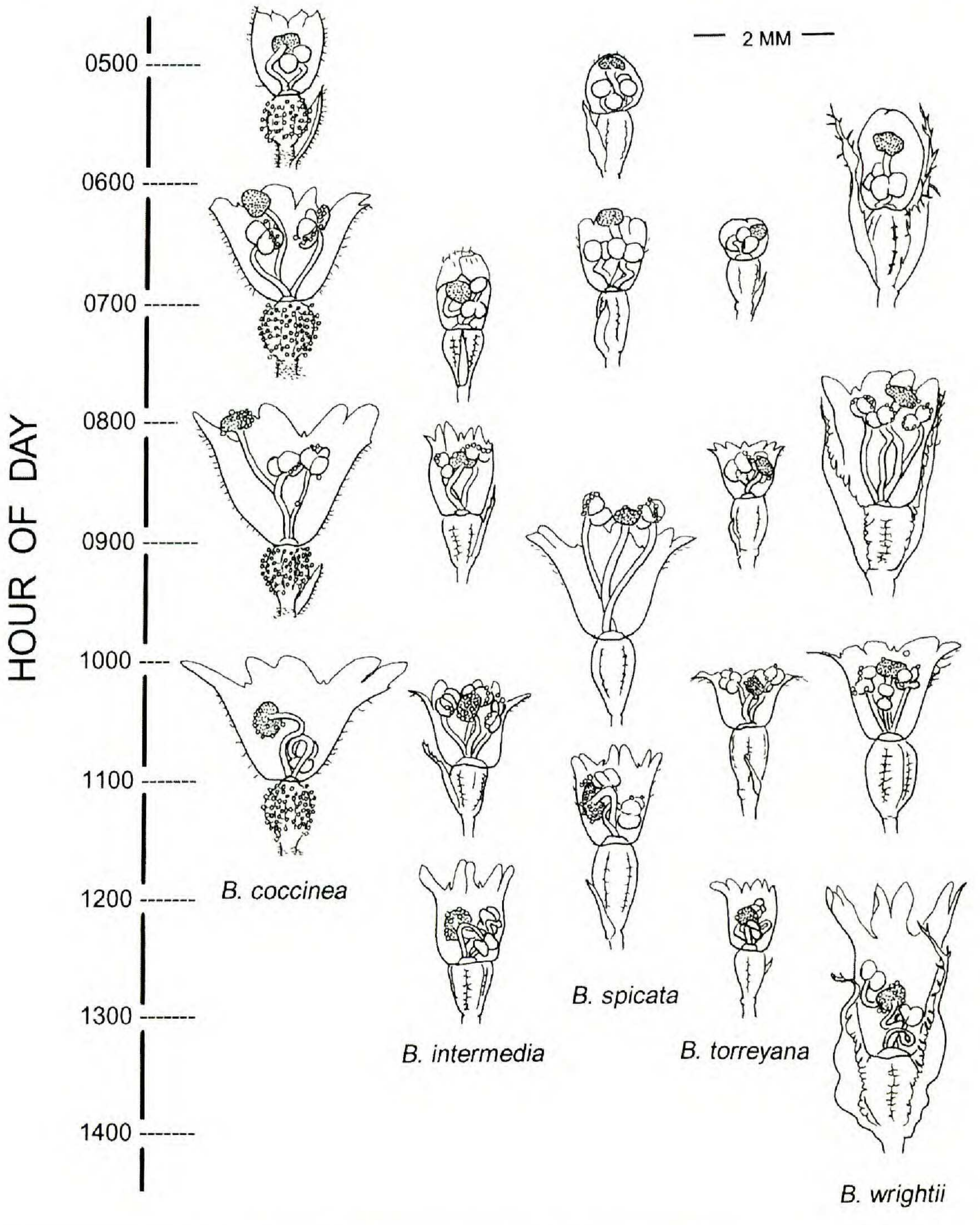

Fig. 1. "Picture graph" of stages of anthesis in five species of *Boerhavia*. Each species is diagramed in one column, anthesis beginning at the top. Hour of day is given on axis at left. All flowers are drawn to the same scale.

slides. Grass and *Salsola* pollen was frequent. For each species the following number of grains were trapped upon the slides and from this data the number of grains per centimeter squared per hour was calculated (number of grains: grains/hr/cm^2): *B. coccinea* (5: 0.025), *B. intermedia* (7: 0.035), *B. spicata* (17: 0.09), *B. torreyana* (0: 0), *B. wrightii* (8: 0.053). One slide from *B. wrightii* was removed from scoring because it had a large clump of

TABLE 1. Total number of insect visitors observed in multiple observation periods for individual plants of each of five species of *Boerhavia*. N is equal to the number of ten minute observation periods. The average number of seconds per visit in given in parentheses. Small Hymenoptera visitors consisted of Bethylidae, Andrenidae (*Perdita*), Halictidae (*Dialictus, Lasioglossum, Halictus*).

	B. coccinea *N = 18*	**B. intermedia** *N = 11*	**B. spicata** *N = 23*	**B. torreyana** *N = 15*	**B. wrightii** *N = 20*
	Total number of visits for all observation periods (average duration of visit in seconds)				
Insect visitor					
HYMENOPTERA					
LARGE					
Scoliidae (*Scolia*)	14(5)		4(7)		
MEDIUM					
Anthophoridae (Mellisodes)	8(5)	5(2)	6(4)	4(0.75)	6(4)
Chrysididae (*Holopyga rudis* Kimsey)	5(1)	8(0.5)		1(3)	5(0.25)
Ichneumonidae	1(3)		4(2)		
Sphecidae (*Ammophila*)			1(60)		
SMALL (see table caption)	25(10)		21(5)	2(1)	1(5)
DIPTERA					
MEDIUM					
Calliphoridae	2(7)		1(2)		
Syrphidae (*Pseudodoros clavatus* [Fab.])			2(6)		
Tachinidae		1(1)		1(0.25)	1(5)
SMALL					
Syrphidae (Toxomerus, Paragus)	6(9)	3(2)	56(7)	2(15)	5(17)
Muscidae	2(10)				
COLEOPTERA					
Nitulidae or Byturidae		8(10)			

pollen, presumably from the landing of a pollen-laden insect. From this data it seems unlikely that wind pollination is significant in *Boerhavia*. Pollen sexine is spinulose, and pollen size is rather large, consistent with that reported for these and other species by Nowicke (1970), and characteristic of insect pollinated plants.

Pollination.—Pollen load on stigmas (as determined by direct observation of pollen grains on stigmas with a 10× hand lens) progressively increased during anthesis, the

TABLE 2. Estimated number of insect visits to individual flower clusters per hour in five species of *Boerhavia*. Estimations are based upon 10 minute observation periods spread throughout the period of anthesis. Number of periods involved in estimations and number of flower clusters indicated in parentheses.

Hour of day	07–0800	08–0900	09–1000	10–1100	11–1200	12–1300	13–1400	Total
B. coccinea (15 ten minute periods; 125 flower clusters)								
	0.0	0.3	1.0	0.3	1.3	1.1	0.0	3.7
B. intermedia (14 ten minute periods; 111 flower clusters)								
	0.0	0.0	0.0	0.6	0.0	0.1	1.0	1.7
B. spicata (21 ten minute periods; 174 flower clusters)								
	0.0	0.0	2.3	0.6	4.0	2.2	0.0	9.1
B. torreyana (14 ten minute periods; 86 flower clusters)								
	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.6
B. wrightii (17 ten minute periods; 124 flower clusters)								
	0.0	0.0	0.0	1.4	1.6	0.7	1.4	5.1

majority of stigmas having more than 6 grains adhered by early afternoon (Table 3). For samples of *B. torreyana* (Table 3), the species with the smallest flowers, data indicate the same trend, though somewhat erratic. This species also received the fewest insect visits during anthesis (Table 2). Four of the five species, *B. spicata* the exception, still had a low to moderate percentage of stigmas without pollen at the time of perianth closure (Table 3).

Even though some stigmas were unpollinated at time of flower closure, percentage of filled fruits in each species was high for both open pollinated and pollinator-excluded inflorescences. Curling of stamens and the style places pollen on the stigma, with the assumption that autogamy results. In each case in the following pairs of data, the number of filled seeds precedes the number of unfilled seeds for plants protected from pollinators and for plants openly pollinated: in plants protected from pollinators – *B. coccinea* 20/0; *B. intermedia* 5/0; *B. spicata* 8/0; *B. torreyana* 19/0; *B. wrightii* 5/0; in plants openly pollinated—*B. coccinea* 21/3; *B. intermedia* destroyed; *B. spicata* 23/0; *B. torreyana* 24/1; *B. wrightii* 13/0.

Pollen/ovule ratios.—Pollen/ovule ratios for the five *Boerhavia* species examined ranged between 28:1 and 102:1. These figures lie between those proposed by Cruden (1977) for obligate and facultative autogamy (Table 4). For each taxon more than 95% of the pollen grains stained well in cotton blue and lactophenol, suggesting a high level of fertility.

Hybridization.—Eleven mature fruits were collected from the single head of *Boerhavia coccinea* that had received pollen from *B. spicata*. All appeared normal. One was opened and the seed was normally filled. The other 10 were planted in native soil in pots outdoors near the end of September, 1984. Even after 16 years, none have

TABLE 3. Percentage of stigmas with number of pollen grains in *Boerhavia* at different hours of the day. Number of stigmas is the total scored for the entire period. Different stigmas were counted during each period.

Species, hour of day, number of stigmas scored	Number of grains on stigma: 0	1-3	6-10	>10
	Percent of stigmas with above number of pollen grains			
B. coccinea (160 stigmas)				
0600–0900	86	10	4	–
0900–1100	69	16	13	2
1100–1300	17	12	32	39
1300–1500		Perianth closed		
B. intermedia (150 stigmas)				
0600–0900	100	—	—	—
0900–1100	83	10	4	3
1100–1300	56	19	13	12
1300–1500	14	12	12	62
B. spicata (210 stigmas)				
0600–0900	64	12	17	7
0900–1100	8	17	37	38
1100–1300	1	6	14	79
1300–1500	—	10	10	80
B. torreyana (150 stigmas)				
0600–0900	100	—	—	—
0900–1100	66	23	11	—
1100–1300	32	30	18	20
1300–1500	32	34	21	13
B. wrightii (150 stigmas)				
0600–0900	100	—	—	—
0900–1100	46	4	50	—
1100–1300	33	7	20	40
1300–1500	22	20	14	44

germinated. The cross may have been too distant (perennial crossed to very different annual). In general, seeds in *Boerhavia* are difficult to germinate in high frequency (personal observation) and dormancy may never have been broken in otherwise "normal" seeds.

GENERAL DISCUSSION

The flowers of the five different types of *Boerhavia* each opened for a few hours in the morning, and then closed permanently. Movement of stamens and style apparently assure self-pollination. These observations conform with those of Chaturvedi (1989) for *Boerhavia*. A similar mechanism was noted by Cruden (1973) and Hernández (1990) for some *Mirabilis*, Mahrt and Spellenberg (1995) for *Cyphomeris*, and Spellenberg and Delson (1977) for *Ammocodon*. Allowing for the exception in the specialized Asclepiadaceae

TABLE 4. Pollen/ovule ratios in five species of *Boerhavia* as related to predicted breeding systems as proposed by Cruden (1977, Table 1).

Breeding system (Cruden) or species of *Boerhavia*	**Mean ± standard deviation, pollen/ovule ratio**	
Cleistogamy	28	±3
B. torreyana	51	±16
B. wrightii	77	±18
B. intermedia	80	±19
B. spicata	86	±20
B. coccinea	102	±39
Facultative autogamy	162	±22
Facultative xenogamy	797	±87
Xenogamy	5859	±937

(Wyatt et al. 2000), pollen/ovule ratios suggest high levels of autogamy (Cruden 1977). In an independent study to determine various sugar concentrations in nectar (unpublished, ratios provided on herbarium vouchers at NMC), I extracted nectar from all species; flowers of *B. coccinea* and *B. spicata* individually produce much more nectar than flowers of the other three; these two species had the most insect visitors, *B. spicata* significantly so. Bittrich and Kühn (1993) review that *Boerhavia* flowers produce nectar in the narrow tube, are melittophilous, and are suited for head pollination by small bees, all observations supported by this study. Insect visitation between plants within a species would allow for occasional outcrossing as noted for autogamous plants by Lewis (1963). This would also allow for the potential of hybridization, which is supported by seed produced (but not germinated) in a very small trial of artificial interspecific pollination. Hybridization may take place occasionally in the field, as suggested by Woodson and Kidd (1961). This is especially likely in closely related, little-differentiated populations, as might be the case between *B. alata* and *B. intermedia* in the Guaymas region in Sonora. Chromosome numbers known in *Boerhavia* are fairly high (n = 13, 20, 26, 27, 58, see Appendix I), especially for annuals, which for those known n = 26 or 27. A high n number would be an important contributor to a high recombination index, promoting a higher number of new gene combinations through segregation and recombination in a limited number of generations (Stebbins 1951) than would a low n number. Hybridization followed by recombination and repetitive inbreeding would be expected to produce a rather fine-grained patchwork of populations homogeneous within and more or less different between. This kind of population structure, reviewed by Lewis (1963) and Stebbins (1957) in discussions of the relationship between autogamy and problems of classification, applies in *Boerhavia*. As noted by Lewis, autogamy *per se* creates no taxonomic problem, and a number of species of *Boerhavia* seem fairly trouble free. When combined with outcrossing, many local phenotypically differentiated populations may be temporarily stabilized by autogamy. This may apply in other *Boerhavia* groups, such as *B. coccinea* and *B. spicata* (both *sensu lato*), and such complexes may be treated in the same manner as those where complex patterns of variation result from outcrossing and/or hybridization without notable inbreeding (Lewis 1963). In such situations, the taxonomist exercises considerable personal judgment, attempting to communicate in a classification a useful taxonomy that corresponds to broad limits on gene flow and/or fidelity to certain ecological situations.

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APPENDIX

Known chromosome numbers in *Boerhavia*. My original counts are indicated by voucher citations, unless otherwise indicated, collection number is mine; voucher specimens are at NMC, with many widely distributed. Other counts were compiled from the literature, the citation provided; for counts reported in the literature, somatic numbers were converted to expected gametic numbers for ease of comparison within the following listing. Within a species, all are organized alphabetically by country. Original counts were obtained from buds fixed in cold modified Carnoy's solution (4:3:1 - chloroform: ethanol:glacial acetic acid), and stained and squashed in hydrochloric acid-carmine (Snow 1963).

Boerhavia coccinea Mill. (perennial). n = 26. Arizona, Maricopa Co., 12 mi. N of Phoenix. *2527*; New Mexico, Doña Ana Co., Doña Ana Mts. N of Las Cruces, *1943*; Bolivia (Fernández Casas & Fernández Piqueras, 1981); Mexico, Vera Cruz, Paso de Ovejas, *Pilz & Strother_683*; n = ca. 26. New Mexico, Doña Ana Co., Las Cruces, *7867*.

Boerhavia diffusa L. (perennial). n = 13. India, (Srivistava & Misra 1966); Tanzania (Gill & Abubakar 1975); n = 26. Hawaii (Carr 1978); n = 27. Hawaii, Oahu, SW part of island, roadside weed along highway H-93, s end of Waianu Range, *6396*; Haleiwa at Waialu Bay, *6406*; n = 58, India (Thombre 1959).

Boerhavia intermedia M. E. Jones (annual). n = 26. New Mexico, Doña Ana Co., Las Cruces, *2080*; Texas, Presidio Co., 24.9 mi. E of Redford, *3431*; n = ca. 27. New Mexico, Doña Ana Co., Las Cruces, *7869*.

Boerhavia linearifolia A. Gray (perennial). n = ca. 26. New Mexico, Chaves Co., 9.2 mi. NW of Roswell, *3431*.

Boerhavia mathisiana F. B. Jones (perennial). n = ca. 26. Texas, San Patricio Co., ca. 2 mi. NW of Mathias, *Turner 80-80M*.

Boerhavia repanda Willd. (perennial). n = 20. India (Gajapathy 1962); n = 21. India (Tandon and Rao 1963).

Boerhavia spicata Choisy (annual). n = 26. New Mexico, Doña Ana Co., Las Cruces, *2080*; n = ca. 26. Mexico, Puebla, 1 mi. W of Acatlan, *Pilz & Strother 671*; n = 27. New Mexico, Doña Ana Co., Las Cruces, *7866*; *8291* [latter *B. torreyana* (S. Wats.) Standl. phase].

Boerhavia wrightii A. Gray (annual). n = 27. New Mexico, Doña Ana Co., Las Cruces, *7870*.

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TAXONOMIC ADDENDUM

This paper was written and submitted so that some of its conclusions could be referenced in an upcoming Flora of North America treatment of *Boerhavia*. The taxonomy followed was that of Reed (1969). As the paper was in galley and virtually "out the door" for publication, the taxonomy of the *Boerhavia spicata* group in the United States yielded to study. This requires name changes from those given in the paper, changes that may be referenced by way of voucher numbers given in the body of the paper. Name changes occur only for those collections originally called *B. spicata* and *B. torreyana*.

Boerhavia coulteri (Hook. f.) S. Wats., *7868*, fourth column of Fig. 1; *8291*, chromosome number, $n = 26$. It has been introduced in the Las Cruces area.
Boerhavia spicata Choisy, *Pilz & Strother 671*, chromosome number, $n =$ ca. 26 (no change in name).
Boerhavia torreyana (S. Wats.) Standl., *7866*, middle column of Fig. 1, *2080*, *7866*, chromosome number, $n = 26$.

In tables 1, 2, 3 and 4 *Boerhavia spicata* now becomes *B. torreyana*, and *B. torreyana* now becomes *B. coulteri*.