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Taxonomy and Natural History of *Bacopa* (Scrophulariaceae) in California

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Abstract. Three of California's four species of *Bacopa* are aliens. *Bacopa rotundifolia,* a tetraploid, native to central United States, was first recorded for California in 1923 and has since become one of the commonest weeds in rice fields of the state. Californian populations of this species were named *B. nobsiana* in 1952. *Bacopa repens,* a neotropical diploid, has been known from a single California station since 1949; its range within the state has not increased in some 30 years. The third alien, the pantropical *B. monnieri,* has been found in California only recently. The native, *B. eisenii,* is tetraploid and has apparently invaded rice fields to a significant degree only recently. Taxonomic interpretation of these species has depended on a synthesis of field, experimental, and herbarium studies.

The phytogeography and migratory histories of alien or immigrant species are seldom well documented (Shinners, 1965; Baker, 1972; McNeill, 1976; Sanders, 1976). Some alien species are given new names in their adopted homes before further studies reveal their correct identity (Moran, 1950; Rodman, 1974; Lonard & Gould, 1974; Rollins, 1978). Our interpretation of the migrational history and taxonomy of Bacopas found in California illustrates how field, herbarium, and experimental studies can be combined to resolve such confusions.

Bacopa comprises some 100 species of aquatic and palustrial herbs distributed throughout the warmer regions of the world (Cook et al., 1974). Current floras (Mason, 1957; Munz, 1959) report two species for California: *B. eisenii* and *B. nobsiana,* both considered native to the state. Recently a third species, the pantropical *B. monnieri,* was reported as adventive in Southern California (Riskind & Patterson, 1975). Following, we present evidence that *B. nobsiana* of California is conspecific with *B. rotundifolia,* a common aquatic weed in central United States. In addition, the neotropical *B. repens,* which has long been misunderstood taxonomically and, in California, confused with *B. nobsiana* is reported for the first time from California.

TAXONOMIC SYNOPSIS OF *BACOPA* IN CALIFORNIA

Bacopa Aublet (*sensu* Pennell, 1946) may be briefly characterized as follows: aquatic or subaquatic herbs; leaves opposite, entire to toothed or finely divided; flowers one to few in leaf axils, pedicellate to sessile, pedicels bearing 0–2 bracteoles near or immediately below the calyx, not at base of pedicel; sepals 5 or 4, unequal to subequal, the inner ones

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narrower, all free to base or nearly so; corollas campanulate to salverform, actinomorphic to somewhat zygomorphic, lobes 5, 4, or rarely 3, usually white or blue, sometimes pink or yellow, often yellow toward the base; stamens inserted on corollas, usually 4, sometimes 5, 3, or 2, anthers often purplish and with filaments inserted dorsally, pollen white to pale yellow; style weakly 2-lobed to 2-cleft, the stigmas globular and papillate; ovary usually subtended by a well-developed nectary; capsules globose or nearly so, bilocular, loculicidal or septicidal; seeds numerous, tiny (0.1–0.3 mm long), evenly sculptured with rectangular pits.

Key to Species of *Bacopa* in California

1. Leaves narrowly spatulate, 1-nerved; pedicels bibracteate just below the calyx; stigmas at least partially united. (sect. *Bramia,* sensu Pennell, 1946) ..... 1. *B. monnieri*
1. Leaves ovate to rotund, palmately 7–15-nerved; pedicels ebracteate; stigmas separate. (sect. *Herpestis,* sensu Pennell, 1946)
   2. Sepals 4 (5), the outer narrowly oblong to ovate-elliptic, margins usually minutely bristly ciliolate; leaves mostly 13–20 mm long, 8–12 mm wide ..... 2. *B. repens*
   2. Sepals 5, the outer broadly ovate to rotund, not ciliolate (inner ones may be ciliolate); leaves mostly 15–28 mm long, 14–20 mm wide.
      3. Pedicels 25 (15–51) mm long, usually much longer than leaves; corollas 12 (10–14) mm long; anthers 2.3 (1.8–2.8) mm long ..... 3. *B. eisenii*
      3. Pedicels 10 (5–18) mm long, usually shorter than leaves; corollas 6 (4.7–8.0) mm long; anthers 0.9 (0.6–1.3) mm long ..... 4. *B. rotundifolia*

1. *Bacopa monnieri* (L.) Wettstein. Plants prostrate to ascending on wet soil or in very shallow water; leaves mostly 5–25 mm long, narrowly spatulate, basally cuneate, apically rounded; pedicels usually longer than leaves; sepals 5, subtended by 2 lance-linear bracteoles, outer sepals lanceolate to ovate, 1.5–5.0 mm wide, not ciliolate; corollas 5-lobed, weakly bilabiate, mostly 8–10 mm long, white to pink or blue.

In California, this species is known only from along the Colorado River in Riverside Co. (Riskind & Patterson, 1975). Perhaps the only remarkable aspect of its presence in the state is its apparently recent arrival. It is a common weed in wet habitats in southern United States and is widespread throughout most of the tropics and subtropics, often as a rice field weed (Sculthorpe, 1967; Cook et al., 1974). Chromosome number for *B. monnieri* is $2n = 64$ (Raghaven, 1959; Lewis et al., 1962).

2. *Bacopa repens* (Swartz) Wettstein. [*Gratiola repens* Swartz, *Herpestis obovata* Poeppig, *Macuillamia limosa* Pennell]. Plants rooted on wet soil and prostrate to ascending or rooted in shallow water and floating on the surface, stems rarely more than 3 dm long; leaves 10–23 mm long, 7–13 mm wide, mostly obovate, l/w = 1.2–2.0; pedicels 0–25 mm long, very slender; sepals 4 (5), the outer ones narrowly ovate to elliptic, 2.2–4.6 mm long, 0.9–2.7 mm wide, l/w = 1.4–2.4, margins

TABLE 1. Chromosome numbers in *Bacopa*. All observations from late diakinesis or early first metaphase in aceto-carmine squashes of pollen mother cells; vouchers at UC.

Bacopa eisenii. $2n = 28$ II. CALIFORNIA: Fresno Co., *Barrett s.n.* (14 Oct 1975), *Barrett 950, Strother 1277*; Merced Co., *Barrett 952*; Sacramento Co., *Strother 1272*; Sutter Co., *Strother 1248*; Yolo Co., *Barrett 954*.

Bacopa repens. $2n = 14$ II. CALIFORNIA: Butte Co., *Barrett 959*. LOUISIANA: Acadia Parish, *Barrett 1036*.

Bacopa rotundifolia. $2n = 28$ II. CALIFORNIA: Butte Co., *Strother 1249*; Merced Co., *Strother 1274, 1276*; Sacramento Co., *Strother 1273*; Sutter Co., *Strother 1245, 1246*; Yolo Co., *Strother 1244*. LOUISIANA: Acadia Parish, *Barrett 1038*. TEXAS: Brazoria Co., *Barrett 1015, 1021*.

usually minutely bristly ciliolate; corollas 4 (5)-lobed, 3.5–5.9 mm long, pinkish to white; anthers 3 (4), 0.3–1.2 mm long.

This rather variable species is common and widespread in the Antilles and Central America, extending north through Pacific states of Mexico to Jalisco and Sinaloa and south into Colombia. The species has also been collected in Hong Kong (*Woo 160* and *170*, 16 Jul 1972, UC). In California, *B. repens* is known only from the vicinity of the Rice Experiment Station near Biggs (Butte Co.: *Barrett 959*, 5 Aug 1976, UC; *Bellue s.n.*, 23 Aug 1949, CDA; *Tucker 2684*, 28 Aug 1953, UC). Although it has been in the state for nearly 30 years or more, *B. repens* has not become widespread, as evidenced by extensive sampling of suitable habitats between 1973 and 1976 (Barrett, unpubl.). The only other collections from the United States that we have seen are from Louisiana and, interestingly, include gatherings from in and near Crowley Rice Research Station (i.e., Acadia Parish: *Barrett 1036*, 11 Aug 1976, UC; *Thieret 31912*, 22 Aug 1969, LAF, LL). The species appears to be diploid, $2n = 28$ (Table 1).

3. *Bacopa eisenii* (Kellogg) Pennell. [*Ranapalus eisenii* Kellogg]. Plants rooted on wet soil and prostrate to ascending or, more commonly, rooted in water to 3 dm deep and floating, stems often to 6 dm long; leaves 12–34 mm long, 8–22 mm wide, obovate to rotund, l/w = 1.2–2.1; pedicels 15–51 mm long, rather stout, much longer than leaves; sepals 5, the outer ones rotund to broadly ovate, 4.3–6.6 mm long, 3.6–6.8 mm wide, l/w = 0.8–1.3, margins not ciliolate; corollas 5-lobed, 10.1–13.5 mm long, usually pure white with yellow in tube/throat, rarely with a flush of pink on the lobes; anthers 4, 1.8–2.8 mm long.

This is probably the only truly Californian *Bacopa*. The type was collected by Eisen in 1876 near Fresno (not found at CAS, presumed lost in 1906 fire). Other early collections of this species were made in 1893 (Calif., San Joaquin Co., *Sanford s.n.*, MO, UC, and in Nev., "east of

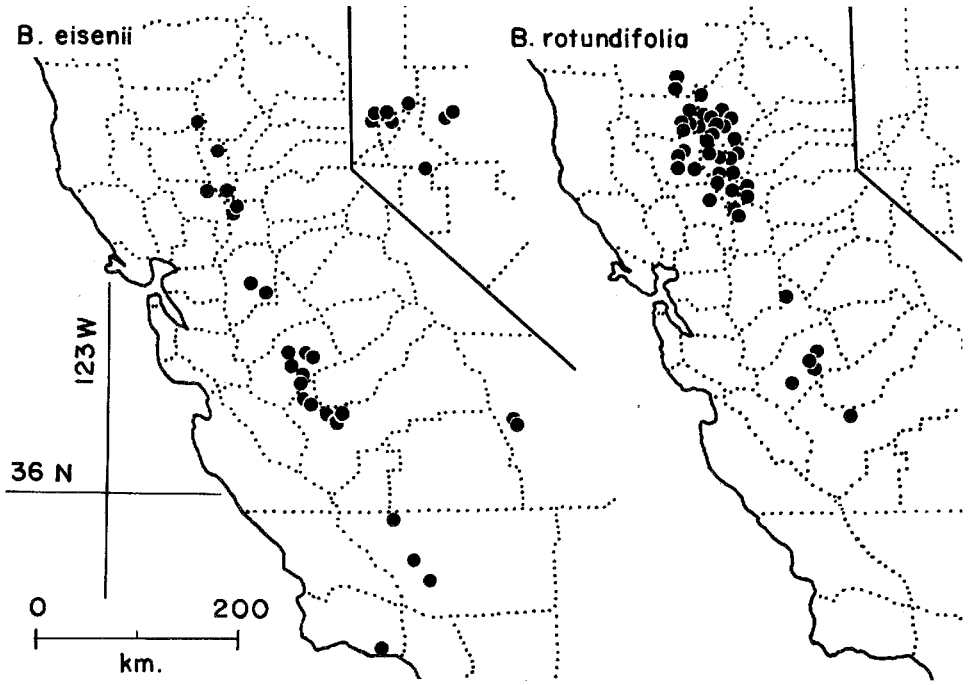


FIG. 1. Distributions of *Bacopa eisenii* and *B. rotundifolia* (California only) based on herbarium records and field observations.

Reno," *Hillman 7325,* POM), in 1912 (Calif., Inyo Co., *Jepson 5155,* JEPS), and in 1915 (Calif., "San Joaquin Valley," *Johnston 68J,* DAV, and *s.n.,* CDA). Although long known from the San Joaquin Valley, *B. eisenii* was not recorded from the Sacramento Valley until 1947 (Glenn Co., *P. V. Harrigan s.n.,* CDA) and was not collected there again until recently. Barrett found *B. eisenii* at only five of 59 sites (rice fields) in the Sacramento Valley in June 1976. He found *B. rotundifolia* at 57 of the 59 sites. Four locations had both species; only one had no *Bacopa.* (See further discussion under *B. rotundifolia*.) Cumulative distribution of *B. eisenii* based on herbarium records and our field observations is mapped in Figure 1. The species is apparently tetraploid, $2n = 56$ (Table 1).

4. *Bacopa rotundifolia* (Michaux) Wettstein. [*Bacopa nobsiana* Mason, *Bacopa simulans* Fernald, *Herpestis tweedii* Bentham, *Monniera rotundifolia* Michaux]. Habit as described for *B. eisenii*; leaves 12–36 mm long, 8–26 mm wide, mostly rotund, l/w = 0.8–1.8; pedicels 5–17 mm long, rather stout, usually shorter than leaves; sepals 5, the outer ones ovate to rotund, 3.1–5.3 mm long, 2.2–4.8 mm wide, l/w = 1.0–1.7, margins not ciliolate (inner sepals may be ciliolate); corollas 5-lobed, 4.9–8.0 mm long, white with yellow in tube/throat, sometimes (especially

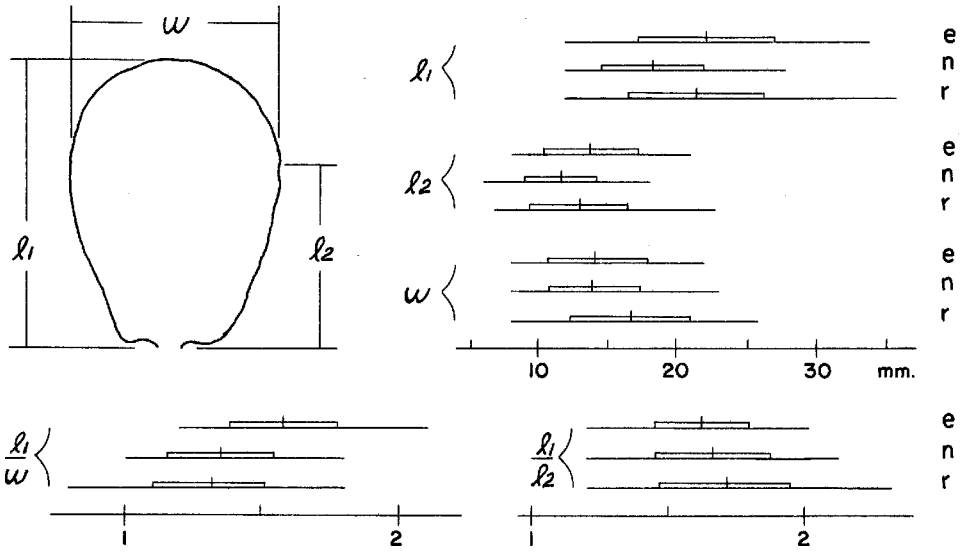


FIG. 2. Comparisons of *Bacopa eisenii* (e, N = 44), "*B. nobsiana*" (n, N = 50), and *B. rotundifolia* (r, N = 49) for range, standard deviation, and mean for measures of leaf shape and leaf size. All measurements from herbarium specimens.

but not exclusively in Arkansas, California, and Oklahoma) with flush of pink on lobes; anthers 4, 0.6–1.3 mm long.

This species is native to central United States, ranging from Mississippi, Louisiana, and Texas north to Indiana, Minnesota, and North Dakota. Collections from Arizona (*Pinney s.n.*, 9 Nov 1912, ARIZ, POM), Idaho (*Tucker 182*, Nov 1933, CIC, ID, NY), and Virginia (*Grimes 4136*, 30 Jul 1921, NY; *Fernald & Long 13749*, GH—*B. simulans*) in the United States and from Chihuahua (*McGill & Keil 8331*, 27 Aug 1971, ASU; *Pinkava et al. 9782*, 4 Aug 1972, ASU) and Jalisco (*McVaugh 17606*, 1 Sep 1958, MICH, NY, TEX) in Mexico appear to be recent, man-associated introductions. Populations in Argentina and Paraguay (*H. tweedii*) may represent a natural disjunction. In one of these collections (Paraguay, Gran Chaco, 1903, *Hassler cat. no. 2828*, MO, NY, UC), the corollas are exceptionally large, suggesting perhaps that *B. eisenii* may have arisen from South American stock.

In California, *B. rotundifolia* is very common in the Sacramento Valley but relatively rare in the San Joaquin Valley (see discussion under *B. eisenii*). The first positive record of *B. rotundifolia* from the San Joaquin Valley dates from 1938 (near Merced, *H. R. Guilbert s.n.*, DAV). Barrett found *B. rotundifolia* at three of eleven sites in the San Joaquin Valley. Eight of those sites had *B. eisenii*; one had both species; one had no *Bacopa*. Cumulative California distribution of *B. rotundifolia* is mapped in Figure 1. The species is apparently tetraploid, $2n = 56$ (Table 1).

Results and Discussion

California plants of *B. rotundifolia* have been known as *Bacopa nobsiana* (Mason, 1952) and have been considered endemic to the Central Valley (Raven & Axelrod, 1978). Our reasons for considering *B. nobsiana* a synonym of *B. rotundifolia* are detailed below; first we consider early records of collections from California.

History.—The earliest unquestionable record of *B. rotundifolia* in California is dated 1923 (Butte Co., rice fields at Nelson, *Copeland 843,* POM). A specimen dated 1915 (Merced Co., Dos Palos, *Johnston s.n.,* DAV) may document an earlier occurrence of *B. rotundifolia* in California, but the specimen cannot be unequivocally identified and other collections by Johnston in the same year (e.g., *B. eisenii,* CDA, DAV) have confusing, contradictory label data. A second collection, also from a rice field, was made in 1925 (Sacramento Valley, *Dunshee s.n.,* DAV). Since these early records are associated with rice culture (as are virtually all collections of this taxon in California), it seems likely that *B. rotundifolia* was introduced from central United States (probably Arkansas or Louisiana) as a contaminant of rice seed. According to an unpublished history of rice culture in California, on deposit at Biggs Rice Experiment Station, Butte Co., rice plantings from Louisiana seed sources were made in 1907 at the start of rice cultivation in California. Other rice weeds native to central United States such as *Heteranthera limosa* (Swartz) Willdenow (Pontederiaceae) have probably been introduced to Californian rice fields in contaminated rice seed (see Tucker & McCaskill, 1967).

Bacopa species are not listed in early surveys of California rice weeds (Kennedy, 1923; Bellue, 1932). Yet today *B. rotundifolia* is perhaps the most abundant and widely distributed of all rice weeds in the state. *Bacopa rotundifolia* occurred in 85.7% of the rice fields (N = 70) included by Barrett in a rice weed survey in 1976. In contrast, the native *B. eisenii,* while more widely distributed in the state (Fig. 1), was found in only 18.6% of rice fields in the 1976 survey. Considering the limited number of early records of *B. rotundifolia* in California, we suggest that the present widespread distribution of the species has been achieved in a relatively short period. Such rapid population expansion and range extension is a well-documented feature of introduced aquatic plants (Ranwell, 1967; Sculthorpe, 1967).

For convenience in the remaining discussion, and in Figures 2–9, we use "*B. nobsiana*" to refer to California plants of *B. rotundifolia.* Unless context indicates otherwise, *B. rotundifolia* refers to plants from central United States.

Morphology.—Bacopa eisenii, "B. nobsiana," and *B. rotundifolia* are remarkably similar in habit. We have been unable to find any single character or combination of characters that reliably distinguishes them in the vegetative condition. Variations in leaf size and shape are summarized

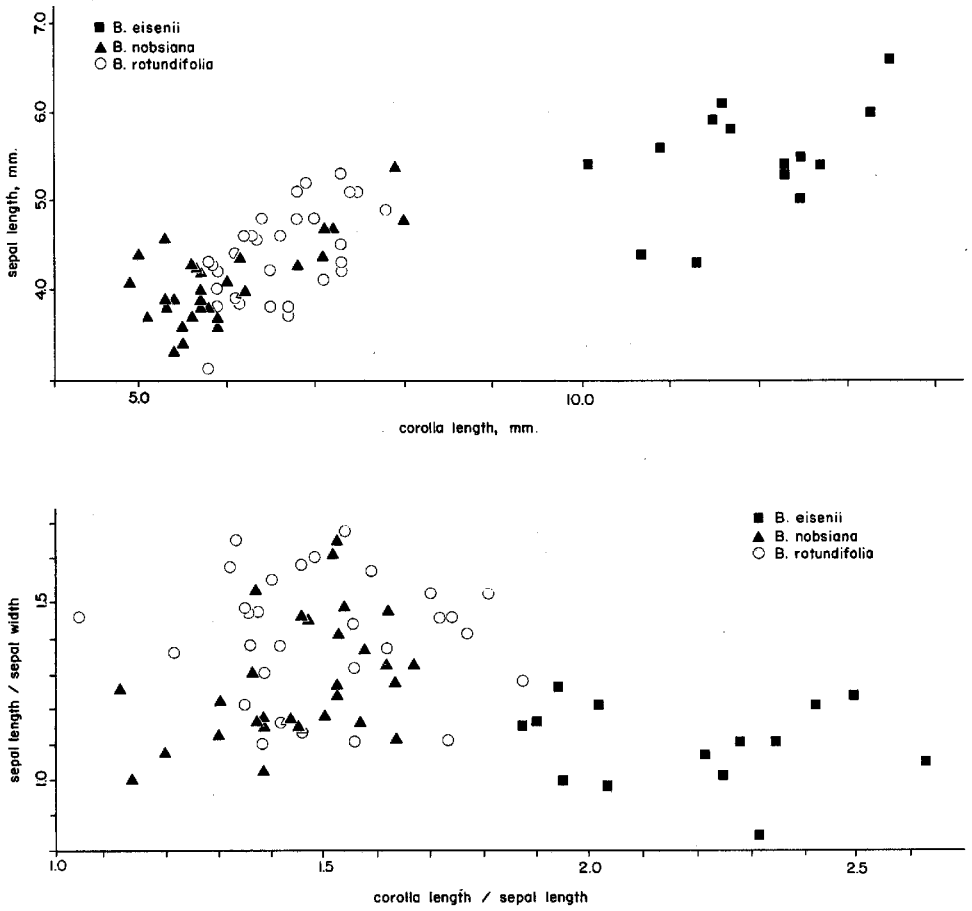
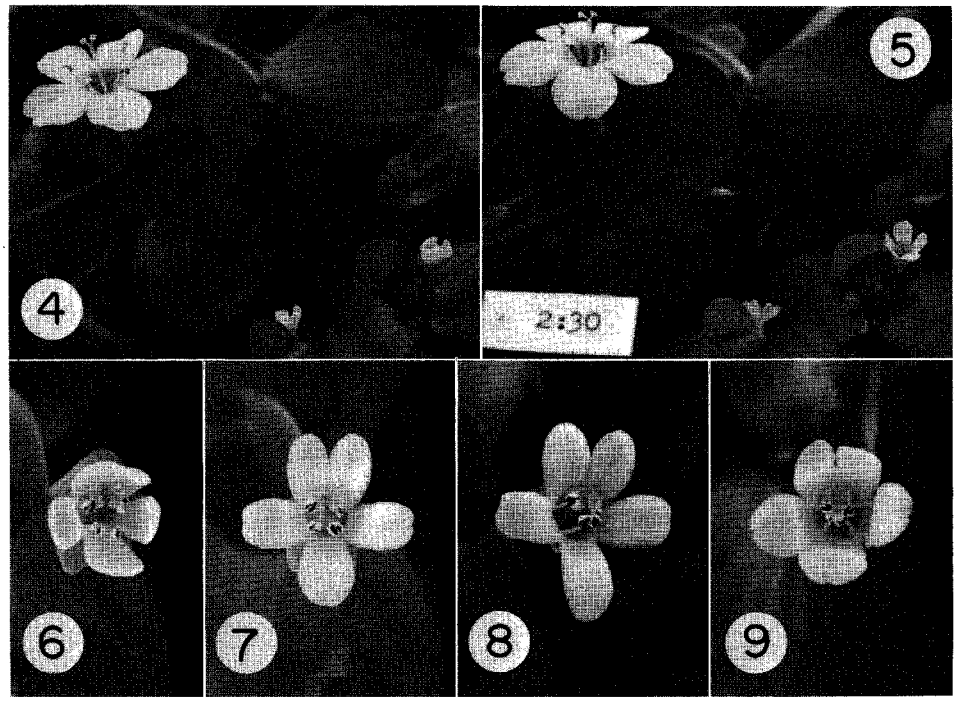


FIG. 3. Scatter diagram comparisons of *Bacopa eisenii*, "*B. nobsiana*," and *B. rotundifolia* for measures of flower size and proportions of floral organs. Measurements from pickled flowers and/or rehydrated dried flowers.

in Figure 2. Longer pedicels and larger flowers readily distinguish *B. eisenii* from "*B. nobsiana*" and *B. rotundifolia*, but "*B. nobsiana*" and *B. rotundifolia* are not distinguishable from each other on floral characters. Although flowers of "*B. nobsiana*" are generally smaller than those of *B. rotundifolia* from most of central United States, many populations in Arkansas, Louisiana, Oklahoma, and Texas have flowers quite as small as in many plants of "*B. nobsiana*" (cf. Fig. 3).

Phenology.—Although the vegetative morphologies of *B. eisenii*, "*B. nobsiana*," *B. rotundifolia*, and *B. repens* are similar, the reproductive phenologies of these plants differ markedly under field and glasshouse conditions. Flowering commences in rice field populations of "*B. nobsiana*" in mid-May and continues until late July. Senescence and death of populations soon follow and few plants remain in rice fields at the end of



FIGS. 4–9. Timing (Daylight Saving Time) of anthesis and stamen movements in *Bacopa eisenii* (*Strother 1275*) and "*B. nobsiana*" (*Strother 1276*) transplants from Merced Co., California. Magnifications: 4–5, ca. 1×; 6–9, ca. 3×. All in Berkeley glasshouse, 13 Aug 1977. 4. 11:00 a.m.; large flower (*B. eisenii*) has been open ca. 3 hours, anthers are held well away from stigmas; small flowers ("*B. nobsiana*") are just opening. 5. 2:30 p.m.; flower of *B. eisenii* is still open and anthers are still held away from stigmas; flowers of "*B. nobsiana*" are fully open, anthers are inflexed toward stigmas as shown in Figs. 8 and 9. 6. 12:00 noon; a flower of "*B. nobsiana,*" not fully open, upper anthers already in contact with stigmas. 7. 1:00 p.m.; same flower as in 6, now fully open with upper anthers in contact with stigmas and lower anthers inflexed toward stigmas. 8. 3:30 p.m.; same flower as in 6, all anthers now touching or in close proximity to stigmas. 9. 2:30 p.m.; another flower of "*B. nobsiana*" with all anthers inflexed toward the stigmas.

August. The demise of "*B. nobsiana*" populations generally occurs as a result of herbicide sprays or heavy shading by rice plants.

Populations of *B. eisenii* occur in Californian rice fields throughout the rice-growing season (April–October) and flowering commences in mid-May. Although herbicide sprays in May and June destroy most emergent plant parts, rapid regrowth occurs and flowering resumes and continues until the draining of rice fields prior to harvest.

The population of *B. repens* at Biggs Rice Experiment Station does not emerge above the water surface to flower until mid-July. Since this species is of tropical origin, its relatively late seasonal appearance in Californian rice fields is probably a result of retardation of growth caused by cool water temperatures early in the growing season. Other tropical

rice weeds, occurring in California, e.g., *Monochoria vaginalis* Presl. (Pontederiaceae) and *Rotala indica* Koehne (Lythraceae), also emerge and flower relatively late in the growing season at Biggs (Barrett, unpubl.).

Under glasshouse conditions, *Bacopa eisenii* plants have grown actively for over one year. In contrast, plants of "*B. nobsiana,*" *B. rotundifolia* (Louisiana), and *B. repens* (California) died 2–4 months after germination. The differences in growth and phenology among Californian *Bacopas* suggest that *B. eisenii* may behave as a perennial under suitable ecological conditions. Jepson (1925) and Robbins et al. (1970) report *B. eisenii* (under the name *B. rotundifolia*) as a perennial although Mason (1952) found no evidence of perenniality.

Floral Biology.—The most significant morphological differences among *B. eisenii, B. rotundifolia* and "*B. nobsiana*" are associated with the flowers. In *B. eisenii,* the flowers are large, showy and held well above the foliage on relatively long pedicels. In contrast, flowers of *B. rotundifolia* and "*B. nobsiana*" are small, inconspicuous, and borne on short pedicels. These differences suggest that the breeding systems of the two species differ. Evidence from observations of flowering behavior and insect foraging activity suggests that *B. eisenii* may be outcrossed to some extent whereas *B. rotundifolia* and "*B. nobsiana*" are predominantly autogamous.

Under field and glasshouse conditions corollas of *B. eisenii* are fully open by 8:00 to 8:30 a.m. (Daylight Saving Time). The smaller corollas of "*B. nobsiana*" and *B. rotundifolia* do not open until about 11:30 (observed in California and in Texas) and on dull, cool days flowers may remain completely closed. By about 3:00 p.m. or earlier, anthers of "*B. nobsiana*" and *B. rotundifolia* are brought into contact with their respective stigmas by inward bending of filaments and self-pollination is effected. By evening, the pedicels bend downward, forcing the flowers under water in floating plants, and the corollas float away. In contrast, there are no such staminal movements in *B. eisenii* in which, in the absence of pollination, corollas may persist and remain open for two days or more. These behavioral patterns are illustrated in Figures 4–9.

Artificial self-pollinations conducted under glasshouse conditions indicate that *B. eisenii, B. rotundifolia,* and "*B. nobsiana*" are self-compatible. Autogamous seed set occurred in all undisturbed flowers of *B. rotundifolia* (N = 40) and "*B. nobsiana*" (N = 40). The facility for autogamy is less well developed in *B. eisenii* and seed set occurred less frequently in undisturbed flowers (percentage fruit production = 52.7, N = 74). *Bacopa repens* is self-compatible and in common with *B. rotundifolia* and "*B. nobsiana*" it produces both cleistogamous and chasmogamous flowers.

Insect visitors to flowers of *B. eisenii* were frequently observed in rice field populations. The introduced honey bee (*Apis mellifera* L.) was the most abundant visitor and was observed collecting pollen and feeding on

TABLE 2. Comparison of floral characters and pollen stainability in *Bacopa eisenii, "B. nobsiana," B. rotundifolia,* and hybrids. All $\bar{x}$ and S.D. from 8 plants, 3 flowers per plant (N = 24). Pollen stainability based on 300 grains per flower.

Character	*"B. nobsiana"*	*B. eisenii* × *"B. nobsiana"*	*B. eisenii*	*B. eisenii* × *B. rotundifolia*	*B. rotundifolia*
corolla length (mm)	6.64 ± 0.66	9.58 ± 1.44	12.58 ± 1.05	10.00 ± 0.96	6.92 ± 0.65
sepal length (mm)	4.02 ± 0.90	5.46 ± 0.83	6.39 ± 0.78	5.92 ± 0.40	4.00 ± 0.30
pedicel length (mm)	7.14 ± 1.58	18.5 ± 4.03	26.58 ± 4.66	19.58 ± 2.22	7.30 ± 2.08
pollen stainability (%)	87.82 ± 23.78	4.38 ± 4.33	95.91 ± 4.87	12.29 ± 20.63	98.58 ± 1.74

nectar. Visitors to flowers of "*B. nobsiana*" and *B. repens* were rarely observed. In a mixed population of *B. eisenii* and "*B. nobsiana*" at Del Paso Rd., Sacramento Co., *Apis mellifera* was observed preferentially visiting flowers of *B. eisenii*. Occasional visits to "*B. nobsiana*" were made. Although infrequent, such interspecies visits may provide an opportunity for natural hybridization between *B. eisenii* and "*B. nobsiana.*"

Hybridization.—Four of eleven flowers of "*B. nobsiana*" collected in a rice field in Sacramento Co. (*Strother 1273*), where *B. eisenii* (*Strother 1272*) also flourished, had poorly staining, irregularly shaped pollen grains. Five of these eleven flowers had large corollas (7.1–8.0 mm long), but not all of the large flowers had poor pollen and poor pollen was also found in two typical, small flowers (corollas 5.4 and 6.2 mm long). This variation suggests that natural hybridization between *B. eisenii* and "*B. nobsiana*" may have occurred. Artificial pollination of emasculated flowers of *B. eisenii* with pollen from "*B. nobsiana*" and *B. rotundifolia* results in good seed-set. Reciprocal crosses were not attempted because of mechanical difficulties in emasculating small flowers.

Hybrid plants grown from artificial hybridizations (*B. eisenii* × "*B. nobsiana*" and *B. eisenii* × *B. rotundifolia*) were morphologically indistinguishable. The 16 hybrids were intermediate in appearance between the two parents. Measurements of the sizes of the corolla, calyx, and pedicel illustrate the intermediate nature of these characters in hybrid plants (Table 2). Pollen stainability of all hybrid plants was low (Table 2) and no seed was obtained from undisturbed flowers. In contrast, pollen stainability of parents was generally high and seed production occurred in all plants.

Conclusion.—Morphological, ecological, and reproductive similarities between "*B. nobsiana*" and *B. rotundifolia* together with the association of earliest records for "*B. nobsiana*" with rice cultivation strongly support our contention that "*B. nobsiana*" and *B. rotundifolia* are conspecific.

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