

CHRYSOTHAMNUS BOLANDERI, AN INTERGENERIC HYBRID

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The genus *Chrysothamnus* (Astereae, Compositae) is closely related to *Haplopappus*, and, particularly, *C. bolanderi* (Gray) Greene has been noted for its similarity to *H. macronema* Gray (section *Macronema*). Gray (1873) and Greene (1895) both suggested *C. bolanderi* could easily be placed in the other genus, and later Greene (1904) did so as *Macronema bolanderi*. This close resemblance to a species of *Haplopappus* makes the identification of *C. bolanderi* essential to an understanding of the systematics and evolution of *Chrysothamnus*. This plant has been, unfortunately, rarely collected. In addition to the earlier collections: *Bolander 6137* in 1866 (GH—holotype, UC!, US!) and *Rattan s. n.* in 1867 (DS!, mixed, *H. macronema* in part), it is now represented by *Reveal 1057* (KSC) and *Anderson & Fish 2923* and *2926* (KSC).

Bolander's type collection is labeled: "At Mono Pass, California, elevation 9000–10000 ft." The only plants we found after extensive independent search (Reveal in 1964, Anderson in 1965) were located east of Mono Pass (elevation 10604 ft.) in Bloody Canyon where they were restricted to a small oasis surrounded by barren rock. A small population was found at 10000 ft. on a steep talus-filled crevasse which rises abruptly from the northwest edge of Lower Sardine Lake (ca. 8 air miles southwest of Lee Vining). A few more plants were found in talus along the trail just below the lake at 9800 ft. A total of 25–50 plants, then, represents the extent of *C. bolanderi*.

Hall (Hall and Clements, 1923) described this taxon as a relict subspecies derived from *C. parryi* (Gray) Greene ssp. *parryi*. However, recent studies (Sharp and Birman, 1963) show that five advances of upper Pleistocene glaciation can be recognized in Bloody Canyon; these are Tioga, Tenaya, and Tahoe (of the Wisconsin), Mono Basin (Illinoian?), and Sherwin (Kansan?). This history of recent repeated glaciation does not support the designation of *C. bolanderi* as a relict. An alternative, as indicated by the extremely limited range and the fact that the plants are growing in very close association with *C. nauseosus* (Pallas) Britt. ssp. *albicaulis* (Nutt.) Hall & Clem. and *H. macronema*, is that it is of recent hybrid origin.

To elucidate the relationship of *C. bolanderi*, comparative studies on gross morphology, cytology, and anatomy were undertaken. Since *C. nauseosus* and *H. macronema* both vary considerably throughout their ranges, only collections associated with *C. bolanderi* are dealt with here. Data collected for *C. parryi* ssp. *monocephalus* (Nels. & Kenn.) Hall & Clem. and *H. suffruticosus* (Nutt.) Gray, also found in Bloody Canyon, indicate they are not related to the problem.

MATERIALS AND METHODS

Methods for gathering data and preparing materials have been previously outlined (Anderson, 1963). Permanent slides and herbarium specimens are filed at Kansas State University. Before detailed studies were begun, Reveal's collection, being a sampling of the entire *C. bolanderi* population, was segregated according to superficial resemblance into three categories by the senior author: *Reveal 1057A*, those plants most similar to *C. nauseosus*; *Reveal 1057B*, those most similar to the type collection (*Bolander 6137*); and *Reveal 1057C*, those most like *H. macronema*.

DISCUSSION

Morphology. On the talus slopes below Mono Pass, *C. nauseosus* is a woody shrub, 2.5–4 dm tall; *C. bolanderi* is less shrubby and intermediate in size (2–3 dm), and *H. macronema* is suffruticose from a woody caudex and 1.5–2 dm tall.

Several aspects of leaf morphology are compiled in Table 1. The arbitrary trichome frequency classes are easily determined under 10 × magnification; they range in series from absent, through occasional, sparse, moderate, and abundant to very abundant. For illustration of frequency classes, see Eiten (1963). Specificity of trichome types and structure permits their use in analysis of hybrids; sometimes they may be used as the primary basis for determination of hybrids (Carlquist, 1961). With *C. nauseosus* having essentially only nonglandular trichomes and leaves of *H. macronema* glandular ones, the trichome complement in specimens of *C. bolanderi* gives an excellent index to degree of intergradation. Leaves of *C. nauseosus* do have a few glandular hairs, but they are not visible under 25× magnification because of the tomentum. Nonglandular trichomes on leaves of *Bolander 6136* (*H. macronema*) are distributed evenly over the leaf surface, whereas in *Reveal 1052* they are restricted to the midribs.

Leaf size and shape are also useful as indicators of the intermediacy of *C. bolanderi*. Leaves of plants most like *H. macronema* (*Reveal 1057C* and *Anderson & Fish 2926*) are larger than those found in either putative parental populations. Leaves of *H. macronema* are unique in having undulate margins.

Several characteristics of floral morphology in *Chrysothamnus* have been demonstrated to be of diagnostic value (Anderson, 1946). Many which apply here are tabulated in Table 2 (omissions due to immaturity of specimens). Other features are discussed in the text.

The inflorescence of *C. nauseosus* is densely corymbose; that of *C. bolanderi* contains fewer heads, and *H. macronema* has a few or sometimes only a single head in the inflorescence. Heads are illustrated for the three taxa in Fig. 1. Involucre height and especially bract number indicate intergradation; further indications are found in bract alignment and structure. Bracts of *C. nauseosus* are in pronounced vertical ranks (a key character for the genus), keeled, and chartaceous. Those of

TABLE 1. COMPARATIVE FEATURES OF LEAF MORPHOLOGY

Taxon and collection	size, mm	shape	apex	trichome frequency	
				glandular	nonglandular
<i>C. nauseosus</i>					
<i>Anderson & Fish 2924</i> (KSC)	27-30 x 1.5-2	linear- oblanceolate	acute-obtuse	absent	very abundant
<i>Bolander 6138</i> (US)	25-35 x 2-3	linear- oblanceolate	acute	absent	very abundant
<i>Reveal 1059</i> (KSC)	30-35 x 2-3	linear- oblanceolate	acute	absent	very abundant
<i>C. bolanderi</i>					
<i>Reveal 1057A</i> (KSC)	30-35 x 2-2.5	linear- oblanceolate	acute-acuminate	occasional	abundant
<i>Anderson & Fish 2923</i> (KSC)	25-28 x 2.5-3.5	linear-oblong	attenuate- cuspidate	sparse	moderate
<i>Bolander 6137</i> (US)	28-33 x 3-4	oblong- oblanceolate	acuminate	moderate	sparse
<i>Reveal 1057B</i> (KSC)	30-37 x 3-4	oblong	acuminate	moderate	sparse
<i>Anderson & Fish 2926</i> (KSC)	30-35 x 5-7	oblong- oblanceolate	obtuse, mucronate	moderate	sparse
<i>Reveal 1057C</i> (KSC)	30-45 x 4-7	oblong- oblanceolate	obtuse, mucronate	moderate	occasional
<i>H. macronema</i>					
<i>Bolander 6136</i> (MO)	23-30 x 4-5	oblong	acuminate	abundant	occasional
<i>Reveal 1052</i> (KSC)	22-24 x 3-5	oblong	acute	abundant	occasional
<i>Anderson & Fish 2922</i> (KSC)	22-24 x 3-4	linear-oblong	acuminate	abundant	absent

C. bolanderi are in obscure vertical ranks, less prominently keeled, and more membranous. Bracts of *H. macronema* are not vertically aligned; they lack keels, and the outermost are green, leaf-like, and covered with glandular trichomes (not shown in Fig. 1).

Elsewhere throughout its range *C. nauseosus* is consistently 5-flowered; therefore, in the case of *Anderson & Fish 2924*, there is evidence of introgression. In addition to flower number, shape of the corolla tubes also suggests intergradation; they gradually flare out in *C. nauseosus*, are somewhat dilated in *C. bolanderi*, and more noticeably so in *H. macronema*. The collections most like *H. macronema* in gross appearance and trichome frequencies are, interestingly, more like *C. nauseosus* in floral morphology.

Cytology. Chromosome numbers as determined from pollen mother cells in meiosis are listed in Table 2; in each taxon, $n = 9$. Chromosomal pairing and other aspects of meiosis appear to be regular in *C. bolanderi*. Pollen fertility as determined by stainability in aniline blue in lactophenol is also listed in Table 2. Apparently normal meiosis and noticeably reduced pollen fertility also characterize the only other presumed hybrid known in *Chrysothamnus* (*Anderson, 1966*). The relatively high pollen fertility in *Reveal 1057A* is possibly due to back-crossing with *C. nauseosus*; this conclusion is supported by many similarities in morphology as reported here. Backcrossing with *H. macronema* is also indicated; the reduced pollen fertility of *Bolander 6136* suggests less compatibility between this parent and *C. bolanderi*. However, these variations in fertility and morphology could also be due to genic recombinations in the F_2 .

The extent of viable seed formation in *C. bolanderi* has not been determined. Only one seed of *Reveal 1057C* successfully germinated, and the seedling died a few days later.

Anatomy. Vegetative anatomy, excluding features of the wood, is similar in most respects among the three taxa. The amounts of primary phloem sclerenchyma tend to vary according to topography and age of the sample; nevertheless, phloem fibers appear to be most abundant in stems of *H. macronema* and least abundant in *C. nauseosus*, with *C. bolanderi* appearing intermediate. Quantitative differences in trichome distribution have already been noted; in addition, there are differences in trichome size and structure. On stems of all samples there are uniseriate nonglandular hairs that are anisotropic under polarized light and biseriate glandular hairs that are isotropic. On stems of *C. nauseosus* the long uniseriate trichomes that form the tomentum cover the less frequent biseriate glandular hairs, the longest glandular hairs being only 9.8μ long. In *C. bolanderi*, the longest glandular trichomes are 12.7 and 13.2μ (*Anderson & Fish 2923* and *2926* respectively); whereas on stems of *H. macronema* the longest glandular trichomes are 32.2μ .

A similar correlation exists for foliar trichomes with one interesting modification. On leaves of *C. nauseosus* the longest glandular trichomes

TABLE 2. COMPARATIVE FEATURES OF THE INVOLUCRE AND FLOWER

Taxon and collection	average bract number	range in bract number	average length of involucre, mm	average flower number	range in flower number	average flower length, mm	% lobe length to total flower length	% appendage length to total style length	gametic chromosome number	% pollen fertility
<i>C. nauseosus</i>										
Reveal 1059 (KSC)	10.0	9-11	8.5	5	5	10.1	18.8	57.2		98.7
Bolander 6138 (US)	11.0	9-12	10.4	5	5	11.0	18.3	52.3		92.3
Anderson & Fish 2924 (KSC)	12.3	11-13		6.4	6-7				9	
<i>C. bolanderi</i>										
Reveal 1057A (KSC)	12.6	12-14	9.5	7.2	6-9	8.5	15.3	58.8		94.0
Reveal 1057C (KSC)	13.5	11-17	12.0	7.4	6-9	10.2	22.5	55.7		34.9
Anderson & Fish 2926 (KSC)	12.5	11-14		8.2	5-13				9	
Reveal 1057B (KSC)	13.5	12-15	14.0	10.0	7-11	8.6	16.2	69.2		32.0
Bolander 6137 (US)	14.1	11-19	10.0	11.0	8-16	10.0	15.0	68.5		33.1
Anderson & Fish 2923 (KSC)	14.7	13-17	10.0	11.3	10-13				9	42.6
<i>H. macronema</i>										
Bolander 6136 (MO)	14.9	11-18	12.1	13.8	8-19	10.3	13.4	69.0		76.4
Reveal 1052 (KSC)	15.4	13-19	11.6	14.9	10-23	10.0	14.0	72.2		98.9
Anderson & Fish 2922 (KSC)	15.7	10-24	12.0	20.4	11-37	9.0	11.1	67.0	9	96.2

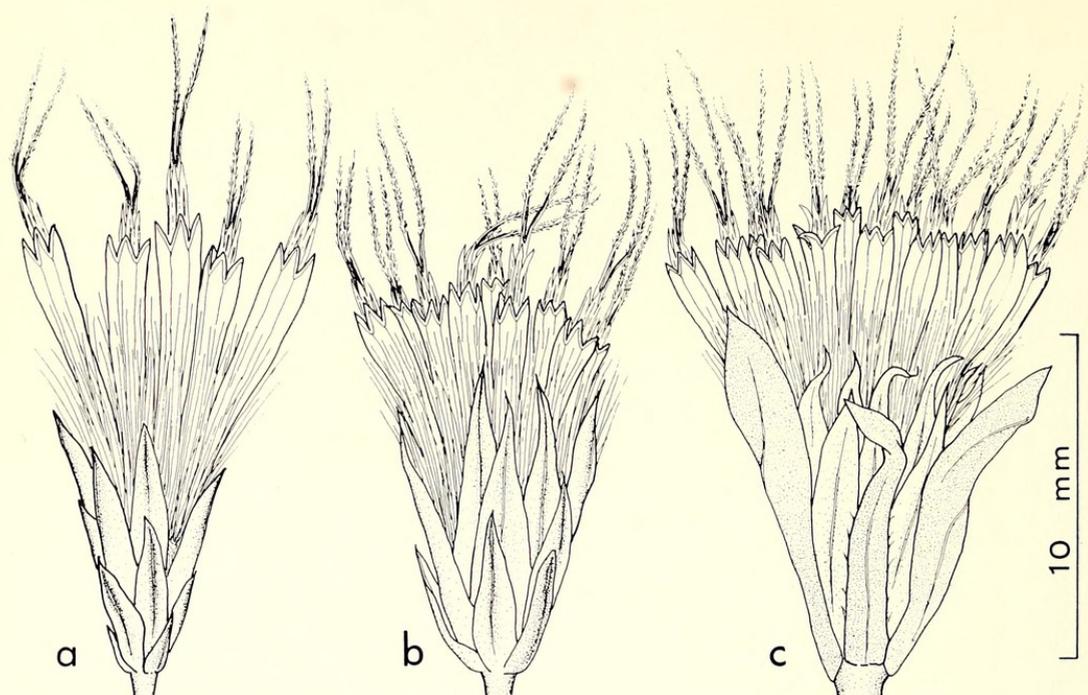


FIG. 1. Representative heads: a, *C. nauseosus*; b, *C. bolanderi*; c, *H. macronema*.

measure 7.3μ and on *C. bolanderi*, 10.4 and 12.0μ . The anisotropic uniseriate, nonglandular trichomes characteristic of leaves of the preceding are converted on *H. macronema* leaves into uniseriate glandular trichomes which are isotropic. These uniseriate glandular hairs are equally as long as the biseriates, the longest measuring 25.0μ .

Selected characteristics of the wood anatomy for the three taxa are summarized in Table 3. The plus symbol indicates the feature is abundantly present, and the minus, present but not abundant. In nearly all features listed in Table 3, *C. bolanderi* is intermediate. Additional xylem features either indicate the possible hybridity of *C. bolanderi* or demonstrate it is more like *Chrysothamnus* than *Haplopappus*.

Vessels in the *Chrysothamni* are angular as seen in transection and appear in large groups of 10 or more; whereas in *H. macronema*, they are roughly circular in transection and average 4.09 per group. Terminal elements of a year's growth are vascular tracheids in each case, but in *H. macronema* they are less abundant; this coupled with other cellular patterns makes age determination of *H. macronema* wood difficult. Uniseriate rays are not frequent in woods of these two genera (Carlquist, 1960); in our samples they are occasional in *H. macronema*, less frequent in *C. bolanderi*, and extremely rare in *C. nauseosus*. Axial wood parenchyma is mostly vasicentric and scanty, being most abundant in *C. nauseosus* and least abundant in *C. bolanderi*.

Most features of floral anatomy are similar in the taxa; however, two are of significance. These are relative abundance and distribution of sclerenchyma in the phyllaries and distribution of secretory canals in the achenes and corollas. Sclerenchyma is less abundant in the phyllaries

TABLE 3. COMPARATIVE FEATURES OF THE WOOD

Taxon and collection	diameter of widest vessel, μ	average diameter of vessels, μ	average length of vessels, μ	average height of multiseriate rays, mm	ray cells isodiametric to procumbent	ray cells isodiametric to erect	average number of cells of maximum multiseriate ray width	average number of rays per mm of tangential section
<i>C. nauseosus</i> Anderson & Fish 2924 (KSC)	74.9	47.2	105.4	1.07	+	—	11.8	3.8
<i>C. bolanderi</i> Anderson & Fish 2923 (KSC)	81.7	46.5	107.7	1.31	+	—	9.1	4.3
Anderson & Fish 2926 (KSC)	99.9	57.6	109.6	1.35	+	—	6.9	4.2
<i>H. macronema</i> Anderson & Fish 2922 (KSC)	102.2	64.3	141.1	1.08	+	+	4.7	5.2

of *H. macronema* as compared to the *Chrysothamni*, *C. bolanderi* again being intermediate. Secretory canals are absent in achenes and flowers of *H. macronema*. They are equally abundant in achenes and style branches in our *Chrysothamnus* samples, but in the corollas they are more extensive in *C. nauseosus*, where they are in the distal portion of the corolla tube as well as in the corolla lobes as in *C. bolanderi*.

CONCLUSIONS

Absolute proof of hybridity, the successful synthesis of *C. bolanderi* from artificially crossing *C. nauseosus* and *H. macronema*, is lacking. Nevertheless, sufficient circumstantial evidence has been amassed from field observations and studies on morphology, cytology, and anatomy to strongly indicate that *C. bolanderi* is indeed a hybrid swarm. Back-crossing, particularly with *C. nauseosus*, is also indicated. In nearly all features, *C. bolanderi* is intermediate; however, in some collections, features such as taller wood rays and larger leaves and involucre suggest a complementary genic action in the hybrids.

Secondly, floral anatomy and especially the wood anatomy of the hybrids is more like that of *Chrysothamnus* than of *Haplopappus*. Therefore, if the genera are treated as distinct, the hybrids should be placed in *Chrysothamnus*. The overall appearance of *C. bolanderi* is that of a subspecies of *C. parryi*. In fact, it is currently treated as *C. parryi* ssp. *bolanderi* (Gray) Hall & Clem. in all floras. Nevertheless, since infra-specific taxa of *C. parryi* are not involved in the origin of this taxon, it is better referred to as *C. bolanderi*.

The hybrid origin of *C. bolanderi* was discovered in preparation of a monograph on *Chrysothamnus* by the senior author. The taxonomic status of the genus in light of this intergeneric hybridization will be considered in the monograph.

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A NEW SPECIES OF BRODIAEA FROM SAN CLEMENTE ISLAND, CALIFORNIA

THEODORE F. NIEHAUS

The island of San Clemente off the southern California coast is noted for its high number of endemics (Raven, 1963). A new species here reported raises the total number of endemics on San Clemente I. to eleven.

Brodiaea kinkiensis Niehaus, sp. nov. *Planta ex cormo tunica fibrosa instructo; perianthii tubo 12 mm longo, 4-5 mm lato, basi rotundato, ejus segmentis patentibus 13-17 mm longis, eis exterioribus oblongis, interioribus obovatis; staminodia paulo involuta, 3 mm lata, 7 mm longa, apice cuspidata, erecta, a staminibus distantia; capsula oblonga; perianthii tubo demum haud fisso.*

Corm with heavy fibrous outer coat; leaves linear, 2-4 dm long; scape 2-3 dm tall; pedicels 3-8 cm long; perianth-tube whitish with brown-purple midribs extending to tips of the segments, rounded at the base, 12 mm long and 4-5 mm wide; perianth-segments violet, 13-17 mm long, spreading at right angles to perianth-tube; outer segments oblong, inner ones obovate; staminodia slightly involute, 3 mm wide, 7 mm long, apically cuspidate, standing erect and well apart from stamens; filaments 1 mm long, anthers retuse, channeled on back, 4-5 mm long; capsule oblong; perianth-tube not splitting as capsule matures; chromosome number $2n = 32$.

Holotype. 0.5 mi W of Stone at junction of road to Stone with main island axis road, San Clemente I., Los Angeles Co., 1395 ft., April 3, 1965, *T. F. Niehaus 407* (UC, 1200400).

Brodiaea kinkiensis is known at present only from San Clemente I. One previous and fragmentary collection was cited as *B. filifolia* Wats. by Hoover (1939) (*Murbarger 219*, UC). It is probable that *B. kinkien-*



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