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TAXONOMY OF THE *ALLIUM TRIBRACTEATUM* (ALLIACEAE) COMPLEX

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ABSTRACT

Allium tribracteatum and related species present a confusing array in California. Previous attempts at classification have been largely unsuccessful and keys that are available are unworkable. Herbarium and field studies were initiated to ascertain if previously overlooked characteristics could be found that would elucidate relationships within the group. Members of the complex were examined morphologically and cytologically. Based on these investigations four of the seven previously described taxa are considered valid: *A. cratericola, A. obtusum, A. tribracteatum,* and *A. yosemitense. Allium tribracteatum* is redefined and *A. obtusum* is divided into two varieties. *Allium obtusum* var. *conspicuum* var. n. is described. A key to the species is presented and relationships within the complex are discussed.

Key words: Alliaceae, *Allium tribracteatum, Allium cratericola, Allium obtusum, Allium yosemitense, Allium obtusum* var. *conspicuum,* taxonomy.

INTRODUCTION

The *Allium tribracteatum* Torr. complex belongs to a group of North American species referred to the *falcifolium* alliance by Ownbey (Saghir et al. 1966). The complex differs from most other species in the alliance by having more or less broadly concave-convex leaves, the margins of which are nearly equal in length, i.e., the leaves are not falcate. Seven taxa have been proposed in the complex in various specific and varietal combinations.

The species belonging to the *Allium tribracteatum* complex are endemic to California with their distribution centering in the Sierra Nevada. One species, *A. cratericola* Eastw., extends into the North Coast Ranges and into the Transverse Ranges in southern California. The complex is characterized by its concave-convex leaves which are decumbent and usually greatly exceed the scape in length. The scapes are low with the more or less compact umbels borne near the soil surface. As with most other members of the *falcifolium* alliance, the scape and leaves break off at the soil surface after the capsule matures. A "tumbleweed" type of seed dispersal occurs as umbels are blown along the ground surface.

As is not unusual in western North America, previous investigators (Jones 1902; Jepson 1923; Ownbey 1959; Mingrone 1968; Munz 1974) have been handicapped by a lack of representative material on which to base their taxonomic decisions. For example, prior to this investigation only five collections from two localities were known for *Allium yosemitense* Eastw. This has led to misinterpretations of morphological variation and reliance on inconsistent characteristics, chiefly leaf number (one or two per scape) to separate taxa. Anyone using the available keys to determine unknowns belonging to the complex is aware of how ambiguous and unsatisfactory they are.

This investigation was undertaken to increase the number of specimens avail-

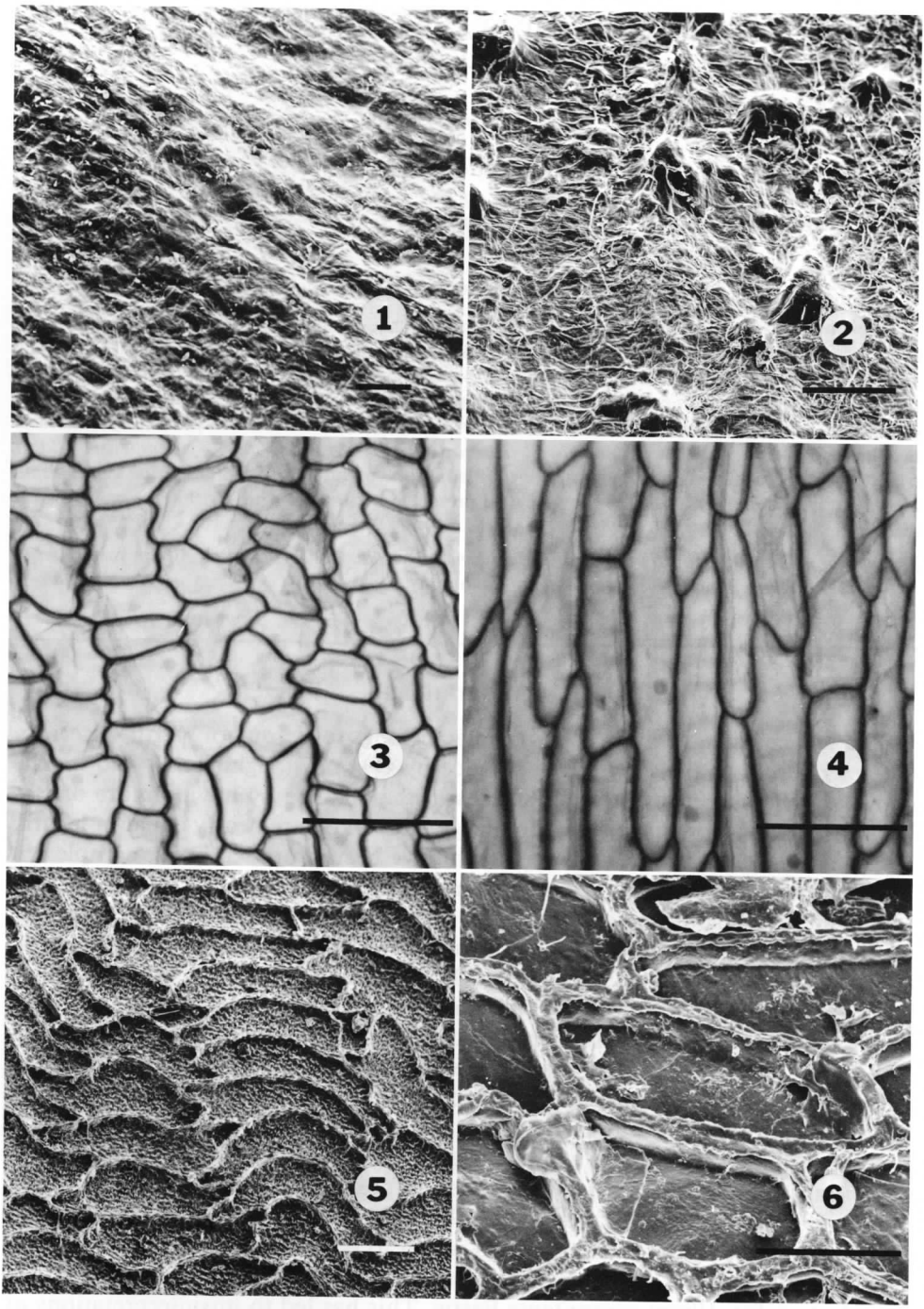

Fig. 1–6. Bulb-coat reticulation and inner leaf-base epidermal cells of the *Allium tribracteatum* complex.—1. *A. cratericola* bulb-coat.—2. *A. yosemitense* bulb-coat.—3. *A. cratericola* epidermal cells.—4. *A. yosemitense* epidermal cells.—5. *A. tribracteatum* bulb-coat.—6. *A. obtusum* var. *obtusum* bulb-coat. (Scale bars = 100 μm.)

Table 1. Chromosome numbers of the *Allium tribracteatum* complex. All collections are from California; vouchers are in CPH.

Taxon	*n*	Collection
A. cratericola	7	4.5 km N of Hwy 140 on Hwy 49, Mariposa Co., 17 Apr 1970, *McNeal 491.*
	7	Hillside E of Redhills Rd., 3.0 km S of Hwy 120 between Yosemite Jct. and Chinese Camp, Tuolumne Co., 19 Apr 1973, *McNeal 1278.*
	14	Table Mtn., W of Cherokee Rd., 10 km S of Hwy 70 at the Cherokee exit, Butte Co., 1 Apr 1977, *McNeal 2011.*
A. obtusum var. *obtusum*	7	Ridgetop above Hwy 88, 1.7 km E of Lumberyard R.S., Amador Co., 23 June 1975, *McNeal 1813.*
var. *conspicuum*	7	S Fork of the Yuba River ca. 1.7 km W of Washington, Nevada Co., 9 May 1975, *McNeal 1596.*
	7	Ridgetop above Hwy 88, 1.7 km E of Lumberyard R.S., Amador Co., 23 June 1975, *McNeal 1814.*
	7	Rest stop on Hwy 20, 30 km E of Nevada City, Nevada Co., 7 May 1976, *McNeal 1909.*
A. tribracteatum	7	3.5 km E of Long Barn on Hwy 108, 30 Apr 1976, *McNeal 1902.*
A. yosemitense	7	1.0 km N of Signal Pk. L.O., Chowchilla Mts., Mariposa Co., 17 June 1976, *McNeal 1913.*

able for study, to analyze all new and extant herbarium material for previously undetected morphologic characteristics on which to base an interpretation of the taxa involved and to construct a more satisfactory key to these taxa.

METHODS AND MATERIALS

As part of a revision of *Allium* in California we have studied a large number of specimens from American herbaria (CAS, CHSC, CPH, DAV, DS, FSC, GH, JEPS, MO, ND, NY, POM, RSA, UC, US, WS) and have made extensive field observations. Voucher specimens and bulbs of putative taxa were collected over a period of years. Bulbs were grown at Stockton, California, for determination of chromosome numbers. We used aceto-orcein squashes for all counts, which were made on pollen mother cells from fresh buds. For investigation of bulb-coat development the adaxial epidermis was peeled from the base of the inner foliage leaf and mounted to ascertain cell shape and arrangement. Mature bulb-coats, developed from this epidermal layer (McNeal and Ownbey 1973) were removed, sputter coated with gold-palladium, and examined on an ETEC SEM.

RESULTS AND DISCUSSION

Much of the confusion surrounding the delimitation of taxa in the *Allium tribracteatum* complex is due to the reliance on leaf number by previous investigators. In two species of the complex, *A. tribracteatum* and *A. yosemitense,* we have found only two-leaved individuals. In the other two species, *A. cratericola* and *A. obtusum* Kell., however, there are populations that are exclusively one-leaved, exclusively two-leaved, and mixed in this regard. This has resulted in

confusion of species boundaries, particularly between *A. tribracteatum* and *A. obtusum* and unwarranted fragmentation of *A. cratericola* into segregate species.

Our investigation has demonstrated that the presence or absence of bulb-coat reticulation and the shape and pattern of the epidermal cells forming this layer are more reliable than leaf number in delimiting species boundaries.

Bulb-coat reticulation results from the sclerification of the adaxial and radial walls of the inner epidermis of the inner foliage leaf base (McNeal and Ownbey 1973). This layer is exposed annually by the disintegration of surrounding bulb tissues. If only the adaxial wall is lignified a cellular pattern does not emerge; however, the cell shape can be determined in these instances by making a peel of the epidermis prior to anthesis.

Allium cratericola and *A. yosemitense* differ from the other two taxa by their lack of cellular reticulation (Fig. 1, 2) and their more robust stature. Peels indicate that the epidermal cells of *A. cratericola* are quadrate or polygonal and seldom more than twice as long as broad (Fig. 3). In *A. yosemitense* the cells are vertically elongate and two to five times as long as broad (Fig. 4). A number of other, more readily discernable characters can be used to differentiate between these species.

Allium tribracteatum and *A. obtusum* both have well-defined patterns of cellular reticulation. In *A. tribracteatum* (Fig. 5) the cells are more or less transversely elongate and form an irregular pattern. In *A. obtusum* (Fig. 6) the cells are quadrate to rectangular. On the basis of leaf breadth, umbel size, and the shape and color of the perianth segments *A. obtusum* can be divided into two varieties, variety *obtusum* with both one- and two-leaved forms and variety *conspicuum* Mortola & McNeal with only a single leaf.

Other California species, belonging to the *falcifolium* alliance, that may be confused with members of the *Allium tribracteatum* complex are: *A. burlewii* A. Davids., *A. hoffmanii* Ownbey ex Traub, and *A. parvum* Kell. The first two are sympatric with *A. cratericola, A. burlewii* in southern California and *A. hoffmanii* in the North Coast Range. Both species can be distinguished by their smaller stature, narrower perianth segments, and stamens, which are equal to or exceed the perianth. *Allium parvum* is sympatric with *A. obtusum* along the Sierra Nevada crest, but differs in having falcate leaves.

With one exception chromosome numbers of all taxa in the complex are $n = 7$, the common number for North American species. The exception is a single population of *Allium cratericola* from Table Mtn., Butte Co., California, which is tetraploid (Table 1).

TAXONOMIC TREATMENT

The following key distinguishes species and varieties of the *Allium tribracteatum* complex. The characteristics used are the best that have been discovered for this purpose. Many of these are subject to rather wide variation, therefore successful use requires considerable understanding of the natural units involved, their distribution, and comparison with descriptions and accurately identified specimens. It is particularly important in collecting *Allium* to preserve the gray or brown coats surrounding the bulb as reticulation patterns will, normally, be visible only on these. In determining cell shape and reticulation patterns, observations should be made near the broadest portion of the bulb as shapes and patterns are usually distorted near the root pad and scape.

KEY TO THE *ALLIUM TRIBRACTEATUM* COMPLEX

1. Outer bulb coats with ± evident cellular reticulation
   2. Cells of the bulb-coat reticulation ± transversely elongate, forming an irregular pattern. Occurring on volcanic soils in Tuolomne Co., Calif. ..... 1. *A. tribracteatum*
   2. Cells of the bulb-coat reticulation quadrate, polygonal or rectangular. Occurring on granitic sands throughout the Sierra Nevada ..... 2. *A. obtusum*
      3. Umbels small, (2–)6–20(–30) flowered; perianth segments oblong-elliptic, obtuse, white with a prominant dark midrib; leaves narrow, 0.5–4(–5) mm broad ..... 2a. *A. obtusum* var. *obtusum*
      3. Umbels larger, 10–65 flowered; perianth segments lanceolate, acute, purple-pink, with darker midribs; leaves broader 2–9(–14) mm ..... 2b. *A. obtusum* var. *conspicuum*
1. Outer bulb coat lacking evident reticulation
   4. Scape 2–12.5 cm; pedicels 1–1.5 times the perianth; stamens ½–¾ as long as the perianth. Scattered through the North Coast Range, along the west base of the Sierra Nevada and in the Transverse Range ..... 3. *A. cratericola*
   4. Scape 6.5–23 cm; pedicels 1–3 times the perianth; stamens $^9/_{10}$ as long as to slightly exceeding the perianth. Restricted to midelevations in the Sierra Nevada from central Mariposa Co. to northern Merced Co. ..... 4. *A. yosemitense*

1. ALLIUM TRIBRACTEATUM Torrey, Pacif. Rail. Rep. 4 (Botany):148. 1857. TYPE: USA, CA, Tuolumne Co., hillsides, Duffield's Ranch, Sierra Nevada, 10 May 1853–54, *Bigelow s.n.* According to Jepson (Fl. Calif., p. 276) this locality is east Sonora, Tuolumne Co., CA (Holotype: NY! Isotypes: GH!, US!).

Bulb ovoid, 1–2 cm long, outer coats brownish, inner coats white, both with obvious transversely oblong, irregularly curved reticulations; leaves 2 per scape, linear, 1–3.5 mm broad, 1.5–3 times as long as the scape; scape 2–7 cm tall; bracts of the inflorescence 2–4 (usually 3), ovate, abruptly acuminate, rarely apiculate; pedicels 6–9(–16) mm long, 1–2 times as long as the perianth; perianth segments 6.5–8 mm long, lanceolate to ± elliptic, acute, white to pinkish or purplish with a darker midvein; stamens ⅔–¾ as long as the perianth segments, anthers dark purple; ovary obscurely crested with 3 acute processes not closely surrounding the style base, style included, shorter than the stamens, stigma punctate to capitellate or obscurely 3-lobed; seeds black and dull, $n = 7$.

DISTRIBUTION (Fig. 7): Tuolumne Co., California. Scattered on volcanic slopes and ridges between 1300 and 3000 m. Flowering late March through July.

Allium tribracteatum is a much misunderstood taxon, almost without exception specimens bearing this name belong to the two-leaved form of *A. obtusum* var. *obtusum*. In addition to its unique bulb-coat reticulation, *A. tribracteatum* differs from the latter in the placement of its ovarian crests at some distance from the style base and in having the style shorter than the stamens.

2. ALLIUM OBTUSUM Lemmon in Greene, Pittonia 2:69. 1890. TYPE: USA, CA, Plumas Co., subalpine regions of Gold lake, 26 June 1889. After careful search of major American herbaria no collection corresponding to the above data was located, leading to the conclusion that the holotype, if one existed, has been lost or destroyed. Neotype (designated here): USA, CA, Sierra Co., above Gold Lake turnoff, 2 June 1976, *McNeal 1918* (NY!: Isoneotype: CPH!).

=*Allium ambiguum* Jones, Contr. W. Bot. 10:18, Fig. 35. 1902. TYPE: USA, CA, Summit, Sierra Nevada, 26 July 1900, *Jones 6660* (Holotype: POM!; Isotype: GH!).

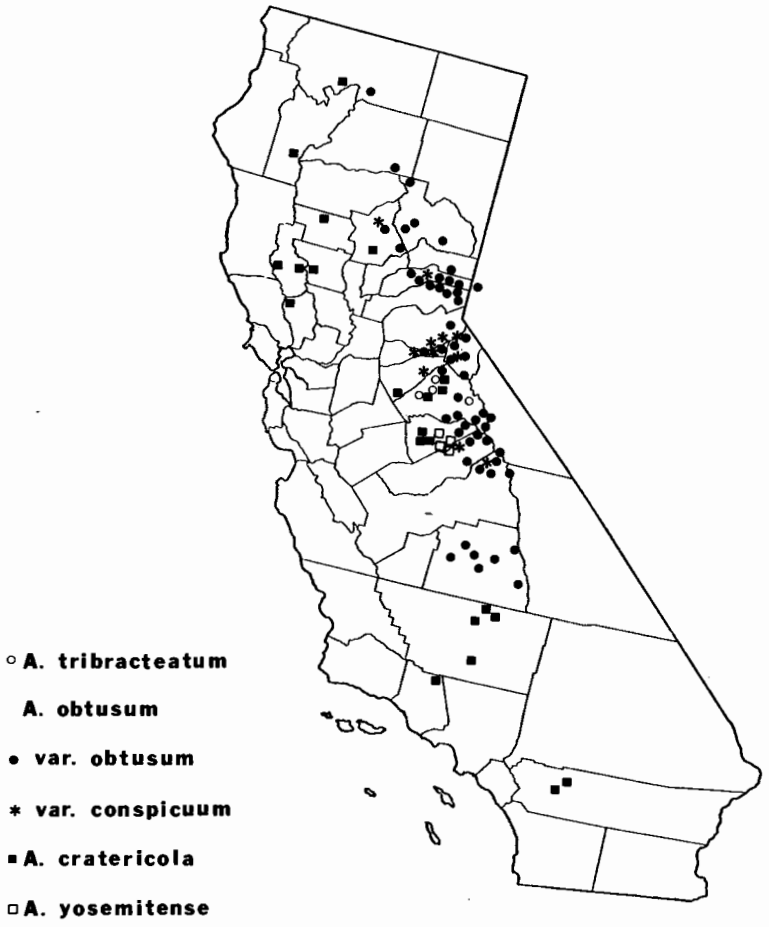

Fig. 7. Distribution of the *Allium tribracteatum* complex.

Bulb ovoid, 1–2 cm long, outer coats brown, inner coats white, both with evident quadrate, polygonal, or ± rectangular reticulations; leaves 1 or 2, linear, 0.5–14 mm broad, 1–3 times the length of the scape; scape 1.5–17 cm tall; bracts of the inflorescence 2–5, ovate, abruptly acuminate to apiculate; pedicels 2–14(–20) mm long, 1–2 times the length of the perianth; perianth segments 4–11.5 mm long, lanceolate to oblong-elliptic, white or purplish pink with darker midveins; stamens ½–9/10 as long as the perianth, anthers purple; ovary obscurely to ± prominently crested with 3 acute or obtuse processes closely surrounding the base of the style; style equal to or exceeding the stamens, included, punctiform, capitellate, or obscurely 3-lobed; seeds black and dull, $n = 7$.

DISTRIBUTION (Fig. 7): From Mt. Shasta, California, south through the Sierra Nevada to central Tulare Co., extending eastward into Washoe Co., Nevada, on Mt. Rose.

2a. ALLIUM OBTUSUM Lemmon in Greene var. OBTUSUM

Leaves 1 or 2 narrow, 0.5–4(–5) mm broad, 1.5–3(–4) times the length of the scape; scape 2–6.5 cm tall, rarely taller; pedicels 2–7(–11) mm long; perianth

segments 4–7(–9) mm long, oblong-elliptic, obtuse, white with dark purplish-brown midveins.

DISTRIBUTION (Fig. 7): As given above for the species. Granitic sands from 1500 to 3500 m.

Variety *obtusum* is a diminutive plant and easily overlooked owing to its white flowers which offer little contrast with the light substrates on which it normally grows. The variety consists of scattered populations, most of which are composed of either 1- or 2-leaved individuals. In a few instances, including the type locality, mixed 1- and 2-leaved populations occur. Approximately 75% of the homogeneous populations sampled and over 90% of the individuals in mixed populations are 1-leaved.

2b. ALLIUM OBTUSUM Lemmon in Greene var. **conspicuum** Mortola & McNeal, var. nov. TYPE: USA, CA, Amador Co., hillside above Hwy 88, 1.7 km E of Lumberyard R.S., Eldorado Nat. For., T.8N, R.15E, Sec. 10, 16 June 1973, *McNeal 1316* (Holotype: NY!).

Folium 1, latum, concavo-convexum, 2–9(–14) mm latum; scapo 2.7–11(–17.5) cm longo; umbella 9–64 floribus; segmenta perianthii lanceolatus, acutis, roses-purpureis (raro albus).

Leaves 1 per scape, 2–9(–14) mm broad, 1–2.5 times the length of the scape; scape 2.7–11(–17.5) cm tall; umbels 9–64 flowered; pedicels 3–14(–20) mm long; perianth segments 4–11.5 mm long, lanceolate, acute purplish pink with dark purple or greenish-purple midveins (rarely white).

DISTRIBUTION (Fig. 7): Scattered in the Sierra Nevada from Butte Co. south to Fresno Co. Granitic Sands from 800 to 3000 m. Most collections of this variety come from Placer, El Dorado, Amador, and Alpine counties but possibly this represents only the more intensive collecting in this area by the authors.

The varietal name refers to the fact that, in contrast to var. *obtusum,* its size, broader leaves, and flower color make the variety quite conspicuous against the light-colored substrates on which it normally grows.

While both varieties of *Allium obtusum* show considerable overlap in size characters, there is little difficulty in differentiating between them. In the type locality, var. *conspicuum* is sympatric with a two-leaved population of var. *obtusum.* Due to its larger size, flower color, and the fact that anthesis occurs one to two weeks later than var. *obtusum,* there is no difficulty in classifying individual specimens. No hybridization between the two varieties is evident.

3. ALLIUM CRATERICOLA Eastwood, Leafl. W. Bot. 1:132. 1934. TYPE: USA, CA, Napa Co., Crater area, Mt. St. Helena, 1 May 1918, *Eastwood s.n.* (Holotype: CAS!; Isotypes: DS!, GH!, POM!, US!).

=*Allium parvum* Kell. var. *brucae* Jones, Contr. W. Bot. 10:12, Fig. 16. 1902. TYPE: USA, CA, Butte Co., Yankee Hill, 17 Apr 1897, *Bruce 1907* (Holotype: POM!; Isotype: US!).

=*Allium parvum* Kell. var. *jacintense* Munz, Manual S. Calif. Bot. 86: 597. 1935. TYPE: USA, CA, Riverside Co., Kenworthy, San Jacinto Mts., 4650 ft, 21 May 1922, *Munz and Johnson 5512* (Holotype: POM!; Isotypes: DS!, GH!, POM!, UC!, WS!).

Bulb ovoid, 1.5–2.5 cm long, outer coats brown or gray, inner coats white, both lacking cellular reticulation; leaves 1 or 2 per scape ± linear, 1–13(–21) mm broad. 1.5–3(–4.5) times as long as the scape; (2–)3.5–9(–12.5) cm tall; bracts of the inflorescence 2–4(–6), ovate, broadly acuminate, often apiculate; pedicels rela-

tively stout, 5–18 mm long, 1–1.5 times as long as the perianth; perianth segments 7–14 mm long, lance-oblong, elliptic, or ± oblanceolate, obtuse, pink to purplish with darker midribs; stamens ½–¾ as long as the perianth, anthers yellow; ovary crested with 3, short, acute or obtuse processes; style included, ca. equal to the stamens, stigma capitellate to capitate; seed black and dull. $n = 7$ or 14.

DISTRIBUTION (Fig. 7): From Napa Co., California, through the North Coast Range to southern Siskiyou Co., scattered through the Sierra Nevada foothills from Butte Co. south to Mariposa Co. and from there disjunct to northern Kern Co. and the Transverse Ranges in southern California. Serpentine, volcanic and granitic soils from 350 to 2300 m.

Like *Allium obtusum, A. cratericola* has both 1- and 2-leaved forms. Southern California material is exclusively 2-leaved while in the Sierra Nevada foothills most populations are 1-leaved except for two populations in Mariposa Co., which are 2-leaved. In the North Coast Range most populations are 1-leaved except for several populations in Lake and Colusa counties, which have both leaf forms.

Munz (1935) described the 2-leaved southern California material as *Allium parvum* var. *jacintense,* later (1974) he reduced this to synonomy with *A. tribracteatum.* Because none of the specimens have reticulate bulb-coats, this latter placement is incorrect. Most of the specimens we have studied bear annotation labels reading "*Allium jacintense* Mingrone and Ownbey." This combination has never been validly published. In view of the close similarity between the southern California material and 2-leaved specimens from mixed populations in Lake and Colusa counties, we conclude that these are conspecific and not sufficiently different to warrant recognition even at the varietal level.

4. ALLIUM YOSEMITENSE Eastwood, Leafl. W. Bot. 1:132. 1934. TYPE: USA, CA, Mariposa Co., Head of Bridal Veil Falls, Yosemite Valley, June 1922, *Michaels s.n.* (Holotype: CAS!; Isotype: GH!).

Bulbs ovoid, 2–3 cm long, outer coats dark brown, inner coats white, both lacking definite reticulation; leaves 2 per scape, linear, 2–18 mm broad, 1–3 times as long as the scape; scape 6–23 cm tall; bracts of the inflorescence 2–4 (usually 3), ovate, acuminate-apiculate; pedicels 7–34 mm long, 1–2+ times the length of the perianth; perianth segments 7–15 mm long, linear-oblong, acute, white to pink with darker midveins; stamens $\frac{9}{10}$ as long as to slightly exceeding the perianth, anthers purple; ovary obscurely lobed with 3, 2-lobed processes; style exserted stigma capitate; seed black and dull. $n = 7$.

DISTRIBUTION (Fig. 7): Iron Mtn., Madera Co., California, Signal Peak (Devil Peak), Chowchilla Mts. and the southwestern portion of Yosemite National Park, Mariposa Co. Sandy soils on the margins of large granite slabs, 800–2200 m. For a detailed habitat description and photographs of *A. yosemitense* see Howard (1980).

Allium yosemitense is a narrow endemic occurring in five known populations in the central Sierra Nevada. It is distinctive in its large stature, long, usually exserted, stamens and long ± spreading pedicels. Its habitat on the margins of, and in cracks in, large granite slabs is also unique.

LIST OF EXSICCATAE

More than 400 herbarium specimens were examined during this investigation. Along with field observations these form the basis for our morphological and distributional data. Lists of these specimens are available from the junior author.

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