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A BIOSYSTEMATIC STUDY OF *TRITELEIA* (LILIACEAE).
I. REVISION OF THE SPECIES OF SECTION *CALLIPRORA*¹

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INTRODUCTION

The question may well be asked why it is necessary to present still another taxonomic treatment of a group so recently studied. Indeed at the time a decision was made to examine cytologically the members of the genus *Triteleia* no thought was given to the possibility that a reexamination of their systematics might be called for. In 1941, R. F. Hoover had published "A systematic study of *Triteleia*" and this was followed by "Further observations on *Brodiaea* and some related genera" (Hoover, 1955) and "Observations on California plants IV" (Hoover, 1957).

According to Hoover (1941), *Triteleia* may be separated into three sections. Of the three, *Calliprora* is the section that was chosen for intensive study. With the discovery of new taxa and the finding that plants from north of San Francisco Bay, from the San Gabriel Mts. in Los Angeles County, and from Guadalupe Island, Mexico, which Hoover had considered to be conspecific, really belonged to three species seemed to indicate that a critical look should be taken of all the members of the section. It was also discovered that types had never been determined for a number of taxa, necessitating the selection of neotypes. The taxonomic portion of this study is being presented at this time in order that the names may be used in future papers.

As will be shown later, members of section *Calliprora* are in a very active state of speciation and as a result they present a number of problems for the taxonomist. It might be argued that each of the reproductively isolated cytotypes should be accorded taxonomic recognition if we are accurately to portray the biological condition existing within the group. To do this would mean the creation of a very large number of names for plants that cannot be satisfactorily differentiated by the usual taxonomic methods. For the working taxonomist this would lead to utter chaos. The other alternative is to give formal standing only to assemblages that can be differentiated on a morphological basis. This is not an entirely satisfactory solution either. No one treatment will satisfy all. My philosophy is that a

¹ In Jepson's Manual of the Flowering Plants of California (1923) and Munz and Keck's A California Flora (1959) these species are included in the genus *Brodiaea*.

systematic work fails in its major purpose if it does not permit the working taxonomist to bring together and recognize formally assemblages of plants that differ morphologically from other assemblages and which have distinct geographical or ecological distributions even though these groups may be composed of populations in which cryptic isolating mechanisms may be operating. It is on this basis that the following taxonomic treatment is offered.

MATERIALS AND METHODS

The present investigation which has been in progress for nearly ten years has, in addition to the usual field and herbarium studies, involved bringing together at Claremont of a large collection of living cultures grown from corms collected over most of the geographical range of the members of the section. This living material has been of great value in studying intra- and inter-populational variability, in performing hybridization experiments, in providing material for meiotic studies, and in determining karyotypes. Individual plants (and clones) where karyotypes have been determined and whose meiotic behavior has been studied are especially useful in attempting to work out the evolutionary history of the group.

All pot cultures were grown under uniform greenhouse conditions, and photographs do not necessarily show plants grown under optimum environmental conditions.

In the field, members of this section bloom from the middle of March until late August depending to a large extent upon the geographical area and altitude. Under uniform cultural conditions there is some variation in peak blooming dates but in all instances there is an overlap which allowed attempts at hybridization to be made between nearly all the taxa.

TAXONOMIC CHARACTERS

In common with many geophytes, plants of the species here under consideration possess relatively few morphological characters useful to the taxonomist. For the most part the taxa differ in quantitative rather than qualitative ways and the probable reasons for this will be considered in a later paper when the evolution of the group is discussed. In past treatments the nature of the scape, whether smooth or scabrous, and the anthers, whether white (or cream) or blue, have been accorded considerable importance; one reason being that on herbarium specimens they are conditions which can be determined readily. Unfortunately, these characters are of little taxonomic significance since all four conditions may be found in a single population. With but one exception, leaves are of minor importance, and many herbarium specimens lack leaves since they are usually withered, or nearly so, at the time that the plant blooms. Corms vary in size, probably influenced in some instances by ploidy level, but in general they are not of taxonomic importance in this section. They, too, are often lacking on herbarium specimens. The position of the perianth segments relative to the perianth tube also shows great variation and although it has been used, it is of little systematic value. All taxa within section *Calliprora*

possess flowers that are cream-colored or some shade of yellow, and both cream-colored and yellow-flowered forms may occur within a single subspecies. The golden-yellow flowers of one species is, however, distinct.

One morphological character I have found to be useful, though it too shows variation, is the nature of the stamen filament, whether triangular, rounded at the apex, or with some form of forked appendages (Fig. 1). The character of the perianth tube is also valuable, particularly when used in conjunction with the form of the stamen filaments.

GEOGRAPHICAL DISTRIBUTION

Members of section *Calliprora* are almost entirely confined to the state of California (Fig. 2) except for one subspecies which extends a short distance north into Oregon and one species which is confined to Guadalupe Island, Mexico. In altitude they range from near sea level to about 10,000 ft and are almost without exception confined to wooded areas ranging from the foothill woodland to upper montane coniferous forests.² One subspecies is occasionally found in grassland.

TAXONOMY

TRITELEIA Douglas *ex* Lindley, Bot. Reg. (Edwards), t. 1293, 1 Jan., 1830.

Type species: *T. grandiflora* Lindl. (*vide* Abrams, Ill. Fl. Pacific States 1: 401, 15 May, 1923).

KEY TO THE SECTIONS

- A. Stamens attached alternately at two levels, forming two rows *Eutriteleia* Hoover
- AA. Stamens all attached at the same level B
- B. Stamens alternately long and short *Calliprora* (Lindl.) Hoover
- BB. Stamens equal in length or nearly so *Hesperoscordum* (Lindl.) Hoover

Section *CALLIPRORA* (Lindl.) Hoover. (Type species, *Calliprora lutea* Lindl.)

KEY TO THE SPECIES

- A. Filaments of the longer stamens rounded at the apex B
- AA. Filaments of the longer stamens not rounded at apex C
- B. Perianth tube funnelform, 4–5 mm long. Lake, Napa, Solano, Monterey, and San Benito cos. $n = 8$ *T. lugens*
- BB. Perianth tube broad funnelform, 7–9 mm long; flowers golden-yellow. Guadalupe Is., Mex. $n = 8$ *T. guadalupensis*
- C. Filaments narrowly triangular or with short blunt appendages; perianth tube slender funnelform to nearly tubular, about equalling the segments in length; high elevations. Fresno, Kern, Los Angeles, Madera, Mariposa, Mono, and Tuolumne cos. $n = 8$ *T. dudleyi*
- CC. Filaments of the longer stamens with straight, incurving to very long recurving appendages; perianth tube much shorter than perianth segments, (nearly equal in one ssp.) funnelform to campanulate. Widely distributed in foothills and mts. from S. Oregon to Kern Co. and from San Mateo to San Luis Obispo cos. $n = 8, 7, (6), 5$, polyploids and aneuploids *T. ixioides*

² Plant community designations are those proposed by R. F. Thorne (in press).

Fig. 1. a. *Triteleia guadalupensis*.—b. *T. ixioides* ssp. *unifolia*.—c. *T. ixioides* ssp. *scabra*.

Fig. 2. Geographical distribution of *Triteleia* sect. *Calliprora*. Guadalupe Island, Mexico, is not shown on the map.

TRITELEIA DUDLEYI Hoover, Amer. Midl. Nat. 25: 86, 1941. Figs. 3, 4, 19

≡ *Brodiaea dudleyi* (Hoover) Munz, Calif. Fl., 1382, 1959.

Corm deeply seated; leaves usually 2, 3–8 mm wide, 1–3 dm long; scape 1–3.5 dm tall, smooth; bracts lanceolate-acuminate; inflorescence few- to

Fig. 3. Geographical distribution of *Tritoleia dudleyi*.

many-flowered, usually few; pedicels to 4 cm long; perianth pale yellow, tube slender-funnelform to tubular, ca. 12 mm long, about equalling the segments; longer filaments ca. 3.5 mm long, triangulate acuminate to oblong, terminal appendages lacking or short, thickened; shorter filaments ca. 1 mm long, narrowly triangular, sometimes almost lacking.

Holotype.—California: Tulare Co. Dennison's Trail, alt. 9,500 ft, region of Upper Tule River, vicinity of Mountain Lake, 30 July, 1895, *Dudley* 932 (DS!).

Etymology.—Named in honor of W. R. Dudley (1849–1911), professor of botany at Stanford University.

Chromosome number.— $n = 8$.

Distribution.—California: Fresno, Kern, Los Angeles, Madera, Mariposa, Mono, Tulare & Tuolumne cos. (Fig. 3) at altitudes of from 4,000 to about 10,000 ft, usually in upper montane coniferous forests where it occurs along edges of meadows and streams in moist soil.

The southernmost station for this species is in the San Gabriel Mts., near

Cloudburst Summit where it is found growing in a moist draw with grasses and sedges at about 6,000 ft, and below Alder Saddle in the Pinyon Flats area at 5,200 ft. The next occurrence of the species is in the Piute Mts. in Kern Co. In both the San Gabriel and Piute mountains it is found in the yellow pine forest.

Figure 4 was drawn from a plant collected at Mammoth, Mono Co., and shows a flower with blunt almost waxy appendages on the longer filaments similar to those on specimens from Cloudburst Summit. Many of the plants from the central part of the range of the species have filaments that are triangular and show no signs of an appendage. All specimens however have the characteristic long slender perianth tube which is about equal in length to the perianth segments. This species favors a more moist habitat than do any of the other members of the section.

Representative specimens.—Fresno Co., 10,000 ft, Big Margaret Lake in little ravinelet above shore of lake, subalpine forest, *Quibell 4086* (JEPS); Kern Co., Saddle Springs, N end of the crest of Piute Mt., loc. common in wet soil, 6,900 ft, *Twisselmann 7347* (CAS); Los Angeles Co., ca. 0.1 mi W of 6,000-ft marker W of Cloudburst Summit, Angeles Crest Hwy, *Lenz 24837* (RSA); Madera Co., Moraine Meadows, Mt. Lyell, 8,800 ft, *Akey 314* (UC); Mariposa Co., grassy damp land, Yosemite, 4,000 ft, *Jepson 4282* (JEPS); Mono Co., Mammoth Lakes Post Office, *Benson 11239A* (POM); Tulare Co., Summit Lake, 9,450 ft, *Niehaus 611* (JEPS, UC).

TRITELEIA GUADALUPENSIS Lenz, *Aliso 7*: 145–147, 1970.

Figs. 5, 20

Corms to 3.5 cm in diam with thick fibrous coats extending into a neck; leaves to 7.5 dm long, 3.2 cm wide; scape to 5 dm tall, smooth or slightly scabrous; pedicels 2.5–4.5 cm long at anthesis; perianth golden-yellow, broadly funnellform, tube 7–9 mm long, segments spreading, 12–14 mm long, 4–5 mm broad, each with a dark midvein; filaments broadly rounded, broader at the tip than at the base, longer ones 5–6 mm long and 3 mm wide, shorter ones 2–3 mm long; anthers 2.5–3 mm long, pale yellow; ovary twice the length of the stipe.

Holotype.—Mexico: Baja California, Guadalupe Is. Occasional in rock crevices, cliff on south side of canyon, E slope of El Picacho, ca. 350 m, 4 March, 1965, *Moran 12036* (SD!, isotype RSA!).

Etymology.—The specific name refers to Guadalupe Is., the only known location where this species occurs.

Chromosome number.— $n = 8$.

Distribution.—Mexico: known only from Guadalupe Is., Baja Calif.

Representative specimens.—Guadalupe Is., head of canyon W of Lobster Camp, *Weber & McCoy 12026* (UC).

The flora of Guadalupe Island, which lies about 165 miles off the mainland of Baja California, is composed of 164 species of higher plants of which 31 are endemic (Raven, 1963). Of the 164 species a number have their closest affinities with species found on the California mainland well to

Fig. 4. *Triteleia dudleyi*.—a. Inflorescence, $\times 1\frac{1}{2}$.—b. Flower opened to show the nature of the stamen filaments, $\times 3$.

the north of the Channel Islands. Among the plants with such northerly distributions are: *Polypodium scouleri* Hook. & Grev., *Polystichum munitum* Klf., *Pinus radiata* D. Don., *Ribes sanguineum* Pursh., *Epilobium minutum* Lindl. ex Hook., and *Eriophyllum lanatum* var. *grandiflorum* (Gray) Jeps. To this list may be added *Triteleia guadalupensis* which is more closely related to *T. lugens* of Lake, Napa, and Solano counties (with disjunct

Fig. 5. *Triteleia guadalupensis*.—a. Inflorescence, $\times \frac{3}{4}$.—b. Flower opened to show the nature of the stamen filaments, $\times 2\frac{1}{4}$.

populations in Monterey and San Benito counties) than it is to plants in southern California. Although Hoover (1941) included the plants from Guadalupe Island and those from Los Angeles Co. with *T. lugens* it is quite evident that the insular material is clearly distinct and is indeed one of the best-marked species in the genus with its large umbels of golden-yellow flowers, peduncles to 2 ft tall and leaves as much as 1.5 in wide. It should make a fine garden plant as soon as corms become available.

I am indebted to Dr. Reid Moran, San Diego Museum of Natural History, for the gift of a single corm of this distinctive plant. All stock of the species now in cultivation has been derived from this single propagule. Although the original plant tended to be self-incompatible it set a few seeds each year and it is from these seeds that the present population has been produced.

TRITELEIA IXIODES (Ait. f.) Greene

KEY TO THE SUBSPECIES

- A. Plants with a single relatively short linear-lanceolate leaf, external portions of flowers usually deeply stained with anthocyanin, moderate elevations. Mariposa to Siskiyou cos., Calif., Jackson Co., Oregon. *n* = 7, 8 ssp. *unifolia*
- AA. Plants with 1-2 linear leaves B
- B. Perianth white or cream, purplish outside, tube nearly as long as the perianth segments. San Luis Obispo Co. *n* = 7 ssp. *cookii*
- BB. Perianth yellow, tube much shorter than segments C
- C. Anthers blue or cream-colored, filaments with short spreading, straight or incurved appendages, moderate elevations. Southern Oregon to Fresno Co. *n* = 7, 21 ssp. *anilina*
- CC. Anthers cream-colored, yellow (occasionally blue), filaments with long slender, often recurving appendages D
- D. Perianth tube 7-10 mm long. San Mateo to San Luis Obispo cos. *n* = 7 ssp. *ixioides*
- DD. Perianth tube 3-7 mm long. Shasta to Kern cos. *n* = 5, (6), 8, polyploids and aneuploids ssp. *scabra*

TRITELEIA IXIODES (Ait. f.) Greene ssp. *ixioides*

Figs. 6, 7, 21

- = *Ornithogalum ixioides* Ait. f., Hort. Kew, ed. 2, 2: 257, 1811 (Basionym).
- ≡ *Themis ixioides* (Ait. f.) Salisb., Gen. Pl. 85, 1866.
- ≡ *Milla ixioides* (Ait. f.) Baker, J. Linn. Soc. Bot. 11: 383, 1871.
- ≡ *Brodiaea ixioides* (Ait. f.) Wats., Proc. Amer. Acad. Arts 14: 238, 1879 (not Sims, 1823).
- ≡ *Triteleia ixioides* (Ait. f.) Greene, Bull. Calif. Acad. Sci. 2(6): 142, 1886.
- ≡ *Hookera ixioides* (Ait. f.) Ktze., Rev. Gen. Pl. 1: 712, 1891.
- ≡ *Calliprora ixioides* (Ait. f.) Greene, Manual of the Bot. of the Region of San Francisco Bay, 319, 1894.
- = *Calliprora lutea* Lindl. Bot. Reg. (Edwards) 19: pl. 1590, 1833 [*Holotype*: N. Calif., Douglas (CGE!)].
- ≡ *Brodiaea lutea* (Lindl.) Mort., Herbertia 7: 318, 1894.

Corms usually deeply seated, to 2.5 cm in diam; leaves usually 2, to 15 mm wide and 4 dm long; scape 2–8 dm tall, smooth or slightly scabrous near the base; pedicels to 7 cm long, spreading and curving upwards; perianth yellow, sometimes pinkish purple on the exterior this accentuated upon drying; tube 7–10 mm long, the segments 10–15 mm long, spreading, lanceolate, outer ones acute, inner somewhat obtuse; filaments broad, flat, appendages long, usually recurved, tapering, the longer filaments 4–5.5 mm mm long including appendages, shorter ones to 3 mm long including appendages; anther to 2 mm long, yellow or blue.

Typification.—William T. Aiton's description of *Ornithogalum ixioides* was based upon material collected by Archibald Menzies and introduced into cultivation in 1796. In the original description, the plant was noted as "Nat of California" and "Fl. May and June." Menzies was botanist and surgeon on the Vancouver Expedition which visited Monterey on three occasions between 1792 and 1794. The first visit was from November 26, 1792, until January 14, 1793; the second was from October 30 until November 6, 1793, and the last from November 6 until December 2, 1794. All three visits were at times when ssp. *ixioides*, which is common in the Monterey area, would not have been in bloom. It is unlikely that Menzies was able to collect corms which would have been dormant and it seems more likely that he was able to find a few seeds which had not yet been shed from their capsules. Since it requires at least three years from seed to obtain blooming-size corms it is reasonable to assume that seed received by the Royal Botanic Garden, Kew, in 1796 could well have produced plants which were described by Aiton in 1811. Aiton's specimens are preserved at the British Museum (Natural History). However according to Mr. John Lewis (pers. com.) there is no sheet of *Ornithogalum ixioides* at that institution. Either no specimen was made or it was destroyed by fire during World War II.

In 1833, John Lindley described *Calliprora lutea* from material collected in California by David Douglas and his type is preserved at Cambridge (CGE). Due to the loss of Douglas's journal describing his travels in California it is impossible to know exactly where or when his collections were made. He arrived at Monterey on December 22, 1830, where he took up residence with a British merchant, William Edward Petty Hartnell, who was to be his host for the next two years. During the spring of 1831, Douglas collected widely in the Monterey area. In flower *Calliprora lutea* (= *Triteleia ixioides* ssp. *ixioides*) is a conspicuous plant and it is reasonable to assume that Douglas collected the species somewhere in the Monterey area. Later that spring he made a trip south as far as Santa Barbara but if he followed the Camino Real linking the California missions between Monterey and Santa Barbara, much of his route would have taken him too far inland for him to find the species.

On November 23, 1831, Douglas wrote to W. J. Hooker telling him of his collecting in California and he ended his letter by saying, "This . . . with many others, I trust you may yet have the pleasure of describing from living specimens, as I have sent to London upwards of one hundred and fifty nondescript plants, which I hope will bloom next season. . . ." How or when the specimens were sent is not known. The plate accompanying the

Fig. 6. Geographical distribution of *Triteleia ixioides* ssp. *ixioides*.

original description of *Calliprora lutea* (Bot. Reg. [Edwards] pl. 1590) is dated, 1 June, 1833. Lindley says only "Received from Mr. Douglas as 'a new genus allied to *Brodiaea*;' it was found in Northern California, but in what situations we are not informed. It proves to be a hardy, very handsome, bulbous plant . . . flowering in July." If the corms had been sent in 1831, the plants would have bloomed the following July at which time it is likely that the drawing was made. The following plate (1591) shows *Mimulus roseus* Dougl. ex. Lindl. (= *M. lewisii* Pursh) and it too is dated 1 June, 1833, but here Lindley says, "This beautiful Monkey-flower was sent by Mr. Douglas from Northern California in 1831."

The farthest north in California that Douglas traveled was 38° 45' N, the latitude of Fort Ross (Sonoma Co.) where it is recorded that he spent one night. *Triteleia lugens* is found at a few locations in Napa, Lake, and Solano counties but Douglas's visit was in late July long after the species would have been in flower and there is no evidence that he collected but the one yellow-flowered species of *Triteleia*.

In the absence of a type of Aiton's *Ornithogalum ixioides* it seems appropriate to designate the type of Lindley's *Calliprora lutea* as the neotype of *Triteleia ixioides* (Ait. f.) Greene ssp. *ixioides*. In addition to the holotype of Lindley's plant there is also a colored plate that illustrates the features of the species.

Distribution.—California: San Mateo, Santa Clara, Santa Cruz, San Benito, Monterey, and San Luis Obispo cos. (Fig. 6) where it is found in the

closed-cone coniferous forest and foothill woodland plant communities at elevations of 100–5,000 ft. It is sometimes found on serpentine.

Etymology.—*Ixia*-like, referring to the resemblance of the flowers to those of the iridaceous genus, *Ixia*.

Chromosome number.— $n = 7$.

Representative specimens.—Monterey Co., Los Burros Cr., 7.5 mi SW of Jolon, *Hardham* 6280 (RSA); San Benito Co., N side of Fremont Peak, S of San Juan Bautista, 2,800 ft, *Stebbins* 3787 (UC); San Luis Obispo Co., rd from north fork of San Simeon Cr. to Rocky Butte, *Hoover* 9082 (CAS); San Mateo Co., King's Mt., *Thomas* 504 (DS); Santa Clara Co., Bald Peak, Mt. Hamilton Range, *Dudley* 419 (DS); Santa Cruz Co., Miller's Ranch, on summit between Gilroy and Watsonville, *Elmer* 4463 (CAS, DS, NY, OSC, UC, US).

Some collections of ssp. *ixioides* show a flush of anthocyanin on the outside of the perianth segments and this becomes intensified upon drying. This condition is also found in *T. ixioides* ssp. *cookii*. In the garden, ssp. *ixioides* blooms several weeks later than the other members of the section, a characteristic noted by Hoover. There is less morphological variation in ssp. *ixioides* than in most of the members of this section; however, plants collected by Stebbins (3290, UC), four miles east of Monterey at the edge of a field among *Quercus agrifolia* Neé have flowers that are smaller than normal for this subspecies and they are superficially like those of *T. lugens* but the stamens are not characteristic of that species. *Stebbins* 3291, collected at the same locality and on the same date, are typical of ssp. *ixioides*.

TRITELEIA IXIOIDES (Ait. f.) Greene ssp. ***anilina*** (Greene) Lenz, comb. nov.
Figs. 8, 9, 22

- = *Calliprora scabra* Greene var. ?*anilina* Greene, *Erythea* 3: 126, 1895 (Basionym).
- = *Calliprora anilina* (Greene) Heller, *Muhlenbergia* 2: 14, 1905 [as *analina*].
- = *Brodiaea scabra* (Greene) Baker var. (?) *anilina* (Greene) Baker, *Gard. Chron. Ser. 3*, 20: 459, 1896.
- = *Brodiaea lutea* (Lindl.) Mort. var. *anilina* (Greene) Munz, *Calif. Fl.*, 1382, 1959 [as *analina*].
- = *Triteleia ixioides* (Ait. f.) Greene var. *anilina* (Greene) Hoover, *Amer. Midl. Nat.* 25: 90, 1941 [as *analina*].
- = *Triteleia anilina* (Greene) Hoover, *Pl. Life* (*Herbertia*) 1: 20, 1955 [as *analina*].

Corms usually small, deeply seated, less than 1.5 cm in diam; leaves 2, slender, usually less than 2.5 dm long; scape not more than 3 dm tall, scabrous or smooth; inflorescences mostly few-flowered; perianth pale to bright yellow, tube short, 3–6 mm long, rather broad; segments to 12 mm long, spreading with conspicuous dark midvein; filaments usually rather narrow, appendages short, spreading, straight or incurved, the longer fila-

Fig. 7. *Triteleia ixioides* ssp. *ixioides*.—a. Inflorescence, $\times 1\frac{1}{2}$.—b. Flower opened to show the nature of the stamen filaments, $\times 2\frac{1}{2}$.

Fig. 8. Geographical distribution of *Triteleia ixioides* ssp. *analina*.

ments to 3.5 mm long, shorter ones sometimes almost obsolete; anthers more often blue than cream-colored.

Neotype here designated.—California: Alpine Co. Just beyond Lake Alpine on Ebbetts Pass Rd., abundant, anthers cream-colored, short broad tube, mostly green-veined flower parts, 27 July, 1971, Lenz 24896 (RSA, duplicate neotype US) (Fig. 18a).

Etymology.—Uncertain. *Aniline* comes from the Sanskrit, *nila* which refers to dark blue and may in this instance refer to the blue anthers.

Chromosome number.— $n = 7, 21$.

Distribution.—Jackson Co., Oregon, south to Tulare Co. (Fig. 8), mostly on the western slopes of the Sierra Nevada at elevations of from 2,800 to 10,000 ft in upper montane coniferous forests where it grows in open places mostly in moist, sandy or gravelly soils.

Fig. 9. *Tritelleia ixioides* ssp. *analina*.—a. Inflorescence, $\times 2$.—b. Flower opened to show the nature of the stamen filaments, $\times 3\frac{1}{4}$.

Representative specimens.—California: Alpine Co., Bear Valley, edge of woods, 6,800 ft, *Lenz* 24868 (RSA); Amador Co., in rocky soil under coniferous forest beside hwy 88 between Tragedy Springs and Ham's Station, *Tucker* 2765 (OSC); Butte Co., Jonesville, 1,550 m, in flat bare opening in pine woods, *Copeland* 351 (CAS, DS, GH, RSA, UC, US); Calaveras Co., sandy flat near North Fork of Stanislaus River, 5,500 ft, *Stanford* 594 (RSA); Eldorado Co., near Echo Camp in open places in the forest in damp granite soil, 7,000 ft, *Heller* 12164 (DS, OSC, PHIL, UC); Fresno Co., Bear Lake, vic. of Huntington Lake, 6,900–7,100 ft, *Russell* 39 (DS); Inyo Co., Andrews Camp, Sierra Nevada above Bishop, *Brandeggee* s.n. (UC); Mari-

posa Co., Yosemite Nat'l. Park, Porcupine Flat, ca. 8,100 ft, *Dourley & Everett 41190* (RSA); Mono Co., E slope of Sonora Pass, open slopes in forested country, 8,500 ft, *Peirson 19379* (RSA); Nevada Co., near Grass Valley, *Heller 13216* (DS); Placer Co., north fork of the north fork of American River, 4,400 ft, *French 365* (UC); Plumas Co., Long Lake, gravel, exposed slopes, 6,800 ft, *Hall 9350* (UC); Shasta Co., Dick's Meadows, 16 mi W of Burney Falls, *Cantelow 2575* (CAS); Sierra Co., 3 mi N on Gold Lake rd from hwy 49, *Niehaus 586* (UC); Siskiyou Co., Castle Lake, in north-facing cirque 14 mi SW Mt. Shasta, 5,434 ft, *Culbertson 95* (RSA); Tehama Co., dry ground, Mineral, 4,800 ft, *Grinnell s.n.* (JEPS); Trinity Co., on dry ridge, rd to White Rock Ranger Station, 5,100 ft, *Alexander & Kellogg 5697* (DS, UC, US); Tulare Co., Kern River, Second Dry Meadow Cr., *Dudley 670* (DS); Tuolumne Co., Strawberry, 5,400 ft, *Jepson 6469* (JEPS).—Oregon: Jackson Co., in the foothills of the Siskiyou Mts. near the line of the So. Pac. Railroad, *Applegate 699* (DS).

TRITELEIA IXIODES (Ait. f.) Greene ssp. *cookii* (Hoover) Lenz, comb. nov.
Figs. 10, 11

≡ *Triteleia ixioides* (Ait. f.) Greene var. *cookii* Hoover. Plant Life (Herbertia) 1: 20, 1955, (Basionym).

≡ *Brodiaea lutea* (Lindl.) Mort. var. *cookii* (Hoover) Munz, Supplement to Calif. Fl., 177, 1968.

Leaves 2, to 2 dm long, 1.5 mm wide; scape to 2.5 dm tall, slightly scabrous; inflorescences many-flowered; pedicels to 12 cm long; perianth cream-white to pale yellow, deeply and conspicuously colored purplish pink on outer portions of the segments, tube 6–10 mm long, segments about the same length; filaments broad and flat, appendages straight or slightly recurved, longer filament about 4 mm long including the appendages, shorter filaments ca. 3 mm long; anthers white, ca. 2 mm long.

Holotype.—California: San Luis Obispo Co., between Rocky Butte and Pine Mt., Santa Lucia Mts. above San Simeon, 21 June 1950, *Hoover 8010* (OBI!, isotypes, CAS!, UC!).

Etymology.—Named for F. L. Cook, Atascadero, Calif. "by first making it possible for me [Hoover] to reach the very interesting locality where it is found."

Chromosome number.— $n = 7$.

Distribution.—California: San Luis Obispo Co. (Fig. 10). Stream sides or wet draws often associated with cypress groves (*Cupressus sargentii* Jeps.) usually on serpentine but apparently not restricted to it.

In establishing *cookii* as a variety of *T. ixioides*, Hoover noted only that the perianth was white, purple-tinged on the outside, and that the segments were reflexed from the mouth of the tube. According to my observations he failed to note the two most extraordinary characteristics of the taxon;

Fig. 10. Geographical distribution of *Tritoleia ixioides* ssp. *cookii*.

the extremely long pedicels and the fact that the perianth tube is about the same length as the segments. The specimens I collected from the type locality did not have white flowers but rather, they were creamy-white. The purple-tinged exterior, while conspicuous in ssp. *cookii*, is not confined to that subspecies but appears in some populations of *T. ixioides* ssp. *ixioides*.

In the original description no mention was made of the habitat. My collection (*Lenz* 24901), was made on a moist west-facing draw where it was growing in wet, black, gummy soil derived from serpentine. The associated plants were sedges and grasses. The area had at one time supported a cypress grove but the trees have disappeared probably due to fire. The only other place where I saw ssp. *cookii* was in a cypress grove a few miles south of the first collection. That ssp. *cookii* is not entirely restricted to serpentine may be seen in the fact that it has been collected at Camp Natoma (San Luis Obispo Co.) which is reported to be on limestone.

Hoover reported that between the extremes of var. *cookii* and var. *ixioides* there were plants which were intermediate both in flower color and in the angle of divergence of the perianth segments. In his "Vascular plants of San Luis Obispo County" (1970) he wrote of *T. ixioides* saying "intergrading with the localized variety [*cookii*] following." Of *T. ixioides* var. *cookii* he says, "Known only in a small area of the Santa Lucia range from near Cypress Mt. to Pine Mt."

Representative specimens.—California: San Luis Obispo Co., Pine Mt. near San Simeon, *Palmer* 531, on the label "*Milla longipes*, Watson, n. sp."; near source of north fork of San Simeon Cr. on rd to Rocky Butte, *Hoover* 8023 (OBI); Burnett Peak cypress groves, *Hardham* 5961 (RSA).

Fig. 11. *Triteleia ixioides* ssp. *cookii*. Collection from the type locality.

TRITELEIA IXIODES (Ait. f.) Greene ssp. *scabra* (Greene) Lenz, comb. nov.
Figs. 12, 13, 23, 24

- = *Calliprora scabra* Greene, Erythea 3: 126, 1895 (Basionym).
- = *Brodiaea scabra* (Greene) Baker, Gard. Chron. Ser. 3, 20: 459, 1896.
- = *Brodiaea ixioides* Wats. var. *scabra* (Greene) Smiley, Univ. Calif. Publ. Bot. 9: 135, 1921.
- = *Brodiaea lutea* (Lindl.) Mort. var. *scabra* (Greene) Munz, Calif. Fl., 1382, 1959.
- = *Triteleia scabra* (Greene) Rattan, West. Coast Bot. 75, 1898.
- = *Triteleia ixioides* (Ait. f.) Greene var. *scabra* (Greene) Hoover, Amer. Midl. Nat. 25: 88, 1941.
- = *Triteleia scabra* (Greene) Hoover, Pl. Life (Herbertia) 1: 20, 1955.
- = *Calliprora aurantea* Kell., Proc. Calif. Acad. Sci., Ser. 1, 2: 20, 1863.

Corms to 4 cm in diam, usually 2–2.5 cm, deeply seated; leaves 2, as much as 5 dm long, 2 cm wide; scape to 5 dm tall, smooth or scabrous; inflorescences usually many-flowered; pedicels to 9 cm long, usually shorter; perianth pale yellow to golden-yellow, tube 3–7 mm long, much shorter than the segments, segments to 2 cm long, outer ones acute, inner ones obtuse, each with a conspicuous dark midvein; longer filaments 5–7 mm long including the appendages, shorter ones 4–5 mm long, appendages long, tapering, straight or recurved, often strongly so; anthers to 2 mm long, cream-colored, yellow or sometimes blue.

Neotype here designated.—California: Madera Co., just W of Coarsegold on hwy 41, 1,750 ft, foothill woodland, 25 May, 1971, Lenz 24856 (RSA, duplicate neotype US) (Fig. 18b).

Etymology.—From Latin, *scabrous* referring to the nature of the scape as described by Greene. Not all specimens of this subspecies have scabrous scapes and the epithet is not very appropriate.

Chromosome number.— $n = 5, (6), 8$, polyploids and aneuploids.

Distribution.—California: Siskiyou Co. S to Kern Co. (Fig. 12) where it is found in valley grassland, foothill woodland and lower montane coniferous forests at elevations of from 500 to 7,200 ft.

Representative specimens.—California: Amador Co., Panther Cr., 5,000 ft, Hansen 1074 (DS); Butte Co., 3.5 mi ENE of Lake Wyandotte, 3 mi N of Rackerby, Powell 1513 (DAV); Calaveras Co., 3.5 mi SE of Vallecito, Deno 42 (DAV); Eldorado Co., along Deer Valley Rd., NW of Resque, 1,000 ft, Robbins 1945 (UC); Fresno Co., Big Sandy Valley, 2,000 ft, Quibell 1554 (RSA); Kern Co., Poso Hills, NW of mouth of Adobe Cr., 800 ft, Twisselmann 7016 (CAS); Madera Co., W of Coarsegold, hwy 41, Lenz 24856 (RSA, US); Mariposa Co., open grass glade below Mt. Bullion village, Jepson 10719 (JEPS); Nevada Co., Penn Valley W of Grass Valley, Heller 13188 (DS); Placer Co., near Loomis, among oaks, Applegate 5366 (DS); Plumas Co., on Oroville-Quincy Rd., 0.5 mi S Bidwell's Bar, 1,000 ft,

Fig. 12. Geographical distribution of *Triteleia ixioides* ssp. *scabra*.

Thomas 2 (RSA); Sacramento Co., $\frac{3}{4}$ mi SW of Mormon Island, 500 ft, *Nordstrom* 21 (UC); Shasta Co., 17 mi N of Redding, 1 mi S of hwy on side rd, 500 ft, *Gould* 745 (UC); Sutter Co., Marysville Buttes (East Butte), *Heller & Brown* 2968 (POM); Tehama Co., open oak woods, Ely, *Jepson* 16335 (JEPS); Trinity Co., summit of Trinity-Shasta Co. line, Eureka to Red Bluff Rd., *Kildale* 3697 (DS); Tulare Co., Last Chance Meadows, upper south fork of Kern River, 7,200 ft, *Kruckeberg* 3357 (RSA); Tuolumne Co., open woods, Grant's Ranch, Columbia, *Jepson* 6303 (JEPS).

Triteleia ixioides ssp. *scabra* is the 'yellow brodiaea' that is such a conspicuous component of the wild flower displays along the foothills of the Sierra Nevada each spring. From my field observations I have found the greatest concentration of plants to exist in Tulare Co. although it is common throughout its entire range. It is also the most variable member of the

Fig. 13. *Triteleia ixioides* ssp. *scabra*.—a. Inflorescence, $\times \frac{3}{4}$.—b. Flower opened to show the nature of the stamen filaments. $\times 2\frac{1}{4}$.

entire section both morphologically and cytologically. Isolated specimens might well be considered as belonging to different taxa except for the fact that a series of intermediates can be shown to exist (see Figs. 23, 24). I have been unable to satisfactorily segregate groups within this subspecies.

The probable reasons for the variability found in *ssp. scabra* will be considered in a later paper.

TRITELEIA IXIODES (Ait. f.) Greene *ssp. unifolia* Lenz, *ssp. nov.* Figs. 14, 15, 25

Scapus minus quam 3 dm altus, glaber vel scaber; folia pleuremque 1, ad 2 dm longa et 1.5 cm lata, erecta vel arcuata; inflorescentia multiflora; pedicelli usque 4 cm longi; perianthium luteum suffusum exteriorum sanguineum; tubus infundibuliformis, 5–7 mm longus; segmentia 9–12 mm longa, acuta; filamenta staminum longior cum appendicibus 3–5 mm longa, filamenta staminum brevior 2–4 mm longa, appendices breves rectae vel incurvae.

Scapes usually less than 3 dm tall, smooth or slightly scabrous; leaves usually 1, to 2 dm long, 1.5 cm wide, erect to arching; inflorescence few to many-flowered; pedicels to 4 cm long; perianth dull yellow, strongly marked deep purplish brown on exterior, tube funnelform, 5–7 mm long, segments 9–12 mm long, acute; longer filaments 3–5 mm long including appendages, shorter filaments 2–4 mm long, appendages short, straight or incurved.

Holotype.—California: Mariposa Co., road from Coulterville to hwy 120, north of Greeley Hill, 3,400 ft, cutover yellow pine forest with oaks, unifoliate, growing in loamy soil, 26 May, 1971, *Lenz 24859* (RSA, isotypes CAS, GH, BM, US).

Etymology.—From the latin, *unifolia*, referring to the single leaf which is characteristic of this subspecies.

Chromosome number.— $n = 7, 8$.

Distribution.—Oregon: Jackson Co.; California: Siskiyou Co. south to Mariposa Co. (Fig. 14) where it occurs in the lower montane coniferous forests mostly at elevations of about 3,500 ft usually in light shade and in more mesic situations than *T. ixioides ssp. scabra* and at elevations below where *T. ixioides ssp. anilina* is usually encountered.

Representative specimens.—California: Amador Co., 8 mi E of Pine Grove on Carson Pass hwy, ca. 3,300 ft, *Wolf 4913* (CAS, UC); Butte Co., roadside bank, treeless summit of Table Mt., *Heller 5032a* (DS, UC); Calaveras Co., Calaveras Grove, *Grant s.n.* (JEPS); Eldorado Co., grassy slope in open woods at CCC camp, Snowline, 3 mi E of Camino, *Robbins 1048* (CAS, UC); Mariposa Co., near Kinsley, *Hoak s.n.* (UC); Nevada Co., in full sun on north-facing slope in yellow pine forest, ca. 2,300 ft, Shaw's Hill, Grass Valley, *Litton 9* (DAV); Placer Co., ca. 1 mi W of Baxter, *Hitchcock 6328* (DS, UC); Shasta Co., level open place along US hwy 299, 5 mi W of Hatchet Summit, ca. 3,500 ft, *Heller 15692* (US); Tuolumne Co., edge of woods, s fork rd, Twain Harte P.O., ca. 4,000 ft, *Alexander & Kellogg 3600* (UC); Yuba Co., Smartsville, *Crambie s.n.* (CAS).—Oregon: Jackson Co., near Ashland, Siskiyou Mts., *Applegate 699* (GH).

Plants collected on the treeless summit of Table Mt. north of Oroville, Butte Co., in thin dry soil (*Heller 5032a*) are typical of the subspecies except for the habitat. Heller noted that "this unusually dark lined form

Fig. 15. *Triteleia ixioides* ssp. *unifolia*.—a. Inflorescence, $\times 1\frac{1}{2}$.—b. Flower opened to show the nature of the stamen filaments, $\times 3\frac{1}{2}$.

TRITELEIA LUGENS Greene, Bull. Calif. Acad. Sci. 2(6): 142, 1886.

Figs. 16, 17, 26

$\equiv$ *Calliprora lugens* (Greene) Greene, Manual of the Bot. of the Region of San Francisco Bay, 319, 1894.

Fig. 16. Geographical distribution of *Triteleia lugens*.

- ≡ *Calliprora ixioides* (Ait. f.) Greene *lugens* Abrams, Ill. Fl. Pacific States, vol. 1, 399, 1923.
- ≡ *Brodiaea lugens* (Greene) Baker, Gard. Chron. Ser. 3, 20: 459, 1896.
- ≡ *Brodiaea ixioides* (Ait. f.) Wats. var. *lugens* Jepson, Fl. Western Middle Calif. ed. 2, 101, 1911.
- ≡ *Brodiaea lutea* (Lindl.) Mort. var. *lugens* (Greene) Mort. Herbertia 7: 81, 1940.
- ≡ *Hookera ixioides* (Ait. f.) Ktze. var. *lugens* Jepson, Fl. Middle Calif., 117, 1901.

Leaves to 3 dm long and 10 mm wide; scape to 4 dm tall, usually less, smooth or slightly scabrous; pedicels to 2.5 cm long; perianth dull yellow

or bright yellow, tube funnellform, rather broad, 4–5 mm long, segments 6–9 mm long, spreading but never rotate; filaments broad, rounded at the apex, appendages absent, longer filaments 3–4 mm, shorter ones 1–2 mm long; anther 1–2 mm long.

Neotype here designated.—California: Solano Co., Vaca Mts., *R. H. Platt s.n.*, 1898 (UC 13,763). This specimen has been cited by Jepson (1922) and Hoover (1941).

Etymology.—From the Latin, *lugent*, to mourn, to wear mourning apparel. Reason for the name is uncertain. Some forms have dull yellow-colored flowers.

Chromosome number.— $n = 8$.

Distribution.—This species has a disjunct distribution, being found in Lake, Napa, and Solano counties north of the San Francisco Bay and in Monterey and San Benito counties south of the Bay (Fig. 16). The two areas are about 140 air miles apart. The species is usually found in foothill woodland and at no place does it appear to be common. Hoover reports it in Sonoma Co. but I have seen no specimens. Plants from north of San Francisco Bay have dull yellow flowers, those from Monterey and San Benito counties are a bright yellow.

Representative specimens.—Lake Co., forest 1.5 mi W of Oat Hill Mine, Wiggans 6741 (DS, UC); Monterey Co., upper Henry Sands Canyon, La Gloria Rd., E of Gonzales, Hoover 9357 (CAS, OBI, ORE, RSA, UC); Napa Co., Howell Mt., ca. 1,400 ft, Raven 4048 (CAS); San Benito Co., 1.5 mi N of site of old Pinnacles Post Office, Hoover 8374 (CAS, DS, OBI, ORE, RSA, UC); Solano Co., near Signal Station, Vaca Mts., Sharpe *s.n.* (JEPS).

PRESUMED NATURAL HYBRID

TRITELEIA × *VERSICOLOR* Hoover (pro sp.) Amer. Midl. Nat. 25: 91, 1941.
= *Brodiaea versicolor* (Hoover) Munz, Calif. Fl., 1382, 1959.

Leaves 7–11 mm wide; scape 3–6 dm tall, densely and minutely scabrous near the base; pedicels spreading, 2–4 cm long; perianth open campanulate, pale yellow when first opening, white at anthesis, often turning purple after anthesis, the tube 6–7 mm long, the segments spreading but not abruptly so, 8–10 mm long, the outer ovate-lanceolate, acute, the inner obovate, obtuse; filaments flat, thin-margined, the longer 5–6 mm long, the shorter 3.5–6 mm long, forks of filaments nearly parallel; anthers white, 2.5–3.5 mm long; stipe of ovary about half as long as the body.

Holotype.—California: Monterey Co., Whaler's Knoll, Point Lobos State Park, Mason & Lee 9351 (UC!, isotypes DS!, GH!).

Etymology.—*versicolor* refers to the change in the color of the flowers after they open (fide, Hoover, 1941).

Chromosome number.—Unknown.

Distribution.—Known only from the type collection.

Fig. 17. *Triteleia lugens*.—a. Inflorescence, $\times 2$.—b. Flower opened to show the nature of the stamen filaments. $\times 3\frac{1}{2}$.

Search in recent years has failed to disclose any plant referable to *T. versicolor* and it seems safe to assume that it is now extinct. *Triteleia versicolor* is morphologically very similar to a presumed natural hybrid between *Triteleia hyacinthina* (Lindl.) Greene and *T. scabra* (= *T. ixioides* ssp. *scabra*) collected by Hoover in Tulare Co. and described by him in 1957. He noted that the two species were locally abundant but showing differences in habitat preference.

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LITERATURE CITED

- Hoover, R. F. 1941. A systematic study of *Triteleia*. Amer. Midl. Naturalist 25: 73-100.
- . 1955. Further observations on *Brodiaea* and related genera. Pl. Life (Hertbertia edition) 11: 13-23.
- . 1957. Observations on California Plants, IV, Leaflet. W. Bot. 8: 129-133.
- . 1970. Vascular plants of San Luis Obispo County. Univ. California Press. Berkeley and Los Angeles. 350 p.
- Jepson, W. L. 1922. A flora of California, vol. 1, part 6, pp. 193-336. Univ. of California, Berkeley.
- . 1923. A Manual of the flowering plants of California. Assoc. Students Store, Berkeley. 1238 p.
- Munz, P. A., and D. D. Keck. 1959. A California Flora. Univ. of California Press. Berkeley and Los Angeles. 1681 p.
- Raven, P. H. 1963. A flora of San Clemente Island, California. Aliso 5: 289-347.

Fig. 18. a. *Tritoleia ixioides* ssp. *analina*. Neotype.—b. *T. ixioides* ssp. *scabra*. Neotype.

Fig. 19. *Triteleia dudleyi*. Rancheria Creek, Huntington Lake, Fresno Co., Lenz 12843. Note long slender perianth tubes.

Fig. 20. *Triteleia guadalupensis*.

Fig. 21. *Triteleia ixioides* ssp. *ixioides*. Carmel Valley, Monterey Co., RSA 24893.

Fig. 22. *Triteleia ixioides* ssp. *analina*. North of McCumber Reservoir, Shasta Co., RSA 24893.

Fig. 23. *Triteleia ixioides* ssp. *scabra*. Terminus Reservoir, Tulare Co., Lenz 13200. Note that the perianth segments are strongly reflexed; compare with Fig. 13a.

Fig. 24. *Triteleia ixioides* ssp. *scabra*. Cultivated plants showing populational variation.—a-b. Intrapopulational variation, Nimbus Reservoir, Sacramento Co.—a. Lenz 12195-4.—b. Lenz 12195.—a-d. Intropopulational (i.e., geographical) variation.—a-b. Nimbus Reservoir, Sacramento Co.—c. Coffee Creek, Tulare Co., Lenz 12136.—d. West of Red Bluff, Tehama Co., Lenz 12755.

Fig. 25. *Triteleia ixioides* ssp. *unifolia*. Meadow Vista, Placer Co., Lenz 12210-4.

Fig. 26. *Triteleia lugens*. Upper Sands Canyon, San Benito Co., Lenz 24855.