

ERYTHRONIUM SHASTENSE (LILIACEAE), A NEW SPECIES FROM
NORTHERN CALIFORNIA

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ABSTRACT

Erythronium shastense D. A. York, J.K. Nelson, & D. W. Taylor is described as a new species restricted largely to limestone outcrops near Shasta Lake, Shasta County, California. Style, leaf, and anther characters are used to distinguish *E. shastense* from the similar *E. californicum* and *E. helenae*.

Key Words: *Erythronium* section *Pardalinae*, fawn lily, foothill woodland, limestone, McCloud River Arm, northern California, Pit River Arm, rare endemic plant species, Shasta Lake.

The genus *Erythronium* consists of ~29 species, with 17 taxa known from western North America (Allen and Robertson 2002, Clennett 2014). The 15 California taxa (Allen 2012) form two groups; the plants with strongly mottled leaves (*Erythronium* section *Pardalinae* of Applegate 1935) generally occurring at lower elevations, and plants without to very faint mottling occurring at higher elevations (*Erythronium* section *Concolorae* Applegate) (Shevock and Allen 1997). An unidentified *Erythronium* of sect. *Pardalinae* was encountered by the third author in 1993 on limestone outcrops adjacent to the McCloud River Arm of Shasta Lake (<30 meters above spillway elevation) at 350 meters elevation. The second author noticed and photographed the same unknown *Erythronium* on the road to Hirz Mountain in 2010. In 2012, the first author independently encountered this novel *Erythronium* in the same watershed, and noted its distinction from congeners. Subsequently, recent collections and photographs of this unique *Erythronium* from limestone outcrops circumscribing Shasta Lake, confirm occurrences at Hirz Mountain, North Gray Rocks above Shasta Caverns, and at Brock Creek adjacent to the Pit River Arm of Shasta Lake (Fig. 1). The discovery of these populations led to our recognition of this new taxon.

TAXONOMIC TREATMENT

Erythronium shastense D. A. York, J. K. Nelson, & D. W. Taylor sp. nov. (Figs. 2–4). ---Type: USA, California, Shasta Co., Shasta-Trinity National Forest, North Gray Rocks adjacent to the McCloud River Arm of Shasta Lake,

N-facing slopes on a limestone outcrop above Shasta Caverns, with *Achillea millefolium* L., *Adiantum* L. sp. nov. (ined.), *Boechera breweri* (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz, *Ceanothus cuneatus* (Hook.) Nutt., *Cercis occidentalis* Torr. ex A. Gray, *Cercocarpus betuloides* Nutt., *Cheilanthes cooperae* D.C. Eaton, *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray, *Cystopteris fragilis* (L.) Bernh., *Erythranthe taylori* Nesom, *Holodiscus discolor* (Pursh) Maxim, *Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E. Wollenw., *Pinus sabiniana* Douglas ex G. Don, *Sedum spathulifolium* Hook., *Selaginella wallacei* Hieron, *Toxicodendron diversilobum* (Torr. & A. Gray) Green, and *Umbellularia californica* (Hook. & Arn.) Nutt., 40.80035°, -122.27475°, 865 m (2840 ft), 10 April 2013, Dana York 3155 (holotype: CAS; isotypes: JEPS, US).

Distinct from *E. helenae* Applegate in its longer style, leaves that are as much as 6 cm longer, and stamens as much as 3 mm longer. Distinct from *E. californicum* Purdy in its bright yellow anthers, larger leaves, and declined style.

Bulb 2.5–9.5 cm long, slender, ovate to elongate, propagating by sessile offsets protruding from the bulb coat. **Leaves** 2, white or brown mottled, 12–26 cm long, 1.7–6.5(11) cm wide, lanceolate to elliptic or ovate, margins undulate. **Scapes** (13)24–30 cm tall; **flowers** 1–3, spreading (nodding). **Tepals** 6, slightly recurved to spreading or campanulate, lanceolate, often pink in bud, tips acute to acuminate, 24–41(45) mm long, 6–15 mm wide, white, fading pinkish to purplish after anthesis, with a 7–9 mm long golden yellow

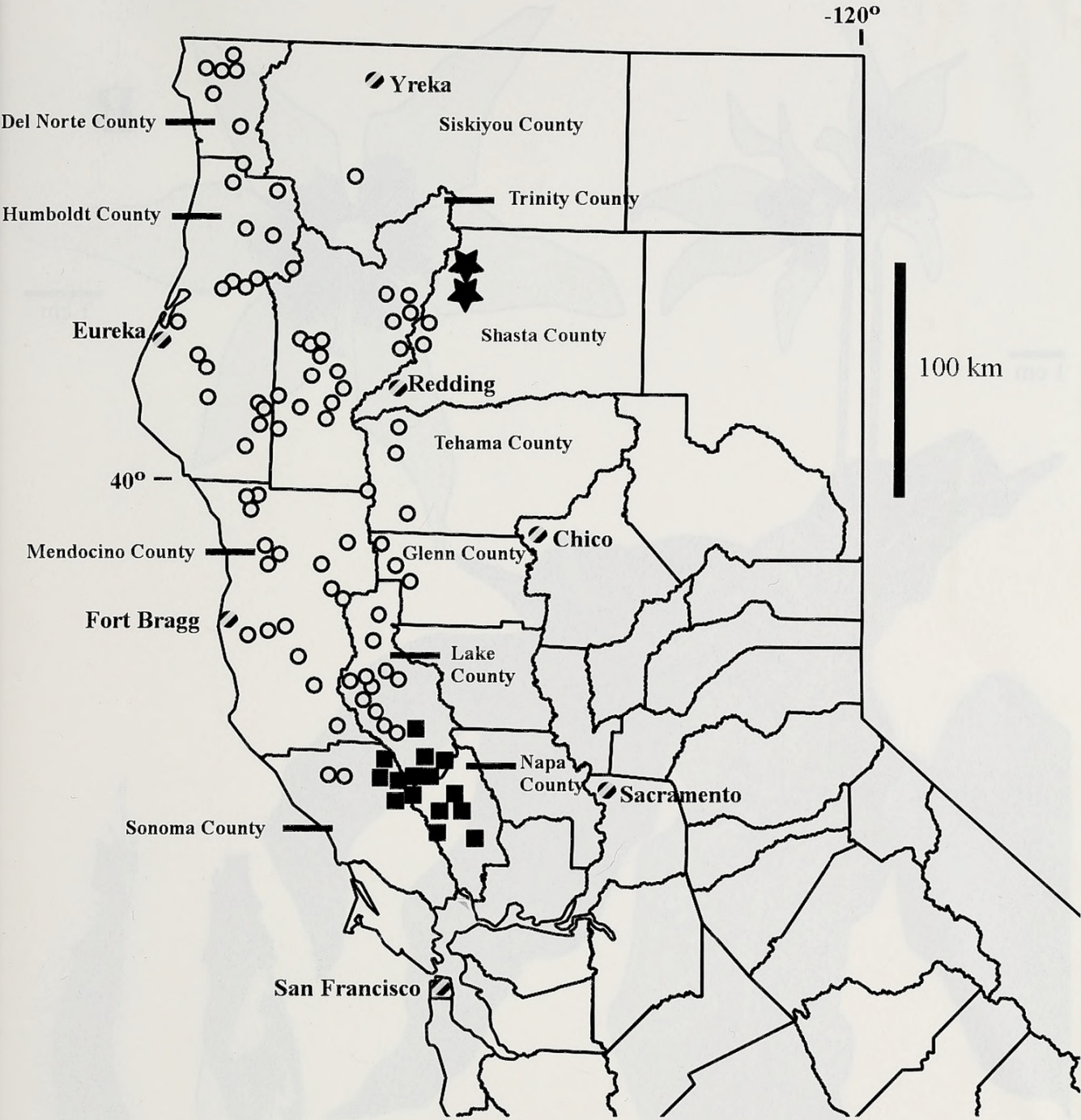


FIG. 1. Map of northern California (with county boundaries) showing the distribution of Consortium of California Herbaria *Erythronium* specimens. ★ = *Erythronium shastense*, ○ = *Erythronium californicum*, ■ = *Erythronium helenae*.

zone at base. Inner three tepals with saclike appendages at base on adaxial surfaces. **Stamens** unequal in two series, 9–12(16) mm long. **Filaments** 5–7(11) mm long, 0.2–0.5 mm wide, white to yellowish; **anthers** 4–5 mm long, yellow. **Style** clavate, 8–14 mm long, white, declined; **stigma** entire to short lobed, the lobes <2 mm. **Capsules** obovoid, 1.3–3.2 cm long.

Paratypes: USA, CALIFORNIA. **Shasta Co.:** Hirz Mountain road, off Gilman Road, east of I-5, north of Shasta Lake, growing on limestone outcrop, roadside, fill slope in shade, on a north aspect, UTM NAD 83 Zone 10 562457E,

4527762N, 3344 ft, 15 April 2014, *Nelson & Lenz 2014-010* (CHSC, RSA); Shasta-Trinity National Forest, along Gilman Road (Road 7H 009) about 0.4 road miles west of the entrance road to Dekkas Rock Campground, TRS 35N3W19, NAD 83 40.87528°, -122.24089°, 1219 feet (371 m), 9 April 2014, *Taylor 21465* (HSC, CHSC, RSA); Gilman Road, east of I-5, north of Shasta Lake above Jennings Creek, UTM NAD 83 Zone 10 564277E, 4528596N, 1200 ft, 14 March 2014, *Nelson et al. 2014-005* (CHSC, HSC, RSA); Shasta-Trinity National Forest, Peak 2968 just north of North Gray Rocks adjacent to the

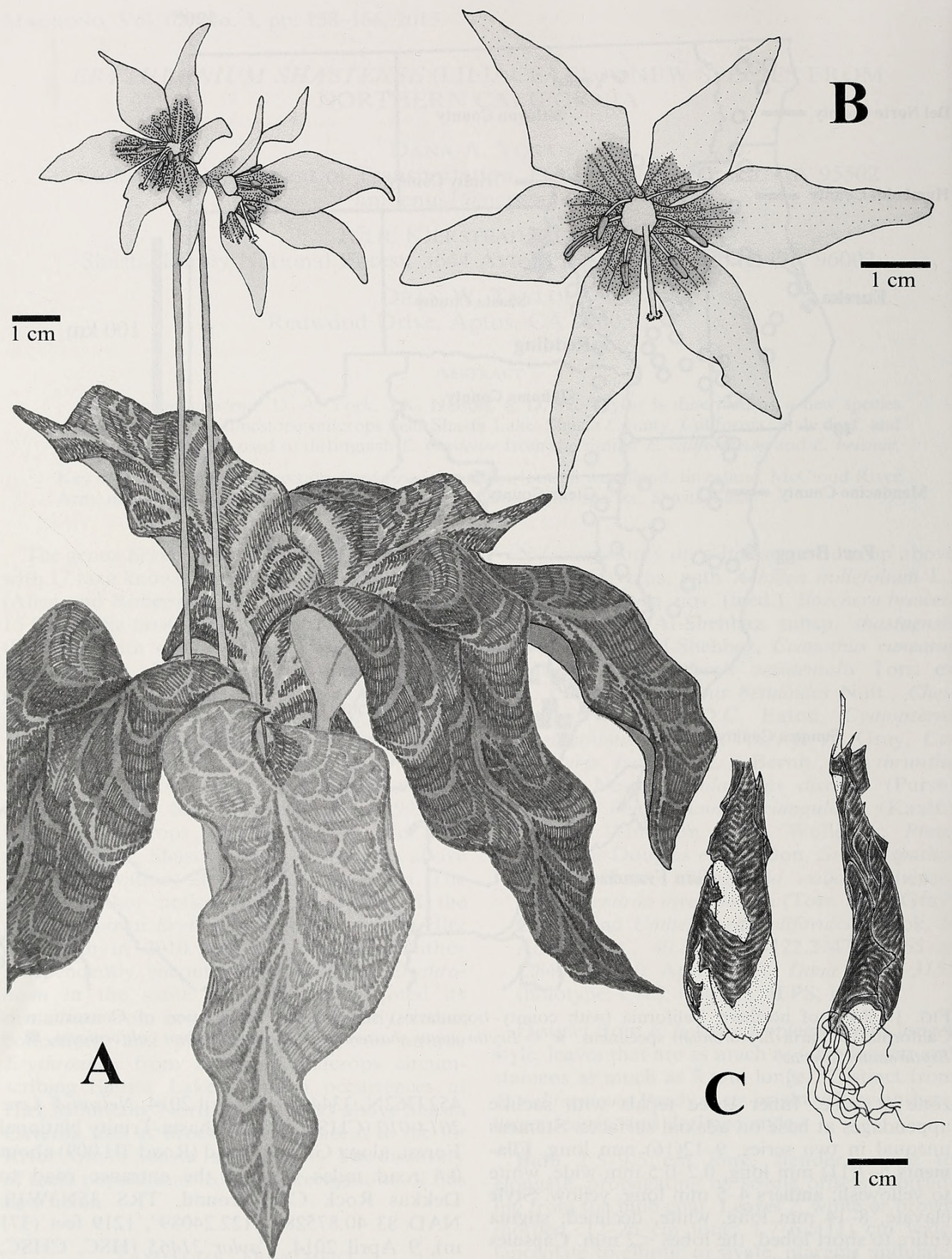


FIG. 2. *Erythronium shastense*. A. Habit, with plant having two flowers above mottled leaves. B. Flower, with declined style. C. Bulbs. Illustrations by Diana D. Jolles.

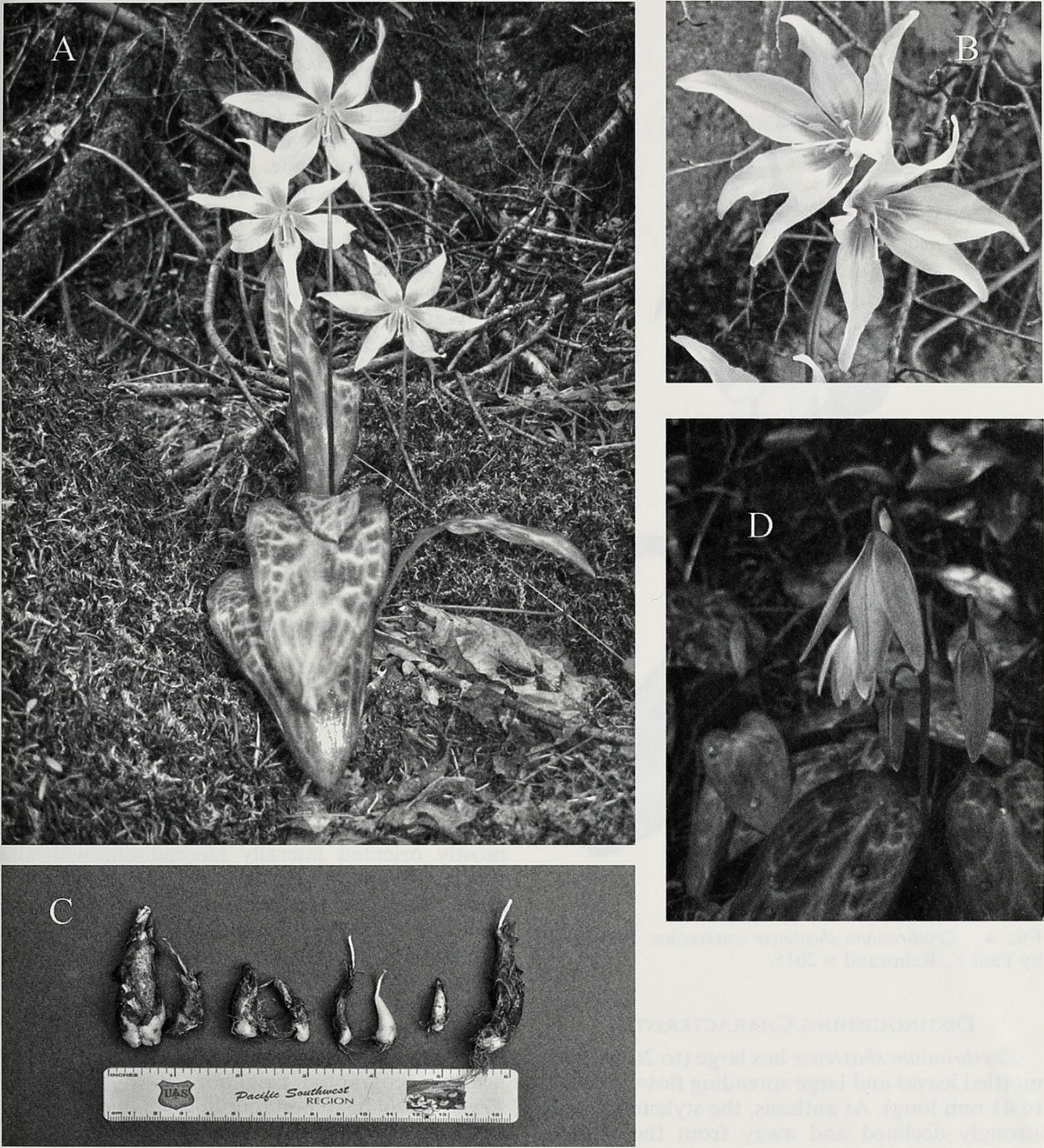


FIG. 3. *Erythronium shastense*. A. Two adjacent plants in limestone habitat. B. Flowers showing declined styles. C. Bulbs from several plants. D. Pendent buds.

McCloud River Arm of Shasta Lake, shaded limestone rock shelves and crevices, 40.80422°, -122.27111°, 900 m (2960 ft), 19 May 2012, *York 3112* (HSC); 1 mile south of McCloud River bridge along road between Ellery Creek and Pine Point Campground, 350 m, 5 March 2003, *Taylor & Reyes 18467* (JEPS100448, UC1755122); McCloud Arm Lake Shasta, along road between Ellery Creek and Pine Point Campground (ca. 1 mile south of McCloud River bridge), 350 m,

17 March 1993, *Taylor 13302* (JEPS96527); 15 miles northwest [sic, northeast] of Redding, 21 April 1935, *Rose 30* (JEPS61880).

ETYMOLOGY

The specific epithet is named for Shasta Lake, Shasta County, where the only known populations occur in close proximity to the reservoir. The suggested common name is Shasta fawn lily.



FIG. 4. *Erythronium shastense* watercolor. Illustration by Paul C. Reinwand © 2015.

DISTINGUISHING CHARACTERISTICS

Erythronium shastense has large (to 26 cm long) mottled leaves and large spreading flowers (tepals to 41 mm long). At anthesis, the style tends to be strongly declined and away from the anthers, resulting in herkogamy. The anthers are bright yellow when they first dehisce. Plants grow in clumps where enough soil exists in cracks and ledges on the carbonate rock substrate. The plant's leaves and flowers easily stand out against the gray limestone rock. Flowers appear in late winter or early spring when occurrence of rainfall is still very likely. During the summer *E. shastense* foliage dies back to its bulb until the following winter and the start of another year's cycle.

TAXONOMIC RELATIONSHIPS

Of the three strongly supported lineages within *Erythronium* (Clennett et al. 2012), all California

taxa fall within an unranked "western North American clade", which has moderately good bootstrap support on combined molecular and morphological phylogenetic analysis (Allen et al. 2003, Clennett 2014). Clennett et al. (2012) found weak support for lineages within the western North American clade. *Erythronium shastense* is morphologically most similar to *E. helenae* Applegate and *E. californicum* Purdy (Table 1). However, *E. helenae* and *E. californicum* often pair together in a clade with *E. hendersonii* S. Watson, *E. howellii* S. Watson, *E. citrinum* S. Watson, and *E. multiscapideum* (Kellogg) A. Nelson & P. B. Kennedy in phylogenetic studies by both Clennett et al. (2012) and Allen et al. (2003), and are keyed in similar fashion (Allen and Robertson 2002). Clennett (2014) recognizes *E. californicum* as having two races; one form with smaller leaves, flowers, and fruits which he attributes to populations from the Trinity Mountains (and which also occur in the High North Coast Ranges) and a larger form occurring in outer North Coast regions of northwest California. Recognition of *E. shastense* now requires that the phylogeny of the North American clade be revisited.

One subtle but significant feature of *E. shastense* is the orientation of flowers at anthesis. Many taxa of *Erythronium* L. offer flowers that are pendant atop a strongly geniculate (distally recurved) scape, with the dehiscing anthers and receptive style dangling below. By contrast, at full anthesis, *E. shastense* flowers are mostly oriented laterally (spreading), with the tepals forming a parabola that is significantly more often oriented horizontally (Figs. 2–4). In bud, the unopened flowers of *E. shastense* are pendant as in congeners; flower orientation features are largely absent on herbarium specimens. The spreading to nodding flowers of *E. shastense* differ somewhat from congeners, including pendant-flowered *E. californicum*, its nearest geographic neighbor—most species of *Erythronium* have nodding or pendant flowers at anthesis, an orientation that provides protection from precipitation potentially damaging flower parts or eroding pollen from the open anthers. Style position is possibly related to flower orientation. Unlike *E. californicum* where the style is exerted well beyond the anthers, *E. shastense* and *E. helenae* achieve herkogamy with declined (having a positive gravitropic response) styles presenting the stigma below and away from the anthers.

In practice, classifications of *Erythronium* (Applegate 1935, Matthew 1992, Allen and Robertson 2002, Allen 2012, Clennett 2014) have treated constituent entities as full species, rather than recognizing closely related, morphologically overlapping, or demonstrated sister taxa as sub-

TABLE 1. COMPARISON OF DIAGNOSTIC CHARACTERS AMONG *ERYTHRONIUM* SPECIES OF CALIFORNIA.

<i>Erythronium</i> taxon	Leaf blades			Inflorescences		Tepals		Filaments		Anthers	Style	Stigma
	Distinctly mottled white or brown	Length (cm)	Width (cm)	# of flowers per scape		Color	Color at base	Color	Width (mm)	Color	Length (mm)	Lobes (mm)
<i>E. shastense</i>	Yes	12-26	1.7-6.5(11)	1-3		White	Yellow	White to \pm yellow	<0.6	Yellow	8-14 (declined)	0-2
<i>E. californicum</i>	Yes	7-15	2.5-5	1-3		White to cream	Yellow	White	<0.8	White to cream	10-15	0-2
<i>E. citrinum</i> var. <i>citrinum</i>	Yes	9-15	1.5-4	1-3		White	Yellow	White to pinkish	<0.8	White to cream	6-10	0-1
<i>E. citrinum</i> var. <i>roderickii</i>	Yes	9-15	1.5-5	1-3		White	Yellow	White to pinkish	<0.8	Pink to dark red	6-10	0-1
<i>E. grandiflorum</i> subsp. <i>grandiflorum</i>	No	5-20	1.4-5	1(3)		Yellow	Pale yellow	White	<0.8	Cream to yellow (dark red)	10-15	2-4
<i>E. helenae</i>	Yes	10-20	0.7-2.2	1-3		White	Yellow	\pm Yellow	<0.8	Yellow	5-8 (declined)	0-1
<i>E. hendersonii</i>	Yes	10-25	2-4.5	1-4		Violet to pink	Dark purple	Purple	<0.8	Pale brown to purple	6-8	0-1
<i>E. klamathense</i>	No	6-17	1.5-2.5	1-3		White	Yellow	\pm Yellow	<0.8	White	4-9	0
<i>E. multiscapideum</i>	Yes	4-15	1-2.5	1-4		White	Yellow	White	<0.8	White to cream	10-13	1-4
<i>E. oregonum</i>	Yes	10-22	3-6	1-3		White to cream	Yellow	White	2-3	Cream to yellow	10-13	3-6
<i>E. pluriflorum</i>	No	7-30	1.5-6	1-10		Yellow	Yellow	Yellow	<0.8	Yellow	6-8	0-1
<i>E. purpurascens</i>	No	6-15	1-2.5	1-6		White	Yellow	Yellow	<0.4	Cream to yellow	4-5	0
<i>E. pusaterii</i>	No	10-35	2-6	1-8		White	Yellow	White	<0.8	Yellow	7-10	0-1
<i>E. revolutum</i>	Yes	10-25	3-6	1-3		Violet-pink	Yellow bands	White to pink	2-3	Yellow	12-18	4-6
<i>E. taylorii</i>	No	18-35	4-9	1-8		White	Yellow	Yellow	<0.4	Cream	9-11	0-1
<i>E. tuolumnense</i>	No	15-35	4-8	1-5		Yellow	Yellow	White to cream	0.4-0.6	Yellow	8-10	0-1

species. We thus treat *E. shastense* by this same method as a full species.

PHENOLOGY

Erythronium shastense flowers from February to April, developing mature fruits in May. Leaves quickly wither with the onset of hot, dry weather in May.

DISTRIBUTION, HABITAT, ECOLOGY, AND CONSERVATION IMPLICATIONS

Erythronium shastense grows in shallow soils on shelves and in crevices in the calcareous rock outcrops circumscribing the McCloud River and Pit River arms of Shasta Lake (Fig. 5). It is restricted largely to the McCloud and Hosselkus limestone formations formed between the Early Permian and Upper Triassic (Demirman and Harbaugh 1965). In the Shasta Lake region, the McCloud limestone formation outcrops form a narrow band approximately one km wide, extending for about 30 km in a north-south orientation (Demirman and Harbaugh 1965). *Erythronium shastense* plants are scattered about the north-facing or shaded limestone rock outcrops in forest and mixed woodland plant communities dominated by combinations of the following species: *Ceanothus cuneatus* Nutt. var. *cuneatus*, *Cercocarpus betuloides* Nutt., *Chrysolepis sempervirens* (Kellogg) Hjelmq., *Garrya fremontii* Torr., *Holodiscus discolor* (Pursh) Maxim., *Pinus sabiniana* D. Don, *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus chrysolepis* Liebm., *Q. garryana* Hook. var. *breweri* (Engelm.) Jeps., *Q. kelloggii* Newb., *Toxicodendron diversilobum* (Torr. & A. Gray) Greene, and *Umbellularia californica* (Hook. & Arn.) Nutt. Known populations of *E. shastense* have one or more of the following associates: *Adiantum* sp. nov. (in press), *Ageratina shastensis* (D. W. Taylor & Stebbins) R.M. King & H. Rob., *Boechera breweri* (S. Watson) Al-Shehbaz subsp. *shastaensis* Windham & Al-Shehbaz, *Cercis occidentalis* A. Gray, *Cymopterus terebinthinus* (Hook.) Torr. & A. Gray var. *californicus* (J. M. Coult. & Rose) Jeps., *Delphinium nudicaule* Torr. & A. Gray, *Erythranthe taylori* Nesom, *Myriopteris cooperae* (D. C. Eaton) Grusz & Windham, *Sedum spathulifolium* Hook., and *Selaginella wallacei* Hieron.

Like *E. helenae* (Applegate 1933), *E. shastense* can form clumps due to bulb offsets (bead-like tissues arising from the bulb). This adaptation is well suited for taxa that tend to grow in rocky conditions with little soil development. Zonal soil development in such rocky habitats is limited; vascular plant establishment is restricted to cracks, fissures or solution pockets in limestone where organic matter accumulates, and where



FIG. 5. Limestone outcrop habitat for *Erythronium shastense*, with Shasta Lake in the background.

seeds find suitable conditions. The clumped growth habit of *E. shastense* is a functional trait adaptive to cliffs and such crevices.

The distribution and abundance of *E. shastense* is doubtless incompletely known, but a substantial portion of suitable habitat has been floristically investigated in recent decades. The 1978 description of *Ageratina shastensis* (Taylor and Stebbins 1978) led the third author to continue to visit limestone outcrops in the Shasta Lake region, resulting in the 1992 discovery of *Neviusia cliftonii* Shevock, Ertter, D. W. Taylor (Shevock et al. 1992). Subsequent surveys, initiated by the second author to elucidate the habitat and rarity of *N. cliftonii* (Lindstrand and Nelson 2006), visited a large fraction of the regional limestone substrate sites without locating any additional *E. shastense* occurrences. It is possible that the surveys were timed too late in the growing season to detect *E. shastense* plants. Other recent spring surveys, targeting the recently described *Erythranthe taylori* (Nesom 2013), only detected two additional Shasta fawn lily occurrences. Adding *E. shastense* to the suite of limestone endemics of the Shasta Lake region strongly suggests that, going forward, comprehensive and fully-vouchered floristic exploration of the region is in order. Many limestone outcrops in this region are remote from roads, are on very steep slopes generally infested with poison oak, and are difficult to access. Consequently, floristic exploration of this region is incomplete.

Safford et al. (2005) rated *E. helenae* as a strong indicator of serpentine affinity, whereas *E. shastense* is a strong calciphile, these substrate preferences indicating divergence between the two species. Other *Erythronium* taxa that have an obvious affinity to a specific and regionally unique geologic substrate include *E. citrinum* S. Watson var. *citrinum* (serpentinite), *E. citrinum* var. *roderickii* Shevock & G. A. Allen (serpentinite), and *E. taylorii* Shevock & G. A. Allen

(metamorphic marine sediments) (Shevock and Allen 1997). *Erythronium shastense* and *E. helenae* are strongly allopatric, situated at, respectively, the north and south ends of the range of *E. californicum* (Fig. 1). *Erythronium californicum* has not been reported from Oregon: vouchers are known within 8 km of the state line (Smith et al. 10274, HSC74878) and might be expected to occur therein.

Because *E. shastense* is restricted to a few known occurrences, mostly on low-elevation limestone in northern California, around or near Shasta Lake, it is of conservation concern. It grows in sympatry with or near the following local endemic plants: *Adiantum* sp. nov. (ined.), *Ageratina shastensis*, *Erythranthe taylori*, *Neviusia cliftonii*, and *Vaccinium* sp. nov. (ined.). Past and current mining of limestone within potential habitat for *E. shastense* is a proximal threat factor. Other threats include planned reservoir expansion of Shasta Lake, road and trail

maintenance/construction, invasive species (some known sites have dense *Rubus armeniacus* Focke), and any habitat changes due to climate change.

In 1935, the novel species of *Erythronium* described herein was first collected and filed as *E. californicum* Purdy by Mrs. C. F. Rose (Rose 30, JEPS6180). The Rose collection is labeled as “15 miles northwest of Redding” which places it in the area of Shirttail Peak, an area without limestone. We surmise that the collection actually came from 15 miles northeast of Redding, placing it in an area where limestone is a common substrate. The 1935 Rose collection was not accessioned at Jepson Herbarium until decades later and bears a typewritten label rather than an autographic one, suggesting that “northeast” might well have been recorded incorrectly as “northwest”. *Erythronium californicum* was documented by the third author from Shirttail Peak in 2004 (Taylor, Molter, and Engstrom 19102, JEPS118209).

KEY TO CALIFORNIA *ERYTHRONIUM* WITH WHITE OR BROWN MOTTLED LEAVES

A revised key, after Allen (2012), based on California taxa with mottled leaves is provided below:

- 1. Filaments 2–3 mm wide; stigma lobed
 - 2. Tepals white with yellow base *Erythronium oregonum*
 - 2'. Tepals violet-pink with yellow base *Erythronium revolutum*
- 1'. Filaments <0.8 mm wide; stigma entire to lobed
 - 3. Tepals violet to pink with dark purple base *Erythronium hendersonii*
 - 3'. Tepals mostly white with yellow base
 - 4. Longest styles >10 mm
 - 5. Anthers yellow; style generally declined; largest leaves >20 cm long *Erythronium shastense*
 - 5'. Anthers white to cream; style straight; largest leaves ≤15 cm long
 - 6. Peduncle, when inflorescence has >1 flower, branched above leaves *Erythronium californicum*
 - 6'. Peduncle, when inflorescence has >1 flower, branched near ground. *Erythronium multiscapideum*
 - 4'. Longest styles ≤10 mm
 - 7. Anthers yellow; style generally declined *Erythronium helenae*
 - 7'. Anthers white, cream, pink, brown, purple, or red; style straight
 - 8. Anthers white to cream *Erythronium citrinum* var. *citrinum*
 - 8'. Anthers pink to brown- or purple-red. *Erythronium citrinum* var. *roderickii*

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