OROBANCHE ROBBINSII (OROBANCHACEAE), A NEW SPECIES OF PARASITIC PLANT FROM COASTAL CALIFORNIA

ALISON E. L. COLWELL

Missouri Botanical Garden P.O. Box 299 St. Louis, MO 63166-0299 aelcolwell@msn.com

GEORGE YATSKIEVYCH

Plant Resources Center University of Texas at Austin Austin, Texas 78712-1711 george.yatskievych@austin.utexas.edu

ABSTRACT

A new species of *Orobanche* (Orobanchaceae) endemic to rocky coastal areas of California is described as *Orobanche robbinsii*. The investigations presented here corroborate and extend those conducted (but not previously published) by G. Thomas Robbins and Lawrence Heckard. The new species is allied to *O. californica* but is distinguished by its glabrous anther sacs, pallid corollas with shorter, less arched tubes with oblong, erect lobes, and its affinity for the host *Eriophyllum staechadifolium*. Chromosome counts of $2n = 24_{\rm II}$ are presented.

The parasitic plant *Orobanche californica* Cham. & Schltdl. occurs along the Pacific Coast of North America, from the Queen Charlotte Islands in British Columbia to Baja California. Six subspecies are currently recognized, each of which occurs in distinct habitats, parasitizes a distinct suite of host plant species, and displays a varied but distinct morphology. Due to their small population sizes and brief appearance above ground, a body of specimens from which to refine range limits and make further morphological assessments has been slow to accumulate. Generations of botanists, including Beck von Mannagetta (1890, 1930), Munz (1930), and Heckard (1973) have contributed iterations of precision to the taxon boundaries of California *Orobanche* species, and the process continues with this paper.

Lawrence R. Heckard advanced our understanding of *Orobanche californica* by correcting misinterpretations of previously cited specimens, actively seeking new specimens, and acquiring chromosome counts (Heckard 1973; Heckard and Chuang 1975). In his 1973 circumscription, Heckard presented *O. californica* as a complex of six subspecies and segregated two species, *O. vallicola* (Jeps.) Heckard and *O. parishii* (Jeps.) Heckard, which showed the best discontinuity in morphology. In that work, he alluded to yet another morphotype in coastal California: "...and the maritime habitat common to most of them **is shared within their range only by a distinctive undescribed species at San Francisco and southwards"** (emphasis added).

Heckard had documented continued presence of this morphotype at the collection sites of Carlquist and of Stebbins, located additional sites (*Heckard 1750, 6725* [UC]), collaborated with Tsan Iang Chuang and Feng Mai Chuang to obtain chromosome counts from four sites, and had drafted a manuscript for publication around 1969. However, Heckard apparently was not convinced that he had gathered enough information, as he never published his manuscript, which came to light during research on the complex.

Heckard's annotations and notes in fragment packets on specimens that he thought belonged to this morphotype inspired field investigations by the first author, resulting in additional locations being documented and a more precise understanding of its habitat, host specificity, and range of variation. The information presented here includes both new investigations and the corroborated investigations of Heckard's manuscript. The combined result is, in our view, sufficient to propose this morphotype as a distinct species.

OROBANCHE ROBBINSII Heckard ex Colwell & Yatsk., sp. nov. TYPE: USA. California. San Francisco Co.: Parasitic on Eriophyllum staechadifolium Lag., on small rock slides on ocean cliff near Lands End, just below Lincoln Park, San Francisco; elev. ca. 150 ft, 13 Aug 1956, G. Thomas Robbins 3730 (holotype: JEPS!; isotypes: GH!, JEPS!, NY!, CAS!). Figure 1.

Differing from Orobanche californica subsp. californica in its short, erect corolla tubes, pallid corolla both interior and exterior, oblong erect corolla lobes, and glabrous (or nearly so) anther sacs.

Annual plants 4–15 (–26) cm in overall length from below-ground host attachment to tip of above-ground inflorescence. Main axis simple or few-branched near base, succulent and fleshy, underground portion of stem thickened and tuber-like or elongate and swollen just above point of host-attachment. Stem glabrous below ground, densely glandular-puberulent distally, entire plant pale yellow, white, or tan, or infused with purple in exposed aerial parts. Roots few to many, fragile, sometimes with short bifurcations, forming an amorphous mass 1-2 cm in diameter around host attachment. Leaves 3–8 mm, spirally arranged, broadly rounded or deltoid, appressed, tips rounded to subacute, margins entire to finely erose. Inflorescence(s) compact, forming a low crown to a hemisphere or cluster in robust specimens (occasionally elongate where obstructed or shaded), the proximal flowers solitary, long-pedicillate, or 2 or 3 on axillary branchlets, the distal flowers nearly sessile. Bracts 5–10 mm, shape obtuse to acute, the tips often retuse or finely erose, erect to slightly reflexed distally. **Pedicels** 2–10 mm (proximal ones to 35 mm in robust specimens), bracteoles 2, similar to calvx lobes. Calvees 6-14 mm, slightly asymmetric, fused portion 1-4 mm, the lobes subulate to narrowly spathulate, sometimes bifid at tip, erect, pallid or tinged dark purple. Corollas (0.8–) 15–25 (–32) mm, exterior pallid, interior with pink or purple venation, sometimes also infused with color beyond the veins (especially Santa Cruz County populations), inconspicuously two-lipped, the margin of sinuses between upper and lower lips rounded, truncate, or narrowly notched, not acute, the interior surface glabrous, moderately glandular-puberulent externally. Corolla tube not distinctly arched or dilated dorsally, slightly constricted above the ovary and slightly widening toward the apex, most flowers held +/- erect. Palatal folds not prominent, cream to pale yellow, slightly inflated, glabrous. Corolla lobes ascending to somewhat outward-curved, sparsely glandular-puberulent internally. Adaxial corolla lobes 4-6 (-9) \times 2-4 mm, oblong to lanceolate, apex rounded to obtuse or truncate, rarely acute, margins finely to moderately erose, the sinus dividing the two lobes 3–4 (–5) mm deep; abaxial lobes +/- equal, 4-6 (-9) \times 2-3 mm, oblong to oblong-ovate, tips rounded to slightly truncate, rarely acute, margins sometimes erose, tips erect, slightly reflexed or slightly incurved. Stamens: filaments glabrous at base; anther sacs glabrous or with a few long hairs along thecae, included or somewhat exserted from tube, held below to above stigma. Stigma somewhat bilobed, irregularly crateriform with thick lobes. Capsules 8–10 mm, shorter than calyx, 2 valved. **Seeds** numerous, 0.3–0.5 mm, brown, +/-ovoid, faceted, favose. 2n = 48.

Topotypes. USA. California. San Francisco Co.: Lands End, San Francisco, 22 Aug 1923, Eastwood s.n. (CAS). Sandy soil at Land's End, San Francisco, the region of the type locality [of Orobanche californica C. & S.], 7 Sep 1930, Howell 5460 (CAS, GH, MO, RSA). Rocky slide near Land's End, below Lincoln Park, 30 Jul 1966, Heckard & Raven 1543 (chromosome voucher) (JEPS). Rocky slide near Lands End, below Lincoln Park, 30 Jul 1966, Heckard 1543a (JEPS). Near Lands End, below Lincoln Park, at base of rocky cliff, along jeep road, elev. ca 150 ft, 30 Jul 1966, Heckard & Raven 1542 (chromosome voucher).

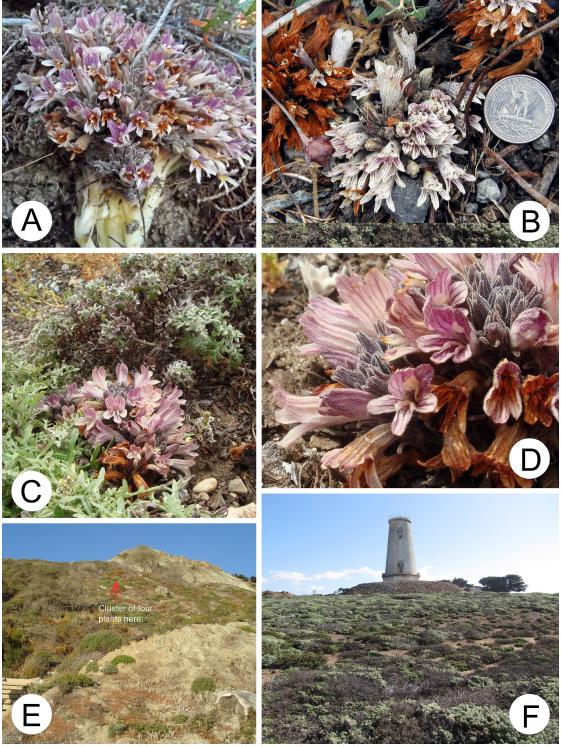


Figure 1. *Orobanche robbinsii* plants and habitats. **A.** Partially excavated plant near Presidio, San Francisco County. **B.** Plant with slightly narrower corolla lobes, near Carmel, Monterey. **C.** Flowering plant at base of *Eriophyllum staechadifolium* (from lighthouse area shown in Part F). **D.** Close-up view of flowers (same individual as in Part C); note the relatively straight (not recurved corolla, somewhat broader lobes. **E.** Bluffy slopes on W side of Presidio, San Francisco County (location of plant in Part A indicated with red arrow). **F.** Lighthouse area at Piedras Blancas, San Luis Obispo County, California. Photos by A. Colwell.



Figure 2. Holotype of Orobanche californica Cham. & Schltdl., Linnaea 3: 134-136. USA. California [San Francisco Co.], S. Francisco, A. von Chamisso s.n. in Aug [1816] (LE. Enlarged insets of label and plant are in red boxes. Photos by Barbara Ertter.

Table 1: Comparison of Orobanche robbinsii and related sympatric Orobanche taxa.

Species	Corolla Color	Corolla shape	Anther indument	Peak Flower ing	Host(s)	Plant Community	Substrate
O. robbinsii	White to cream exterior and interior; interior lobes with pink or purple venation, occasionally also tinged pink	Tube straight to slightly curved, slightly dilated midway; upper corolla lobes oblong, erect at full anthesis, corolla 18-20 mm*	Anther sacs glabrous or occ with few long hairs	April- July	Eriophyllum staechadifolium	Coastal rock outcrops and rocky or sandy slopes at ocean, or slide material thereon	Crevices of metamorphose d ocean floor rock outcrops (Franciscan Complex), or gravel, scree or sandy soil derived from same.
O. californica subsp. grandis	Pallid to yellow exterior; interior of upper lobes infused pink to solid brick red, lower lobes paler with pink venation	Tube arched, abruptly dilated midway; upper corolla lobes flared, frilly, reflexed at full anthesis, lower lobes erect, corolla 25-30 mm*	Anther sacs woolly	July- August	Lessingia filaginifolia, Isocoma menziesii var. vernonioides	Coastal dunefields, especially in the lee of the foredunes	Semi-stabilized ocean sand dunes
O. californica subsp. californica	Solid lavender to solid red- purple exterior and interior, with darker venation	Tube arched, gradually widening; upper corolla lobes lanceolate to lance-ovate, diverging, recurved at full anthesis, corolla 25-55 mm*	Anther sacs woolly	August - Septem ber	Grindelia stricta var. platyloba and other Grindelia spp.	Coastal prairie, coastal bluff (Pleistocene marine terraces), coastal strand; estuary & lago on borders	Ancient alluvial deposits, composed of clay, silt, sand and gravel

^{*}measurements indicate overall corolla length from base of flower to tip of upper lobes.

Representative specimens. USA. California. County unknown: California, 1868–1869, Kellogg & Harford 651 (NY, right-hand plant only). Coast Range, Central California, 1876, Palmer 337 (YU). Monterey Co.: Point Lobos State Park, on Artemisia pycnocephala, sands, 16 Jun 1935, Lee & Mason 9024 (UC). Along State Highway No. 1 between Little Sur River & Point Sur, bluffs facing sea in sandy soil, 31 May 1948, Stebbins 3950 (UC); 27 Jun 1966, Heckard 1600 (chromosome voucher) (JEPS). Coastal bluff just NW of restaurant, Rocky Point, S of Carmel, cleft in rock with Corethrogyne californica, Eriophyllum staechadifolium, coastal bluff, 27 Jul 1988, Heckard & Taylor 6725 (fragment in packet; JEPS); Jul 2004, Colwell & Taylor 04-313 (UC). San Francisco Co.: San Francisco, sand dunes, Aug 1914, Miere s.n. (CAS). Coastal dune, 26 July, 1922, Degener s.n. (NY). Above the Golden Gate to the E of Land's End, Lincoln Park, on crumbling rocky slopes. 5 Oct 1967, Heckard 1750 (JEPS). San Luis Obispo Co.: 0.5 mi N of Piedras Blancas, on seaward face of bluffs, just above beach, 22 Apr 1951, Carlquist 127 (DS, JEPS). Piedras Blancas, about ½ mi N of Point Piedras Blancas, same location as Carlquist 127, in sand of stabilized bluff about beach, 27 Jun 1967, Heckard 1598 (chromosome voucher) (JEPS). Piedras Blancas Light House, native plant restoration area W of lighthouse, Adams s.n. in 2014 (UC). San Mateo Co.: Pacifica, Shelter Cove, eroding faces of bluffs facing sea, 24 Jul 2014, Colwell 04-

196 (UC). Golden Gate National Recreation Area, Pacifica, W of Highway 1 at Mori Point, gravel bench at base of coastal bluff, 23 Jun 2013, *Schneider & Colwell 293* (JEPS). <u>Santa Cruz Co.</u>: Santa Cruz, Jun 1881, *Jones 242* (RSA). Sand Bluff, 4 mi N of Santa Cruz, on ancient shell mound, 28 May 2015, *Neubauer s.n.* (JEPS); 5 Jun 2015 *Colwell 15-006* (JEPS). Pigeon Point Light, in restoration area on lighthouse campus, 6 Jun 2015, *Colwell 15-007* (JEPS).

Additional specimens cited in the unpublished Heckard 1969 manuscript as at CAS, but not found during research for this paper. Marin Co.: Lime Point, 29 Jun 1921, Eastwood s.n. San Francisco Co.: Ingleside, on Eriophyllum staechadifolium, Bergman s.n. in 1920. The last was also cited by Howell et al. (1958).

Table 2. Comparison of *Orobanche robbinsii* with the *O. californica* type specimen at LE (an inflorescence from a single plant) and *O. californica* subsp. *californica* specimens from San Francisco and vicinity.

De la la destaca de la compansión de la	O. robbinsii	O. californica type specimen (LE)	O. californica subsp. californica	
Main flowering period	April–July	October	Aug-October .	
Anther sac vestiture	ther sac vestiture Glabrous or a few long hairs		Woolly	
Corolla color White with pink or lavender veins, drying proving to brown		Dried dark (apparently violet in color when fresh)	Lavender to violet, drying dark	
Inflorescence A corymb, few- to many- flowered, often congested		A corymb, appears to have at least ten flowers and buds, not congested	A corymb, few- to many- flowered, but not congested	
Corolla length	15-23 mm	19-22 mm	22-30 mm	
Corolla lobe length	3-4 (-8) mm	6-10 mm	5–13 mm	
Calyx length	8-13 mm	11–15 mm	12–15 mm	
Calyx lobe length	4–10 mm	6–9 mm	9–18 mm	
Corolla throat	Barely constricted above ovary	Strongly constricted above ovary	Strongly constricted above ovary	
Corolla shape	Upper corolla lobes with more or less parallel sides and evenly rounded or truncate apices; their shared notch is deep, half to nearly same length as upper lobes	Upper corolla lobes are slightly flared medially and their distal outer edge is tapered inward towards a shallow shared notch, shorter than upper lobes	Upper corolla lobes are slightly flared medially and their distal outer edge is tapered inward towards shallow shared notch, shorter than upper lobes	
Sinus between upper and lower corolla lobes	Rounded	Acute	Acute	
Position of upper corolla lobes	Erect, flared slightly at tips	Some indication of flared lobes	Flared, outer margins sometimes also recurved	

Etymology

The specific epithet was chosen by Larry Heckard to commemorate G. Thomas Robbins (1916–1960), assistant to Rimo Bacigalupi at the Jepson Herbarium, University of California, Berkeley. According to Heckard, it was Robbins who first recognized the distinctness of this species. Heckard chose Robbins' 1956 collection as the type.

The genus *Orobanche* has heretofore borne the common name of broomrape, a name of European origin, which refers to the parasitism of some members of Fabaceae tribe Genisteae Dumort. (brooms) by species in the Eurasian sections of *Orobanche*. New World sections of *Orobanche* do not parasitize legumes. Therefore, we suggest an alternative common name: daisydrops. This name refers to the primary host plant family (Asteraceae) for this and related *Orobanche*

species and to its flowering at the soil surface near its host. In the case of the plant described here, the suggested common name is Robbins' daisy-drops.

Ecology and distribution

The vegetative stages occur mainly underground, attached to host roots. Inflorescences appear above ground April through June in the southern part of the range, and in June and July farther to the north; rarely at other times of year in response to atypical rainfall patterns. Elevational range is 0-100 m.

This species is endemic to the central California coast. It occurs in sandy or gravelly openings among rocky outcrops, eroding slopes of seaside bluffs and on prehistoric shell mounds. Two specimens, Miere s.n. and Degener s.n., also list sand dunes as habitat in San Francisco on their labels, but this requires confirmation.

Host relationships

Orobanche robbinsii has been confirmed by excavation multiple times to be connected to roots of Eriophyllum staechadifolium Lag. (Asteraceae: Heliantheae). Eriophyllum staechadifolium is the most frequently reported host on specimen labels. Artemisia pycnocephala (Less.) DC. (Asteraceae: Anthemideae) and *Phacelia californica* Cham. (Hydrophyllaceae) have been reported as the host on one specimen label each, and both species are frequent in O. robbinsii habitat. However, neither was physically confirmed to be the host.

North American *Orobanche* species tend to have one or sometimes two primary host species, although they will utilize other host species in cultivation (Hill 1892; pers. obs.), and occasionally a population will be found on a unique primary host species. Therefore, the host species (and its habitat) is an excellent identifying characteristic for these parasite species and care should be taken to obtain this information for herbarium specimen labels.

Taxonomic relationships

Relation to sympatric Orobanche californica subspecies. Orobanche robbinsii shares its coastal California distribution with two other Orobanche taxa: O. californica subsp. californica and O. californica subsp. grandis Heckard. Because these three taxa are sympatric, and populations of each are closely juxtaposed, recognition of their distinctness has been delayed. However, each has a distinct primary host species and is found on a distinct substrate type in a distinct plant community. Each has a different primary flowering time and differs in floral traits related to pollinator affinity, resulting in less opportunity for interspecific gene flow than a solely geographic distance measure would suggest. See Table 1 for a comparison of traits between these three taxa.

Schneider et al. (2016 in press) have recently studied the molecular phylogeny of New World Orobanche and included samples of O. robbinsii. They have confirmed that O. robbinsii is part of the O. californica complex. This might support describing the new taxon as a subspecies of O. californica, and indeed the taxon may be reclassified as such following more intensive studies. For now, we prefer to maintain it at the species level, both because of its unique host specificity and ecology and because the placement of O. robbinsii within the complex differed in trees generated using plastid sequence markers and those from nuclear markers, and thus has not been fully resolved. Future studies should focus on phylogenetic relationships of the O. californica complex using additional, more rapidly evolving markers.

Distinctness from the type of Orobanche californica. The type locality chosen for Orobanche robbinsii is in the vicinity of the type locality of Orobanche californica, described by Adelbert von Chamisso as: "...e vicinia portus St. Francisci Californiae..." (Heckard, 1973). Howell noted: "in the region of the type locality" on his 1930 collection (Howell 5760), and Robbins apparently thought his 1956 collection (Robbins 3760) matched descriptions of the Chamisso &

Schlechtendal type, as he put "Topotype" on his labels. However, the port of San Francisco at the time of the von Chamisso collection (1816) was in San Francisco Bay, surrounded by strand and estuary plant communities, a preferred habitat of O. californica subsp. californica and its host genus, Grindelia Willd. (Asteraceae: Astereae). In von Chamisso's (1836) account of his visit to San Francisco, he included repeated trips from his ship to the Presidio (he was functioning as the ship's interpreter) and a brief trip to the North shore of the bay on October 9, where he observed a "dry, arid field" and a "swamp" (red-brown rocks there siliceous schist). The rocky sea-bluff and sand dune habitat occupied by O. robbinsii and its host occur 3-5 miles west of the port location of that time, and southwards on the coast from the promontory of the "Golden Gate". Furthermore, it is O. californica subsp. californica that would have been in bloom during von Chamisso's visit.

The holotype of Orobanche californica, a single inflorescence, is at the V.L. Komarov Botanical Institute, Saint Petersburg, Russia (LE). Heckard borrowed the type and examined it, and concluded that it is most similar to the plants that he treated as O. californica subsp. californica (Heckard 1973). In 2008, Barbara Ertter photographed photographed this type specimen while visiting LE (Fig. 2). Table 2 compares characters of this specimen with those of O. californica subsp. californica from the area and with O. robbinsii.

Note on corolla characters on herbarium sheets. Holoparasitic Orobanchaceae are succulent plants with strong oxidation activity when their tissue is cut or dried. Herbarium sheets therefore do not preserve the shape or the color of these plants well. In life, the corolla tube of Orobanche robbinsii is primarily pallid within and without, with purple or pink venation on the interior of the corolla lobes (Fig. 1A–D). In some plants, the upper lobes are also suffused with pale purple or pink (Fig. 1A, C, D). On herbarium sheets, the flowers of this species often dry dark, suggesting a deeper purple color than in life. Thus specimens can appear similar to those of O. californica subsp. californica, whose corollas (except where covered by the calyx) are uniformly reddish purple both inside and out, as their external and internal epidermal layers are composed of heavily pigmented cells. Orobanche californica subsp. californica tends to dry blackish purple or very dark brown (as is the case with the von Chamisso type). Orobanche californica subsp. grandis, in contrast, is strongly pink to brick red on the interior of the upper corolla lobes, with pallid lower lobes with pink veins, but this species is uniformly pallid on the exterior of the corolla due to the outer epidermal layer of cells lacking pigment. This trait can be seen on well-preserved herbarium specimens, the external epidermal cells of which maintain a 'frosted' appearance when viewed under a dissecting scope. This taxon tends to dry rust brown in less well-preserved specimens, although the deeper tint in the inside of the upper corolla lobes usually remains visible.

Infraspecific variation

As in other taxa in sect. Nothaphyllon, the size of Orobanche robbinsii plants varies considerably. Individuals in shallow, rocky soil present with compact, tuber-like belowground axes topped with many short, stout branchlets supporting a congested crown of few to many 1 cm-long flowers at the soil surface (Fig 1B). Such plants may be as small as 4 cm from host attachment to tip of inflorescence. Individuals that germinate in loose, deep soil and attach to robustly growing hosts, such as in fresh landslides or recently cleared sites, can exhibit an elongate, thick, fleshy, underground stem from a deeper host root attachment, either with a single flowering axis, or branched below the soil surface near the base of the axis, resulting in multiple adjacent crowns of flowers at the soil surface (Fig. 1A). Robust individuals (e.g., Robbins 3730 [UC]) can be as long as 26 cm from attachment point to tip of inflorescence. The inflorescence in that case may present as a hemisphere of flowers at the soil surface, rather than a congested, flat crown (Fig. 1A).

Flower color and shape, as for other North American *Orobanche* species, is labile in this group, varying markedly between populations and even between individuals within a population. This variability could be an effect of genetic drift between these small, isolated populations or of differential selection by local pollinators. The variation between plants is foremost a consequence of differences in vigor of the host plant, or of the particular host plant root to which the parasite is attached. Plant size, flower number, and flower size are especially a function of host vigor, depth of germination of the parasite and amount of light an individual receives upon surfacing. In contrast, the hue of the entire plant or corolla, corolla shape and corolla lobe margin type may be genetically controlled, with a high degree of variability between individuals, as evidenced by differences in these traits in plants attached to the same host either in the wild or in cultivation (personal observation). The degree of shading that plants receive may also factor into the amount of anthocyanin production.

Habitat

This species inhabits coastal bluff and slope habitat, in rocky or sandy soils, where its host plant, Eriophyllum staechadifolium, is frequent. Several of the known locations are on steep, eroding faces of sea-bluffs, on substrates belonging to the Franciscan Complex (metamorphosed rock derived from ocean floor and pelagic detritus) (Fig. 1E). The host plant occurs in seaside habitats from Coos County, Oregon, to San Diego County, California, but is most abundant and often dominant on Franciscan Complex substrate, between Del Norte and Ventura counties; within this region of host plant abundance additional populations of *Orobanche robbinsii* should be sought.

Conservation status

This new taxon has not yet been assessed for conservation status. This species has been documented to date in fourteen distinct locations (greater than 0.25 miles apart). Of these, ten are on county, state, or federal land. Two sites, Ingleside (Degener s.n. [NY]) and Sand dunes, San Francisco, (Miere s.n. [CAS]), have been converted to urban landscape and the Orobanche populations thereon likely have been extirpated. At the other twelve sites, there remains significant intact habitat where this species could persist or has been confirmed to be extant recently. A portion of this plant's past and potential habitat has been lost to non-native invasive plants (as is the case at type locality, where it has not been relocated in recent years), and to trampling associated with nearby development (Rocky Point and Lime Point locations). Removal of invasive species, or removal of vegetation followed by regrowth of the host species, has resulted in the reappearance of populations of Orobanche robbinsii at Piedras Blancas Light Station (Lewis and Adams 2009-2010), at Pigeon Point Light Station, and at the bluffs on the west side of the Presidio in San Francisco. Concentrations of rodents are a threat to O. robbinsii survival in some locations, such as at the Presidio, where most plants observed blooming in the past ten years have been devoured prior to setting seed.

With the exception of the restoration area at Pigeon Point Light, where more than 100 individuals were in bloom in 2015, fewer than 20 individuals have been observed to be flowering at any location, with 1–5 individuals typically observed at one time in a given location.

The typical habitat is steep, slippery with loose soil and rock, and difficult to access. Therefore, further inspection of likely habitat likely will reveal additional populations. However, due to the restricted amount of the preferred habitat (sparsely vegetated sea-cliffs with both a non-granitic rock substrate and abundant host plants), the number of occurrences of this plant are unlikely to be increased significantly. Therefore, the authors suggest the California Native Plant Society Rare Plant Inventory (http://www.cnps.org/cnps/rareplants/inventory/) consider this taxon for evaluation and eventual ranking.

Chromosome counts

Meiotic figure drawings and chromosome counts were made from four Heckard collections by Fei Mai Chuang in 1966 and 1967. A sample camera lucida drawing is used to illustrate these counts (Fig. 3). The methods were as reported in Heckard and Chuang (1975). All four collections

exhibit the diploid n = 24 number typical of sect. *Nothaphyllon*, and shared with most other California Orobanche species.

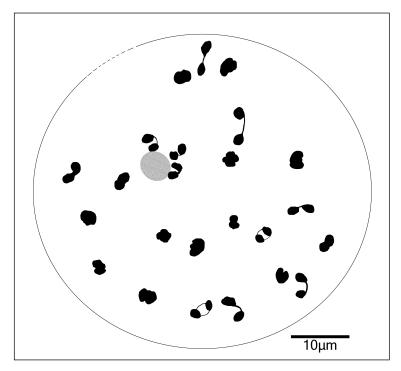


Figure 3. Camera lucida drawing at diakinesis of a representative meiotic chromosome count of Orobanche robbinsii $2n = 24_{\parallel}$. Voucher: Heckard & Raven 1543. Other counts of $2n = 24_{\parallel}$ are based on Heckard & Raven 1542, Heckard 1598, and Heckard 1600. All vouchers at JEPS. Original counts and camera lucida drawing by F.M. Chuang. See the exsiccatae for voucher locality data.

ACKNOWLEDGEMENTS

Gratitude is extended to the following people and institutions for their contributions to the study of this taxon: Paul Silva for his recollections about this manuscript and advice on how to honor Larry Heckard's contribution; Fei Mai Chuang, for the chromosome counts and original camera lucida drawings of the squashes; Barbara Ertter, for photographing the type at LE; Margriet Wetherwax, for preserving Larry Heckard's files, including his unpublished manuscript; UC/JEPS herbaria for permission to reproduce his figures and quote from the text of his manuscript, and to the following herbaria: CAS, GH, MO, NY, RSA, UC/JEPS, YU for loaning the specimens used in this paper, and for allowing the senior author to visit their collections. The Flora of North America Project kindly provided funds to the senior author for a research visit to the Missouri Botanical Garden, where both authors benefited from discussions with our daisy-drop collaborator, Turner Collins. Gratitude is expressed to the following people for their assistance in the field: Michael Chasse for bringing the continued existence of this species in San Francisco to our attention and for searching the type locality for this plant (with Emily Magnaghi, Peter Brastow, and other intrepid GGNRA staff); to Carole Adams for bringing an extant population in the vicinity of the earlier Carlquist collection to our attention; to Dylan Neubauer and Tim Hyland for locating the Sand Bluff population; to Adam Schneider and Bruce Ponman for combing the bluffs of central California with the senior author. Special thanks go to the many volunteers and staff at Piedras Blancas and Pigeon Point Light Stations and at the Golden Gate National Recreation Area, whose diligence in weed removal and native plant restoration has had a positive impact on the presence of this species at all three locations.

LITERATURE CITED

- Beck von Mannagetta, G. 1890. Monographie der Gattung Orobanche. Biblio. Bot. 4: 78-85.
- Beck von Mannagetta, G. 1930. Orobanchaceae. Pp. 1–348, in A. Engler (ed.). Das Pflanzenreich: Regni vegetabilis conspectus IV (261), issue 96. Wilhelm Engelmann, Leipzig.
- Heckard, L.R. 1973. A taxonomic re-interpretation of the Orobanche californica complex. Madroño 22: 41–70.
- Heckard, L.R. and T.I. Chuang. 1975. Chromosome numbers and polyploidy in Orobanche (Orobanchaceae). Brittonia 27: 179-186.
- Hill, E.J. 1892. The host plants of Aphyllon fasciculatum. Bull. Torrey Bot. Club 19: 17–21.
- Howell, J.T., P.H. Raven, and P. Rubtzoff. 1958. A flora of San Francisco, California. Wasmann J. Biol. 16: 1–157.
- Lewis, R. and C. Adams. 2009–2010. Native plant restoration at Piedras Blancas Light Station Outstanding Natural Area. Fremontia 37(4)/38(1): 34–39.
- Munz, P.A. 1930. The North American species of Orobanche, section Myzorrhiza. Bull. Torrey Bot. Club 57: 611-624.
- Schneider, A.C., A.E.L. Colwell, G.M. Schneeweiss, and B.G. Baldwin. 2016 (in press). Extensive cryptic host-specific diversity among western hemisphere broomrapes (Orobanche s. l., Orobanchaceae). Ann. Bot.
- von Chamisso, A. 1836. A Sojourn at San Francisco Bay 1816 by Adelbert von Chamisso, Scientist of the Russian Exploring Ship Rurik, Illustrated by a Series of Drawings First Published in 1822 by the Rurik's Artist Louis Choris. Book Club of California, San Francisco (Grabhorn Press) [a reformatted partial reprinting of: Choris, L. 1822. Voyage Pittoresque Autour du Monde, Avec des Portraits de Sauvages d'Amerique, d'Asie, d'Afrique, et des Iles du Grand Ocean; des Paysages, des Vues Maritimes, et Plusieurs Objets D'histoire Naturelle; Accompagne de Descriptions par M. Le Baron Cuvier, et M. A. De Chamisso, et D'observations sur Les Cranes Humains, par M. Le Docteur Gall. Impr. de Firmin Didot, Paris.]