DUDLEYA GNOMA (CRASSULACEAE): A NEW, RARE SPECIES FROM SANTA ROSA ISLAND

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ABSTRACT

Dudleya gnoma is endemic to a single California island. It appears most similar to a Channel Islands endemic, D. greenei, and the more widespread D. caespitosa. It differs from D. greenei and D. caespitosa chiefly by its smaller size, smaller rosettes, shorter leaves, narrower peduncles, shorter and less-branched inflorescences, earlier flowering season, and habitat. Glaucous forms of D. candelabrum Rose have now been found on two of the northern Channel Islands, but that species is not easily confused with D. gnoma. Dudleya gnoma is placed in subg. Dudleya based on its evergreen leaves with broad bases, broad rather than terete leaves, and erect or fairly erect petals.

The name *Dudleya greenei* forma *nana* was originally proposed in a dissertation (Moran 1951) and was applied to a population of small plants found only on East Point, Santa Rosa Island. The plants had been discovered the previous year by Reid Moran. Though other aspects of the dissertation were published (e.g., Moran and Uhl 1952; Uhl and Moran 1953), the name itself was never validly published. Moran decided not to formally recognize the taxon. His reluctance was due at least in part to unresolved taxonomic problems in *D. greenei* and the *D. caespitosa* complex and also due to the presence of *D. greenei* on the same island (Moran 1951 and Moran, personal communication April 1994).

By 1993, "forma nana" was still only known from Moran's original collection site on infrequently visited East Point. In May 1993, I examined many dudleyas on Santa Rosa Island with the cooperation of the National Park Service. Sarah Chaney (of the NPS) and I found two additional colonies of "forma nana", not realizing that those two colonies had been discovered shortly before by Steve Junak of the Santa Barbara Botanic Garden.

Shortly afterwards, Thomson (1993) described a new species based on the Santa Rosa Island plants, *D. nana* Moran ex P. Thomson. Moran (personal communication 1994) thinks it would be better to refer to the name as *D. nana* P. Thomson (incorrectly attributed to Moran). Thomson based his description of *D. nana* on Moran's (1951) unpublished description of "forma nana" and on material of the cultivar 'White Sprite' (Thomson, personal communication, March 1994). Thomson (1993) mentioned 'White Sprite' without referring to collection data. In the late 1970s, Abbey Garden named

and distributed *D. greenei* 'White Sprite,' which they had propagated from a cutting or plant given to them by Dorothy Dunn (Higgs, personal communication 1996). She obtained her material from Reid Moran. The International Succulent Institute distributed Moran 3364 (from UC Berkeley) as 'White Sprite' in 1977 (Kimnach and Lyons 1977).

Thomson published the name *D. nana* Moran ex P. Thomson without citation of a type specimen. In the description there was no discussion regarding the reasons for recognizing this taxon separate from *D. greenei*. The arrow on the map on p. 197 is an accurate approximation, but the table on p. 17 (Thomson 1993) incorrectly lists *D. nana* as occurring on Santa Cruz Island, rather than on Santa Rosa Island. The lack of collection number, collector, collection date, type specimen, or location of a type specimen in an herbarium indicate Thompson's protologue did not constitute a valid publication according to the International Code of Botanical Nomenclature in effect at the time (Greuter 1988) or according to the Code in effect now (Greuter 1994).

In his monograph, Thomson described 12 new species and made 11 new combinations. He recognized most taxa previously named as subspecies (and many taxa previously reduced in synonymy) as full species. He separated *Hasseanthus* from *Dudleya* as had been done prior to 1953 (Thomson 1993; Uhl and Moran 1953; Moran 1951, 1953). In Thomson's book, there are references to only seven herbarium specimens and to one set of duplicates for those seven. Although I disagree with Thomson on several other points, for reasons mentioned below, I do think the plants he referred to as *D. nana* are distinct enough to be recognized at the species level.

SPECIES TREATMENT

Dudleya gnoma S. McCabe, sp. nov. (Fig. 1).—Type: USA, California, Santa Barbara Co., Santa Rosa Island, approximately 200 m W of East Point, found in shallow soils on top of a bare, rocky knoll, elevation 20 m, 7 May 1993, ex hort 20 May 1993, *S.W. McCabe* 792 (holotype: CAS; isotypes: SBBG, UC).

Plantae caespitosae ad 10 cm latae. Rosulae 8–51 mm latae. Caudices 5–26 mm longae diametro (1.5–)12–20 mm. Rosulae foliis 8–19, triangularis vel trianguli-ovatis, 6–25 mm longis, 5–13 mm latis, acutis, glaucis. Rami floriferi, 25–129 mm alti 2–5 mm crassi. Folia caulina 10–15, triangularia, turgida, 5–10 mm longa, 4–6 mm lata, acuta, glauca. Rami 2 vel 1–3 simplices vel bifurcati. Pedicelli 1–3 mm longi. Calyces segmentis triangularis 3.5–4 mm longis 2–3 mm latis, acutis, glaucis. Petala ca. 1–2 mm connata, elliptica, 8–9(–11) mm longa, 3 mm lata, flavus-aureus, acuta. Filimenta

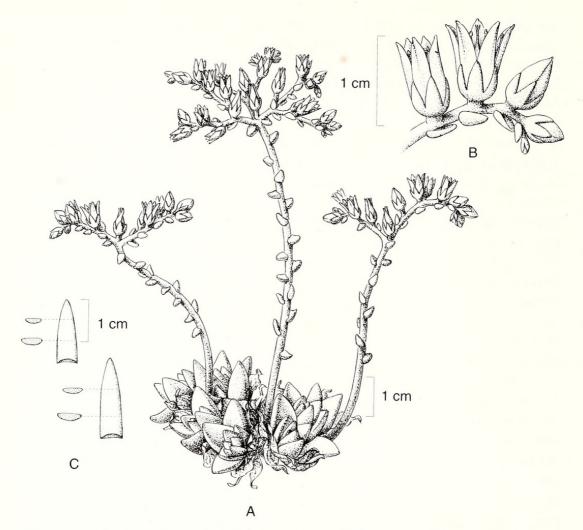


Fig. 1. *Dudleya gnoma*. A, entire plant. B, detail of flowers. C, leaves and cross-sections. All from *McCabe* 792, drawn primarily in Jun 1993 from live plants used as isotypes and using photos of the holotype. Drawing by Carol Barner, 1993.

6.5–8 mm longa. Carpella erecta. Ovariis 4–6 mm longis. Stylis 2–3 mm longis. Chromosomatum numerus n=34.

Low, cryptically colored succulent plants to 10 cm across. Roots shallow, rapidly tapering. Rosettes 1–57; 8–51 mm in diameter. Caudex caespitosely branching, 5–26 mm long \times (1.5–)12–20 mm thick; maximum of 12 mm between branches; covered below rosette with dried leaves; caudex and leaf bases not changing to burgundy-purple in response to leaf removal or other wounding. Leaves 8–19 per rosette; tinged with burgundy color underneath wax, especially on leaf tips; triangular or triangular-ovate; (6–)9–25 mm long \times 5–13 mm wide; convex abaxially, plane or concave or slightly convex adaxially; leaf margins acute adaxially; apices acute; faces heavily glaucous, single wax line on adaxial surface apparently from "bud-printing". Floral stems usually with 2 branches, occasionally

1 or 3 or more, rebranching 0-1 time; terminal flower of inflorescence 0-2 mm from point of branching; cincinni spreading initially to horizontal or recurved as flowers mature; $25-129 \text{ mm long} \times 2-$ 5 mm thick; glaucous; lightly tinged with burgundy; 0-24 mm to first leaf. Floral stem leaves 10-15 per inflorescence; changing to burgundy-purple in response to leaf removal or other wounding; horizontal to 20° above perpendicular to axis; triangular, 5-10 mm $long \times 4-6$ mm wide; turgid, clasping, acute. Pedicels erect, 1-3 mm long. Sepals lightly tinged with burgundy; tips red-burgundy or greenish-yellow; triangular, 3.5-4 mm long × 2-3 mm wide; acute; glaucous. Petals fused 1-2 mm; slightly twisted in bud; erect to slightly outcurving at tips, some flowers with petals ascending-erect with upper margins not quite touching, scarcely outcurved at tip; pale yellow to bright yellow, often tinged slightly with red especially on and near keel and towards petal tips—on some appearing almost orange; elliptic, 8-9(-11) mm long \times 3 mm wide, acute; lightly glaucous on keels, especially towards tips. Stamens 6.5–8 mm long, epipetalous shorter by less than 0.5 mm. Nectar glands 1 mm. Ovaries 4-6 mm long; styles 2-3 mm long. Seeds fusiform, flattened on one side, tapering more on one end; 0.7-1.0 mm long. Chromosome number n=34 (C. H. Uhl in Uhl and Moran, 1953). The epithet, derived from New Latin, means diminutive, fabled being and refers to the small size of the plants and their parts.

PARATYPES: USA, California, Santa Barbara Co., Santa Rosa Island, "Thin gravelly soil of a barren knoll 200 yards from East Point, Santa Rosa Island (near 33°56.5′N, 119°58.2′W". voucher for Dr. Uhl's chromosome count, 13 Mar 1950, ex hort 8 Jun 1951 *Reid Moran 3364* (UC 015364); ex hort 15 Jun 1950, some of the flower stalks appear etiolated, *Moran 3364* (UC 918949); ex hort. 8 Jun 1951, *Moran 3364* (SBBG) formerly housed at SBM; on bare, ridge several hundred meters west of East Point, 40 m west of East Point bench mark, 7 May 1993, ex hort Apr 1994, *McCabe 794* (CAS); 400–500 m W of East point, the middle of the three known colonies, petals in bud with some red, 7 May 1993, *McCabe 795* (US).

Additional information on the plant description. The differences between Moran's (1951) description and my field notes are probably a reflection of individual variation between plants and the differences between field-grown and cultivated specimens. In cultivation, plants of McCabe 792 had leaves up to 4 mm longer and rosettes 13 mm wider than recorded in the field. Moran's (1951) description differed in minor details from my field notes and those details have been incorporated above and in Table 1. Some plants of this species in cultivation more than 10 years (e.g., McCabe 179) have caudices that have become longer and have thus branched more often than those I saw in the wild. Because collection data were not certain.

measurements from *McCabe 179* were not included in the description. In low light, inflorescences elongate, petals may become less erect, and the leaves become somewhat more lanceolate and less triangular than in field-collected plants.

Habitat. Dudleya gnoma occurs on low, rounded hills at elevations of 20–70 m on the extreme southeast portion of Santa Rosa Island on gravelly, poorly developed, very shallow volcanic soils, where it is essentially the only higher-plant species. The otherwise bare patches of ground where this *Dudleya* grows are surrounded by low grassland vegetation.

Substrate. Several rocks collected from the surface of the soil at the type location and from outcrops at the highest colony are Miocene volcanoclastic sandstones. This contrasts with the Monterey formation, a diatomaceous rich formation, which has been mapped as the predominant rock type in the vicinity of *D. gnoma* on the southeastern tip of the island (Dr. Robert Garrison, UCSC Earth Sciences, personal communication, 1994). McEachern (1994) noted several other rock types in the bare patches. Further field work is needed.

Distribution and population size. Dudleya gnoma is known only from the type locality and two additional colonies within a few hundred meters west of the type locality. The type locality occupies an area less than 34 m \times 12 m. Sarah Chaney and I estimated the total number of known plants on 7 May 1993 to be roughly 3200. Totals for the farthest east and west colonies were estimated and the total for the middle colony was counted (230 individuals).

Inclusion in subgenus Dudleya. Dudleya gnoma differs from other members of subg. Dudleya by having some flowers on some plants more wide-spreading than flowers of typical members of the subgenus, approaching the petal attitude of members of subg. Stylophyllum, such as D. traskiae. The open, relatively flat habitats and very shallow soils D. gnoma inhabits are typical of habitats occupied by members of subg. Hasseanthus. In other respects, such as the evergreen nature of the plants, broad leaf bases, and petal attitude of the "average" flower, D. gnoma is most similar to members of subg. Dudleya. Although the division of species into subgenera in this genus may be artificial due to possible reticulate evolution, D. gnoma is placed in subg. Dudleya.

Comparison with other taxa. Dudleya gnoma differs from D. greenei by its smaller rosettes and shorter, mostly triangular to triangular-ovate leaves vs. larger, variously shaped leaves that are not triangular (See Table 1). Dudleya gnoma has shorter stem leaves, smaller flowers, and shorter pedicels than in D. greenei. In the in-

florescences of D. gnoma, the base of the pedicel of the first flower is usually 2–4 mm from the base of the lowest cincinnus. In D. greenei the base of the pedicel of the first flower may be 0–5 mm from the base of the first cincinnus, but it is usually 0 mm, i.e., at the base of the first cincinnus.

In D. gnoma, there are usually two branches to the inflorescence and the two infrequently rebranch. In D. greenei, there are usually three inflorescence branches, which more often rebranch and become more upright (ascending) as the cincinni uncurl. In the field in 1993, some D. gnoma had inflorescences with additional branching below the main floral branches. Such branching occurs normally in some species, such as D. edulis and occasionally (after heavy rain years or under lush horticultural conditions) in other species, such as D. greenei, D. caespitosa, and D. lanceolata. In the last three species the additional branches arise below what would normally be the first flower and depart from the floral stem at an angle slightly above the horizontal rather than ascending as in typical primary inflorescence branches. The production of some secondary branches in D. gnoma and D. greenei (observed in 1993) may have resulted from the wet winter of 1992-1993. Even the smallest flowering plants of D. greenei (McCabe 798), which looked quite young, differed from D. gnoma by having blunter leaf apices and leaves more oblong and more rounded in cross-section.

The habitat of relatively level, bare, shallow soil contrasts with the habitats of *D. greenei*, which are usually steep, rocky coastal cliffs, steep areas with rocky soils, or canyons. Unlike the easily visible bright white or green leaves of *D. greenei* on the common habitats of reddish-brown soil or dark colored cliffs, *D. gnoma* is cryptically colored and inconspicuous in its habitat. Although *D. gnoma* is very similar in color to the glaucous forms of *D. greenei*, *D. gnoma* is difficult to spot even though it grows with few other species of higher plants and on fairly level ground. Non-glaucous forms have not been found in *D. gnoma*, but both glaucous and non-glaucous forms are common in *D. greenei*.

At the population of *D. greenei* found closest to East Point (near the Torrey Pine Grove), only a few plants of *D. greenei* were even beginning to flower when plants of *D. gnoma* appeared to be past the halfway point of their blooming season. There thus appears to be at least some temporal and geographic isolation of *D. gnoma* from *D. greenei*. The steep cliffs below the upper East Point colony were not examined for additional *Dudleya* plants.

Dudleya greenei is a polymorphic species not always easily distinguished from D. candelabrum. Dudleya candelabrum differs from D. gnoma in much the same manner noted previously for D. greenei, although plants of D. candelabrum tend to be even larger (Table 1). Additionally, D. candelabrum differs from D. gnoma by the pres-

DUDLEYA FOUND ON SANTA ROSA ISLAND. Some measurements of D. greenei and D.

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	D. gnoma	D. greenei	D. candelabrum
Leaf			
	£ 13	28_110	55–170
length (mm)	51-13	011 07	07.71
width (mm)	6–25	9-35	0/-/1
thickness (mm)	2-4	4–8	4-7
Rosette width (mm)	8–51	50-150	100–300
Floral stem leaf			
length (mm)	5–10	10–30	30-70
width (mm)	4–6	5–12	10-20
shape	triangular, thick	lanceolate to oblong, ± thick	lanceolate, ± thin
attitude	0–20° above horizontal	$0-20^{\circ}$ above horizontal	90-0 below nortzonital
Inflorescence			
thickness (mm)	2–5	3-13 (usually 5.5–9)	150 540
length (mm)	25–129 (1 at 291 in cult.)	110-500	150-540
no. of branches	usually 2, occasionally 3	usually 3, rarely 2	usually 3 of more
Base of 1st pedicel from			C
1° infl branch (mm)	rarely 0, usually 2-4	usually $0 (0-5)$	0
Caudex thickness (mm)	1.5–17	14–50	20-100
	toget (to accounting areas	erect (to ascending-erect in	erect, tips outcurved
Petal attitude	in cultivation)	cult.) tips slightly out-	
	Max Inn	Im_III	Jun-Jul

ence of thick caudices that are swollen at the base, usually quite long, reflexed floral stem leaves, usually green leaves, and three or more branches to the inflorescences. The habitat for *D. candelabrum* is steep, inland to coastal canyons, often north-facing or shaded cliffs, and often on deeper soils than *D. greenei*.

Dudleya gnoma is clearly separate from Dudleya caespitosa. Dudleya caespitosa is very similar to D. greenei, differing chiefly by its bright yellow flowers as opposed to usually pale yellow flowers and by more variation in leaf shape and size. Phenotypic dwarf forms of D. caespitosa have been found in San Mateo County, approximately 430 km north—northwest of D. gnoma. The morphology of the dwarf forms grade into normal forms in the area. The dwarf plants of D. caespitosa respond more vigorously to cultivation than do those of D. gnoma; they further differ by having the base of the pedicels of the first flowers at the base of the cincinni, brighter yellow and more erect petals, broader leaf apices, and less glaucous leaves.

The various forms of *D. greenei* and *D. caespitosa* respond well to summer water. When *D. gnoma* receives supplemental summer water it retains its leaves as usual, but there is little new growth and the roots may actually be killed. In summary, compared with what may be its closest relatives, *D. greenei* and *D. caespitosa*, *D. gnoma* is unusual in its habitat requirements, petal attitude, short and thin-stalked inflorescences, and near-obligate summer dormancy period.

Even though *D. gnoma* grows only 2 km from *D. blochmaniae* subsp. *insularis* in somewhat similar habitats, it differs from its close neighbor by not possessing an underground corm, by having broad rather than narrow leaf bases, by having evergreen rather than vernal leaves, and by having fairly upright rather than widespreading petals.

Dudleya parva grows on the mainland adjacent to the location of the Channel Islands. Like D. gnoma, D. parva is a dwarf member of subg. Dudleya and also appears to be restricted to Miocene volcanic substrates. Dudleya parva, however, has narrower, less glaucous summer-deciduous leaves and is restricted to north-facing slopes.

Specimens from Prince Island (off San Miguel Island), topotypes of *D. hoffmannii* Johansen and *D. regalis* Johansen, are clearly different from *D. gnoma*, but within the range of variation for *D. greenei*. The leaves of *D. hoffmannii* were described (Johansen 1932a, b) as over twice the length of those of *D. gnoma*. The leaves of *D. regalis* were described as over four times as long.

Although *D. echeverioides* Johansen has been described as having an odor "unmistakably resembling that of woodland violets" (Johansen 1935), I noticed no such odor from any member of subg. *Dudleya* on the island. Johansen's (1935) description of *D. eche-*

veriodes with leaves linear, spatulate, or oval, 34–45 mm long and obtuse and having inflorescences with several branches, differs from the triangular to lanceolate, acute leaves 6–25 mm long and 2–3 branches of the inflorescences found in *D. gnoma*. Therefore, *Dudleya echeverioides* clearly differs from *D. gnoma*.

Glaucous plants in D. candelabrum. Although it has been previously reported that D. candelabrum, another northern Channel Island endemic, is non-glaucous (Moran 1951, Munz 1968, and Bartel in Hickman 1993), I found somewhat glaucous plants of D. candelabrum on Santa Cruz Island (McCabe 692 and McCabe 694) and heavily glaucous plants on Santa Rosa Island that appeared in other respects to be D. candelabrum (McCabe 801). The leaves were 55–97 mm long, the caudices 45 mm thick, and the floral stem leaves were reflexed on some of the inflorescences. These and other plants of D. candelabrum are easily distinguished from plants of D. gnoma. Seed germination and seedling establishment were poor for seeds of McCabe 801 (out of 30 seeds, 1 seedling survived to one month and then died) indicating the possibility of low fertility in this plant.

Taxonomic rank. With the segregation of D. verityi (Nakai 1983) and the recognition of D. palmeri separate from D. caespitosa (e.g., Bartel 1993 and Munz 1968), the main characteristic separating D. caespitosa from D. greenei is petals bright yellow vs. petals pale yellow. (I also consider the red-petaled plants of southern Monterey County to be more similar to D. palmeri than to D. caespitosa in most cases.) The discovery of relatively bright yellow petals in D. greenei (e.g., McCabe 803 on Santa Rosa Island below the Torrey Pine Grove) further lessens the distinction between D. caespitosa and D. greenei. Even though plants from near the Torrey Pine Grove could possibly be considered to be D. caespitosa, they are left as D. greenei as had been done by Uhl and Moran (1953).

Because of the minor differences between *D. caespitosa* and *D. greenei*, the possibility that *D. greenei* could later be reduced to a subspecies of *D. caespitosa*, and because of the differences between *D. gnoma* and other species, it makes more sense to treat *D. gnoma* as a species than as a subspecies. Although an argument could be made to treat it as a subspecies of *D. greenei*, *D. gnoma* is more easily separable from all other species and subspecies than the following species pairs are from each other: *D. farinosalD. caespitosa*, *D. caespitosalD. palmeri*, *D. caespitosalD. greenei*, and *D. greeneil*, *D. candelabrum*.

Threats. Dudleya gnoma is threatened by erosion, at least during heavy rain years. Large, non-native grazing mammals such as cattle, elk, and deer probably exacerbate this erosion. In 1993, approximately 5% of the plants were uprooted in some sections. Later sam-

pling by Park Service research staff (McEachern 1994) yielded results similar to my estimates. For example, McEachern (1994) found the colonies to have the following percentages of uprooted plants: lower 5.0%, middle 3.6%, and upper 9.0%. I noted many broken floral stems (perhaps from hooves or small animal herbivory). Although I found some small plants with single rosettes indicating some reproduction, I saw no first-year seedlings. Given the small population size, the uprooted plants, and the apparent slow rate of replacement, there is cause for concern about the long-term viability of the populations.

The National Park Service has placed a fence around the colonies since work on this article began. Uprooted plants have also been replanted.

Additional specimens examined. My specimens will be housed at CAS and collection numbers, unless otherwise noted, are mine.

Dudleya greenei Rose.—USA, California, Santa Barbara Co., San Miguel Island: Prince Island off of San Miguel Island, 10 May 1932, Ralph Hoffmann (holotype of D. hoffmannii, CAS); Prince Island, 10 May 1932, Hoffmann (syntype of D. regalis, CAS); Prince Island, n=51, 30 Jun 1950, Moran 3443, 3443A (topotype of D. regalis, UC, CAS); San Miguel Id., North Point, 29 Jun 1950, Moran 3440 (UC); Hoffmann Cliff (Eagle Cliff), n=51, 27 Jun 1950, Moran 3438 (UC, CAS). Santa Cruz Island: Jul and Aug 1886, Edw. L, Greene (holotype, CAS); Pelican Bay, 1 May 1931, Ira W. Clokey 5358 (UC, CAS); Pelican Bay, n=34, "1935?, cultivated at La Canada, California," Moran 242 (UC); north coast, e. of West Point, near the top of a nearvertical cliff, 21 May 1991, 754. Santa Rosa Island: "Vicinity of Bletcher's Bay," 30 Jun 1931, L. R. Abrams and I. L. Wiggins 222 and 243 (UC, CAS, SBBG); Arlington Cyn. 550', n=51, ex hort 19 Jun 1950, C. F. Smith 2537A (UC); Water Canyon, on canyon slope, 1 1/2 miles inland, 5 Dec 1930, Ralph Hoffmann (Note this is the same year, collector, and island as lost D. echeveriodes type, but there is no indication that this was a type. CAS); above Cherry Canyon, on a ridge top, on shallow soil above a Lyonothamnus floribundus var. asplenifolius grove, 8 May 1993, 798; at the base of the Pinus torreyana grove, at the base of a dry streambed/dry cascade, 12 m above the main road, 9 May 1993, 803.

D. candelabrum Rose.—USA, California, Santa Barbara Co., Santa Cruz Island, Jul and Aug 1886, Edw. L. Greene (holotype, CAS); Santa Cruz Island, Willows Anchorage, n=17, 11 Mar 1950, ex hort 2 Jun 1951, Moran 3354; near Valley Anchorage, first small arroyo e. of stairs, 9 Apr 1990, 692; in canyon near 50–100 m north of Rancho del Sur., 9 Apr 1990, 694. Santa Rosa Island, mouth of Old Ranch Canyon, n=17 count by Uhl, 8 Apr 1941, Moran 829; mouth of Old Ranch Canyon, mouth of marsh, n.-facing cliffs, elev. 3 m, 31 May

1996, 858; mouth of Cherry Canyon, n.-facing slope, overlooking NPS compound, growing near *D. greenei*, 9 May 1993, 802; along road 0.65 km by road n. of "road's end" at Johnson's Lee, 8 May 1993, 799; 4 km e. by road of Johnson's Lee, near mouth of Jolla Vieja Canyon, 801 very glaucous, 8 May 1993, 800, 801.

D. blochmaniae subsp. insularis (Moran) Moran—USA, California, Santa Barbara Co., Santa Rosa Island: Old Ranch Point, ca. 10' elev. (near 33°57.7'N, 119°58.6'W), 10 Mar, 1950, ex hort 15 Jun 1950, n=17 count by Uhl, Moran 3352 (holotype, UC); just s. of a small point, Old Ranch Point, also called "Oat Point" on some maps, elev. 3–5 m, 6 May 1993, 791.

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