A HETEROSTYLOUS *GILIA* (POLEMONIACEAE) FROM CENTRAL NEVADA

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ABSTRACT

Gilia heterostyla occurs in deep alluvial sands on floors and lower slopes of north–south valleys of northern Nye County in central Nevada. It is morphologically similar to *G. nyensis, G. subacaulis,* and *G. hutchinsifolia* differing from these species by its distylous flowers, as well as several floral and leaf features. It is the first member of the Polemoniaceae found to be heterostylous.

An attractive, magenta-flowered annual *Gilia* (Polemoniaceae) from southern Nevada was noted in the early 1960's by Janice Beatley during her ecological studies at the Atomic Energy Commission Test Site in Nye County (now the Department of Energy Nevada Test Site). The conspicuous, many-branched plants, with abundant flowers and exserted stamens, were found growing in deep white sand at the base of volcanic tuff outcrops. Numerous collections were made, many by James Reveal, who described the species as *Gilia nyensis* (Reveal 1969).

During subsequent surveys of the Test Site and adjacent regions with William Rhoads and Michael Williams during the late 1970's, the first author observed and collected specimens of a *Gilia* that appeared morphologically similar to *G. nyensis,* but with longer, paler corollas. Closer examination revealed that the plants were distylous. Within a population some individuals had flowers with long styles and short stamens while other individuals had flowers with short styles and long stamens. This represents the first documented example of heterostyly in the Polemoniaceae. The morphological distinctions between these two entities and the heterostylous condition of the newly discovered populations support the recognition of the latter as a distinct species:

Gilia heterostyla S. Cochrane and A. Day, sp. nov. (Fig. 1)—TYPE: USA, Nevada, Nye Co., T3S R49E sect. 3, Gold Flat Rd 3.7 mi S of Cedar Pass Rd, Cactus Flat, 1705 m, 14 June 1978, *Susan A. Cochrane 1300* (holotype CAS; isotypes BRY, NY, RENO, RSA, UNLV, US).

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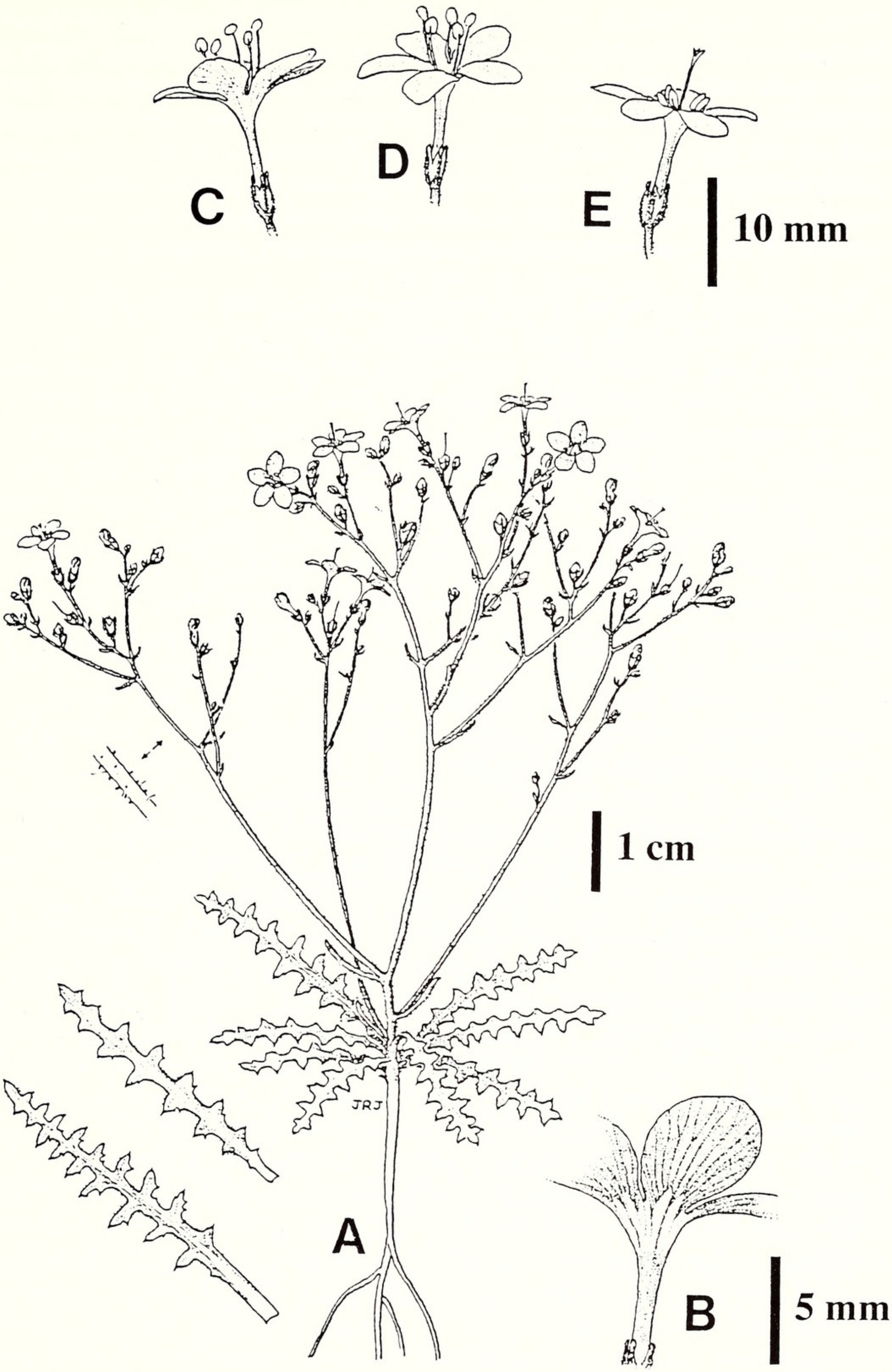

FIG. 1. *Gilia heterostyla.* A. Habit. B. Abaxial surface of corolla showing veins. C and D. Pin flowers. E. Thrum flower.

Planta annua, erecta, glandulifer. Folia basalia et caulina, lineara-oblonga, pinnatifida bipinnatifidave, loba ad angulum 90 ad rhachis mucronata. Flores distyles. Corolla infundibuliforma, tubo 2–3 plo calycem, rosa-violacea vel alba liniis rosis-violaceis, faux dilatata anguste, longa quam lata, corolla macula bilobata flavo-virenti bilateraliter super venam roseo–violaceum instructa; lobi supri rosei vivide, infra rosei pallidi nervis atroviolaceis. Capsula calyce exserta. Semina 30–50 per capsulam. Chromosomatum numerum n = 8.

Erect annual 4–12 cm tall, branches 1–many from near base, moderately glandular puberulent throughout. Basal leaves in rosette, extended 1–3 cm up the stem, sometimes elevated on stem more than 1 cm above soil, glandular-puberulent and dotted with sand grains. Leaves linear-oblong, 0.5–7 cm long, 2–13 mm wide, rachis 0.4–2 mm wide, lower leaves pinnatifid to bipinnatifid, lobes at right angle to rachis, mucronate, 1–5 mm long, secondary lobes 0.5–2 mm long when present, usually on proximal margin of primary lobes. Lower cauline leaves 5–25 mm long, entire to pinnatifid; upper cauline leaves entire, gradually reduced to bracts 1–2 mm long at terminal branching points. Inflorescence corymbose-paniculate, in open to dense semi-hemispherical crown in many-branched individuals, pedicels 1–5 mm long. Flowers distylous. Calyx (pin and thrum) 2–3.5 mm long in flower, 3–4 mm in fruit, midrib green, sometimes purplish near tip or throughout, tip acuminate-apiculate, lobes ⅓–½ length of calyx, hyaline membrane in the sinuses V-shaped, extended along margins to apex, growing with and usually not ruptured by capsule. Corolla (pin and thrum) funnelform, 11–17 mm long; tube narrow, 3–6 mm long, commonly 2(–3) times calyx, pink-violet or white with pink-violet streaks; throat narrowly flared, mostly as long as wide, 1–3 mm long, white with green-yellow bilobed spots centered on pink-violet midvein; lobes broadly ovate, subacute, 3–6.5 mm long, 4–6 mm wide, bright light pink above, paler below with darker veins. Stamens inserted near sinuses, filaments of pin flowers 1 mm long, anthers at orifice or to 1 mm above, filaments of thrum flowers 3–5 mm long, anthers exserted 3.2–5.5 mm above orifice; pollen cream colored. Ovary (pin and thrum) 2.5–3.3 mm long, green; styles of pin flowers 8–11 mm long, exserted 3.5–5 mm beyond corolla orifice; styles of thrum flowers 4–6(–9) mm long, not exserted beyond orifice. Stigmas white in both morphs, 1.1–1.2 mm long in pin flowers, 0.6–0.8 mm long in thrum flowers. Capsule (pin and thrum) 3.5–5 mm long, exserted beyond calyx, oblong ovoid, often purple-speckled at apex. Seeds 30–50, both pin and thrum plants setting abundant, normal-appearing seed. n = 8 in both morphs.

PARATYPES: USA: Nevada, Nye Co: In vicinity of "Five Mile," along Tonopah-Ely Hwy, 17 Jul 1937, *Goodner and Henning 766*

(RENO); 12 mi S of Hot Creek, 14 May 1941, *Eastwood and Howell 9448* (CAS); 10 mi NE of Warm Springs, 14 May 1941, *Eastwood and Howell 9454* (CAS, US); 7 mi S of Calloway, 26 May 1941, *Ripley and Barneby 3628* (CAS); 13 mi S of Hwy 25, N of playa, Kawich Valley Rd, 1 Jun 1968, *Reveal and Beatley 1116* (BRY, DS, NY, RENO, RSA, US, UTC); 14.2 mi NE of Warm Springs, Hwy 6, 28 May 1978, *Williams and Williams 78-74-5*; Alpha Gate (main entrance), Tonopah Test Range, Cactus Flat, 20 May 1978, *Williams 527* (CAS, NTS, UC); 2 mi N of Hwy 6, Saulsbury Wash Rd, S end Toquima Range, 27 May 1978, *Williams and Williams 78-62-1*; 5 mi NW of Gold Reed Pass, NE Gold Flat, 5250 ft, 3 Jun 1978, *Cochrane, Williams and Rhoads 1262* (CAS, NTS, RENO, RSA, US, UNLV); S of Monitor Hills, NW Cactus Flat, T1N R46E Sect 31 NW¼, 5 Jun 1978, *Cochrane, Williams and Rhoads 1281* (CAS, NTS); 0.4 mi E of Gold Flat Rd on Trailer Pass Rd, N Gold Flat, 5300 ft, 14 Jun 1978, *Cochrane 1302* (CAS, NTS, NY, RSA, UNLV); N boundary of Tonopah Test Range, W of main gate, N Cactus Flat, T1S R46E Sect 3, 15 Jun 1978, *Cochrane 1305* (CAS, NTS, UNLV, US, UTC); 14.2 mi NE of Warm Springs, Hwy 6, 26 June 1978, *Williams 78-142-3* (CAS); 0.4 mi E of Gold Flat Rd on Trailer Pass Rd, N Gold Flat, (chromosome count voucher), 15 May 1979, *Cochrane 1705* (CAS, NY, RENO, UNLV, US); Hwy 6, central Stone Cabin Valley, T3N, R48E, 20 May 1979, *Cochrane and Niles 1747* (CAS, NTS, RENO, UNLV); S end Hot Creek Valley, 20 May 1979, *Holland and Niles 2367* (CAS); 1 mi E of Five Mile Spring, Stone Cabin Valley, 20 May 1979, *Holland and Niles 2356* (CAS); Blue Jay Maintenance Station, Hwy 6, Hot Creek Valley, T6N, R51E, 28 May 1979, *Cochrane and Safford 1869* (CAS, NTS); along road, 1.0 mi W of Alpha Gate, N entrance to Tonopah Test Range, N Cactus Flat, T1S, R46E, Sect 1, 1 Jun 1979, *Cochrane 1895* (CAS, NTS); along power line rd, NE boundary of Tonopah Test Range, N Cactus Flat, T1S, R47E, Sect 4, 1 June 1979, *Cochrane 1899* (NTS); Ralston Valley S of Hwy 6, T1N, R45E, S27, 23 May 1981, *Williams and Tiehm 81-22-2* (CAS); E side Stone Cabin Valley, T4N, R49E, Sect 20, 23 May 1981, *Williams and Tiehm 81-21-1* (CAS); S of Locke's, Railroad Valley, 4.4 mi S of Hwy 6, T7N, R55E, Sect 4, 23 May 1981, *Williams and Tiehm 81-20-3* (CAS); between Currant and Nyala, 5.3 mi S of Currant, 11 Jun 1982, *Wilken 13849* (CAS); S end Pancake Range, E edge Big Sand Springs Valley, 2 rd mi N of Hwy 6 at the Black Rock lava flow, 5000 ft, T7N, R53E, Sect 9, 13 May 1987, *Knight 1564* (NY).

Distribution. Gilia heterostyla occurs in deep alluvial sands on floors and lower slopes of north–south trending Basin and Range valleys of northern Nye County, Nevada, at an elevational range of 1463–1828 m. It is known from Cactus Flat, southeast of Tonopah,

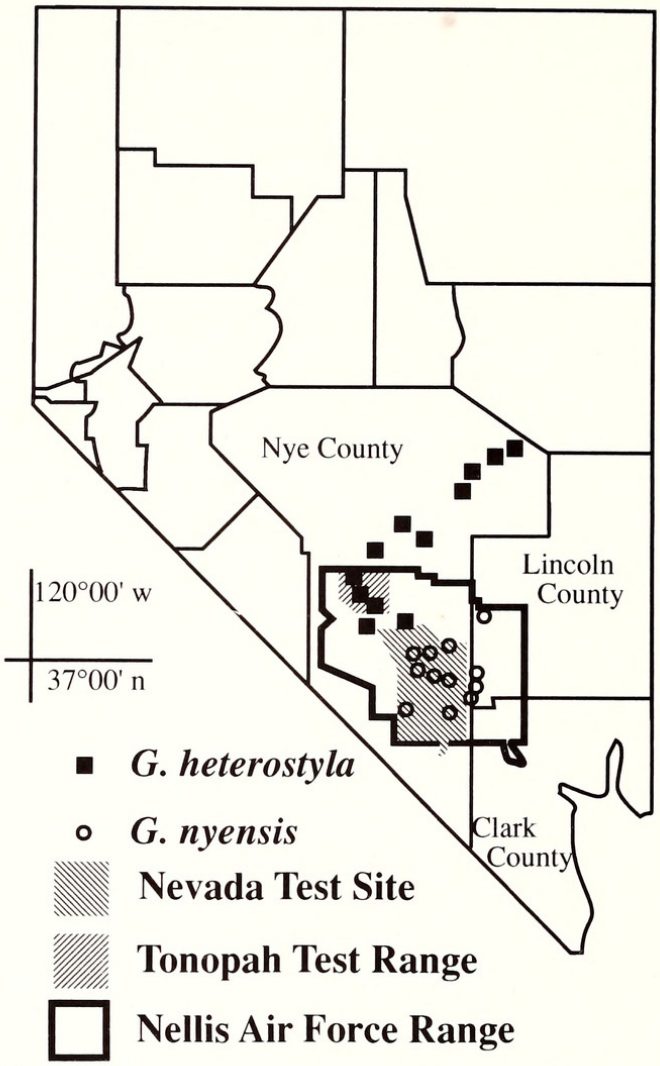

FIG. 2. Distribution of *Gilia heterostyla* and *Gilia nyensis* in south central Nevada.

east and north to the dunes in eastern Railroad Valley (Fig. 2). Recent treatments have considered these populations as *G. nyensis* (Cronquist, 1984).

Habitat and phenology. Gilia heterostyla flowers from May to early July. It grows in open areas and under shrubs in Great Basin vegetation typical of sandy valley floor habitats dominated by *Atriplex canescens* and *Achnatherum hymenoides.* Other commonly associated shrubs include *Chrysothamnus greenei, Tetradymia glabrata* and *Psorothamnus polydenius.*

Morphology. Pin and thrum flowers do not differ morphologically except in stamen, style, and stigma lengths. Stigmatic papillae appear the same in both morphs. Estimates of pollen fertility appear equally high (89–99%) in pin and thrum flowers of *G. heterostyla,* as determined from staining grains with lactophenol-cotton blue. Measure-

TABLE 1. COMPARISON OF MORPHOLOGICAL FEATURES OF *GILIA HETEROSTYLA* AND *G. NYENSIS*.

Character	*G. heterostyla*	*G. nyensis*
Floral morphology	Distylous	Homostylous
Leaf lobe posture	Right angle to rachis	Ascending tipward
Leaf lobe width	Broad at rachis	Narrow at rachis
Corolla lobe color		
Upper surface	Bright light pink	Dark magenta
Lower surface	Bright light pink	Pale milky pink
Corolla lobe veins	Purple	Not apparent
Corolla tube	Well-exserted	Included in calyx
Corolla throat	Gradually expanded	Abruptly expanded
Capsule	Exserted from calyx	Generally included
Seeds/capsule	30–50	Generally 14–30

ments of pollen grain diameters in the two morphs also showed no significant differences. Pollen is zonocolporate with striato-reticulate sexine in pin and thrum flowers.

One population of *G. heterostyla* sampled in the field showed nearly equal numbers of pin and thrum plants. Herbarium collections with large numbers of plants on single sheets also had nearly identical numbers of pin and thrum plants.

Chromosome counts of $n = 8$ for *G. heterostyla* were made from pollen mother cells of pin and thrum plants (voucher *Cochrane 1705*). We also counted $n = 8$ for *Gilia nyensis* (voucher *Cochrane 1904* CAS). This differs from a report of $n = 9$ for *G. nyensis* by Reveal & Styer (1973). We have seen a duplicate of their cited voucher and verified that it is *G. nyensis.* Diploid chromosome numbers of both $n = 8$ and $n = 9$ are known in section *Giliandra* (Grant 1959), as in the related *G. hutchinsifolia* Rydb. with $n = 9$ (Grant l. c.) and *G. subacaulis* Rydb. with $n = 8$ (Day 1993). Further studies of chromosome number and relationships in sect. *Giliandra* are to be reported elsewhere by the second author.

Relationship with G. nyensis. Gilia heterostyla differs from *G. nyensis* most significantly by its distylous flowers; however, there is an array of floral and vegetative characters that distinguish these species of section *Giliandra* (Table 1).

Corolla color differs noticeably between the two species in fresh material. Corollas of *G. heterostyla* are bright light pink, whereas those of *G. nyensis* are dark magenta, almost hot pink. In herbarium specimens the corollas of both species dry to blue, but those of *G. nyensis* become darker blue than those of *G. heterostyla.* The outer (abaxial) surface of the lobes of *G. heterostyla* is the same color as the inner (adaxial) surface, with darker veins prominent, while the abaxial surface of *G. nyensis* lobes is paler milky pink than the adaxial surface, and veins are not apparent. The corolla tube of *G.*

heterostyla is the same color as the lobes; in *G. nyensis* the tube is violet. Both species have green-yellow spots in the throat below each corolla lobe, as do *G. hutchinsifolia* and *G. subacaulis* also of section *Giliandra.* In *G. heterostyla* the spots appear paired, as they are bisected by a purple midvein, while the spots in *G. nyensis* appear singly, and are not bisected by a colored midvein. Furthermore, the stigmas of *G. heterostyla* are always white, while those of *G. nyensis* are often streaked with purple.

These two species also differ in corolla size and shape. The corolla tube of *G. heterostyla* is over twice the length of the calyx, while that of *G. nyensis* is slightly if ever exserted beyond the calyx. The throat of *G. heterostyla* is more gradually and narrowly flared than that of *G. nyensis,* which flares abruptly at almost a 45 degree angle, and is often wider than long.

The pinnatifid leaf segments of *G. heterostyla* extend perpendicular to the rachis, as seen in *G. subacaulis,* while in *G. nyensis* the segments angle forward, a characteristic shared with *G. hutchinsifolia* and *G. pinnatifida.* Nutt.

These species are also distinguished by ecological preferences. *Gilia heterostyla* occurs in open sandy flats in large valleys, while *G. nyensis,* found mostly to the south of *G. heterostyla* (Fig. 2), is restricted to deep sands derived from volcanic tuff on mountains, mesas and in valleys. It grows in the Great Basin–Mojave Desert transition zone, in *Artemisia*-Piñon-Juniper, *Grayia-Tetradymia-Artemisia tridentata-Atriplex confertifolia-Psorothamnus polydenius, Coleogyne* and *Larrea-Ambrosia* vegetation. These two species have not been found growing sympatrically, although potential areas of sympatry may exist on restricted-access military lands. Populations of these species have been found at opposite ends of Kawich Valley. No morphological intergradation between these species has been noted.

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NOTE

EXTRAFLORAL NECTARIES ON *ARBUTUS MENZIESII* (MADRONE).—John C. Hunter, Section of Plant Biology, University of California, Davis, CA 95616.

From April to July 1993, I made observations on the vegetative buds of *Arbutus menziesii* (Ericaceae) growing at the University of California's Northern California Coast Range Preserve in Mendocino County. During bud burst and the early stages of leaf expansion, these buds appeared to function as extrafloral nectaries. This has not been previously documented for *Arbutus*.

On branches where the apical bud had begun to swell and burst, a droplet of fluid exuded from the tip of the apical and the upper axillary buds. This fluid tasted faintly sweet, and tested positive for reducing sugars (using Benedict's solution). I observed various Coleoptera, Diptera, and Hymenoptera on the buds, the most abundant of which was the ant *Prenolepis imparis* Say.

Inside the buds, the nectar was exuded from the adaxial surface of the bud scales. On this surface, free-hand sections revealed glandular trichomes that may be the source of the nectar. These trichomes were typically 250–600 nm long and consisted of up to two dozen cells arranged into a basal stalk and a wider head. The trichomes, and frequently adjacent epidermal cells, were densely stained with neutral red, as is commonly seen in active nectaries (Kearns and Inouye, Techniques for Pollination Biology, 1993).

On four trees, I monitored 18 apical and 117 axillary buds on 18 marked branches. During the period of bud burst (April–May), all apical buds and 63 of 117 axillary buds exuded nectar. During leaf expansion, the bud scales reflexed, withered, and abscised. Only 3 of the 63 axillary buds that produced nectar gave rise to fully developed shoots; the others abscised during the summer along with the previous year's leaves and bark.

Extrafloral nectaries are often most active during the period of leaf expansion (Darwin, Journal Linnean Society of London 15:398–409, 1876; Tilman, Ecology 59: 686–692, 1978; Curtis and Lersten, American Journal of Botany 61:835–45, 1974). They are suggested to reduce herbivory by attracting ants that deter herbivores (Bentley, Annual Review of Ecology and Systematics 8:407–427, 1977), and experimental evidence supports this interpretation (Oliviera et al., Oecologia 74:228–230, 1987; Koptur, Ecology 65:1787–1793, 1984). The extrafloral nectaries of *Arbutus menziesii* also may serve this function.

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