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(CAMPANULACEAE, NEMACLADOIDEAE) AND A KEY  
TO THE SPECIES**

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NEW SPECIES AND A NEW VARIETY OF *NEMAACLADUS* (CAMPANULACEAE,  
NEMAACLADOIDEAE) AND A KEY TO THE SPECIES

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ABSTRACT

In the course of preparing the treatment of *Nemacladus* (Campanulaceae, Nemacladoideae) for Volume 18 of *Flora of North America north of Mexico*, it has become apparent that several new taxa must be described and others recircumscribed. These are: two new species of uncertain affinities from the White Mountains and Inyo Mountains; in the *N. longiflorus* A.Gray group, a new species and a variety elevated to species; four new species in the *N. sigmoideus*/*N. secundiflorus* complex; and a new variety of *Nemacladus twisselmannii* J.T.Howell.

Key words: California, Campanulaceae, *Nemacladus*.

*Nemacladus* Nutt. is one of two genera in the Nemacladoideae M.H.G.Gustafsson (Campanulaceae Juss.), which is endemic to southwestern North America and central Mexico and most closely related to Cyphocarpoideae Miers, a Chilean endemic. Together these two subfamilies are sister to Lobelioideae Burnett, although the exact relationships are still unclear (Crowl et al. 2016). *Pseudonemacladus* McVaugh, the other genus in the subfamily, is monotypic and known only from the Sierra Madre Oriental in Mexico (Rzedowski 2019). *Pseudonemacladus* differs from *Nemacladus* in being perennial with a woody caudex, lacking a basal rosette, and having sub-opposite cauline leaves. In *Pseudonemacladus*, the flowers are not resupinate; in contrast to *Nemacladus* and all Lobelioideae, the filament tube and style bend away from the medial sepal before curling over. *Pseudonemacladus* lacks the conspicuous nectary glands and large cells attached to the filaments found in *Nemacladus*.

*Nemacladus* is annual, with a basal rosette, and few, if any, cauline leaves, which, when present, are alternate. *Nemacladus* flowers are resupinate or not, distinctly bilabiate or not, the petals distinct to base or connate proximally. Unlike Lobelioideae, the corolla lobes are not connate into lips, but the corolla may be 2-lipped, in which three lobes are opposite the other two, or 1-lipped, in which all five lobes are on one side, or nearly radially symmetric, with lobes evenly distributed. The ovary is partially inferior in all but the *N. longiflorus* A.Gray group, which have superior ovaries. The filaments are connate at least part of their length and recline or bend toward the medial sepal. The two filaments flanking the medial sepal bear conspicuous clusters of single, elongate cells sometimes attached to a multicellular pad. Most species have large nectar glands on the ovary apex. Pollen is presented on the

tip of the closed stigma lobes, which are exposed after the anthers flip back, compared with lateral hairs or papillae on the style in Campanuloideae (Shetler 1979), or pushed through the tube of connate anthers in Lobelioideae, or in a “pollen box” in Cyphioideae (Leins and Erbar 2003). The function of the large cells attached to the filaments is unknown. These cells reflect light, so they may mimic nectar, although the nectar glands appear to produce copious nectar as well. The cells may serve as heat repositories to warm pollinators, or they may perform a mechanical function in the movement of the filament tube/style. In summary, this is a very unusual genus within Campanulaceae.

Several factors make it difficult to identify *Nemacladus* in the field or in the herbarium. Small-flowered species tend to be self-compatible, self-pollinating, and may mature fruit even after being pressed (Morin unpublished data); specimens of these may only have capsules and senesced flowers even if collected in full bloom. Species of *Nemacladus* may grow intermixed or near each other, thus herbarium specimens are frequently mixed sheets composed of multiple species (Morin unpublished data). Since different species develop at different times, a collection may include immature plants of one species and mature plants of another. Most species of *Nemacladus* are very difficult to see in the field: the basal rosette is generally shriveled when in flower, the pedicels are so thin as to be nearly invisible, leaving only the flowers and fruits to be seen about 5 to 10 cm above the ground surface, which is often sand or fine gravel the color of the corollas.

Munz (1924) published the first comprehensive work on *Nemacladus*. He retained *Parishella* A.Gray as a separate genus and in *Nemacladus* recognized eight varieties grouped in three species (Table 1):

TABLE 1. COMPARISON OF PREVIOUS TAXONOMIC TREATMENTS OF *NEMAACLADUS*.

Munz (1924)	McVaugh (1939)	Robbins (1958)	Morin (2008, 2012)
<i>Parishella californica</i> A. Gray	<i>Parishella californica</i>	n/a	<i>Nemacladus californicus</i> (A.Gray) Morin
<i>N. longiflorus</i> A. Gray	<i>N. longiflorus</i> var. <i>longiflorus</i> /var. <i>breviflorus</i> McVaugh	n/a	<i>N. longiflorus</i> var. <i>longiflorus</i> , var. <i>breviflorus</i>
	<i>N. glanduliferus</i> Jeps. var. <i>glanduliferus</i>	n/a	<i>N. glanduliferus</i>
	<i>N. glanduliferus</i> var. <i>orientalis</i> McVaugh	n/a	<i>N. orientalis</i> (McVaugh) Morin
<i>N. ramosissimus</i> Nutt. var. <i>ramosissimus</i>	<i>N. ramosissimus</i>	n/a	<i>N. ramosissimus</i>
<i>N. ramosissimus</i> var. <i>gracilis</i> (Eastw.) Munz	<i>N. gracilis</i> Eastw.	<i>N. gracilis</i> s.s.	<i>N. gracilis</i> s.s.
<i>N. ramosissimus</i> var. <i>pinnatifidus</i> (Greene) A. Gray	<i>N. pinnatifidus</i> Greene	n/a	<i>N. pinnatifidus</i>
<i>N. rigidus</i> Curran var. <i>rigidus</i>	<i>N. rigidus</i>	n/a	<i>N. rigidus</i>
<i>N. rigidus</i> var. <i>australis</i> Munz	<i>N. glanduliferus</i> var. <i>australis</i> (Munz) McVaugh	n/a	<i>N. australis</i> (Munz) Morin
<i>N. rigidus</i> var. <i>capillaris</i> (Greene) Munz	<i>N. capillaris</i> Greene	n/a	<i>N. capillaris</i>
<i>N. rigidus</i> var. <i>interior</i> Munz	<i>N. rubescens</i> var. <i>interior</i> (Munz) McVaugh	<i>N. interior</i> (Munz) Robbins	<i>N. interior</i>
<i>N. rigidus</i> var. <i>montanus</i> (Greene) Munz	<i>N. montanus</i> Greene	n/a	<i>N. montanus</i>
<i>N. rigidus</i> var. <i>rubescens</i> (Greene) Munz	<i>N. rubescens</i> Greene var. <i>rubescens</i>	n/a	<i>N. rubescens</i>
	<i>N. rubescens</i> var. <i>tenuis</i> McVaugh	n/a	<i>N. tenuis</i> (McVaugh) Morin var. <i>tenuis</i> /var. <i>aliformis</i> Morin
		<i>N. secundiflorus</i> Robbins	<i>N. secundiflorus</i> var. <i>secundiflorus</i> /var. <i>robbinsii</i> Morin
		<i>N. sigmoideus</i> Robbins	<i>N. sigmoideus</i>
			<i>N. twisselmannii</i> J.T.Howell
			<i>N. calcaratus</i> Morin

long-flowered *N. longiflorus*, campanulate-flowered *N. ramosissimus* Nutt., and petals distinct nearly to base in *N. rigidus* Curran. McVaugh (1939) published a revision of *Nemacladus*, and Robbins (1958) addressed issues in *N. gracilis* Eastw. Morin (2008, 2012) published the only recent treatments of the genus. Here we describe two new species from the White Mountains of uncertain affinity, a revision of the *N. longiflorus*, *N. secundiflorus* G.T.Robbins, and *N. sigmoideus* G.T.Robbins groups, and a new variety of *N. twisselmannii* J.T.Howell.

#### METHODS

Over the course of this study, more than 3500 herbarium specimens of *Nemacladus* from the herbaria listed in the Acknowledgments and more than 100 populations of *Nemacladus* in the field have been studied. Because so many characters are lost or difficult to see on herbarium specimens, a concerted effort to see as many populations of *Nemacladus* as

possible in the field began in 1993. Plants were photographed in the field and in the laboratory. Freshly collected plants were maintained in small vases until they could be photographed in the lab and pressed to best maintain characters. Flowers were preserved in formalin-acetic acid-alcohol (FAA) or 70% ethanol. Preserved whole flowers or with corollas removed were dehydrated, critical point dried, coated with gold-palladium, and viewed with the SEM to study the glands and staminal appendages. Samples for molecular sequencing were dried using silica. Study of morphological characters revealed consistent differences in architecture, leaf size and shape, bract shape and aspect, pedicel shape, flower orientation, sepal shape and aspect, corolla size, shape, and coloration, filament and anther coloration, and capsule shape. In most cases, these correlated well with geographical distribution and results of preliminary molecular analyses (Neff and Ayers unpublished data). Differences in flowering time, flower orientation, and corolla size and shape

can be expected to result in reproductive isolation between distinct species in *Nemacladus*. Supplemental Materials 1 lists images of holotypes included as Supplemental Figures.

#### Notes on Terminology and Measurements

On any flowering branch, generally there are one or two flower buds in the distal-most portion, one open flower below those, and developing capsules below that. Measurements of bract length, pedicel length, and internode length in the descriptions refer to the area just above and below an open flower. Angles of pedicels and of branches relative to the adjoining axis are approximate, to give an idea of openness or compactness of the plant. Abaxial or adaxial position of sepals and petals or corolla lobes refers to flowers as they appear when they open, whether they are resupinate or not. Therefore, in non-resupinate flowers there are two abaxial petals, whereas in resupinate flowers there are three abaxial petals. In non-resupinate flowers (Fig. 1A, B), the calyx consists of two paired adaxial sepals, two paired lateral sepals—called flanking sepals here, and a median unpaired abaxial sepal. For ovary and capsule dimensions, the percentage inferior approximates how much of the ovary is below the point at which the hypanthium ends. However, this changes as the capsule develops, with the ovary dome expanding above the hypanthium line, or the lower portion enlarging, or the distinction between hypanthium and ovary wall disappearing (as in *N. pinnatifidus* Greene), the sepals seeming to arise directly from the capsule wall.

#### TAXONOMIC TREATMENT

##### Two New Species from the White Mountains and Inyo Mountains of Uncertain Affinities

Populations from near the California/Nevada state border with sigmoid pedicels and small flowers usually have been identified as *Nemacladus sigmoideus*. Some of these plants proved to have a corolla similar to *N. orientalis* (McVaugh) Morin, sepals similar to *N. rigidus*, and pedicels similar to *N. sigmoideus* (Fig. 1A, B). A collection made in 1897 by Marcus E. Jones near Bishop, Owens Valley, California, may be the first collection of this taxon. Although often collected with *N. orientalis* or *N. sigmoideus*, or both, some collections of the new species by itself were also found. Photographs of this unusual form by Steven Matson (Fig. 1A, B) showed that the coloring of the corolla was also different from other species. We relocated two populations based on collections by James Morefield, making it possible to examine fresh material and preserve material for molecular analysis and SEM, from which we concluded this was an undescribed species.

***Nemacladus morefieldii*** Morin & T.J.Ayers, sp. nov.—Type: USA, California, Inyo County.

Near the SW base of Black Mountain, 1.8 mi, N4° of Wilkerson Springs, T8S R34E S33. Coarse mixed alluvium sloping 5°WSW with *Atriplex*, *Haplopappus*, *Psorothamnus*, *Menodora*, *Grayia*. Sporadically common annuals. Owens Valley drainage. Alt. 4350 feet. 06 May 1986. *James D. Morefield and Douglas H. McCarty 3587* (Holotype: UC1545302!, Supplemental Fig. 1, Isotypes: ARIZ!, MO!, NY!, RSA!, RSA-POM!, UCR!)

*Nemacladus morefieldii* differs from other species of *Nemacladus* in having the combination of a sigmoid pedicel, nonresupinate flower, sepals different in size and shape, the two lateral sepals about 1/3 larger than the others, ovate, giving a winged appearance, the corolla bilabiate, with lobes distinct to base, adaxial 3 lobes white with maroon or orangey-brown shading on the margins (Fig. 1A, B).

**Plants** erect, 4–14 cm tall, branched from base at 20–30° angles to the main stem, or 1.5–2 cm above base at about 70°, branches dichotomous in lower nodes, straight, angles narrow, secondary branches few or none. **Stems** brownish purple proximally, with short fine hairs proximally. **Leaves** rhombic to nearly round, 3–8 × 2–5 mm, ± fleshy, narrowed to broad base, margins entire, wavy, apex obtuse, surfaces with very fine, very short hairs adaxially, felty or granular abaxially. **Inflorescence** axis shallowly zig-zagged, internodes 5–8 mm long (progressively shorter distally); bracts appressed to and enfolding pedicel base, broadly ovate, 1–3 × 0.6–1.5 mm, ± fleshy, apex acute. **Pedicels** ascending at about 60° to axis, 8–15 (–22) mm long, about 0.2 mm diam., straight, becoming sigmoid and declining, abruptly upturned at tip. **Flowers** non-resupinate, held facing outward; hypanthium obconical, 0.5–1 mm tall, sepals fleshy, abaxial sepal deltate, adjacent sinuses wide, straight, adaxial 4 sepals unequal, the flanking 2 ovate, 1.2–1.5 × 0.4–0.8 mm, about 1/3 longer and wider than central 2, bowed, giving a winged appearance, central adaxial sepals lanceolate, 0.8–1.1 × 0.2–0.3 mm; corolla bilaterally symmetric, slightly cup-shaped at base, petals distinct to base, abaxial 2 lobes white, oblong-lanceolate, apex acute, tips appressed at anthesis, 1.2–1.6 mm long, adaxial 3 lobes white with maroon or orangey-brown shading on margins abaxially and adaxially, triangular, outer two bowed on outer margin giving a winged appearance; filaments connate in distal about 1/3, declined, white proximally, white or faintly maroon distally, (1–)1.5–1.8 mm long, transparent cells 4–6 per group, cylindrical, tip rounded, attached at base of filaments and at right angles to filaments, anthers white, about 0.2 mm long, pollen white; ovary 1/2–3/4 superior, stigma blue or rose-pink; nectaries flat, round in outline, yellow. **Capsules** about 4/5 superior, ± obconic, round in cross section, somewhat compressed horizontally, 1.5–2.6 × 1.5–2.4 mm, base rounded, apex rounded; sinuses flanking lower sepal not clearly differentiated from upper part of capsule,

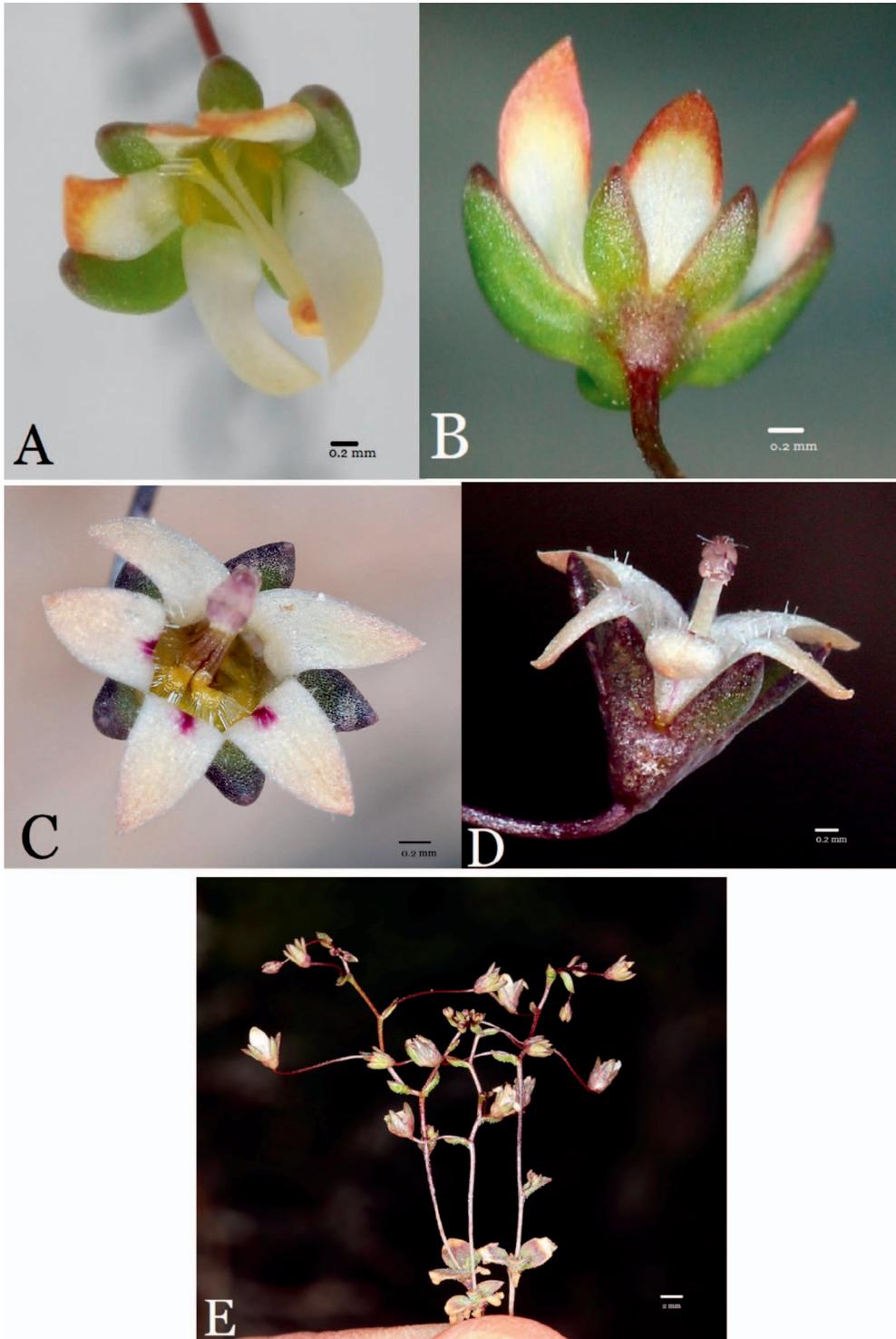


FIG. 1. *Nemacladus morefieldii* and *N. inyoensis*: *N. morefieldii*, A. flower front; B. flower back; *N. inyoensis*, C. flower front, D. flower side, E. entire plant. (photos: S. Matson).

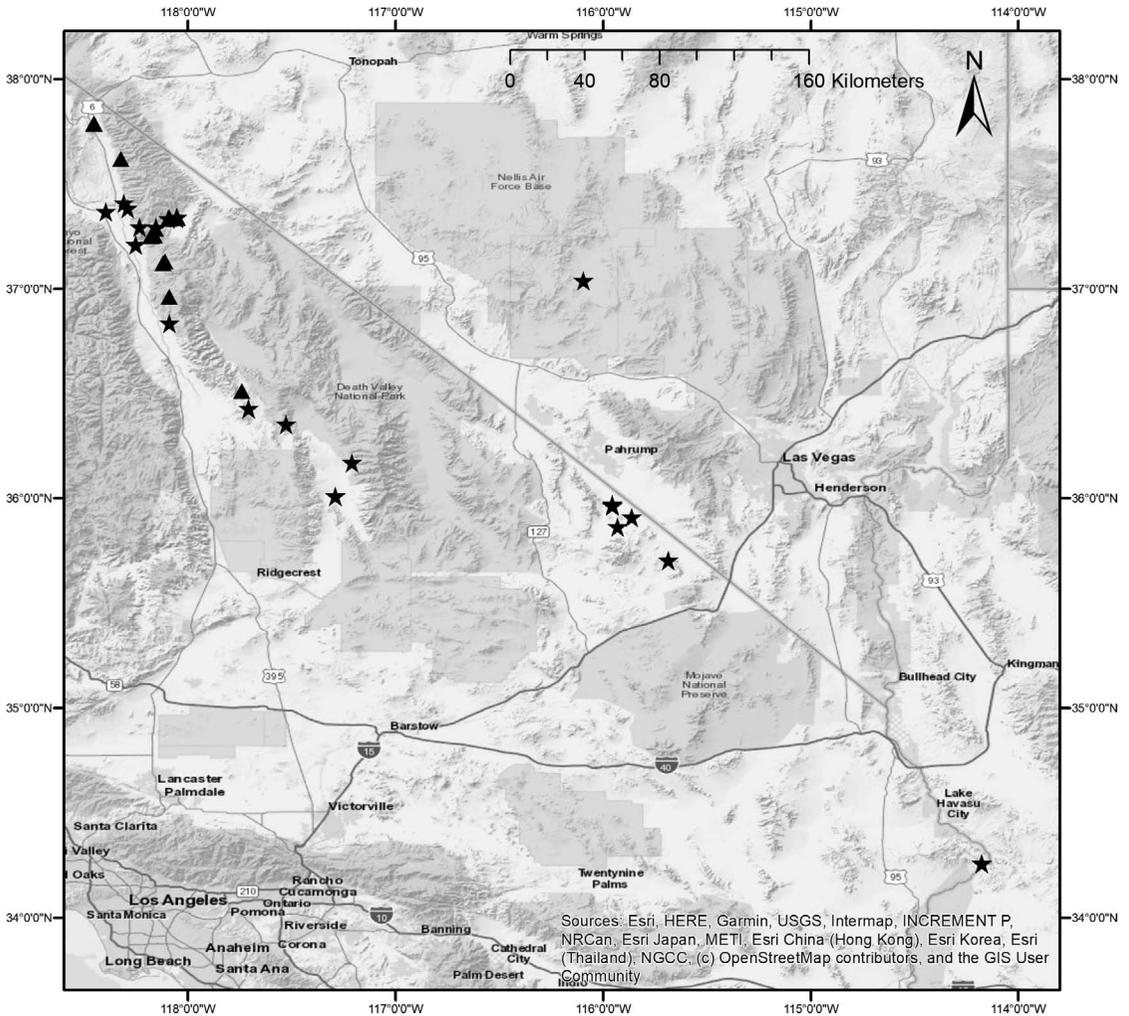


FIG. 2. Distribution of *Nemacladus morefieldii* (stars) and *N. inyoensis* (triangles).

abaxial sepal cocked downward, adaxial 4 sepals clasping in fruit. **Seeds** oblong, 0.5–0.6 mm long, surface reticulate.

**Distribution and ecology.** *Nemacladus morefieldii* occurs at 300–2200 m on volcanic and gravelly calcareous soil, shale talus, and in sandy, gravelly, desert washes, in the White and Inyo Mountains south along the California/Nevada state border to the Whipple Mountains (Fig. 2). Herbarium specimens of *N. morefieldii* usually have been identified as *N. sigmoideus*. Reports of *N. capillaris* from the eastern side of the Sierra Nevada are *N. morefieldii*.

**Phenology.** Flowering April through June.

**Etymology.** The species is named for Dr. James Morefield, Supervisory Botanist with the Nevada Natural Heritage Program, in recognition of his extensive work in the White Mountains of California and Nevada.

**Representative specimens (localities abbreviated).** USA. CALIFORNIA. **Inyo Co.:** Inyo Mountains, east of Independence, Mazourka Canyon, *DeDecker 4059, 4060* (RSA 2 sheets, each with *N. sigmoideus*, *N. orientalis*, and *N. morefieldii*); Black Canyon, *Duran 2730A*; Cedar Flat, *Duran 3290* (JEPS, UC); Bishop, Owens Valley, *Jones s.n.* (RSA-POM); between Jail and Hall Canyons, Panamint Valley, *Kerr 452* (CAS); 5 mi NE of Darwin on old Death Valley Road, *Kerr s.n.* (CAS, RSA); 7.8 miles southwest of Deep Springs Maintenance Center, *LeDoux, Dunn & Morris 807* (NY); Canyon to Santa Rosa Mine, 1.7 mi N38E of Poleta Mine, 3.3 mi ESE of Laws, *Morefield 3400* (UC); Canyon to Santa Rosa Mine, south end of Inyo Mountains, *Munz 11755* (CAS, NY, RSA WTU, (with *N. orientalis*)); Keanes Spring, *Munz 12578* (MO, POM, UC); Slate Range, E of Trona, *Peñalosa 2381* (CAS); NE Mojave Desert, southern Pahrump Valley, SW edge of Calvada Springs, 794 m, *Sanders 39378b* (UCR);

NE Mojave Desert, southern Pahrump Valley, WSW of Calvada Springs, 802 m, *Sanders & Onkar Singh 39398* (UCR); west side of Pahrump Valley, *Wolf 10593* (CAS, JEPS [JEPS sheet has *N. morefieldii* and *N. orientalis*], RSA, TEX, UC, WTU [UC and WTU sheets have *N. morefieldii*, *N. orientalis* and *N. sigmoideus*]). **Mono Co.:** East of Sierra Nevada: White Mtns, west base Piute Creek drainage c. 0.2 mi ne of powerhouse on Chalfant Loop Rd., 1319 m, *Howald 4065* (UCR); North wall of Coldwater Canyon near its mouth, *Morefield 3433* (ARIZ, GH, MICH, MO, NY, RSA, UC, UCR). **San Bernardino Co.:** 6.5 mi NNW of Horse Thief Springs, *Castagnoli et al. 104* (CAS); Mesquite Mountains ca. 1.5 air miles northeast of Winters Pass, 1213 m, *Bell 2624* (RSA, with *N. orientalis*); Sonoran (Colorado) Desert, Whipple Mountains, Dune OHV area near Echo Point/Echo Lodge, *DeGroot et al. 2733* (with *N. orientalis*) (ARIZ, CAS, RSA, UCR). USA, NEVADA. **Clark Co.:** Las Vegas, on the mesas, *Goodding 2319* (MO, NY). **Nye Co.:** Nevada Test Site, *Beatley 3605* (DS [with *N. orientalis*], RENO).

Steve Matson discovered, photographed, and collected an unusual *Nemacladus* in the Inyo Mountains in 2010. The collection was of just a few small plants, not enough to determine whether it was an odd *N. sigmoideus* or a new species. Most notable in the photographs were dark maroon lines on the midveins of the three abaxial corolla lobes of the small, cup-shaped corolla. Three large populations were found by Matson, A. Schusteff, and M. Purdy in May and June, 2019, providing enough material to confirm this as an undescribed species that shares with *Nemacladus rigidus* dark stem, leaves, bracts, hypanthium, sepals, and mature capsule, and broadly deltate sepals; with the new species with small cup-shaped corolla described later in this paper, it shares a shallowly cup-shaped corolla, the three abaxial lobes oblong-lanceolate and the two adaxial lobes divergent (Fig. 1C, D, E).

***Nemacladus inyoensis*** Morin & T.J.Ayers, sp. nov.—

Type: USA, California, Inyo County; Inyo Mountains, Harkless Flat Road, Forest road 9S13, 37.1167, -118.1158. Rocky limestone soils in sparse pinyon juniper woodland. 22 May 2019. *Matson 2820*, with *Aaron Schusteff* and *Martin Purdy*. Holotype: UC!; isotype ASC!

*Nemacladus inyoensis* differs from other *Nemacladus* species in its combination of bracts, hypanthium, and sepals having a very dark purplish-green color, corolla being cup-shaped, white to cream-colored with maroon stripe from throat to base on abaxial 3 lobes, and small, 2.1–2.4 mm; transparent cells being thin, cylindrical, attached to oblique appendage on filaments; and capsule dark brownish greenish purple, large, base flat to obtuse.

**Plants** erect, height above rosette 2–10 cm, (in some plants the rosette is 14–20 mm above the root/stem interface), reddish brown, branches few, from

base and upper nodes, at about a 45° angle from main axis, first branch 1–2.5 cm above rosette. **Stems** dark reddish brown, glabrous. **Leaves** elliptic to ovate, 1–4 × 0.5–3 mm, base cordate to obtuse, margins entire, apex acute to obtuse, surfaces glabrous or with sparse or dense broad or slender white hairs abaxially and adaxially. **Inflorescence** axis shallowly zigzagged, internodes 2–4 mm; bracts straight, aligned with pedicel, green with reddish margin, broadly ovate, 1–1.5 mm long, base cupped under but not enfolding pedicel base. **Pedicels** at 90° to axis, 5–12 mm long, 0.1 mm diam., shallowly curved, in fruit nearly straight. **Flowers** resupinate, bilaterally symmetric, hypanthium dark purplish green, obconic, 1.1–1.5 mm long, sepals erect, dark purplish green, broadly deltate, 1–1.5 mm long, flanking sepals longer than abaxial sepals, somewhat fleshy, base slightly narrowed, apex acute, apiculate, surface with clear, crystalline raised areas; corolla bilaterally symmetric, total length 2.1–2.4 mm, petals connate about 1/2 proximally to form a shallow cup, abaxial 3 lobes white to cream colored with deep maroon line on central vein from throat to base, oblong-lanceolate, adaxial lobes divergent, white to cream-colored, lower margin somewhat curved, upper margin straight; filaments connate in distal 1/2–1/3, arched over, grayish white to pale blue, apex glabrous or with few long hairs, transparent cells 6–8 per group, attached to broad, hockey-stick shaped pad on filaments, very slender, cylindrical, blunt-tipped, anthers pale blue, about 0.3 mm long; ovary about 9/10 inferior, nectaries yellow. **Capsules** 3/10–1/2 inferior, dark purplish green, base obtuse to flat, apex rounded to acute, 2.5–3 × 2–3 mm, sepals longer than valves, erect in fruit. **Seeds** oblong, 0.8–0.9 mm long, surface of rows of shallow pits separated by low ridges.

**Distribution and ecology.** *Nemacladus inyoensis* occurs in limestone, sandstone, and granite rubble and granite washes in pinyon juniper woodland and upper desert shrubland, at 1680–2600 m in the Inyo and White Mountains (Fig. 2).

**Phenology.** Flowering May–June.

**Etymology.** *Nemacladus inyoensis* was first discovered in the Inyo Mountains, Inyo County, California. The species name reflects its original discovery in the Inyo Mountains of eastern California.

**Paratypes.** USA. CALIFORNIA. **Inyo Co.:** Inyo Mountains, Ridge just south of Badger Flat, open pinyon juniper forest with *Penstemon*. 36.958, -118.0878. 2636 m. 20 June 2010. *Matson 2539* (UC). White Mountains, side canyon running north from Westgard Pass road (CA Hwy 168) about 1 mi. ENE of Batchelder Spring and about 1 mile WSW of the narrows. Owens Valley drainage. Locally abundant. Gravelly calcareous alluvium in dry open wash along bottom of canyon draining southward, with *Eriogonum nidularium* Coville, *Diplacis parryi* (A.Gray) G.L.Nesom & N.S.Fraga, *Eriogonum*

TABLE 2. COMPARISON OF MORPHOLOGICAL FEATURES OF *NEMAACLADUS BREVIFLORUS*, *N. LONGIFLORUS*, AND *N. RICHARDSIAE*.

	<i>Nemacladus breviflorus</i>	<i>Nemacladus longiflorus</i>	<i>Nemacladus richardsiae</i>
Height	1–7 cm	(2.5–)7–21 cm	5–15 cm
Basal leaves	1.5–4 mm long	3–12 mm long	1.5–7 mm long
Internodes	2–5 mm long	3.5–7 mm long	4–7 mm long
Bracts	ascending, lanceolate	appressed to pedicel, elliptic to ovate	appressed to and enfolding pedicel base, linear-lanceolate
Pedicels	5–8 mm long	6–25 mm long	10–20 mm long
Sepals	linear lanceolate	elliptic	lanceolate
Corolla tube shape, lobes aspect	cylindrical, lobes rotate	cylindrical, lobes rotate	infundibuliform, lobes spreading
Corolla tube length	1.5–3 mm long, 1–1.5 times as long as sepals	5–8 mm long, 4–8 times as long as sepals	2.5–3 mm long, 2 times as long as sepals
Capsule	urceolate, 2–3 mm tall	fusiform, 3–5 mm tall	oblong-ovoid, 3–3.5 mm tall

*fasciculatum* Benth. var. *polifolium* (Benth.) Torr. & A.Gray, *Stipa speciosa* Trin. & Rupr., *Phlox stansburyi* (Torr.) A.Heller, *Lupinus flavoculatus* A.Heller, *Eriogonum inflatum* Torr. & Frém., etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 6470 ft (1972 m), 37.24931° N, –118.17576° W  $\pm$  10 m. 9 June 2019. James D. Morefield 5896 (UC). Westgard Pass, Cedar Flat just east of White Mountain Road about 0.4 miles northwest of its intersection with California Hwy 168. Owens Valley drainage. Abundant on the flats. Level calcareous gravel and silty soil among shrubs, with *Pinus monophylla* Torr. & Frém., *Juniperus osteosperma* (Torr.) Little, *Artemisia nova* A.Nelson, *Artemisia tridentata* Nutt., *Oreocarya hoffmannii* (I.M. Johnst.) Abrams, *Cordylanthus kingii* S.Watson ssp. *helleri* (Ferris) T.I.Chuang & Heckard, *Cryptantha gracilis* Osterh., *Phlox stansburyi*, *Eriastrum wilcoxii* (A.Nelson) H.Mason, *Lupinus brevicaulis* S.Watson, etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 7350 ft (2240 m), 37.28540°N, –118.15690°W. 23 June 2019. James D. Morefield with Steve Matson, Martin Purdy 5902 (UC). Mono Co.: White Mountains, north side of Jeffrey Mine Canyon near bottom, 0.1 miles WSW of Jeffrey Mine map marker, Hammil Valley-Owens Valley drainage. Light colored metamorphic scree and colluvium in bed of foot trail sloping 5° south near bottom of steep canyon, with *Pinus jeffreyi* Grev. & Balf., *Pinus monophylla*, *Artemisia tridentata*, *Artemisia nova*, *Chamaebatiaria millefolium* (Torr.) Maxim., *Eriogonum rupinum* Reveal, *Diplacis parryi*, *Festuca octoflora* Walter, etc. Corollas white to cream colored, 3 lobes medially maroon streaked near base. 7105 ft (2166 m), 37.61858°N, –118.32289°W ( $\pm$  5m). 22 June 2019. Morefield 5897, with Matson and Purdy. See also online images (Supplemental Materials 2).

#### *Nemacladus longiflorus* Complex

*Nemacladus longiflorus* is conspicuous with its resupinate flowers, long, bilabiate corollas, (Fig. 3D) and superior ovary and capsule. It was the second

species named in the genus, by Asa Gray (1877). Var. *breviflorus* was added by McVaugh in 1939 based on its shorter corolla, much shorter filament tube, smaller stature, and more pubescence. *Nemacladus breviflorus* is smaller than *N. longiflorus* and has a corolla tube about equal to slightly longer than the sepals, versus 4–8 times the length of the sepals in *N. longiflorus*. *Nemacladus breviflorus* often has a compact, curly look, with a zigzagged axis (vs. nearly straight axis in *N. longiflorus*), much shorter internodes, short, very curved pedicels, and small, very hairy basal leaves (Table 2, Figs. 3A, B). The difference in corolla length alone would be a barrier to cross-pollination, and although the two taxa occur in close proximity to each other in some localities, *N. breviflorus* is more common in Transverse Ranges and San Jacinto Mountains, whereas *N. longiflorus* is more common in the Laguna, Palomar, Cuyamaca, Volcan, and San Jacinto mountains and Anza Borrego desert. Plants somewhat intermediate between these two taxa are rare, but have been reported from Whitewater Canyon, Riverside County.

*Nemacladus longiflorus* occurs in chaparral, oak woodland, and mixed conifer forests, in sandy washes and burned areas at 100–2200 m. It is found in the San Bernardino, San Gabriel, South Coast, and Peninsular Ranges, south to Sierra San Pedro Martír in Baja California (Fig. 4). A collection by Clokey (6928), north of Barstow, well out of the range of *N. longiflorus*, contains a few plants of *N. longiflorus* with mostly *N. rubescens*.

***Nemacladus breviflorus*** (McVaugh) Morin & T.J.Ayers, comb. nov. *Nemacladus longiflorus* A.Gray var. *breviflorus* McVaugh, Amer. Midl. Naturalist 22: 526. 1939.—Type: USA, Arizona, Pima County, near Roadside Mine on the Tucson Ajo Highway. Mar. 27, 1927. Peebles et al. 3754 (holotype: US1367475!; isotypes ARIZ!, RSA!).

**Plants** erect, 1–7 cm tall; branches many from base, narrow, at 25° angle to main stem, secondary branches few, at 70–90°. **Stems** reddish brown,

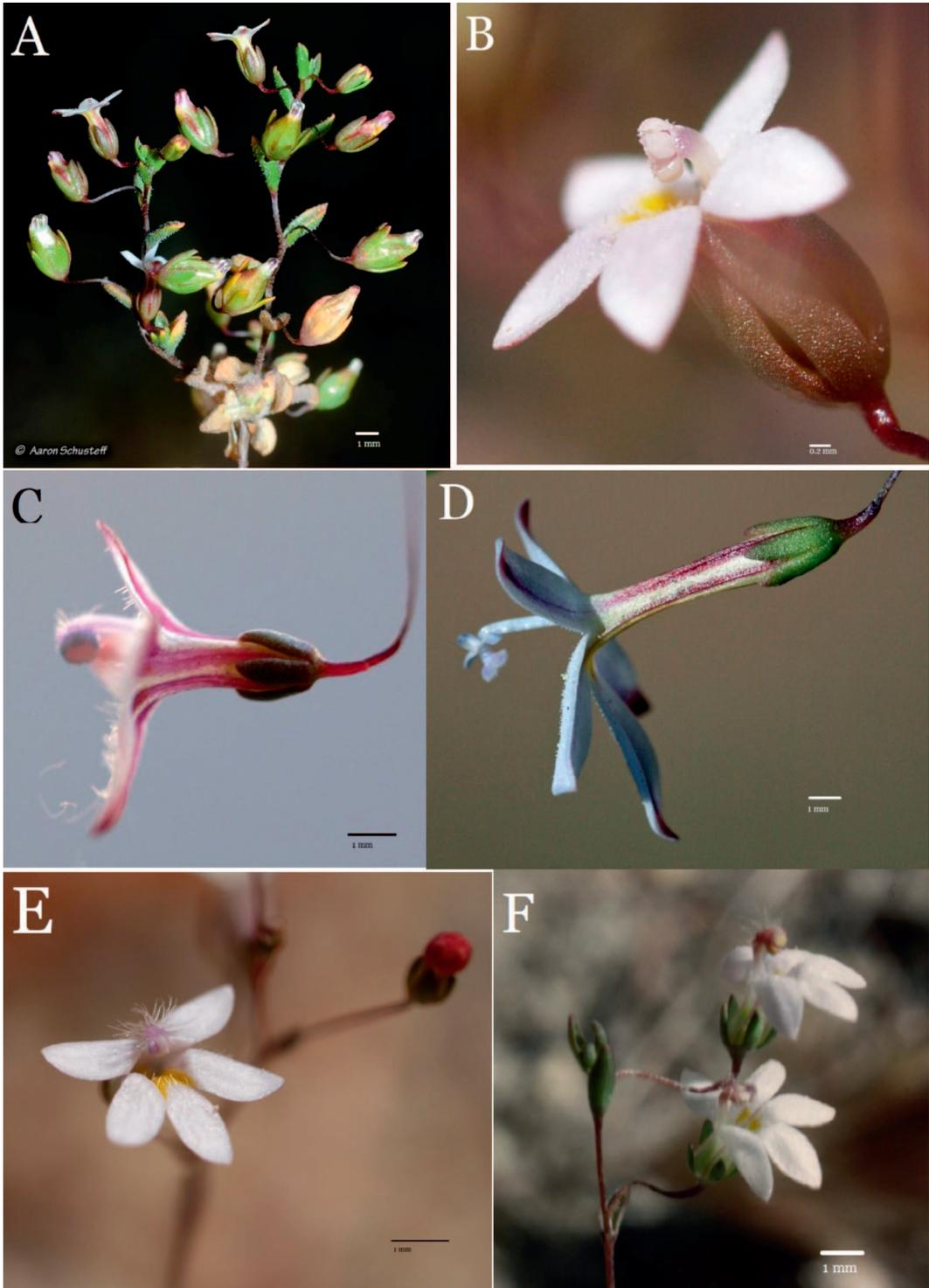


FIG. 3. *Nemacladus* flower comparisons: *Nemacladus breviflorus* A. habit., photo by A. Schusteff. B. flower, photo by N. Morin; *Nemacladus richardsiae*, C. flower, photo by N. Morin; *Nemacladus longiflorus*, D. flower, photo by Jon Rebman. *Nemacladus bellus*, E. flowers, photo by N. Morin; *Nemacladus secundiflorus* var. *secundiflorus*, F. flowers, photo by N. Morin.

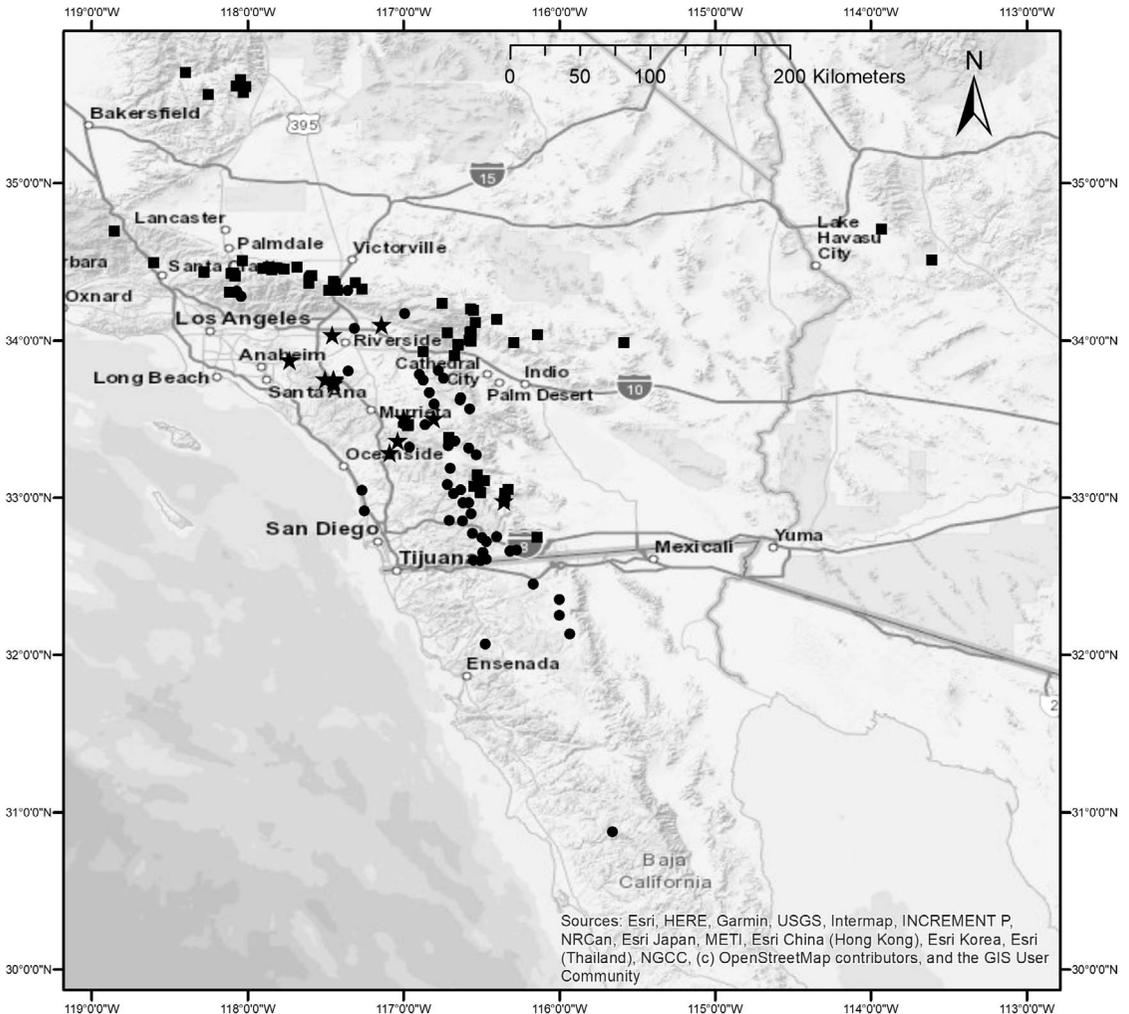


FIG. 4. Distribution of *Nemacladus richardsiae* (stars), *N. longiflorus* (circles), and *N. breviflorus* (squares). The locations of the *N. breviflorus* populations in Arizona and Utah are not shown.

glabrous or densely hairy. **Leaves** oblanceolate to ovate or oblong,  $1.5\text{--}4 \times 1\text{--}3$  mm, base tapered or abruptly narrowed to a winged petiole, margins entire to finely crenate, apex broadly acute to obtuse, surfaces usually densely hairy, sometimes nearly glabrous. **Inflorescence** axis strongly zigzagged, internodes 2–5 mm long, bracts ascending, lanceolate to broadly lanceolate, 2–3 mm long, apex acute. **Pedicels** widely spreading,  $70\text{--}90^\circ$  to axis, often declined below its node, 5–8 mm long, about 0.1 mm diam., deeply sigmoid, proximally forming an ascending arch, distally deeply curved, tip abruptly curved. **Flowers** resupinate; hypanthium 0, sepals all alike, erect, appressed to corolla, linear lanceolate, 1.5–2 mm long; corolla salverform, bilaterally symmetrical, conspicuously 2-lipped, divided 1/2 or less to base, tube white with maroon lines abaxially, cylindrical, 1.5–3 mm long, 1–1.5 times as long as sepals, abaxial lobes 3, spreading, white with yellow

spot on base, 3–3.5 mm long, central lobe elliptic, acute, 2 flanking lobes oblique-elliptic, about 4/5 length of central lobe, acute, adaxial surface with short, erect, white papillae, adaxial lobes 2, erect to slightly spreading, elliptic, acute, surface with short, erect, white papillae; filaments straight, connate in about distal 1/2, extended just beyond corolla tube, white, 2–3 mm long, tip abruptly curved down, hairs very short, transparent cells attached about 2/3 from base, slender, acute, 0.05–0.1 mm, anthers white or grayish, 0.25–0.3 mm long; ovary superior, oblong-ovoid, nectaries green, low mounds on side of ovary. **Capsule** superior, urceolate, 2–3 mm tall, base rounded, narrowed distally, rounded at tip, valves entire. **Seeds**  $\pm$  round, 0.4 mm long, surface with rows of large pits.

*Distribution and ecology.* *Nemacladus breviflorus* occurs on sandy or gravelly slopes and in washes, in juniper woodland, sagebrush scrub, Joshua tree

woodland, and gray pine-oak woodland, at 300–1400 m. in the Transverse and Peninsular ranges and westernmost Mojave Desert, south to northern Baja California; disjunct populations occur in the Kern River and Cyrus canyons, Kern County (Fig. 4). Collections from the Colorado Plateau in Utah (e.g. *Fertig 21062*) are highly disjunct and occur in sandy openings and in undisturbed biological soil crust areas and orangish-red deep stabilized sand dunes. The Arizona collections, from Mohave County, are also disjunct. The type locality, in Pima County, Arizona (*T. H. Kearney; R. H. Peebles & G. J. Harrison, 3754*), is the only collection from that area. This species is found near, and sometimes mixed with, *N. longiflorus* in California.

*Phenology.* Flowering March–June (July).

In 2010, Thomas Chester alerted the senior author to a population of *Nemacladus longiflorus* in the Temescal Canyon. Although the plants generally resemble *Nemacladus longiflorus*, the funnell-form shape of the corollas is unlike any other species in the genus, so significantly that recognition as a separate species is warranted. Lee Lake, in Indian Wash, Temescal Canyon, the type locality for the new species, has been a common botanical collecting spot at least since the early 1900s, and collections of *Nemacladus* from here date back to 1922.

***Nemacladus richardsiae*** Morin & T.J.Ayers, sp. nov.

TYPE: USA, California, Riverside County. Temescal. Sandy Wash. April 28, 1922. *Munz 5024* (Holotype: UC 219192!, Supplemental Fig. 2; isotypes CAS!, DS!, MO!, POM!, RSA!, UC!).

*Nemacladus richardsiae* differs from other *Nemacladus* in having the combination of a large, 5–6.3 mm, infundibuliform corolla, the tube gradually widening and the lobes spreading from the same plane as the tube, and a superior ovary (Fig. 3C).

**Plants** erect, 5–15 cm tall; branching 1.5–5 cm above base, at 60–80° to main stem, rarely branching from base, secondary branches few, at 40–50°. **Stems** reddish brown, glabrous. **Leaves** lanceolate to ovate, obovate, or rhomboid, 1–7 × 0.5–3 mm, base tapered, margins shallowly crenate or with a few sharp teeth, apex obtuse to sharply pointed, surface glabrous or densely hairy, hairs short, white, appressed, some of them curly. **Inflorescence** axis nearly straight, internodes 4–7 mm long; bract bases appressed and enfolding pedicel base, straight, or proximal ones bent back at middle, otherwise erect and aligned with axis or aligned with pedicel base, lanceolate to linear-lanceolate, 1.5–3 × 0.6 mm, apex attenuate. **Pedicels** at 70–90° to axis, 10–20 mm long, about 0.1 mm diam., sigmoid, proximal curve broad, distal curve abrupt, tip abruptly curved. **Flowers** resupinate; hypanthium 0, sepals all alike, erect, lanceolate, 1.4–1.5 (–4) × 0.4–0.5 mm, narrowed at base; corolla infundibuliform, bilaterally symmetric, conspicuously 2-lipped, total length 5–6.3 mm,

divided 1/2–3/5 to base, pale pink, or cream-colored with broad pink stripes on tube and maroon splotches on lobes abaxially, a yellow spot on base of each abaxial lobe, adaxially hairy and papillate; tube flared, 2.5–3 mm long, about twice the length of the sepals, lobes extend from tube, not abruptly rotate, central abaxial lobe elongated obovate, about 3 mm long, about 1/4 longer than flanking lobes, obtuse, flanking lobes obovate, obtuse, about 2.5 mm long, 2 adaxial lobes ovate, acute, about 2 mm long; filaments slightly arched, extended well beyond corolla tube, connate in about distal 1/2, pale lavender blue, tube 2–4 mm long, tip curved down, apex densely short-papillate, appendages attached about 2/3 from base, cells slender, acute, 0.15 mm long; anthers pale lavender blue, 0.3–0.5 mm long, pollen cream-colored; ovary superior, oblong-fusiform, nectaries green, low mounds on side of ovary. **Capsule** superior, oblong-ovoid, 3–3.5 × 1.5–2.2 mm, base rounded, apex blunt, opening by two valves, the valves entire. **Seeds** nearly round, 0.4 mm long, surface with rows of large pits.

*Distribution and ecology.* *Nemacladus richardsiae* occurs on sandy flats of alluvial fans, in creosote scrub at 300–500 m, in Temescal Canyon, Riverside County south to San Luis Rey, San Diego County (Fig. 4), with an outlying population northeast of San Bernardino collected by Parish in 1888, supported by an image in iNaturalist taken in 2019 (Echols 2019) from just north of Mentone, San Bernardino County. In a good year, with many plants blooming, the pink color of the corollas makes a kind of pink haze over the ground.

*Phenology.* Flowering March through June.

*Etymology.* The species is named for Dr. Jennifer H. Richards, professor of Biology at Florida International University, who has studied the plants in the field with the senior author while accompanying her on many *Nemacladus* collecting trips. Dr. Richards's insight into the floral morphology of the genus has been invaluable.

*Representative specimens.* USA. CALIFORNIA. **Riverside Co.:** Lee Lake, *Baer s.n.* 1923 (POM); Temescal Canyon: east side of Indian Wash between I-15 and Temescal Canyon Road, *Boyd 1700* (ARIZ, HSC, NY, RSA, TEX, UCR); Temescal Canyon: Alluvial benches of Indian wash just south of Interstate 15, *Boyd 1753* (ARIZ, NY, RSA, TEX, UCR); Wilder's near Riverside, *Brandege s.n.*, 1905, (POM, UC); 9 mi W of Anza, *Campbell 16133* (RSA); Temecula River, *Jepson 1555A* (JEPS); Cleveland Forest, *Maxfield 51* (CAS); Temescal Canyon: east side of Indian Wash between I-15 and Temescal Canyon Road, *Morin & Richards 657* (UC); Temescal Canyon, *Peirson 2920* (CAS, DS, RSA); Temescal Valley: Indian Wash, SW of I-15, S. side of De Palma Rd., 700–1100 ft WNW of intersection with Glen Eden Rd., *Provance 417-68* (UCR); Temescal Mts., *Reed 5140* (POM); Eastern foot of Santa Ana Mtns., Temescal Canyon near Lee

(Corona) Lake, 0.1 mi. SW of the dam, south of Temescal Canyon Rd., *Sanders 41530* (UCR). **San Diego Co.:** Wilderness Gardens, *Scott s.n.*, 1983 (SD); Pala: alluvial fan of Magee Creek, southern foothills of the Agua Tibia Mtns. and adjacent San Luis Rey River Valley, *White & DeVries 7328* (RSA). See also online images (Supplemental Materials 2).

#### The *Nemacladus sigmoideus* Complex

More difficult to study and less well understood than the showier species of *Nemacladus* are the ones with small white corollas. *Nemacladus ramosissimus*, which has cup-shaped corollas, was the first species described in the genus, and initially all small-flowered species were placed here. *Nemacladus ramosissimus* is easily recognized by its straight axis and erect, linear to oblong-lanceolate bracts. Munz (1924) included *N. gracilis*. and *N. pinnatifidus* in *N. ramosissimus* as varieties; McVaugh (1939) recognized them as species, but maintained Munz's general concept of *N. gracilis*, which is to say everything with a sigmoid pedicel and small white flower not *N. pinnatifidus* or *N. ramosissimus* was included in *N. gracilis*.

Robbins (1958) determined that *N. gracilis* should be split into three species: *N. gracilis*, *N. secundiflorus* G.T.Robbins, and *N. sigmoideus* G.T.Robbins. *Nemacladus gracilis*, as Robbins circumscribed it, is limited to the Inner South Coast Range from Merced County south to Kern County, and in the foothills of the Tehachapi Mountains (Fig. 9). It has short internodes, short, very thin pedicels, and corolla tube base wider than the hypanthium.

Robbins (1958) included in *N. secundiflorus* plants with a "relatively long corolla-tube which often noticeably surpasses the calyx (for about a distance of 1 mm or slightly more); its wide-spreading upper corolla-lobes; its relatively stout pedicels that commonly spread at right angles to the branches (although in older plants they may display more or less of a sigmoid curve); its often strongly secund racemes, and its huge anthers." These plants were from the South Coast Range. He noted two exceptions to this general description: plants with small corollas from San Benito County, now recognized as *N. secundiflorus* var. *robbinsii* Morin, and plants from the Greenhorn Mountains in Kern County that "show considerable variation in the degree of pedicel arching, and secund racemes are evident only on an occasional branch." The Greenhorn Mountain populations are recognized here as a distinct species. In addition to characters mentioned by Robbins, they differ from *N. secundiflorus* var. *secundiflorus* (Fig. 3F) and var. *robbinsii* in having basal leaves broadly elliptic to ovate-deltate, 1.2–4 mm long, with margins shallowly toothed or wavy. *Nemacladus secundiflorus* basal leaves are oblanceolate to spatulate, 1.5–12 mm long, the margins irregularly lobed.

***Nemacladus bellus*** Morin & T.J.Ayers, sp. nov.—Type: USA. California. Kern Co., dominant associated

species: *Quercus wislizeni* var. *frutescens* Englm., *Cercocarpus montanus* [probably *Cercocarpus betuloides* Nutt. var. *betuloides*]. Upper reaches of the *Pinus sabiniana* D.Don belt on southwesterly facing slope, in loose granite gravel along road over Greenhorn Mountain (on the eastern side of the mountain) exactly 5 miles above junction of this road with road to Kernville; elevation 4,000 ft. June 1, 1954. *Bacigalupi and Robbins 4538* (Holotype JEPS5490!, Supplemental Fig. 3). Additional note by G. Thomas Robbins on the specimen, 16 Feb. 1956: "Provisionally assigned to *N. secundiflorus* G.T.Robbins ined. on the basis of the rather large corollas and the outline of the basal leaves. Racemes are not secund, however, and the pedicels are somewhat more variable in curvature than in *N. secundiflorus*."

*Nemacladus bellus* differs from other species of *Nemacladus* in having the combination of basal leaves broadly elliptic to ovate-deltate, margins shallowly toothed or wavy, not irregularly lobed; inflorescence zigzagged, internodes 2–5 mm long, flowers not (or very rarely) secund (Fig. 3E); corolla with cylindrical tube 2–2.5 mm long, lobes 2–2.5 mm long; filaments and anthers white or pale lavender, the anthers about 0.4 mm long, transparent cells on filaments narrow, attenuate; capsule about 1/4 inferior, round, sepals erect in fruit.

**Plants** erect, 5–11 cm tall, branched 1.5–2.5 cm above base, many secondary branches distally at 60° angle to axis, not wandlike. **Stems** reddish-brown, glabrous, or sparsely hairy at base. **Leaves** broadly elliptic to ovate-deltate, 1.2–4 mm long, base narrowed to petiole, margins shallowly toothed or wavy, apex obtuse or broadly acute, surfaces with scattered short, white hairs. **Inflorescence** axis zigzagged, internodes 2–5 mm long, flowers not secund; bracts usually aligned with pedicel, linear, 0.8–2 mm long, base not enfolding pedicel base, apex acute. **Pedicels** diverging at 50–90° angle to axis, shallowly sigmoidally curved, 3–10 mm long, about 0.1 mm diam., tip curved up. **Flowers** resupinate; hypanthium obconic, 0.5–1 mm long, sepals slightly spreading, lanceolate to deltate (sometimes quite broad at base), 0.8–1.2 mm long, all shaped alike, 2 flanking sepals larger than the others, sinuses "u-shaped", apex acute; corolla bilaterally symmetrical, ± 1-lipped, the adaxial lobes diverging, 4–4.5 mm long, petals connate proximally 3/10–1/2, tube white, veins faintly lavender, cylindrical, (twice as long as wide), slightly narrower just below lobes, 2–2.5 mm long, abaxial surface of lobes faintly lavender at tip, adaxial surface of lobes with erect white hairs, abaxial lobes white, with yellow blotch at base, 2–2.5 mm long, central lobe elliptic, flanking lobes asymmetrically ovate, the lower margin bowed, the upper margin straight, adaxial lobes sometimes folded back, the lower margin bowed, upper margin straight; filaments erect, connate in about distal 2/3, exserted from corolla tube, white, apex densely hairy,

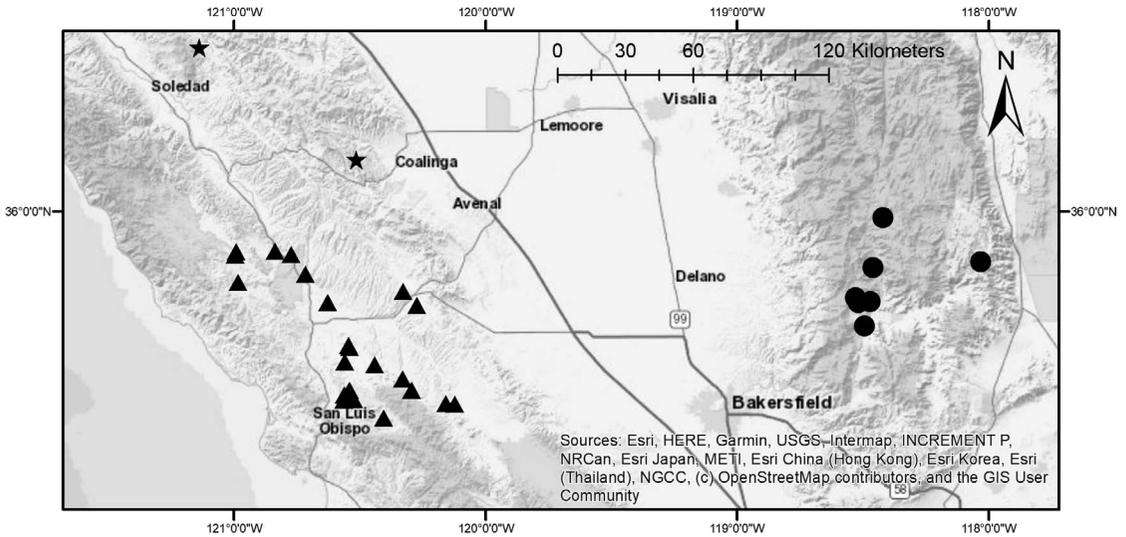


FIG. 5. Distribution of *Nemacladus secundiflorus* G.T.Robbins var. *secundiflorus* (triangles), *N. secundiflorus* var. *robbinsii* Morin (stars), and *N. bellus* (circles).

hairs moniliform, about 0.5 mm long, transparent cells 6–9 per cluster, slender, long-attenuate, sometimes held erect, attached just below connate portion of filaments to broad thick stub of tissue, anthers white to faintly lavender (about 0.4 mm long), nectary a rounded cushion at base of ovary with short, broad-based sharp-tipped hairs, ovary nearly superior, obconical. **Capsule** about 1/4 inferior, round, 1.5–2 mm diam., slightly oblique at base, sepals remain erect. **Seeds** round, 0.4–0.5 mm long, surface reticulate.

*Distribution and ecology.* *Nemacladus bellus* occurs on granitic gravel and sandy flats in Joshua tree woodland or mixed oak and conifer woodland, at 800–1800 m, on the Kern Plateau and in the Greenhorn Mountains of California (Fig. 5).

*Phenology.* Flowering May–July.

*Etymology.* The specific epithet, “bellus,” refers to the beautiful appearance of the plants when they are covered with delicate flowers.

*Representative specimens (localities abbreviated).* USA. CALIFORNIA. **Kern Co.:** between Isabella Dam and Keyville, *Howell 51777* (CAS); Eastern Slope Sierra Nevada, along Calif. Hwy 178 E of Walker Pass, *Keil & Holland 24043* (OBI). **Tulare Co.:** Upper part of Brush Creek Canyon on Cherry Hill Road, *Howell 53758* (CAS); Kern River Canyon near Roads End Post Office, *Howell 33166* (NY, CAS); Kern River Canyon north of Kernville, 0.2 miles south of intersection with Salmon Creek, *Morin 626* (UC); Greenhorn Mountains ca. 5.5 miles north of Kernville, near the road to the Greenhorn Summit Store, *Smith 411* (JEPS); Kern River Canyon, 5.5 miles north of Kernville, *Twisselmann 3566* (CAS, NY).

### Three New Species Separated from *Nemacladus sigmoideus*

*Nemacladus sigmoideus* as Robbins (1958) circumscribed it occurs “in the Mojave Desert and on desert slopes of the bordering mountains, less frequent on the western borders of the Colorado Desert; Tehachapi Mountains and Mount Pinos region; east to western Nevada and Arizona; south to Lower California.” Robbins’s concept of *N. sigmoideus* was based on characters of at least four species, two of which are represented on the holotype (JEPS7686, Fig. 6). Five plants are mounted on the sheet: four have small tubular corollas and are mostly in fruit; the fifth is mostly in bud, the few open flowers being larger with corollas cup-shaped. Plants on isotypes at CAS, MO, NY, and RSA all have small tubular corollas. Robbins’s (1958) “specimens to verify range” included representatives of all three species described below, as well as *N. sigmoideus* narrowly defined, the revised description of which follows here.

***Nemacladus sigmoideus*** G.T.Robbins, *Aliso* 4: 144. 1958.—TYPE: USA, California. Los Angeles Co., slopes of South Fork of Little Rock Creek Canyon at an elevation of 5100 feet, San Gabriel Mountains, June 14, 1953. *R. Bacigalupi & G. T. Robbins 4190* (Holotype: JEPS7686!, Fig. 6; isotypes CAS!, MO!, NY!, RSA!).

**Plants** erect, (6–)11–15 cm tall, basal branches at about 30° from axis, first secondary branches about 1.5 cm above base at about 70°. **Stems** brown or reddish brown, glabrous or with scattered hairs at base. **Leaves** rhombic to broadly lanceolate or elliptic, 1.5–11 × 1–5 mm, base wide, margins entire or shallowly crenate, apex obtuse or broadly acute,

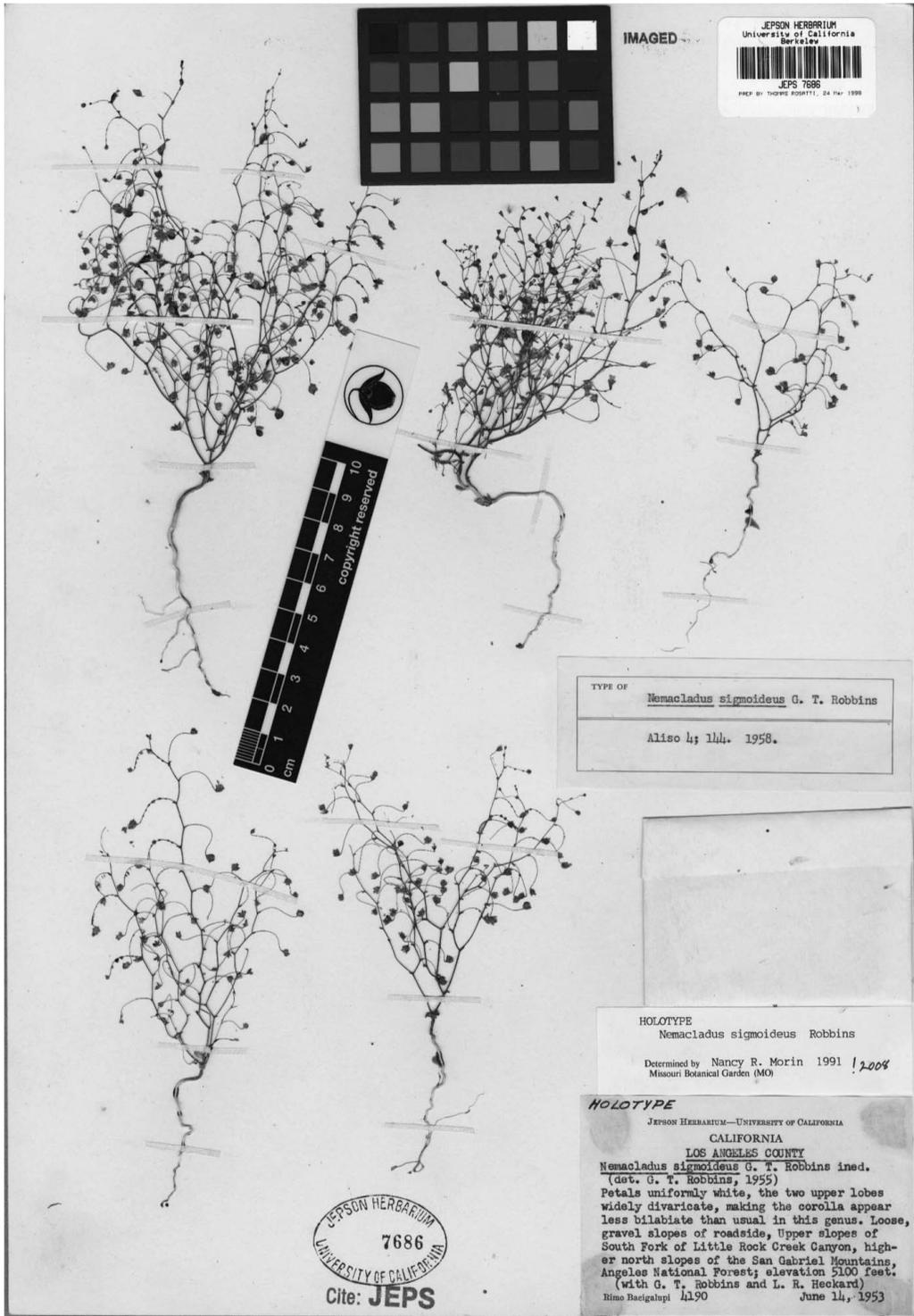


FIG. 6. *Bacigalupi* & G. T. Robbins 4190, holotype of *Nemacladus sigmoideus* G. T. Robbins. The center plant in the top row has an open flower with a cup-shaped corolla and is not *Nemacladus sigmoideus*. The other plants have smaller, tubular flowers typical of *N. sigmoideus sensu strictu*.

surfaces densely hairy abaxially, sparsely hairy adaxially. **Inflorescence** axis zigzagged, internodes 6–10 mm long; bracts aligned with pedicel, ovate to oblong-lanceolate, 0.8–2 mm long, base cupped around base of pedicel, apex obtuse to bluntly acute. **Pedicels** at about a 90° angle to axis, straight initially, becoming sigmoid, or deeply curved so flower is held at level of previous internode, 12–20 mm long, 0.1–0.2 mm diam. **Flowers** resupinate; hypanthium obconic, 0.8–1 × 1–1.2 mm, narrowed to base, base oblique, sepals all alike, spreading, lanceolate or broadly deltate, narrowed just at base, 1–1.3 × 0.5–0.6 mm, sinuses V-shaped; corolla bilaterally symmetrical, ± 1-lipped, the adaxial lobes divergent, petals connate in proximal 1/2–7/10, tube white, throat sometimes yellow, urceolate, 1.4–2.5 mm long, base rounded, narrowest just proximal to lobes, sometimes striate, or slipper-like, barely expanded at base, equal to or longer than the sepals, lobes white, sometimes yellow at tips, sometimes lavender abaxially, 1.8–2.5 mm long, central abaxial lobe oblong-elliptic, flanking lobes bowed on inner edge, straight on outer edge, adaxial lobes lanceolate to oblong-acute; filaments straight, slightly or well-exserted from corolla tube, connate in about distal 1/2, white or pale lavender, 1.5–2.6 mm long, abruptly bent down, somewhat constricted immediately below anthers or not, hairs at apex sparse, long, transparent cells attached just below ovary apex directly on filaments or to a narrow pad of tissue on filaments, slender, acute, anthers white or pale lavender, about 0.2 mm long; ovary about 1/2 inferior, nectaries yellow, low mounds on edge of ovary dome. **Capsules** about 2/5 inferior, almost round, 2–2.8 × 1.5–2.8 mm, base acute or oblique and flattened, apex broadly pointed, sepal tips and valve tips at about the same level or sepals longer, sepals spreading, sinus about 0.5 mm, valves and sepals widely spreading when seeds released, then sepals becoming narrower, sometimes darkening. **Seeds** widely elliptic, 0.5–0.8 mm long, surface reticulate. (Figs. 8A, B, C).

*Distribution and ecology.* *Nemacladus sigmoideus* occurs on sandy or gravelly soils at 200–2200 m in southern California (Fig. 7) and probably western Nevada and Arizona, south into Sonora, Mexico.

*Phenology.* Flowering April–June.

Specimens in a broadly defined *Nemacladus sigmoideus*, those with a small tubular corolla, sigmoid pedicel, and ovate or rhomboid basal leaves, have been collected from the southern and eastern Sierra Nevada and adjacent Nevada, Mojave Desert and northwestern Sonora Desert, Transverse Ranges, Peninsular Range, and southern Inner Coast Range. Plants most similar to the type specimen occur in the southern Sierra Nevada, Transverse Ranges, primarily on the north side, and west and north to the southern Inner Coast Range (Fig. 7). The bracts of this form are narrower than in other forms and more spreading. Their mature capsules are somewhat expanded above the hypanthium/sepal intersection,

and are surrounded by stiff, spreading, deltate sepals. The capsule valves are often shiny. Plants in the Walker Pass area of the southern Sierra Nevada have very small basal leaves and sepals that clasp the mature capsule. Also found in the southern Sierra Nevada are plants with very short corolla tubes and comparatively large capsules, and plants with long corolla tubes, both of which in other respects seem to be *N. sigmoideus*. Some plants have flowers with extremely small anthers, small enough to suggest the plants may be cleistogamous. Even given this range of variation, there are many forms that seem to have small tubular corollas, in which other aspects, such as pedicels, bracts, capsules, architecture, or basal leaves, do not fit within *N. sigmoideus* (Fig. 7, insert); although these specimens must remain annotated with this name, further study is needed to determine their true affinities.

*Nemacladus sigmoideus* has been confused with *N. secundiflorus* var. *robbinsii* and *N. gracilis*. *Nemacladus gracilis* has a cup-shaped corolla compared with the urceolate corolla of *N. sigmoideus*. *Nemacladus secundiflorus* var. *robbinsii* has basal leaves narrowly oblanceolate to spatulate, the margins irregularly lobed, sepals somewhat fleshy and blunt-tipped, and a cylindrical corolla tube, compared with *N. sigmoideus*, which has basal leaves rhomboid to broadly lanceolate or elliptic, the margins entire or shallowly crenate, sepals not fleshy, apex acute, and an urceolate corolla tube. *Nemacladus secundiflorus* var. *robbinsii* appears to occur only in Pinnacles National Monument, San Benito County, and Hanging Valley, Monterey County.

*Representative specimens of plants closely matching the type specimen (localities abbreviated).* USA. CALIFORNIA. **Kern Co.:** Southern Sierra Nevada Range; Piute Mountains, lower Esperanza Canyon at eastern base of Sorrell Peak and western edge of Kelso Valley, *Boyd 11947* (RSA); Western Transverse Range, San Emigdio Mountains Tecuya Ridge, *De Vries 7751* (RSA); Cortez Canyon, south of Bob Rabbit Canyon, *Fraga 199* (RSA); Tejon Ranch, *Jensen 1244, 1960, 1979, 2076, 3498* (RSA, UC); 1960 (RSA, UC); Tehachapi Willow Springs Rd, Parikh & Gale 3163, 3172, 3197, 3205 (SBBG). **Los Angeles Co.:** Junction of road to Horse Flat Public Camp and main paved road from Upper Chilao Recreation Area, *Bacigalupi et al. 4187* (JEPS); Mojave Desert, Hwy 138, 4 mi E of jct w Hwy 18 NE of Pinyon Hills, *Boyd & Mistretta 1558* (RSA); Liebre Mtns, head of the North Fork Fish Canyon, *Boyd & Raz 9817* (RSA); Transverse Ranges: San Gabriel Mountains region West terminus of Holcomb Ridge, west of Big Rock Creek, *Gross 2217* (RSA); San Gabriel Mtns region, *Mistretta 354* (RSA); San Gabriel Mountains, Little Rock Creek, drainage E of creek and N of Forest Rd. 4N15, *Mistretta 1223* (RSA); San Gabriel Mountains region Aliso Creek, slopes W of Angeles Forest Hwy., *Mistretta 5173* (RSA); San Gabriel Moun-

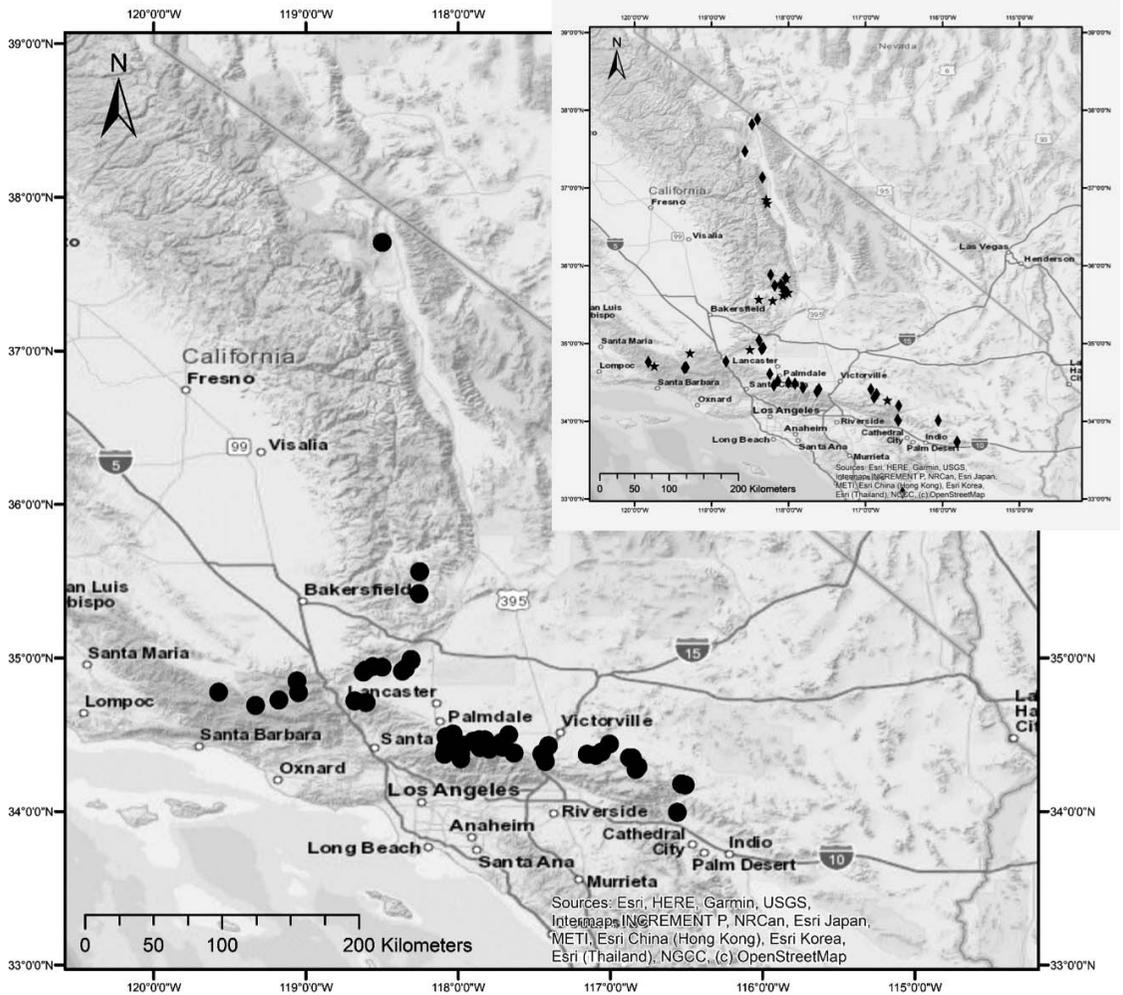


FIG. 7. Distribution of *Nemacladus sigmoideus* specimens most closely resembling type specimen (circles). Figure 7 insert. Varying degrees of resemblance to type specimen (many specimens cannot be identified yet with confidence): very probably *N. sigmoideus* (diamonds), large-capsuled *N. sigmoideus* (stars).

tains, Mill Creek Canyon, *Mistretta 5241* (RSA); Little Rock Creek, north base of San Gabriel Mountains, *Peirson s.n.* (POM); Pinyon Ridge, between upper Little Rock Creek and the San Andreas Rift Zone, *Ross et al. 3747* (CAS, RSA); Big Pines Hwy, midway between Caldwell Lake and Big Rock Springs, *Ross & Boyd 2671* (RSA); Liebre Mountain, west summit, *Ross & Boyd 7893* (CAS, RSA); Pacifico Mountain, *Ross & Banks 7994* (RSA); west summit of Liebre Mountain, *Ross & Boyd 8658* (CAS, RSA); San Gabriel Mountains/Mojave Desert, Mescal Highlands, *Swinney 6076* (RSA, UCR); San Gabriel Mtns.; SW of Pinon Hills, *Swinney 6182* (RSA, UCR); San Gabriel Mtns., nameless canyon immediately west of Jesus Canyon, *Swinney 7389* (RSA, UCR); San Gabriel Mtns., Devils Punchbowl Co. Park, *Swinney 8927, 8938* (UCR); San Gabriel Mtns. Sulphur Springs Campground, *Swinney 10955* (RSA, SD, UCR); San Gabriel Mountains, NNE of

Oracle Hill Summit, *Swinney 12841* (UCR); Transverse Ranges; San Gabriel Mountains, N of Bob's Gap, *Thorne 43469* (MO, RSA, UC); San Gabriel Mountains region, North of Shoemaker, *Thorne 43511* (MO, RSA, UC); San Gabriel Mts., Juniper Hills, c. 2 mi S of Ft Tejon Road, *Thorne 43524* (RSA); Mojave Desert Slope, Junction of Pallett Creek & Longview Road, *Thorne 43410* (MICH, RSA); San Gabriel Mountains, near Shoemaker Canyon, *Vanderplank et al. 50506* (RSA); San Gabriel Mts., Juniper Hills, *Wheeler s.n.* (RSA); San Gabriel Mtns. Mill Creek Summit, *Wood 789* (RSA); San Gabriel Mountains, Vicinity of Little-rock creek; *Wood 1623b* (RSA). **Riverside Co.:** Dry Morongo Wash, nw end of Coachella Valley, *Munz 16239* (NY, RSA). **San Bernardino Co.:** Mojave Desert along Pioneertown Road, just west of Black Hill, *André 17163* (UCR); The Pioneertown Mountains Preserve, *Bell 6607* (RSA); 6 mi w of Hesperia,

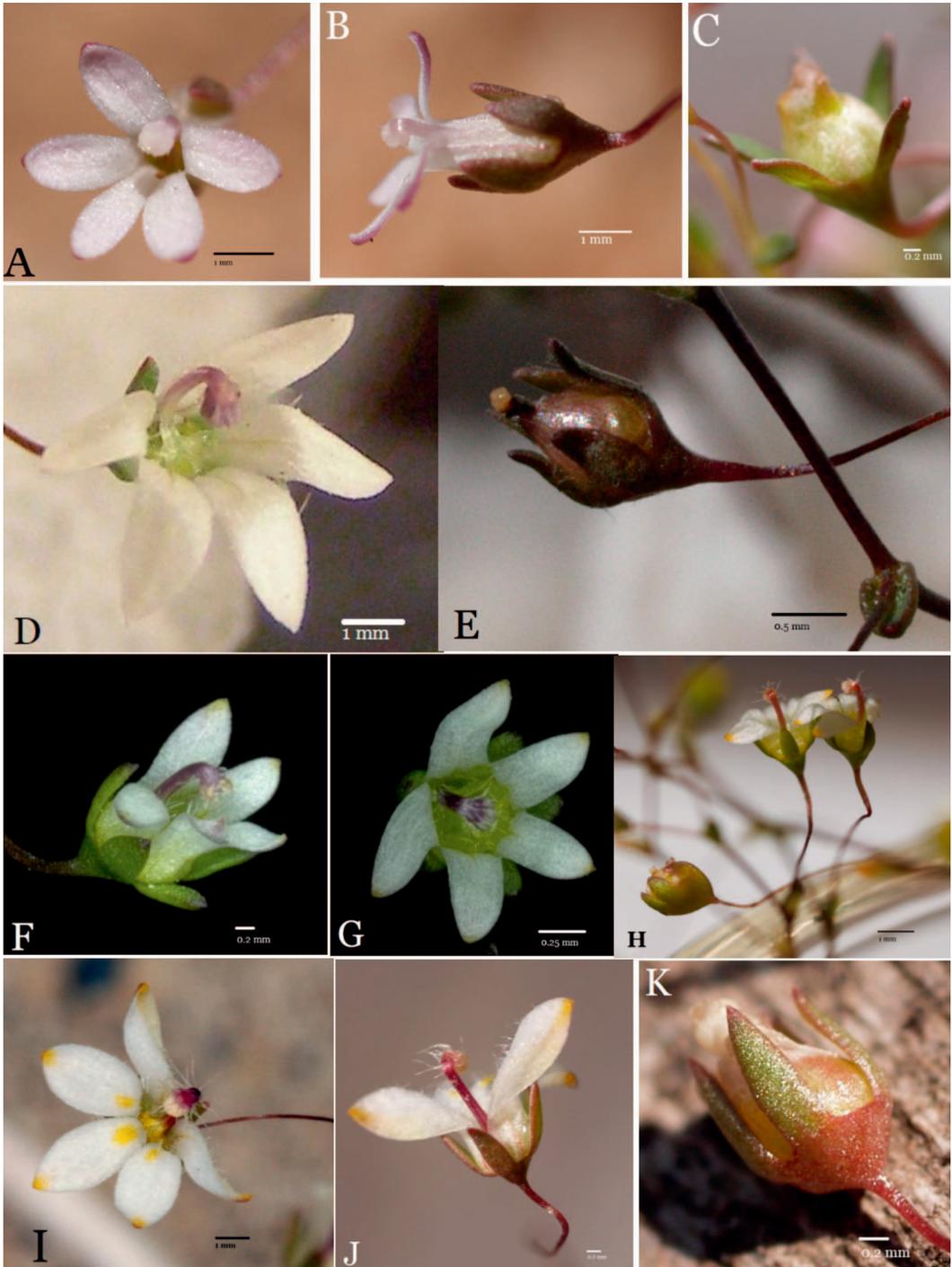


FIG. 8. *Nemacladus* flower and capsule comparisons: *Nemacladus sigmoideus*: A. flower front view. B. flower top view. C. capsule. *Nemacladus parikhiae*: D. flower, front view. E. capsule. *Nemacladus eastwoodiae*: F. flower side, G. flower front, H. flower top and side, and capsule. *Nemacladus matsonii*: I. flower front, J. flower top, K. capsule (photos: A, B, C, D, E, H, K, N. Morin; F, G, T. Ayers; I, J, S. Matson).

Johnston (POM.); Cushenbury Canyon., *Morin 617* (UC); Cajon Pass, *Parish & Greata 1931* (RSA); Baldwin Lake, *Peirson 6747* (DS, RSA); Cajon Summit, *Sanders 6502* (UCR); San Bernardino Mts, wash below Rattlesnake Spring, *Sanders 17091* (UCR); Mojave desert: Baldy Mesa, north of Cajon Summit, *Sanders 21791* (UCR); Pinyon Hills, ridge-top E of Oak Springs Canyon, *Swinney 3968* (RSA, UCR); Transverse Ranges; Baldwin Lake: W end of lake, *Thorne 52284* (RSA); San Bernardino Mtns. relay station on Grapevine Canyon Road, *Thorne 53027* (RSA); 1 mi ENE of Bowen Ranch, *Thorne & Prigge 52915* (RSA); S of Lucerne Valley on alluvial slope below Pfizer limestone quarry in Marble Canyon, *White s.n.* (UCR). **Santa Barbara Co.:** east end of San Rafael Mountains, upper reaches of Santa Barbara Canyon, south from the mouth of Alamo Canyon, *Gross 3383* (RSA); Big Pine Basin, San Rafael Mountains, *Hoffmann s.n.* (SBBG). **Ventura Co.:** Near summit of grade along road south of and overlooking Lockwood Valley, *Bacigalupi 4522* (JEPS); Near Camp Ozena, *Chandler 3500* (MO); Lockwood Valley Road west of Seymour Creek, *Morin 578* (UC); Camp Ozena, *Morin 579* (UC).

The fifth plant on the type specimen of *Nemacladus sigmoideus* is placed here in *Nemacladus parikhiae*.

***Nemacladus parikhiae*** Morin & T.J.Ayers, sp. nov.—

Type: USA, California, Los Angeles Co., Slopes W of Angeles Forest Hwy about 0.6 mi N of jct with Aliso Cyn Rd, 34.43411°N, 118.09149°W. Alt. 1189m/3900ft. Coarse soils, full sun. Former chaparral/scrub association, completely burned in Station Fire in 2009. Currently rich assemblage of mostly native annuals and seedling/stump sprouting perennial shrubs and trees, including *Mentzelia veatchiana* Kellogg, *Gilia modocensis* Eastw., *G. ochroleuca* M.E.Jones, *Cryptantha muricata* var. *jonesii* (A.Gray) I.M.Johnst., *Chaenactis glabriuscula* DC., *Poa secunda* J.Presl., *Eriodictyon crassifolium* var. *nigrescens* Brand, *Lotus strigosus* (Nutt.) Brouillet, *Lupinus bicolor* Lindl., *Ericameria linearifolia* (DC.) Urbatsch & Wussow, *Claytonia parviflora* Hook., *Adenostema fasciculatum* Hook. & Arn., *Cercocarpus betuloides* Nutt. Uncommon, Corolla irregular, 20 May 2010. *Orlando Mistretta 5160* with *Christine Mistretta* (Holotype: RSA777928!, Supplemental Fig. 4; isotype SFV).

*Nemacladus parikhiae* differs from other *Nemacladus* in having a 2–4 mm long, cup-shaped, bluetinged corolla, the filament tube dark purple to reddish purple distally, transparent cells very slender, tapered; anthers dark blue, 0.2–0.3 mm, empty anthers gray (Figs. 8D, E).

**Plants** 5–12 cm tall, branches from base and 1–2 cm above, at 45° to axis or more, secondary branches at 50–60°. **Stems** reddish brown, glabrous or with scattered hairs. **Leaves** broadly deltate to elliptic, 2–

4.5 × 1.7–1.8 mm, base broad, abruptly or gradually narrowed, margins toothed, apex acute, surfaces glabrous. **Inflorescence** axis slightly zigzagged, internodes 2.5–5 mm long; bracts aligned with pedicel but not clasping, narrowly ovate, 1–1.2 mm long. **Pedicels** 6–18 mm long, about 0.1 mm diam., at about 90° to axis, straight to shallowly curved, tip curved up. **Flowers** resupinate; hypanthium broadly obconic, 0.5–0.6 mm long, sinuses flat, sepals erect, deltate, 0.5–1 mm long; corolla bilaterally symmetrical, 1-lipped, the adaxial lobes divergent, petals connate 1/10–1/4 proximally, white with a faint blue tinge, with dark pink or greenish veins, 2.5–4 mm long, tube broadly cup-shaped, about 0.5–1 mm long, slightly gibbous at base, medial sinus slit nearly to base, ovary dome clearly visible, pentagonal, green, corolla lobes 2–3 mm long, long hairs scattered adaxially, 1.2–2 mm long, abaxial lobes elliptic, acute, adaxial lobes slightly asymmetrical, oblong, acute, folded back; filaments connate nearly to base, arched over, dark purple to reddish purple distally, abruptly curved at tip, few very long hairs at apex, transparent cells numerous (10+ per group) attached to pad at base of filaments, very slender, attenuate, anthers dark blue, 0.2–0.3 mm long, empty anthers gray; ovary about 3/4 inferior, nectaries pale yellow or pale green. **Capsule** ellipsoid, 0.8–1.5 × 1.6–3 mm, base oblique, narrow, apex narrow, sepals erect or flared outward from middle. **Seeds** oblong-elliptic, 0.5–0.6 mm, surface reticulate.

*Distribution and ecology.* *Nemacladus parikhiae* occurs in chaparral and creosote bush scrub on coarse gravelly soils at 800–1800 m. It is found in the Transverse Ranges, with gaps in distribution between the western San Gabriel Mountains, Los Angeles County, the San Bernardino Mountains, San Bernardino County, and San Jacinto Mountains, Riverside County (Fig. 9).

*Phenology.* Flowering (March) April–July.

*Etymology.* *Nemacladus parikhiae* is named in honor of Dr. Anuja Parikh, who, with Nathan Gale, for years has provided extremely helpful photos, specimens, and observations of many *Nemacladus* taxa. They have done the same for many other genera and Southern California botanists, including rediscovery the San Fernando Valley spineflower, *Chorizanthe parryi* var. *fernandina* (S.Watson) Jeps. at Newhall Ranch (Spratt 2018). We are very grateful to both of them for their help with *Nemacladus*.

*Representative specimens (localities abbreviated).* USA. CALIFORNIA. **Los Angeles Co.:** Mount Wilson, *Abrams 1899* (NY, DS, POM RSA); 4 miles northeast of Lancaster on the Muroc Road, *Ferris 9480* (DS, GH, ORE); Upper Big Tujunga Canyon, 0.3 km ENE of Shortcut Station, 0.7 km N of State Highway 2 (Angeles Crest Hwy), *Anuja Parikh, Nathan Gale 3595* (SBBG); from alder saddle along s. fork Little Rock Creek, *Gross 2385* (RSA); San Gabriel Mtns: Mill Creek Canyon, near spur road to

falcon Mine, *Mistretta* 5223 (RSA); San Gabriel Mountains region North Fork Mill Creek, *Mistretta* 5296 (RSA, UC); Western extension of Waterman Mountain, along Waterman Mountain trail, *Soza* 1683 (RSA); near Chilao Creek, Upper Chilao Campground, *Thorne* 38285 (RSA); Big Tujunga, ridge E of Coldwater Canyon, *Wheeler* 6641 (RSA). **San Bernardino Co.:** Sawtooth Mountains, *Bell* 1136 (RSA); Bighorn Mountains 1.25 air miles nw of Viscera Spring, *Bell* 6769 (RSA); Burns Canyon, *Morin* 644 (UC); mouth of Burns Canyon, 0.5 mi W of end of pavement near Rimrock, *Sanders* 12279 (UCR); 2.1 mi above Rimrock Rd just below Burns Springs, *Sanders* 16861 (UCR).

A population from Aliso Canyon, San Gabriel Mountains, Los Angeles County (*Parikh & Gale* 3485) with small, lavender tinged, nearly actinomorphic, cup-shaped corollas and dark purple filament tips may be a small-flowered version of *N. parikhiae*. More study is needed to determine whether plants with flowers like *N. parikhiae*, but with paler filaments and long, upwardly curved pedicels and large capsules found in the Lake Arrowhead and Bear Lake region warrant recognition. At least at Crab Flat, east of Lake Arrowhead, San Bernardino Mountains, this form grows with *N. sigmoideus* s.s. in some years. Representative collections of these are: 3.5 air miles east of junction of Pacific Crest Trail and forest service road 1N05, *Bell* 1377; Bighorn Mountains, central Ruby Canyon, *Bell* 6681 (RSA); San Bernardino Mountains region; FS Rd 3N34, on the slopes above Hooks Creek, just east of its confluence with Bear Creek, *Fraga* 1619 (RSA); San Bernardino Mountains region, on Pacific Crest Trail, 0.25 mi N of FS Road 2N04, east of YMCA camp, Camp Oaks, near Arrastre Creek, *Fraga* 2171 (RSA); San Bernardino Mountains region; West of South Fork Campground, north of Hwy. 38 & Santa Ana River, *Gross* 1139 (RSA); N of Baldwin Lk, 0.8 mi W of Smart's Ranch, *Sanders* 17304 (UCR); Barton Flats area, Hathaway Flat along Glass Road, near Barton Creek, *Sanders* 17370 (UCR); San Bernardino Mtns., Little Bear Creek, c. 1.5 mi. ENE of Lake Arrowhead, above confluence with Hooks Creek, *Sanders* 28342 (UCR).

Although G. T. Robbins (1958) considered all plants in the Mojave Desert and adjacent regions with sigmoid pedicels and very small white corollas to be *Nemacladus sigmoideus*, these can be resolved into two distinct groups—those described in the more narrowly circumscribed *N. sigmoideus* as usually having entirely white or pale lavender, tubular corollas and white or pale lavender filaments and anthers, and plants with white or cream-colored, cup-shaped corollas, the throat and lobes yellow-tipped, filaments maroon distally, and gray or white anthers, described here as *N. eastwoodiae*.

***Nemacladus eastwoodiae*** Morin & T.J.Ayers, sp. nov.—Type: USA. California. San Bernardino Co., Mesquite Mountains, Winter's Pass. Sandy

wash with *Larrea tridentata* (DC.) Coville, *Yucca schidigera* Roetz ex Ortgies, *Y. baccata* Torr., *Salvia dorrii* (Kellogg) Abrams, *Hymenoclea salsola* Torr. & A.Gray [= *Ambrosia salsola* (Torr. & A.Gray) Strother & B.G.Baldwin], *Acacia greggii* A.Gray [= *Senegalia greggii* (A.Gray) Britton & Rosei], *Eriophyllum wallacei* (A.Gray) A.Gray, *Camissonia brevipes* (A.Gray) P.H.Raven [= *Chylismia brevipes* (A. Gray) Small], *Nemacladus* spp., *Salazaria mexicana* Torr. [= *Scutellaria mexicana* (Torr.) A.J. Paton], *Dyssodia cooperi* A. Gray [= *Adenophyllum cooperi* (A. Gray) Strother], *Mimulus bigelovii* A. Gray [= *Diplacus bigelovii* (A. Gray) G.L. Nesom], *Eriogonum inflatum*, etc. Delicate annual, 3500 ft. May 10, 1978. *Thorne et al.* 51354 (Holotype: RSA 275909!, Supplemental Fig. 5; isotype MO!).

*Nemacladus eastwoodiae* differs from other *Nemacladus* in having a combination of small, 1–1.6 mm, cup-shaped corollas, maroon filaments, white or gray anthers, very long, slender, deeply curved pedicels, and sepals clasping the capsules, which bear few, relatively large seeds (Figs. 8F, G, H).

**Plants** erect, (4–)8–12 cm tall, branches from base at 30–50° from main stem and 1.5 cm above at 60–70°, secondary branches many, at 40–50°, tertiary branches few, at 40–50° angles. **Stems** light brown or reddish brown, glabrous. **Leaves** rhombic to elliptic, 3–6 × 1.5–2 mm, base narrowed, margins sharply but shallowly toothed, apex acute, surfaces glabrous or pubescent. **Inflorescence** axis ± shallowly zig-zagged, internodes 4–6 mm long; bracts straight or arched back, aligned with pedicel, narrowly lanceolate, 1–1.6 mm long, base enfolding pedicel base, apex acute. **Pedicels** 10–15 mm long, <0.1 mm diam., at least 2x longer than internode, much thinner than axis, 90° to axis, deeply sigmoidally curved, tip erect. **Flowers** resupinate; hypanthium green, obliquely obconic to hemispheric, (0.4–) 0.5–0.6 mm long, sepals erect, ± alike, oblong-deltate, 0.6–1.2 mm long; corolla bilaterally symmetric, ± 1-lipped, petals connate in proximal 1/4, tube cup-shaped, wider than deep, 0.2–0.4 mm long, lobes white or cream-colored with yellow tips and throat, oblong elliptic, 0.8–1.2 mm long, with scattered long hairs adaxially, 3 abaxial lobes spreading, 2 adaxial lobes divergent and folded back; filaments connate in distal 1/2, tube maroon distally, connective maroon, 1–1.3 mm long, transparent cells narrowly deltate, attenuate, attached to a short stalk connected near the base of the filaments, anthers white or gray, 0.15–0.2 mm long, pollen white; ovary 1/2 inferior, nectaries greenish yellow, low mounds on edge of ovary dome. **Capsule** 1/4 or less inferior, straw-colored, round, 1–2 × 1–2 mm tall, base acute, apex rounded, abaxial sepal remaining cocked, adaxial sepals clasping the capsule, sinuses U-shaped, valves ultimately opening widely. **Seeds** elliptic, 0.5–0.6 mm long, surface reticulate.

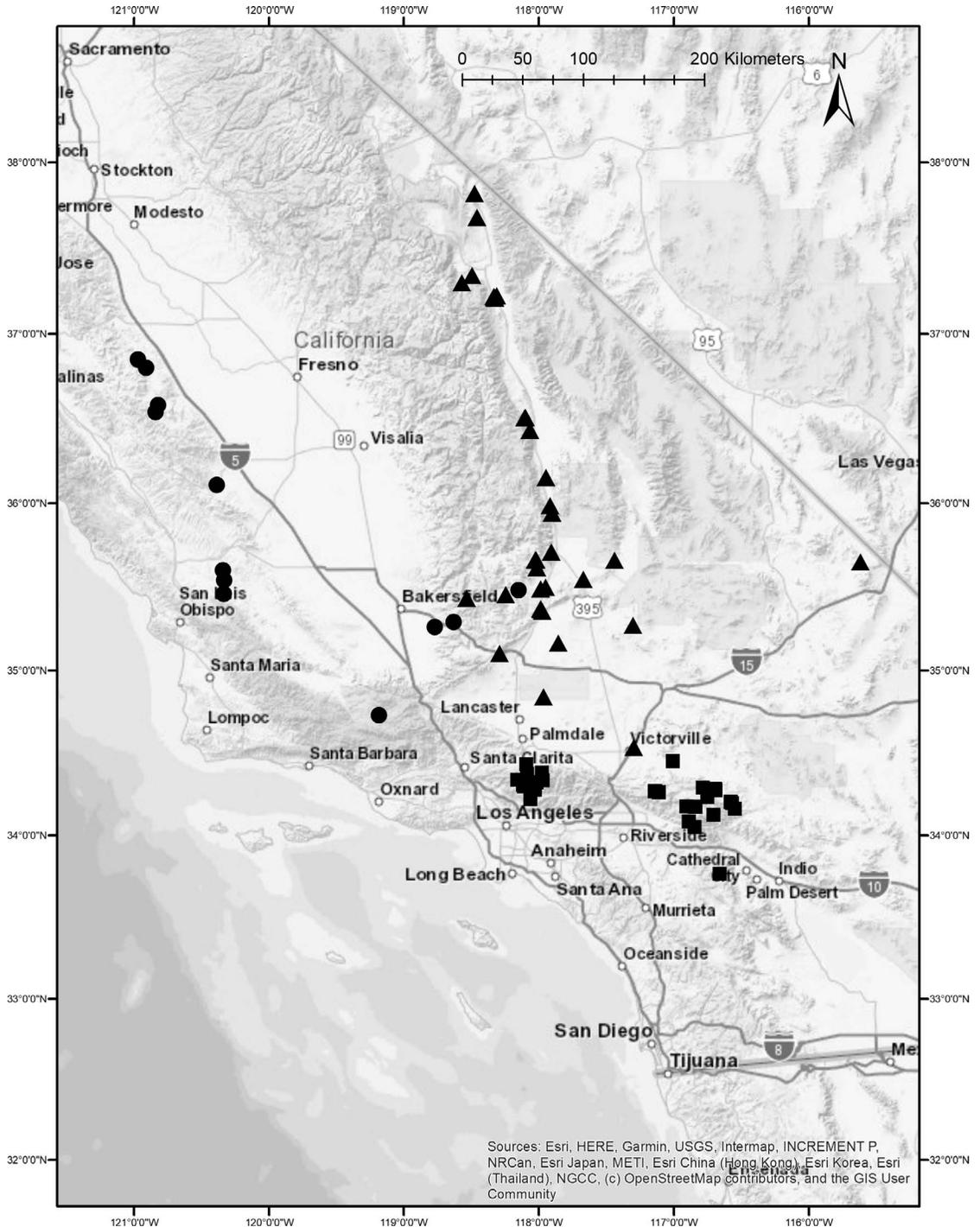


FIG. 9. Distribution of *Nemacladus matsonii*-(triangles), *N. parikhiae*-(squares), and *N. gracilis*-(circles).

**Distribution and ecology.** *Nemacladus eastwoodiae* occurs in sandy washes and openings, on rocky slopes, in Joshua Tree woodland, and creosote bush scrub; at 900–2200 m, in California and Nevada, primarily in the Mojave Desert and Owens Valley (Fig. 10).

**Phenology.** Flowering April–June.

**Etymology.** *Nemacladus eastwoodiae* is named for Alice Eastwood, 1859–1953, quintessential California botanist, who collected *Nemacladus* throughout the

state. She collected *N. eastwoodiae* near Baker, San Bernardino County, with Tom Howell; this locality is where the senior author first saw this lovely plant.

*Similar species.* Although very similar to *N. sigmoideus* in its sigmoid pedicel and broad basal leaves, *N. eastwoodiae* can be distinguished on herbarium specimens because the filament tube often is extended above the corolla and generally is still visible above the dried corolla, whereas in *N. sigmoideus* the filament tube is wrapped in the remains of the corolla.

*Nemacladus tenuis* (McVaugh) Morin var. *tenuis* also has small white corollas and can be distinguished from *N. eastwoodiae* in having the two adaxial lobes tipped with reddish brown, the three abaxial lobes with a deep rose chevron, and deeply toothed or pinnately lobed leaves.

*Selected specimens (localities abbreviated).* USA. ARIZONA. **Mohave Co.:** 7 miles southeast of Yucca, *Gould & Darrow 4312* (UC, CAS, ARIZ). CALIFORNIA: **Inyo Co.:** Sierra Nevada Mtns., Big Pine Canyon, along Glacier Lodge Road, *André 11660* (UCR); About 22 miles south-southeast of Olancho, *Henrickson 17922* (RSA, CHICO, NY, TEX); Desert flats, *Robbins 3488C* (JEPS). **Kern Co.:** Branch Park, 1 mi N and 1 mi W of South Gate to Edwards AFB, *Charlton 5332* (RSA); W Mojave Desert, *Hoffmann s.n.* (SBBG); 0.8 km N of Tehachapi Willow Springs Rd., just W of 100th St West, *Parikh & Gale 3173* (SBBG); south end of Soledad Mountain, *Twisselmann 4312* (CAS); Rademacher Hills, Summit of Hwy 395, *Twisselmann 7063* (CAS); El Paso Mountains: Last Chance Canyon, *Twisselmann 4354* (CAS, JEPS); Mojave-Randsburg Region, *Twisselmann 4439A* (JEPS). **Los Angeles Co.:** Lancaster, *K. Brandegee, s.n.* (POM); Transverse Ranges, San Gabriel Mtns. region, *Mistretta 600* (RSA); Transverse Range; San Gabriel Mtns./Western Mojave Desert Carr Canyon, *Swinney 10596* (UCR); Transverse Range; San Gabriel Mtns., lower Brainard Canyon, *Swinney 10749* (UCR). **San Bernardino Co.:** Monkeyflower Wash s of Kane Wash, N Ord Mtn area, *André 5112* (UCR); Ivanpah Valley, *André 12777* (RSA); southwest of Cima dome along Mojave Road at Cedar Wash, *André 14658* (UCR); Old Woman Mountains, north end of range at historic Enterprise Mine area, near corral, *André 24903* (RSA); Kelso, *Baldwin 256* (RSA); Turquoise Mountains about 2.75 air miles north of Halloran Spring, *Bell 4845* (RSA); Pioneer town Mountains Preserve; Pipes Wash, between Black Hill and Flat Top, *Bell 6734* (RSA); *Bell 7972* (RSA); *Bell 6538* (RSA); Kingston Wash at Coyote Holes, *Castagnoli et al. 99* (RSA); Mohave Desert, along Hwy 18, ca. 0.5 mi E of jct w/ Hwy 66–91, *Davis 130* (UCR); At turnoff to the Fossil Pit road from the paved highway, *Dunn 5611* (UCR); near Baker, *Eastwood & Howell 8895* (CAS); Halloran Summit exit on Interstate 15 in the Mojave Desert, halfway between Barstow and Las Vegas, *Ertter 9957* (UC); Mojave Desert, *Hall 6819*

(UC (w/ *orientalis* and an odd *rubescens*)); Eastern Mojave Desert large wash crossing Kelbaker Road 5 mi north of Kelso, *Helmkamp s.n.* (UCR); Garlic Springs, *Hoffmann s.n.* (SBBG); half way between Adelanto and Johannesburg, Mohave Desert, *Jaeger s.n.* (POM); 15 mi S of Warren's Well, Little San Bernardino Mts., *Jaeger s.n.* (POM); Stoddard Well, *Jepson 5915* (JEPS); Barstow, by Iverson Hill, *Jepson 17188B* (JEPS); Barstow, *Jepson 5822* (JEPS, NY); Mojave Desert, *Jepson 20509* (JEPS); 5.5 miles northeast of Kelso, *Jepson 20573* (JEPS); Along road to Baker on mountain slopes above Kelso, *Jepson 20585* (JEPS); Mojave Desert, *Jepson 20512A* (JEPS, MICH, US); SE of Victorville, *Johnston s.n.* (POM); Along Wildhorse Canyon Road, *Junak 1176* (SBBG); Near Calico, *Lemmon s.n.* (UC); Transverse Ranges; Santa Ana River Canyon, Junction of Stetson Creek Road (Forest Road 1N36) and Round Cienega Creek, *Mistretta 3795* (RSA); 20 mi. N of Box "S" Ranch, *Munz 12440* (UC, POM); South base of Sugarloaf Mountain, *Munz 17118* (POM); 3 mi E of Warrens Well, *Munz & Johnston 5191* (POM); New York Mts. e Mojave Desert, *Prigge 2879* (RSA); Kramer Hills, *Roos 5634* (RSA, UCR); 3.9 mi E of the Field Rd. exit on I 15, ca. 7 mi NW of Afton Cyn., *Sanders 256* (UCR); Mojave Desert/San Bernardino Mtns; north foot of mtns below the Partin Brothers Mine (Terrace Springs), 4.6 mi. SSW of Old Woman Springs Road, *Sanders 16927* (UCR); Eastern Mojave Desert Ivanpah Valley, alluvial slopes below Clark Mountain, *Sanders 38165* (UCR); Southeastern end of the Kingston Range. 6.8 miles northwest of Kingston road on Excelsior Mine road, *Sanders 263* (SBBG, UCR); Cushenbury Canyon, off Hwy 18 to the west near Cal Trans 5000 ft elevation sign, *Soza et al. 233a* (RSA); Mojave Desert; Southcentral Mojave Desert region New Dixie Mine Road, *Stoughton et al. 1258* (RSA); Riggs Wash, south of Kingston Range Wilderness on C0743, approximately 10 miles E/NE of Hwy127, *Stoughton et al. 1320* (RSA); Mojave Desert; S of Hwy 247 in Johnson Valley, *Swanson 534* (RSA); Mojave Desert; East Mojave Desert region New York Mountains, *Thorne 51311* (RSA); Mojave Desert, Mesquite Mountains, Winter's Pass, *Thorne 51354* (RSA); Lucerne Valley, 0.3 miles west of Lucerne Valley, *Thorne 51796* (RSA); Southcentral Mojave Desert 1 mi SW of S end of Rabbit Dry lake, *Thorne 53034* (UCR); Southeast end of Kelso Sand Dunes. 7 miles south of Kelso on Amboy Road, *Wolf 10214* (CAS, NY, RSA); Excelsior Talc Mine, *Wolf 10383* (DS, RSA); San Bernardino Mountains Ridgeline west of Mohawk Mine, *Wood 2002* (RSA). NEVADA. **Esmerelda Co.:** Oriental Wash, 0.4 road miles ENE of junction with Tule Canyon Road, *Tiehm 14657* (CAS, NY, UTC). **Lincoln Co.:** Kane Springs Valley, Kane Springs Wash 9 road mi NE of hwy 93 on road to Elgin, *Tiehm 7638A* (CAS, NY, USA). **Nye Co.:** Nevada Test Site, *Beatley 12842* (RSA, UNLV).

Photographs in CalPhotos by Steve Matson (2010) alerted the authors to the following new species. Thomas Howell and Ernest Twisselmann both collected *N. sigmoideus*-like plants with large corollas, maroon filaments, and white anthers extensively. Twisselmann on his collection number 3536 noted the maroon filaments and bright white anthers. Heller, on his collection number 8878, noted that the plants might be distinct.

***Nemacladus matsonii* Morin & T.J.Ayers, sp. nov.—**

Type: USA, California, Inyo Co., 9 miles sw Lone Pine (Carrol Creek Pack Station). Sandy desert. 5500 ft. May 25, 1958. *Lewis S. Rose 58072* (holotype: UC 1106156!, Supplemental Fig. 6; isotypes DS!, GH!, MO!, NY!, RSA!, US!, WTU!).

*Nemacladus matsonii* differs from other *Nemacladus* in having the combination of a large flower, 3.5–5 mm, the corolla tube cup-shaped, the medial sinus deeper than the others, the lobes cream-colored with a yellow splotch at the base, the filament tube and connective red to faded magenta, the anthers white or cream-colored. (Figs. 8I, J, K.)

**Plants** erect, (2.5–)7–16 cm tall, branched from base and 1–1.5 cm above base, at lowest 1–3 nodes, secondary branches numerous, branch angles wide, (60–)85–90° to main stem. **Stems** dark red, glabrous or with scattered hairs. **Leaves** ovate, elliptic, lanceolate, to obovate, 2–8 × 1.5–4 mm, base narrowed, margins entire or teeth very shallow, apex obtuse or acute, surfaces glabrous abaxially or sparsely hairy, densely hairy adaxially. **Inflorescence** axis zig-zagged, internodes 4–8 mm long; bracts mostly aligned with pedicel, or bent back, narrowly lanceolate to ovate, 1–2.5 mm long, base folded against but not around pedicel base, apex acute, surface hairy abaxially, the hairs white. **Pedicels** at 80–110° angle to axis, 8–18 mm long, 0.1–0.15 mm diam., sigmoid, proximal portion straight or curve broad, distal curve abrupt (zigzag of axis amplifies width). **Flowers** resupinate; hypanthium broadly obconic, 0.3–0.8 mm long, sepals slightly spreading, ± alike, lanceolate, 0.7–1.5 mm long, apex acute, sinus broad, straight, adaxial sepal cocked back, sepals longer than corolla tube; corolla bilaterally symmetric, ± 1-lipped, 3–4.5 mm long, tube cream-colored, cup-shaped, length equal to or less than width, medial sinus deeper than other sinuses, lobes cream-colored with yellow splotch at base, tip cream-colored or yellow, drying darker, 2.2–4.5 × 0.6–0.7 mm, apex acute, with white, erect hairs on adaxial surface, hairs about 0.1 mm long, central abaxial lobe spatulate-elliptic, flanking lobes elliptic, adaxial two lobes straight on upper (adaxial) edge, slightly bowed on lower edge; filaments connate entire length, tube straight then curved over, tube and connective red to faded magenta, 1.1–2 mm long, apex with sparse moniliform hairs, transparent cells broadly deltoid, base broad, tip pointed, attached to a broad pad of tissue that is attached at the level of the ovary apex, anthers white or cream-colored, 0.4–0.6 mm long,

shiny, pollen cream-colored; ovary elongated, almost superior; nectaries yellow, round, on wall of ovary near base. **Capsules** 1/5–3/10 inferior, darkish, becoming straw-colored, round or broadly ovoid, 2–3 mm diam., base rounded or oblique, apex rounded, sepals erect to slightly spreading, with wide, flat sinuses, valves broad, translucent, sepals and valves erect in open capsules. **Seeds** oblong, 0.5–0.6 × 0.3 mm, surface with wavy ridges separated by large cells.

**Phenology.** Flowering April–June.

**Distribution.** *Nemacladus matsonii* occurs on compact sand and stabilized dunes, in Joshua tree woodland and creosote bush scrub, at 700–1700 m in the Owens Valley south through the Red Rock Canyon area to at least the Tehachapi Mountains. (Fig. 9.)

**Etymology.** The species is named in honor of Steve Matson, who has been documenting the plants of the western U.S., especially the Owens Valley, making his excellent images (nearly 24,000) available through CalPhotos (<http://calphotos.berkeley.edu>).

**Representative specimens (localities abbreviated).** USA. CALIFORNIA. **Inyo Co.:** Owens Valley along transmission line road, c. 4 miles north of Big Pine, 1 mile east of Hwy 395, 0.5 mi. north of Klondike Reservoir, *André 11548* (RSA, UCR); near Oak Creek Campground just N of Whitney Fish hatchery, *André 11641* (UCR); Eastern Sierra Nevada Cottonwood Creek, Wormhole Canyon, along Cottonwood Road, 2.1 mi west of US Hwy 395, c. 11 mi north of Olancho, *André 17882* (UCR); Little Lake, south of cinder cone, sandy soil, elev. 3500 ft, *DeDecker 2041* (RSA); Owens Valley: 3.5 mi N of Big Pine, *DeDecker 3450* (RSA); Near Little Lake, *Hall 7362* (UC, UNLV, POM); Foothills west of Bishop, *Heller 8278* (CAS, DS, GH, JEPS, NY, UC, US); About 23 air miles south-southeast of Olancho, *Henrickson 18058b* (CHICO, NY, RSA); 6 mi SW of Bishop along Hwy 168 near 5000' elev. sign, along dirt road N of Highway, broad decomposed granite sand and gravel alluvial fan, *Honer 2321* (RSA); on road from Lone Pine to Whitney Portal road, 6500', *Howell 33310* (CAS); Carroll Creek, morainal slopes, *Howell 33372* (CAS, MO, NY); north of Big Pine near power transformers, *Morin 683* (UC); Bishop Highway 3.8 mi N of Big Pine, *Twisselmann 15537a* (CAS); 3.25 mi e of US Hwy 395 and 3.5 mi s of Coso Rd., *Zemba CHSA 196*, with *N. sigmoideus* (RSA). **Kern Co.:** Gravelly wash at north end of Walker Basin at crossing of road to Havilah, *Bacigalupi 4528* (CAS, DS, GH, JEPS, RSA, SLO). Tehachapi Pass, Piute Mountain Range, *Benson 3500* (RSA, US, WTU); E of Mojave, *Carter and Kellogg 3167* (UC); Red Rock Canyon, *Dearing 4637* (SBBG); Owens Peak eastern watershed, Short Canyon, *Fraga 1099* (RSA, UC); Mojave Desert, California City land development, *Holmgren & Holmgren 7689* (CAS, NY); 5 miles east of Claraville, *Howell s.n.* (CAS); 8 miles north of Ricardo, Kern Co., *Howell 4997* (CAS); East side of Walker Pass, *Howell 37206* (CAS, MO); Southern Sierra Nevada, Scodie Mtns, Kiavah Wilderness, Cow

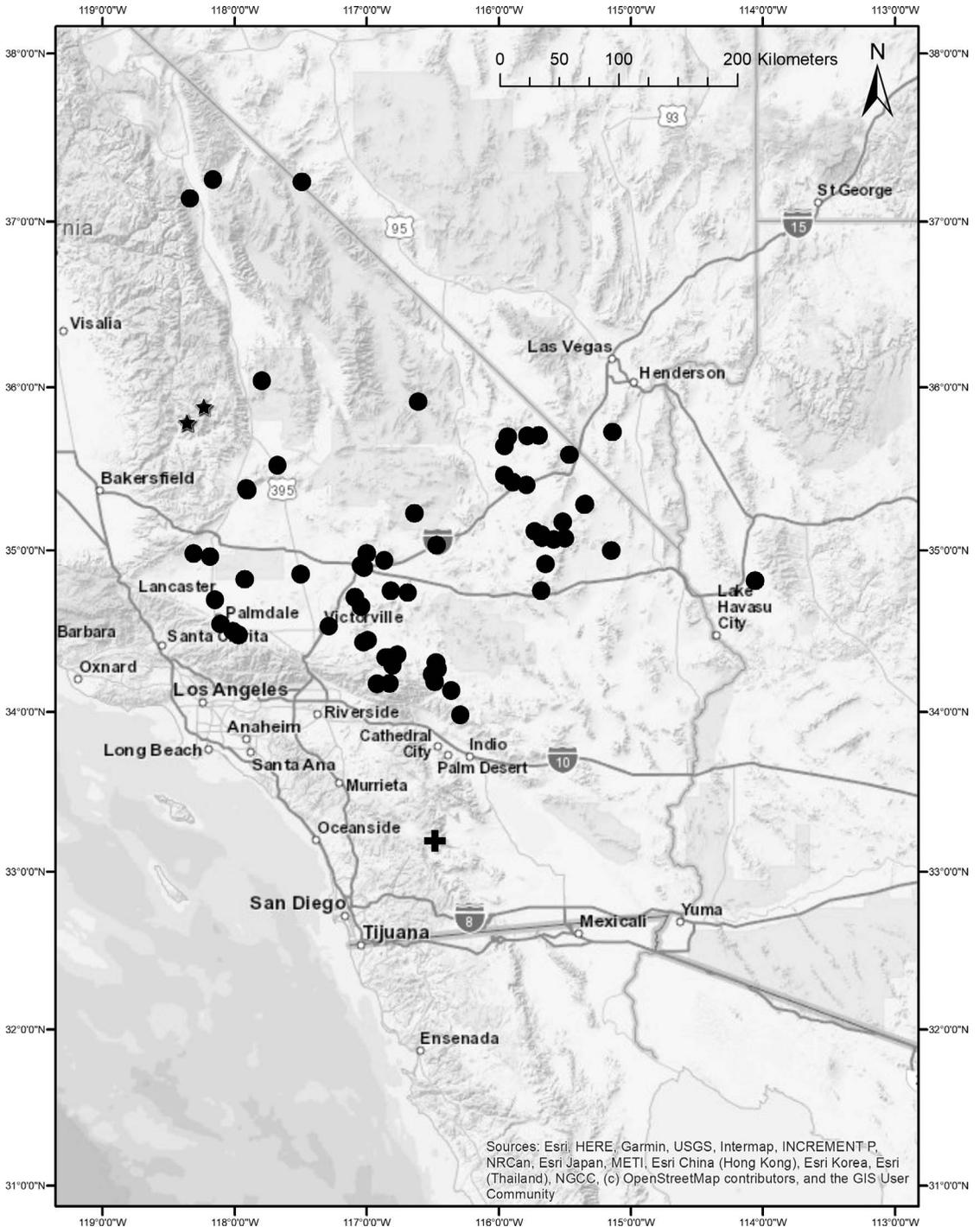


FIG. 10. Distribution of *Nemacladus eastwoodiae* (circles); *Nemacladus twisselmannii* var. *twisselmannii* (stars) and *N. twisselmannii* var. *botanywomanae* (cross).

Haven Canyon, west side of the main road, *Gardner & Poutasse 833* (RSA); Mojave, *Jones s.n.* (UC, US); Sandy flats, 9 mi. north of Ricardo, *Munz 12463* (POM, UC); 0.5 miles east of summit of Walker Pass, *Munz 13362* (POM, RSA, WTU); 8 mi n of Ricardo,

Indian Wells Valley, *Peirson 8821* (RSA); Walker Pass, e slope, *Rose 62040* (CAS, JEPS, MICH, RSA); East fork of Red Rock Canyon, *Twisselmann 3536* (CAS, JEPS); East slope of Walker Pass, *Twisselmann 4497* (with *N. sigmoideus*) (CAS, JEPS); Rademacher Hills:

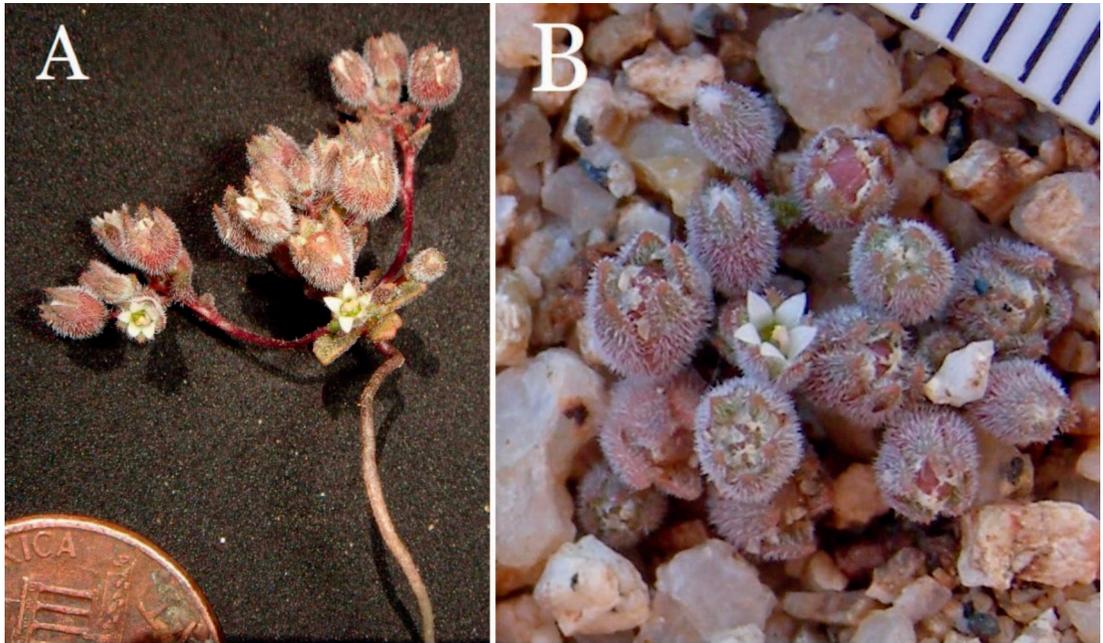


FIG. 11. *Nemacladus twisselmannii* var. *botanywomanae* (photos K. Morse).

summit of Highway 395, *Twisselmann 7063* (CAS, JEPS, SBBG); Northeast end of Buckhorn Lake, *Twisselmann 10681* (CAS, JEPS, OSU, RSA, SBBG); Dunes at the northeast end of Buckhorn Lake, *Twisselmann 10829* (with *N. rubescens*) (CAS, JEPS); Slope at the head of Tarweed Canyon, *Twisselmann 15344* (CAS); Gravel slopes at the head of Tarweed Canyon, *Twisselmann 15371* (CAS); Head of the canyon fork west of Ricardo, *Twisselmann 15431* (CAS, JEPS). **Mono Co.:** south of Benton Hot Springs along Fish Slough Road, 16.1 mi north of Mono/Inyo County line, *Andr  18403* (UCR); Benton Station, *Jones s.n.* (JEPS, POM). **San Bernardino Co.:** Mojave Desert; 33 air mi. NW of Barstow, c. 10 mi. north of Black Canyon, 3 mi. west of the SW corner of the Naval Weapons Center, *Henrickson 17366* (RSA, UCR); Victor, *Jones s.n.* (US, POM); Poison Canyon, *Mason 8281* (UC, US).

#### A New Variety of *Nemacladus twisselmannii*

Discovered in 1963 by Ernest Twisselmann, *Nemacladus twisselmannii* J.T.Howell has been known from only two localities on the Kern Plateau, totaling about 400 individuals in a 10 acre area. A new population was discovered in April 2012, in Culp Valley, Anza Borrego Desert State Park, Riverside County, a disjunction of about 350 km. The group who made the original discovery surveyed and mapped 53 plants in 2012, most in an active wash and a few in a side wash. In 2013, 23 plants were found in the original location (five in the active wash, 18 in the side wash). The type locality was considerably disturbed due to foot traffic of firefight-

ers battling the Vallecito Fire in August 2012. Similar habitats nearby were surveyed in 2012 and 2013, but no other plants were found; however, in April, 2019, about 30 plants were found in the original location. The significant geographical disjunction and presence of some notable morphological differences warrants recognition of this new population as a separate variety.

***Nemacladus twisselmannii* var. *botanywomanae*** Morin & T.J.Ayers, var. nov.—Type: USA. California. San Diego Co. Anza-Borrego Desert State Park, Pinyon Ridge above Culp Valley, across the road from the Wilson Trailhead; small flattish wash 2 3/4 mi SE of Ranchita, with deep sand made of small quartz grains. 33.1944 –116.4844, 1214 m. Habitat: Sandy Wash in Desert Transition. *Lasthenia gracilis* (DC.) Greene, *Eriophyllum wallacei*, *Erodium cicutarium* (L.) Aiton, *Gilia diegensis* (Munz) A.D.Grant & V.E.Grant, *Stephanomeria exigua* Nutt., *Salvia columbariae* Benth., *Lotus strigosus*, *Nemacladus longiflorus* var. *breviflorus*, Apr 28, 2012. *Kate Harper, Tom Chester, Keir Morse, RT Hawke, Shaun Hawke, 1712* (Holotype: SD225143!, Supplemental Figure 7).

*Nemacladus twisselmannii* var. *botanywomanae* differs from var. *twisselmannii* in having the flower non-resupinate, sepals broadly deltate, and occurrence in desert habitat (Figs. 11A, B).

**Stem** base sparsely hairy. **Leaves** often only 2 cotyledons and 2 basal leaves, which subtend the first branches, oblong-acute, 2–3.5 mm, margins entire or teeth 2, minute, surfaces hairy. **Inflorescence** bracts

ovate, 1.5–2.5 mm; pedicels 3.5 mm. **Flowers** not resupinate; hypanthium 1.6 mm, densely hairy; sepals 1.6–2.2 mm, broadly deltate, apiculate; petals connate only at base, 2 abaxial lobes divaricate, asymmetrically deltate, outer margin nearly straight, inner margin bowed, 0.5–1.5 mm, acute, 3 adaxial lobes erect, lanceolate, 0.5–1.5 mm, acute; filaments declined, connate only at apex; ovary 3/5 inferior. **Capsules** 9/10 inferior.

*Distribution and ecology.* Anza Borrego Desert State Park, in desert washes at 1200 m. Known only from the type locality (Fig. 10).

*Phenology.* Flowering June.

*Etymology.* The variety is named for Kate Harper, Senior Consulting Botanist and Wildlife Biologist, Harper Biological Consulting, who saw the plants first. She has been part of a group that has been documenting the plants of Anza Borrego Desert State Park for many years. When advised that the authors wished to name the plant for her in recognition of her discovery, she requested that the epithet be the name by which she is known in the group, which is Botany Woman.

KEY TO SPECIES OF *NEMAACLADUS*

- 1. Plants prostrate or cushionlike; rosettes 1 or more, linked by leafless, prostrate branches; inflorescences capitate (sometimes somewhat elongated)
  - 2. Herbs 1–10 cm diam.; corolla lobes 1.5–2 mm; capsules circumscissile . . . . . *Nemacladus californicus*
  - 2' Herbs 0.5–1 cm diam. or tall; corolla lobes 0.5–1.5 mm; capsules opening by valves
    - 3. Flowers resupinate, sepals narrowly lanceolate, Greenhorn Mountains . . . . . *Nemacladus twisselmannii* var. *twisselmannii*
    - 3' Flowers non-resupinate, sepals deltate, Anza Borrego Desert . . . . . *Nemacladus twisselmannii* var. *botanywomaniae*
- 1' Plants erect or spreading to decumbent; rosette 1, basal; inflorescence an open raceme
  - 4. Ovaries and capsules superior, capsules oblong-fusiform, urceolate, or oblong-ovoid, valves entire
    - 5. Corollas funnellform, pale pink or cream-colored, with wide maroon splotches . . . . . *Nemacladus richardsiae*
    - 5' Corollas salverform, white with maroon stripes and sometimes narrow to wide maroon blotches adaxially
      - 6. Corolla tube 5–8 mm; inflorescence axis often shallowly zigzag, internodes 3.5–10 mm; pedicels shallowly sigmoid . . . . . *Nemacladus longiflorus*
      - 6' Corolla tube 1.5–3 mm; inflorescence axis strongly zigzag, internodes 2–5 mm; pedicels deeply sigmoid . . . . . *Nemacladus breviflorus*
  - 4' Ovaries and capsules at least partially inferior, capsules round, ellipsoid, obconic, or cup-shaped, each valve splitting in two
    - 7. Flowers not resupinate; petals distinct nearly to base, corolla 2-lipped, lobes white or cream-colored with maroon, dark pink, or orangish or brown markings, 2 abaxial lobes declined, 3 adaxial lobes erect, filament tube declined
      - 8. Sepals unequal in size and shape, abaxial petals 0.4–1.6 mm
        - 9. Capsules round, 3–4 mm, leaves fleshy; Great Basin . . . . . *Nemacladus rigidus*
        - 9' Capsules obconic, 1.5–2.7 mm, leaves not fleshy; White and Inyo mountains or Coast Ranges, Sierra Nevada, Cascade Range, and Modoc Plateau
          - 10. Pedicels sigmoid; White and Inyo mountains . . . . . *Nemacladus morefieldii*
          - 10' Pedicels straight or arched; Coast Ranges, Sierra Nevada, Cascade Range, and Modoc Plateau . . . . . *Nemacladus capillaris*
      - 8' Sepals equal in size and shape, abaxial petals 1.3–4 mm
        - 11. Basal leaf blades broadly elliptic, remaining green through flowering; corolla lobes with brown, yellow, and orange markings at tip; base of stem silver-gray . . . . . *Nemacladus rubescens*
        - 11. Basal leaf blades oblanceolate to elliptic or ovate, generally senescing early; corolla markings maroon, base of stem brown or reddish brown
          - 12. Flowers with maroon or brownish maroon markings on tips of adaxial corolla lobes; deserts
            - 13. Capsules hemispherical, 1.5–2 mm diam.; widespread in southwestern deserts . . . . . *Nemacladus orientalis*
            - 13' Capsules spherical, 3.5–4 mm diam.; central Baja California . . . . . *Nemacladus australis*
          - 12' Flowers with maroon or deep pink markings near base of adaxial corolla lobes; Coast Ranges and Sierra Nevada
            - 14. Filaments 2 mm; capsules narrowly obconic, 2–2.5 mm; seeds 0.5 mm, with clearly pitted rows; leaf blade margins irregularly serrate; Sierra Nevada . . . . . *Nemacladus interior*
            - 14' Filaments 2–2.5 mm; capsules broadly obconic, 2.5–3 mm; seeds 0.9–1 mm, with deeply impressed, vertical lines; leaf blade margins entire or obscurely toothed; Coast Ranges . . . . . *Nemacladus montanus*

- 7' Flowers resupinate or not; corolla 1-lipped or nearly radially symmetric, petals usually connate 1/2–3/5 from base, lobes white or pale pink, pale blue, or pale lavender, midvein on lobes sometimes pink, lavender, or maroon, or (in *N. tenuis* var. *aliformis*) adaxial lobes orangish brown, otherwise without darker marks; filaments declined, curved, erect, or arched
15. Flowers not resupinate, corollas usually cup-shaped, white, pale pink or pale blue, sometimes with dark pink or lavender veins
16. Corollas bilaterally symmetric, 1-lipped, lobes all held on adaxial side of flower, bases of 2 lowest lobes fused into spur . . . . . *Nemacladus calcaratus*
- 16' Corollas nearly radially symmetric, lobes evenly distributed, not 1-lipped, not spurred
17. Inflorescence axis straight; leaf blade margins irregularly toothed or  $\pm$  pinnately lobed; bracts linear to oblong-lanceolate, erect, aligned with axis . . . . . *Nemacladus ramosissimus*
- 17' Inflorescence axis zigzag or nearly straight; leaf blade margins deeply pinnately lobed; bracts linear to lanceolate or elliptic, aligned with pedicel
18. Sepals erect; hypanthium 0.5–0.7 mm; capsules hemispheric to ellipsoid; inflorescence axis nearly straight . . . . . *Nemacladus pinnatifidus*
- 18' Sepals spreading; hypanthium 0.8–1 mm; capsules nearly round; inflorescence axis strongly zigzag. . . . . *Nemacladus glanduliferus*
- 15' Flowers resupinate, corollas cup-shaped or tubular, white or cream-colored, sometimes lavender tinted or with tinted veins, lobes sometimes with yellow spots or tips, or adaxial lobes brownish
19. Corollas tubular
20. Corolla tube urceolate . . . . . *Nemacladus sigmoideus*
- 20' Corolla tube broadly cylindrical
21. Leaf blades broadly elliptic to ovate-deltate, margins shallowly toothed or wavy; inflorescence flowers not second . . . . . *Nemacladus bellus*
- 21' Leaf blades narrowly lanceolate to +/- spatulate, margins deeply toothed; inflorescence flowers second . . . . . *Nemacladus secundiflorus*
22. Corolla 5–6 mm, anthers 0.5–0.7 mm . . . . . *Nemacladus secundiflorus* var. *secundiflorus*
- 22' Corolla 0.8–1.3 mm, anthers 0.1–0.2 mm . . . . . *Nemacladus secundiflorus* var. *robbinsii*
- 19' Corollas cup-shaped.
23. Corolla lobes 2.2–3 mm
24. Anthers white or cream-colored, 0.4–0.6 mm, filament tube red to faded magenta; capsules round or broadly ovoid; sepals in fruit erect or flared from base . . . . . *Nemacladus matsonii*
- 24' Anthers dark blue, 0.2–0.3 mm, filament tube dark blue to dark purple or reddish purple; capsules narrowly ellipsoid; sepals in fruit erect, flared from middle . . . . . *Nemacladus parikhiae*
- 23' Corolla lobes 0.5–2.2 mm
25. Leaf blades lanceolate, oblong, or spatulate, margins deeply toothed or pinnately lobed; corollas white or cream-colored, adaxial lobes brown, deltate to nearly linear, arched, or with deep pink or pinkish brown and yellow chevrons; sepals erect in fruit, extending above capsule; filament cells cylindrical, blunt
26. Corolla lobes similar, oblong-elliptic, white, tips pink or +/- yellow; capsules 1–2 mm. . . . . *Nemacladus tenuis* var. *tenuis*
- 26' Corolla lobes dissimilar, adaxial 2 linear, arched outward, maroon or brown, abaxial 3 lobes white with yellow and +/- brown markings; capsules 2–2.5 mm . . . . . *Nemacladus tenuis* var. *aliformis*
- 25' Leaf blades rhombic to elliptic, narrowly oblanceolate to oblong, or spatulate, margins entire, irregularly dentate, to +/- pinnately lobed, or sharply but shallowly toothed; corollas white, cream-colored, or pale lavender, lobes unmarked or with yellow tips or with maroon line from throat to base on abaxial lobes
27. Sepals in fruit erect to spreading from base, broadly deltate, transparent cells on filaments cylindrical, obtuse; hypanthium and capsule dark purplish green, base flat, apex acute . . . . . *Nemacladus inyoensis*
- 27' Sepals in fruit flared from base or clasping capsule, oblong-deltate or narrowly deltate, transparent cells on filaments attenuate, hypanthium green, capsule straw-colored, base acute, tip rounded
28. Inflorescence internodes 4–6 mm; corollas white or cream-colored with yellow markings, filaments maroon distally, anthers maroon, white or gray, 0.15–0.2 mm; capsules round; bracts narrowly lanceolate or lanceolate-ovate, 1–1.6 mm, straight or arched back . . . . . *Nemacladus eastwoodiae*
- 28' Inflorescence internodes 2.5–4 mm; corollas entirely white to pale lavender, midvein on lobes lavender; filaments white, anthers white, 0.2–0.3 mm; capsules broadly obconic; bracts linear-oblong, 2–4 mm, recurved . . . . . *Nemacladus gracilis*

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