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Hidden in Plain Sight: A New *Cuscuta* Species from Southwest Utah and Northwest Arizona (Section *Californicae*, Subgenus *Grammica*, Convolvulaceae)

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Abstract*—*Cuscuta nuwuviana, a new species from southwest Utah and northwest Arizona is described and illustrated. The phylogenetic analyses revealed that the new species belongs to a subclade of *C.* sect. *Californicae* (subg. *Grammica*) that also includes *C. draconella* and *C. decipiens*. Although not statistically significant, a topological incongruence between the plastid and nuclear data suggests that *C. draconella* resulted from the homoploid hybridization of *C. nuwuviana* and *C. decipiens*, accompanied by plastid introgression. Optical and scanning electron microscopy were employed to morphologically distinguish *C. nuwuviana* from *C. draconella* and *C. decipiens*, and an identification key was provided. Field investigations allowed the description of the habitat and plant community of the new species, which is currently known from only two populations in which it parasitizes solely *Gutierrezia microcephala* (Asteraceae). Evolutionary relationships, infrastaminal scales, and the presence of floral stomatiferous protuberances in *C.* sect. *Californicae* are discussed.

***Keywords*—**Dodder, host specificity, hybridization, parasitic plants, phylogeny, plastid capture.

Cuscuta section *Californicae* is the most investigated infrageneric group of *Cuscuta* L. (dodder), both from taxonomic and evolutionary points of view. Starting with *C. californica* described by Hooker and Arnott (1839), *Cuscuta* sect. *Californicae* currently includes 12 species that have diversified in western North America (Costea et al. 2015a). Engelmann (1859) and Yuncker (1921, 1932, 1965) provided the species-level taxonomic foundation, however, only in the last ca. 20 years has this clade become the focus of numerous studies: clade circumscription and phylogenetic relationships (Stefanović et al. 2007, García et al. 2014), typification of taxa (Costea et al. 2006), species-level molecular phylogenetics, morphometrics, floristics, and host range/specificity (Costea and Stefanović 2009a, 2009b, 2012; Costea et al. 2009, 2020). The latter studies led to the discovery of three new species: *C. pacifica* Costea & M.A.R.Wright, *C. draconella* Costea & Stefanović, and *C. difficilis* Stefanović & Costea, as well as brought back to the attention of the botanical and conservation communities some little-known species such as *C. jepsonii* Yunck., which was thought to be extinct. Species of this clade have been included in broad scale evolutionary studies of dodders, such as evolution of the plastid genome (Braukmann et al. 2013), plant community structure (Pennings and Callaway 1996), long-distance-dispersal via endozoochory (Costea et al. 2016), character evolution of pollen (Welsh et al. 2010), gynoecium (Wright et al. 2011), breeding systems (Wright et al. 2012), infrastaminal scales (Riviere et al. 2013), stomatiferous protuberances (Clayson et al. 2014), fruits (Ho and Costea 2018), seeds (Olszewski et al. 2020), and inflorescences (Glofcheskie et al. 2023). New chromosome counts were published for some of its species (García et al. 2019), and were also included in a genus-wide study of the karyotype and genome size evolution (Ibiapino et al. 2022).

Upon embarking on our first broad scale molecular phylogenetic research of *Cuscuta* subgenus *Grammica* (Stefanović et al 2007; Stefanović and Costea 2008), plastid (*trnLF*) and nuclear (ITS) DNA sequences obtained in 2005 from an herbarium specimen collected in the extreme NW corner of Arizona in 1980 (*Bundy 210*, ARIZ) strongly suggested that this plant belonged to a hitherto unknown species in *Cuscuta* sect. *Californicae*. However, despite extensive searches in many regional herbaria, we could not find any additional specimens to corroborate this discovery. After nearly two decades, we searched for this plant in the wild and located it in the SW corner of Utah, not far from the area of the original collection in Arizona. The objective of our current work is to present this new species using both morphological and molecular evidence, as well as to discuss its evolutionary relationships and ecology.

Materials and Methods

***Material and Outgroup Selection*—**We have studied *Cuscuta* specimens from over 100 herbaria in connection with the treatments of the genus for the second edition of the *Jepson Manual* (Costea and Stefanović 2012), *Flora of North America* Project (Costea and Nesom 2023), and a future monograph of the genus. In addition, we have conducted extensive collection trips throughout western North America. Most relevant to this study are field trips conducted in Arizona, Nevada, and Utah in the summer of 2023 and the fall of 2024, which led to the discovery of additional populations of this new species in SW Utah (Appendix 1).

Based on the results of our previous, more inclusive phylogenetic analyses of *Cuscuta* sect. *Californicae* (Stefanović et al 2007; Costea and Stefanović 2009a, 2009b; Costea et al. 2020), the first split within this section occurs between two clades, one containing species of main interest in this work (*C. draconella*, *C. decipiens*, and the new species described here) and the other clade containing the remaining ten species belonging to this section. We used ten individuals, each representing one of the species in the latter clade as a collective functional outgroup (Appendix 1).

***Morphology and Micromorphology*—**Descriptions are based on rehydrated herbarium material and observations in the field. We examined the basic morphology of rehydrated flowers under a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 6.8 software (MIS Inc., Villa Park, Ilinois). Additional photographs illustrating details of the floral and fruit morphology are available on the Digital Atlas of *Cuscuta* website (Costea 2007). Photos and measurements of pollen were taken at 10 kV using a Hitachi S-570 scanning electron microscope. Dry anthers were crushed on stubs and coated with 30 nm gold using an Emitech K 550 sputter coater.

***Molecular Methods and Alignments*—**In addition to the DNA samples used in previous studies (Stefanović et al 2007; Costea and Stefanović 2009a, 2009b; Costea et al. 2020), total genomic DNA was isolated from newly obtained specimens by the modified CTAB method (Doyle and Doyle 1987) and purified using Wizard® minicolumns (Promega, Madison, Wisconsin). Double-stranded DNA fragments for the regions of interest were obtained via PCR from total genomic DNA. The plastid genome (ptDNA) region containing the *trnL* intron, 3′ *trnL* exon, and intergenic spacer between this exon and *trnF* (i.e., the *trnLF* region) was amplified using primers designed by Taberlet et al. (1991) while the *rbcL* gene was amplified using primers published by Olmstead et al. (1992). The internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) containing ITS1, 5.8S, and ITS2 (here called ITS) was obtained using primers described by Baldwin (1992). To amplify a ca. 950 bp portion at the 5′ end of the nuclear large-subunit ribosomal DNA (26S rDNA), primers described by Kuzoff et al. (1998) were used. PCR reagents and conditions as well as amplicon purification followed the protocols detailed in Costea and Stefanović (2009b). All cleaned PCR products were sequenced, including both strands to ensure accuracy, at the McGill University and Génome Québec Innovation Centre (Canada). Sequences newly generated in this study are deposited in GenBank (accession numbers PV567642-PV567659 and PV568068-PV568087; see Appendix 1). Sequences were aligned manually using Se-Al v.2.0a11 (Rambaut 2002). Alignments of sequences used in this study were deposited in Dryad (Costea and Stefanović 2025).

Phylogenetic Analyses and Topological Incongruence Testing—Sequencher 4.8 (Gene Codes Corp., Ann Arbor, Michigan) was used to assemble and edit chromatograms of complementary strands. Albeit sequences of all accessions were readily alignable in both the plastid and nuclear matrices, a number of gaps had to be introduced in the alignments of the non-coding regions. Preliminary phylogenetic analyses were conducted to explore the distribution of phylogenetic signal in the individual matrices with and without coded gaps. Neither resolution nor support was affected in a substantial way by inclusion of gaps (results not shown), and therefore gaps in the alignments were treated as missing data in subsequent analyses.

Phylogenetic analyses were conducted using PAUP* v. 4.0b10 (Swofford 2002) under both parsimony and maximum likelihood criteria. Given the moderate number of terminal units (20 OTUs for all matrices), the parsimony searches were conducted with a Branch-and-Bound algorithm, ensuring recovery of all of the most parsimonious (MP) trees. Nucleotide characters were treated as unordered (Fitch 1971), and all changes were weighted equally.

ModelFinder (Kalyaanamoorthy et al. 2017) was used to determine the model of sequence evolution that best fit each dataset. For individual datasets, some version of the GTR model (Tavaré and Miura 1986) with rate variation among nucleotides following a discrete gamma distribution (Yang 1994) was selected. The exact models employed for each matrix, including combined plastid and combined nuclear sequences, are listed in Table 1. The full heuristic searches for maximum likelihood (ML) trees were performed using corresponding models of DNA evolution, each involving 100 replicates with stepwise random taxon addition, tree bisection-reconnection (TBR) branch swapping, and MULTREES option on.

Under both optimality criteria, the support for clades was inferred by non-parametric bootstrapping (Felsenstein 1985), using 500 heuristic bootstrap pseudoreplicates, TBR branch swapping, and MULTREES option on. Nodes receiving bootstrap (BS) values $< 75\%$, 75–90%, and $> 90\%$ were considered weakly, moderately, and strongly supported, respectively. Potential conflict between datasets was evaluated by visual inspection, looking for the presence of strongly supported but conflicting topologies from individual data partitions.

To investigate a discrepancy between topologies obtained from plastid and nuclear data sets, in particular regarding the position of *Cuscuta draconella*, we constructed constrained trees by imposing a plastome-derived topology onto nuclear-derived dataset and vice versa. To statistically test and compare these reciprocally enforced phylogenetic hypotheses with the optimal trees, two statistical tests were conducted under the maximum likelihood criterion: one-tailed Shimodaira-Hasegawa test (SH test; Shimodaira and Hasegawa 1999; Goldman et al. 2000) as well as the Approximately Unbiased test (AU test; Shimodaira 2002), using 10,000 resampling with the RELL method (Kishino et al. 1990) and full parameter optimization of the model in PAUP* v.4.0b10 (Swofford 2002).

Results

Molecular Phylogenies—Several preliminary phylogenetic analyses were conducted to explore the distribution of phylogenetic signal in the different individual matrices, with and without coded gaps. Clades recovered in each analysis were congruent with the tree structure recovered using data from the other matrices derived from the same genome, with similar levels of support. Being present on the same organellar genome, *trnLF* and *rbcL* are on the same linkage group and thus were treated as one locus (ptDNA). Similarly, nuclear ITS and 26S rDNA sequences were treated as one locus (nrDNA). We present here only the maximum likelihood results for the combined ptDNA data and the combined nrDNA data (Fig. 1). The trees from individual matrix analyses are not shown, but their results are summarized in Table 1. The relationships derived under the parsimony criterion are topologically consistent with those inferred through the ML approach (Fig. 1) and have received similar levels of support (not shown).

Overall relationships among species of *Cuscuta* sect. *Californicae* are congruent with those obtained in previous studies (Stefanović et al 2007; Costea and Stefanović 2009a, 2009b; Costea et al. 2020). All sampled individuals and populations belonging to *C. nuwuviana*, a species newly described here, form a distinct lineage based on a combination of their individual strong bootstrap support (100% and 99% from ptDNA and nucDNA, respectively) and molecular distinctiveness, as evidenced by the substantial branches subtending them (Fig. 1). These molecular results corroborate the morphological distinctiveness of the new species (see below). *Cuscuta nuwuviana* is most closely related to *C. draconella* and *C. decipiens*, and the support for the clade containing all three of them is uniformly very strong (100% BS; Fig. 1).

We observed some minor discrepancies between plastid- and nuclear-derived phylogenies regarding the placement of some species (e.g., *C. jepsonii*, *C. subinclusa*) which have received very week support ($<$ 75% on the ptDNA tree; Fig. 1A). However, we have also observed two major topological incongruences which have received stronger support

Table 1. Summary descriptions for sequences included in, and phylogenetic trees derived from, individual and combined analyses of *Cuscuta* sect. *Californicae* species. Twenty operational taxonomic units (terminals) were included in all datasets. CI = consistency index (excluding parsimony uninformative characters); nrDNA = nuclear ribosomal data combined; ptDNA = plastid data combined; RI = retention index.

	trnLF	*rbcL*	nrITS	26S rDNA	ptDNA	nrDNA
Sequence characteristics:						
Aligned length	516	1290	639	864	1806	1503
Variable sites	80	109	132	75	189	207
Parsimony informative sites	53	68	75	36	121	111
Mean AT content (%)	61	57	50	45	58	47
Maximum Parsimony tree characteristics:						
Number of trees	8	1	2	24	6	1
Length (steps)	102	130	168	147	233	256
CI/RI	0.87/0.95	0.92/0.96	0.86/0.93	0.91/0.95	0.89/0.95	0.88/0.94
Maximum Likelihood tree characteristics:						
Model of DNA evolution	TPM1uf+G	TVM+G	GTR+G	TIM3+G	GTR+G	GTR+G
log likelihood (lnL)	−1310.844	−2651.596	−1877.859	−1745.257	−3997.0665	−3668.8731

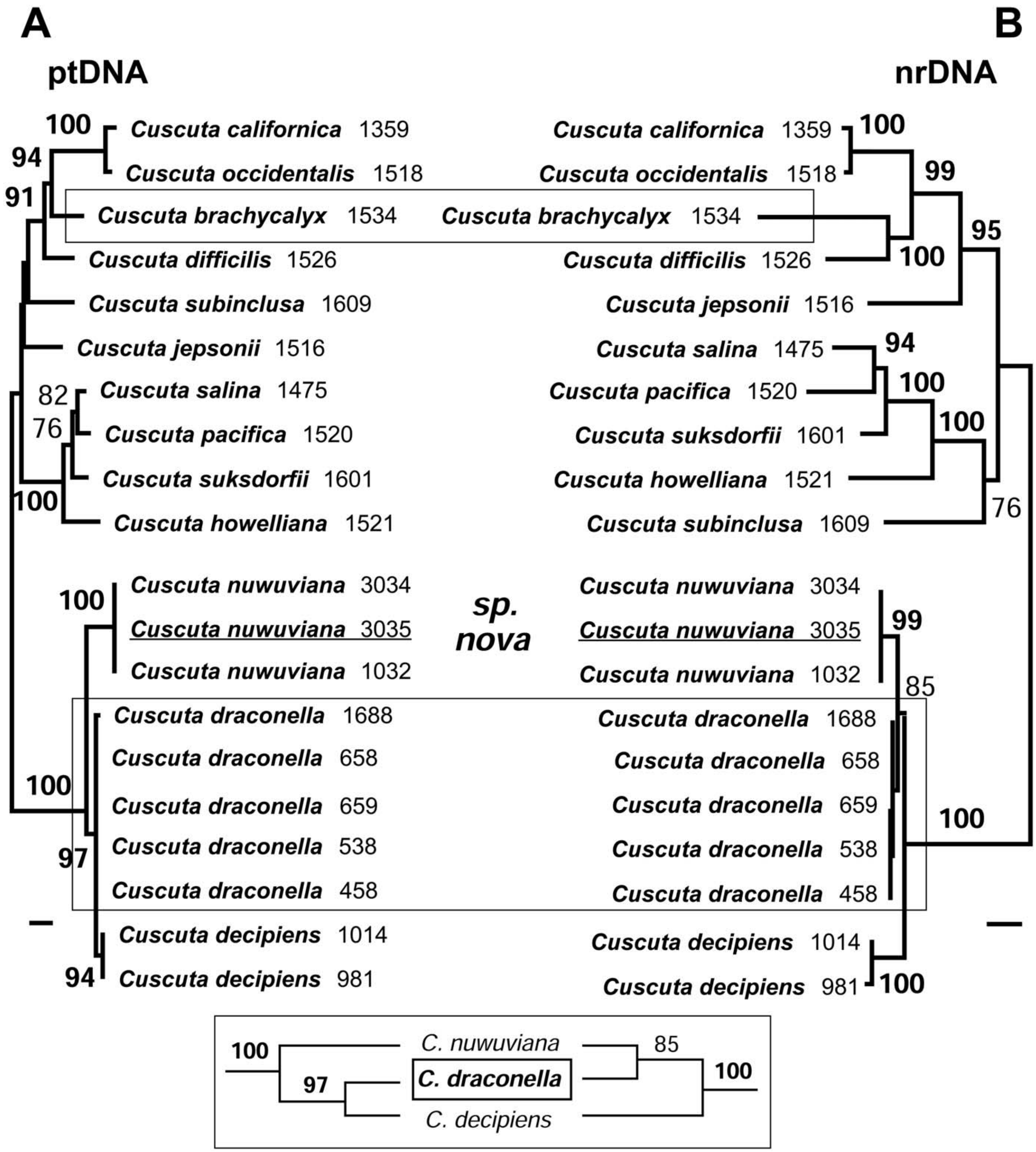

FIG. 1. Phylograms derived from maximum likelihood analyses of plastid DNA data (A. *trnLF* plus *rbcL*) and nuclear ribosomal DNA data (B. ITS plus 26S rDNA) obtained from the *Cuscuta* sect. *Californicae* species. Phylogenetic placement of the newly described species, *C. nuwuviana*, is shown (type specimen underlined). The trees are rooted using the first split within *C.* sect. *Californicae* based on previous phylogenetic results (Stefanović et al. 2007; Costea and Stefanović 2009a, 2009b) as functional outgroup. For simplicity, maximum likelihood bootstrap values are indicated only for nodes supported moderately-to-strongly (≥ 75%). Strongly supported incongruences are highlighted (boxed and inset) and discussed in the text. Numbers following species names correspond to DNA accession numbers (see Appendix 1). Bars indicate 0.005 substitutions per site; note the different scale for plastid and nuclear phylograms.

(> 90%; highlighted in Fig. 1). One of them, the differential placement of *C. brachycalyx*, was already documented previously in detail (Costea et al. 2020) and is here confirmed. The other one is novel for this study. Namely, plastid data place *C. draconella* as sister to *C. decipiens*, while nuclear data resolve *C. draconella* as sister to the newly described *C. nuwuviana* (Fig. 1). These results received moderate-to-strong bootstrap support, 97% and 85% from ptDNA and nucDNA, respectively (see inset in Fig. 1). However, the Shimodaira-Hasegawa (SH) and Approximately Unbiased (AU) tests, performed in both directions, resulted in trees that were not significantly different from the ML trees (ΔlnL = 5.018, p-SH = 0.112, p-AU = 0.059; ΔlnL = 0.913, p-SH = 0.254, p-AU = 0.214, respectively), commensurate with the support these topological alternatives have received.

Discussion

Distinctiveness of Cuscuta nuwuviana, C. decipiens, and C. draconella in C. sect. Californicae—Both morphologically and phylogenetically, these three species are distinct from the other members of *Cuscuta* sect. *Californicae*. What separates them morphologically from the remainder of *C.* section *Californicae* are the well-developed infrastaminal scales (IFSs) with numerous fimbriae, and the strongly inflexed and often cuspidate corolla lobes. As indicated by Riviere et al. (2013), *C.* sect. *Californicae* is the only infrageneric group of *Cuscuta* in which the gradual reduction of the infrastaminal scales can be traced across the entire clade, ranging from species with fully developed IFSs, such as in the flowers of these three species, to species in which the IFSs have become completely reduced (*C. californica*, *C. occidentalis*, *C. brachycalyx*, and *C. difficilis*). IFSs, called by Engelmann (1859) "the most peculiar organs of the [*Cuscuta*] flower," were suggested by (Riviere et al. 2013) to protect the ovary/ovules against herbivorous insects. They possess internal laticifers that remain exposed at the tips of fimbriae, releasing the toxic latex at the slightest physical contact.

Stomatiferous (multicellular) protuberances (SPs) have been recently documented on the corolla and/or calyx of *Cuscuta* species from multiple sections of *Cuscuta* subgenera *Grammica* and *Cuscuta* (reviewed by Clayson et al. 2014). In *C.* sect. *Californicae*, only *C. draconella* and *C. nuwuviana* possess them solely on the calyx lobes. Floral SPs become visible early on floral buds; they are diversely shaped (e.g., tubular, hemispherical, conical, crests) and have systematic significance (Costea et al. 2011a, 2011b, 2013). The water loss through the SPs forces the roots of the hosts to absorb more water by increasing the negative pressure/tension in the xylem of the host via the haustoria connection (Clayson et al. 2014). Floral SPs evolved numerous times in *Cuscuta* species growing in arid areas or areas characterised by a dry season (Clayson et al. 2014). While this is consistent with *C. draconella* (Chihuahuan Desert) and *C. nuwuviana* (southeastern periphery of the Great Basin Desert and adjacent sub-desert area), *C. decipiens* from the Chihuahuan Desert does not possess floral SPs.

Topological incongruence in Cuscuta draconella—Previous evolutionary studies of *Cuscuta* have presented evidence of reticulate evolution based on conflicting phylogenetic signals between the uniparentally (i.e., maternally; Corriveau and Coleman 1988; Reboud and Zeyl 1994; Mogensen 1996) inherited plastid sequences (such as *trnLF*, *rbcL*) and biparentally inherited nuclear ribosomal array sequences (such as nrITS, 26S rDNA). In the most studied and species-diverse *Cuscuta* subgenus, *Grammica*, with ca. 155 species, we see both relatively recent as well as more ancient reticulation events, corresponding to intra- and intersectional hybrids (Stefanović and Costea 2008; Costea and Stefanović 2010; García et al. 2014, 2018; Costea et al. 2015b). Some of these cases have been studied in great detail using not only phylogenetic approaches but also corroborated through fluorescence/genomic in situ hybridization (FISH/GISH) studies (Ibiapino et al. 2019, 2025), chromosome counts (García et al. 2019), and host/ecological differentiation (García et al. 2018). Other subgenera of *Cuscuta* also show various cases of hybridization (e.g., García and Martín 2007). In addition, recently a case of plastid introgression ("capture") was invoked to explain a case of observed tree discordance (Costea et al. 2020) for *C. brachycalyx*, a representative of which is included in our current study as well (Fig. 1, highlighted). Collectively, these studies lead to the conclusion that reticulation is an important diversification mechanism in *Cuscuta*, with potentially 10% of its species being of hybrid origin (Stefanović and Costea 2008).

It therefore comes as no surprise that an additional case of topological conflict was detected between our current datasets, the one involving *Cuscuta draconella*. This species has previously been included in *Cuscuta* sect. *Californicae* phylogenetic studies and was always found in a clade with *C. decipiens* (e.g., Costea and Stefanović 2009a, 2009b). These two species together were in the position of sister-group to the rest of species of *C.* sect. *Californicae*, without any incongruence. It was only after the inclusion of the third species in this clade, the newly described *C. nuwuviana*, that discordant positions of these three lineages became apparent: plastid data place *C. draconella* with *C. nuwuviana* (Fig. 1A), while nuclear data show *C. draconella* as sister to *C. decipiens* (Fig. 1B). These placements have received strong (97%) to moderate (85%) bootstrap support (Fig. 1; inset). Given its prevalence across *Cuscuta*, and specifically *C.* subgenus *Grammica*, hybridization presents itself as the most obvious explanation for these results. Yet, in this particular instance, caution is warranted. First, while the support for the discordance is substantial, it is not as strong as was the case in many other examples of hybridization in *Cuscuta*, such as those found in *C.* sect. *Denticulatae* (García et al. 2018) or *C.* sect. *Umbellatae* (Costea and Stefanović 2010). This is most evident from the nuclear topology which is only moderately supported (85%; Fig. 1B). Second, both the SH and the AU topological incongruence tests, conducted in a reciprocal fashion (i.e., enforcing *Cuscuta draconella* as sister to *C. decipiens* with the nrDNA matrix and as sister to *C. nuwuviana* with the ptDNA matrix), resulted in trees not significantly different from the optimal trees. Finally, the available cytological information for species across the entire *Cuscuta* sect. *Californicae* indicates that all of them are diploids, with $2n$ = 30 (García et al. 2019). Preliminary data suggest that *C. draconella* itself is also a diploid ($2n$ = 30; Amalia Ibiapino pers. comm.). This last point argues at least against the polyploid hybridization in the case of *C. draconella*, but leaves the possibility of hybrid speciation without change in ploidy level (i.e., "diploid" hybrid speciation) accompanied by "plastid capture," as was suggested for the case of *C. brachycalyx* (Costea et al. 2020) as a viable option.

We posit that, in the case of *C. draconella*, phenomena other than hybridization/introgression, be it analytical or biological, are more likely to explain the topological incongruence. From the analytical point of view, because the affected subclade includes only three species and a root (Fig. 1; see the inset), a simple topological distortion, such as nearest-neighbor interchange (NNI), would result in trees compatible between plastid and nuclear data. Such a spurious transformation, caused for example by the long-branch attraction (Felsenstein 1978), could explain observed topological differences because the internal branches and the root branch subtending the subclade are of substantially different lengths, most pronounced in the nuclear-derived phylogeny (Fig. 1B). Also, the simplicity of an NNI swap could explain why the SH and AU tests have uniformly failed to find the significance in observed likelihood differences between the optimal and constrained trees for both plastid and nuclear data sets despite moderate-to-strong support for this incongruence. However, at low (species) phylogenetic levels, potentially the strongest explanation for the observed topological discrepancies is lineage sorting (i.e., random sorting of ancestral polymorphism or "deep coalescence"; Avise 1986; Wu 1991; Doyle 1992). Because the plastid genome is both uniparentally inherited and haploid, it has a significantly smaller effective population size when compared to nuclear loci (Moore 1995). Hence, the plastid haplotype tree has a substantially higher probability of more rapid coalescence time, leading to the relatively rapid elimination of any polymorphism. The same cannot be said for the biparentally inherited nuclear ribosomal arrays, to include nrITS and 26SrDNA sequences, which show some polymorphism within *C. draconella*, and suggest lower support for its phylogenetic position as sister to *C. nuwuviana* instead of *C. decipiens*.

Key to Species of *Cuscuta nuwuviana*, *C. decipiens*, and *C. draconella*

For a key that includes the reminder species of *Cuscuta* sect. *Californicae*, see Costea et al. (2009b, 2020), as well as Costea and Nesom (2023).

1. Flowers 1.8–2.2. mm long; calyx shallowly and broadly cupulate with lobes broader than long, auriculate at the base; anthers round, 0.2–0.4 × 0.3–0.4 mm . . . . ***C. nuwuviana*, sp. nov.**
1. Flowers 2.5–4 mm long; calyx campanulate with lobes longer than wide, not auriculate at the base; anthers broadly elliptical, 0.5–0.8 × 0.4–0.5 mm 2
    2. Multicellular protuberances present on the bracts and calyx lobes; bracts 1(–2) at the base of pedicels, 2.4–3.5 mm long; calyx angled, divided 1/2–2/3 to the base, with overlapping lobes . . . . *C. draconella*
    2. Multicellular protuberances absent; bracts usually absent at the base of pedicels, if present, 0.9–1.1 mm long; calyx not angled, divided 1/2 to the base, lobes do not overlap . . . . *C. decipiens*

Taxonomic Treatment

Cuscuta nuwuviana Costea & Stefanović, sp. nov. Type: USA. Utah: Washington Co., S of Hwy 59, ca. 2.5 mi S on Gould Wash Rd., 37°06′38.5″N, 113°14′01.1″W, 2 Sep 2023, *S. Stefanović 23-48B* (holotype: NY; isotypes: MO, TRTE).

Cuscuta nuwuviana resembles *C. draconella* and *C. decipiens*, but differs from them in the smaller flowers, 1.8–2.2 mm long, with shallowly and broadly cupulate calyx having the lobes broader than long, auriculate at the base, and the smaller, round anthers, 0.2–0.4 mm long. In addition, from *C. draconella* it contrasts in the shorter bracts, 1.1–2 mm long, without multicellular protuberances and infrastaminal scales that are longer than the corolla tube; moreover, from *C. decipiens* it diverges in the presence of multicellular protuberances with stomata on the calyx lobes.

Stems filiform, yellow to pale orange. **Flowers** solitary or in fasciculate cymes of 2–3(–5) flowers; **pedicels** 0.4–2(–5) mm; **bracts** one at the base of cymes and sometimes 1(–2) on the pedicels, membranous, ovate-triangular to lanceolate, 1.1–2 × 0.5–0.8 mm, without multicellular protuberances along the midveins, margins entire, apex acute. **Flowers** 5-merous, 1.8–2.2 mm long, membranous; papillae absent on the pedicels, calyx and corolla; laticifers isolated or in longitudinal rows, ovoid to elongated, visible in the calyx and corolla lobes along the midveins and in the ovary; **calyx** 1.1–1.5 mm long, membranous, reticulate and shiny, straw-yellow when dry, shallowly and broadly cupulate, ± angled (a feature more evident in the flower bud), equaling corolla tube, divided 1/3–1/2 to the base, tube 0.6–0.7 mm long, lobes 0.6–1 mm long, broadly ovate, broader than long, each with 1 dome-like or hemispherical multicellular protuberance at their middle or in the 3/4 distal part on the midveins, 0.1–0.2 mm in diameter; apices rounded or obtuse, often apiculate, broadly overlapping at the base, at least 2 or 3 lobes auriculate; margins membranous, irregularly serrulate or denticulate; **corolla** 1.7–2.1 mm long, white when fresh, creamy-yellow when dry, the tube 0.9–1.1 mm long, globose-campanulate, lobes 0.8–1.1 mm long, triangular-ovate, equaling the corolla tube, slightly spreading at full anthesis, margins overlapping at the base, irregularly denticulate, apex ± cucullate, acute or truncate, cuspidate, inflexed; **stamens** included, shorter than the corolla lobes, anthers round, 0.2–0.4 × 0.3–0.4 mm; filaments 0.3–4 mm long; **pollen** tricolpate 17–21 × 10–14 µm, subsphaerical to prolate, rounded at the poles, tectum imperforate; exine granulate; **infrastaminal scales** 1.1–1.4 mm long, spatulate to obovate, longer than the corolla tube, well developed, fimbriae 0.2–0.3 mm long; **styles** 2, slightly unequal, cylindrical, 0.3–0.5 mm long, shorter than the ovary; stigmas small, globose; **ovary** ovoid to obovoid or globose, apically thickened and with an interrupted collar at the style bases. **Capsules** indehiscent with the dried corolla at the base (mature capsules and seeds were not examined). Figure 2.

Phenology—Flowering from late August to early October.

Ecology—Grows at elevation of 1100–1300 m in subdesert shrub plant communities dominated by *Coleogyne ramosissima* Torr., *Gutierrezia microcephala* (DC.) A.Gray and *Ericameria nauseosa* (Pall. ex Pursh) G.L.Nesom & G.I.Baird. Other companion species observed locally were: *Artemisia filifolia* Torr., *Ambrosia dumosa* (A.Gray) W.W.Payne, *Atriplex canescens* (Pursh) Nutt., *Baileya multiradiata* Harv. & A.Gray, *Dasyochloa pulchella* (Kunth) Willd. ex Rydb., *Ephedra viridis* Coville, *Eriocoma hymenoides* (Roem. & Schult.) Rydb., *Eriogonum inflatum* Torr. & Frém., *Neltuma odorata* (Torr. & Frém.) C.E.Hughes & G.P.Lewis, *Opuntia polyacantha* Haw., *Sphaeralcea parvifolia* A.Nelson, and *Stephanomeria pauciflora* (Torr.) A.Nelson. It is important to mention that *C. nuwuviana* was encountered only on *Gutierrezia microcephala*, a species that occurs from Mexico to SW Colorado and south-central Utah (US) in Chihuahuan, Sonoran, Mojave, and Great Basin deserts (Lane 1985). Geologically, the collection area consists of well-drained alluvial and eolian deposits (Biek et al. 2022).

Distribution—Apparently localized E of Hurricane, in SW Utah and neighboring territory in NW Arizona. Two targeted

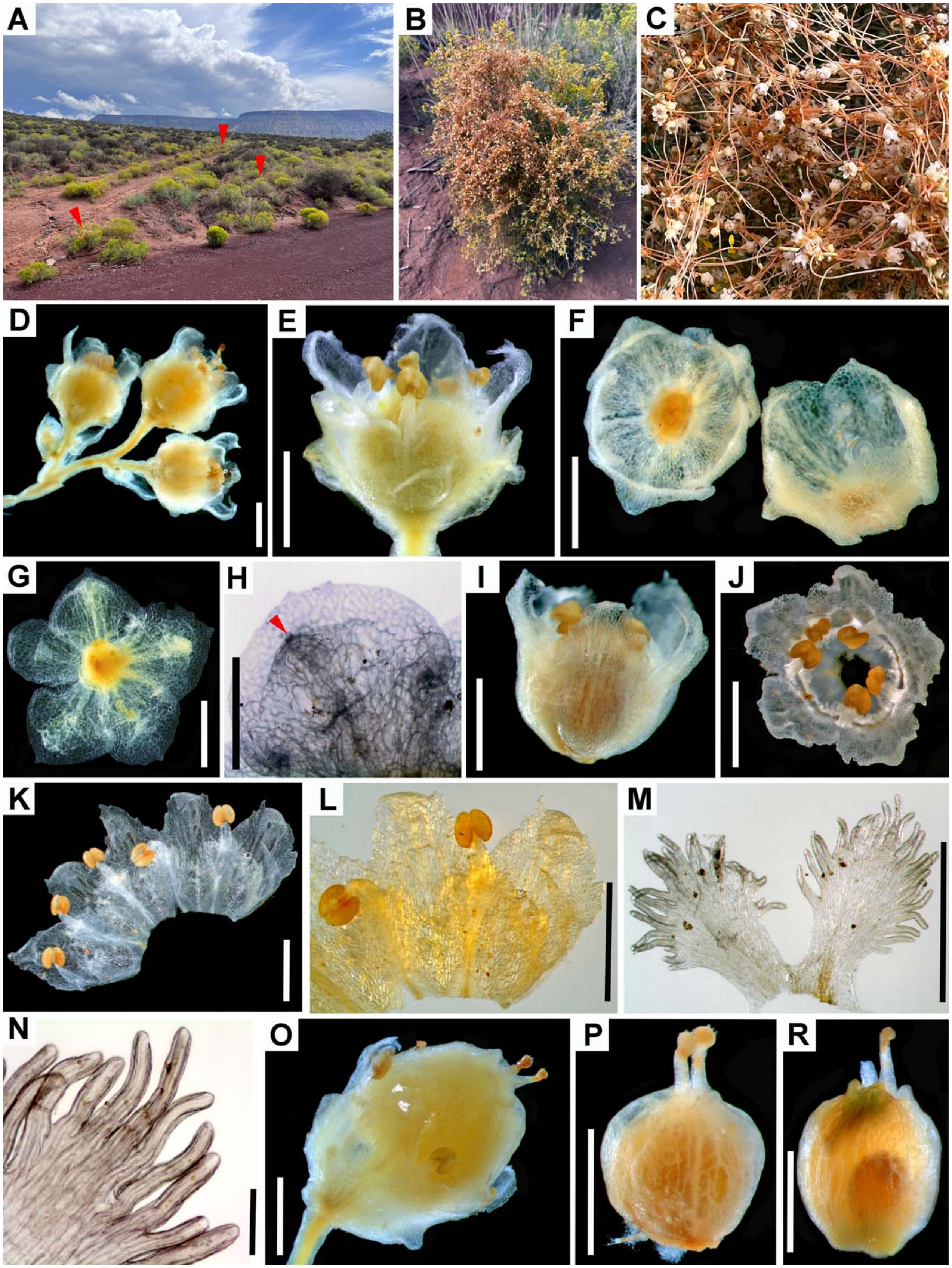

FIG. 2. Habitat and morphology of *Cuscuta nuwuviana*. A. Habitat (arrows indicate *Cuscuta* plants). B. Individual *C. nuwuviana* plant parasitizing *Gutierrezia microcephala*. C. Flowers and stems of living plant. D–R. Morphology based on the rehydrated type material. D. Inflorescence. E. Flower. F. Calyces, 3D. G. Dissected calyx, flattened. H. Calyx lobe with stomatiferous protuberance (arrow). I. Corolla, 3D, lateral view. J. Corolla, 3D, view from the top (gynoecium removed). K–L. Corolla dissected, flattened. K. Overview. L. Detail of corolla lobes and stamens. M. Infrastaminal scales removed from the corolla. N. Detail of infrastaminal scale fimbriae. O. Gynoecium with corolla at the base. P–R. Gynoecia after removal of corolla. Scale bars = 1 mm except H = 0.5 mm, N = 100 μm.

field searches in the area, in the summer of 2023 and the fall of 2024, failed to reveal additional populations in surrounding areas. However, it should be noted that the populations observed in SW Utah in 2023 were relatively abundant locally, with several dozen individuals/clusters growing on *Gutierrezia microcephala*.

Preliminary Conservation Status—Considering that the species is currently known from two locations/populations located at ca. 16 km from one another, *C. nuwuviana* is most likely Critically Endangered whether using IUCN (2025) or NatureServe (2025) conservation status ranks. It is unknown what ecological or biological factors limit its distribution considering that the host is common in N America (see above).

Etymology—The specific epithet honors the Nuwuvi People (Nuwu or Southern Paiute) whose traditional lands spanned across southern Nevada, southern Utah, as well as Northern and Western Arizona and southeastern California (Van Vlack 2015).

***Additional Specimens Examined*—USA.** —Arizona: Mohave Co., N of Antelope Spring, T41N R09W S10 (36°58′08.4″N 113°15′11.2″W), 3 Sep 1980, *Bundy 211* (ARIZ, ASU, BRY). —Utah: Washington Co., S of Hwy 59, ca. 1.5 mi on S Gould Wash Rd, 37°07′21″N 113°14′44″W, 2 Sep 2023, *Stefanović 23-48A* (TRTE, WLU).

Note—The discovery of this species from a clade that has received considerable attention and within a general geographical area that has been explored by numerous botanists, suggests that the diversity of *Cuscuta* (in general) is still incompletely known even in N America, and certainly more so worldwide.

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Author Contributions

MC wrote the first draft of the article, did fieldwork, examined the herbarium material and imaged the relevant morphological traits. SS did field work; conducted the molecular phylogenetic analyses, wrote the corresponding sections as well as edited the rest of manuscript.

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APPENDIX 1. List of herbarium specimens examined for molecular analyses of the *Cuscuta* sect. *Californicae*. Country, locality details, date, collectors, and herbaria in which the specimens are deposited are provided for all specimens. In addition, DNA extraction and GenBank accession numbers (plastid *trnLF* and *rbcL*, nuclear ITS rDNA, 26S rDNA) are given in the square brackets. Newly generated sequences are indicated in bold. Abbreviations of herbaria follow Index Herbariorum (Thiers 2017).

Cuscuta decipiens Yunck. **Mexico.** —ZACATECAS: NE of Estatión Camacho, *Henrickson 13394* (MEXU) [**981;** EF194509, PV568084, PV567647, EU883498]; Hwy 54, near Majoma, 19 Oct 2001, *Henrickson 22781* (TEX) [**1014;** EF194510, EU883450, EF194718, EU883499].

Cuscuta draconella Costea and Stefanović**. USA. —**TEXAS: Brewster Co.; Hwy 118, 47 mi S of Alpine, 29°44′10″ N, 103°33′43″ W, 15 Aug 2016, *Stefanović 16-71* (TRTE, WLU) [**1688;** PV568073, PV568083, PV567646, PV567656]; El Paso Co.; *Tharp 46072* (IND) [**458;** EF194508, PV568081, EU883482, EU883500]. —New Mexico: Catron Co.; E of Mogollon, 9 Aug 1977, *Wagner 3359* (UNM) [**538;** PV568072, PV568082, EU883483, PV567655]; Doña Ana Co.; White Sands Missile Range, San Augustin Mts., ca. 17 km NE of Las Cruces, 1.5 km N of US Hwy 70 & 2 km E of San Augustin Pass, Black Prince Arroyo, SW corner Sec. 28, 1990, *Mahrt 10497* (NMC) [**659;** EU883437, EU883452, EU883485, EU883501]; Socorro Co.; extreme SE corner of county, on White Sands Missile Range Center, on Range rt. 7, 1988, *Herman 462* (NMC) [**658;** EU883436, EU883451, EU883484, EU883500].

Cuscuta nuwuviana sp. nov. **USA. —**Arizona: Mohave Co.; N of Antelope Spring, 3 Sep 1980, *Bundy 211* (ASU) [**1032**; PV568074, PV568085, PV567648, PV567657]. —Utah: Washington Co.; S of Hwy 59, 1.5 mi on S Gould Wash Rd., 37°07′21" N, 113°14′44" W, 2 Sep 2023, *Stefanović 23-48A* (TRTE, WLU) [**3034**; PV568075, PV568086, PV567649, PV567658]; S of Hwy 59, 2.5 mi on S Gould Wash Rd., 37.110689° N, 113.233624° W, 2 Sep 2023, *Stefanović 23-48B* (NY, TRTE, WLU) [**3035**; PV568076, PV568087, PV567650, PV567659].

Functional outgroups*: *Cuscuta brachycalyx Yunck.: **USA. —**California: Monterey Co.: along Hwy 198, halfway between San Lucas and Coalinga, 36°10′18.3" N, 120°40′13.3" W, 6 Jun 2015, *Stefanović 15-21* (TRTE, WLU) [**1534**; MT070389, MT070361, MT070216, MT070182]. ***Cuscuta californica*** Hook. & Arn.: **USA. —**California: San Bernardino Co.: San Bernardino National Forest, Hwy 38, 20 Apr 2013, 34.103660° N, 117.009580° W, *Stefanović 13-04* (TRTE, WLU) [**1359**; MT070370, MT070341, MT070191, MT0701162]. ***Cuscuta difficilis*** Stefanović & Costea: **USA. —**California: Glenn Co.: Sacramento National Wildlife Refuge, 39°25′33.6" N, 122°11′16.9" W, 3 Jun 2015, *Stefanović 15-09* (TRTE, WLU) [**1526**; MT070390, MT070363, MT070218, MT0701184]. ***Cuscuta howelliana*** Rubtzoff: **USA. —**California: Sonoma Co.; Santa Rosa, Annadel State Park, False Lake meadow, 38.438726 N, 122.6365802 W, Jun 2015, *Stefanović 15-04* (TRTE, WLU) [**1521**; PV568071, PV568080, PV567645, PV567654]. ***Cuscuta jepsonii*** Yunck.: **USA. —**California: Mariposa Co.: Yosemite NP, Wawona, along Chowchilla Mt. Rd, 0.6 road mi from the junction with Hwy. 41, 9 Jul 2009, *Taylor et al. 20761b* (YOSE) [**1516**; MT070401, MT070369, MT070227, MT0701190]. ***Cuscuta occidentalis*** Millsp.: **USA. —**California: Tehama Co.: A16 Ono-Platina Rd., 6 mi NE of road #36, 40°22′59.8" N, 122°50′34.3" W, 3 Jun 2011, *Stefanović 15-11* (TRTE, WLU) [**1518**; MT070375, MT070346, MT070199, MT0701167]. ***Cuscuta salina*** Engelm.: **USA. —**Nevada: Pershing Co.; along I-80, mile post 97/96, 40° 05′28.4" N, 118° 35′47.8" W, 20 Jul 2014, *Stefanović 14-03* (TRTE, WLU) [**1475**; PV568068, PV568077, PV567642, PV567651]. ***Cuscuta subinclusa*** Durand & Hilg.: **USA. —**California: San Diego Co.: Hwy 94, Dulzura, Marron Valley Rd., 32°37′20" N, 116°46′16" W, 3 Apr 2016, *Stefanović 16-09* (TRTE, WLU) [**1609**; MT070399, MT070367, MT070225, MT0701188]. ***Cuscuta suksdorfii*** Yunck.: **USA.** —California: Siskiyou Co.: Siskiyou Mountains, 6.8 mi from Dry Lake Lookout on road to Horse Creek, 4 Jul 1934, *Wolf 5946* (WTU) [**1601**; PV568070, PV568079, PV567644, PV567653]. ***Cuscuta pacifica*** Costea & M.A.R. Wright: **USA. —**California: Marin Co.; along Hwy 1, Stinson Beach, Stinson Gulch, 37°54′22.5" N, 122°39′02.1" W, 1 Jun 2015, *Stefanović 15-03* (TRTE, WLU) [**1520**; PV568069, PV568078, PV567643, PV567652].