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Molecular Phylogeny of the *Cuscuta californica* Complex (Convolvulaceae) and a New Species from New Mexico and Trans-Pecos

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Abstract*—**Multiple DNA sequences from plastid (*trnL–F* region and *rbcL*) as well as nuclear (ITS and 26S rDNA) genomes were used to infer the phylogeny of the *Cuscuta californica* complex. This group is currently circumscribed to include nine species distributed mostly in western North America. Four well-supported lineages have been revealed within this complex. The first lineage includes the controversial *C. californica* s. l., an assemblage of taxa characterized by their lack of infrastaminal scales; the second lineage consists of a single species, *C. subinclusa*, with short fimbriate scales. The third lineage groups *C. howelliana*, *C. salina*, and *C. suksdorfii*, with scales that exhibit a reduction trend, while the forth includes *C. decipiens* and a new species from New Mexico and trans-Pecos Texas, ***C. draconella, both with well-developed infrastaminal scales. Stereo, compound, and scanning electron microscopy were used to investigate the new species and compare it with *C. decipiens*, its closest relative, as well as to update the taxonomic treatment of *C. californica* s. l. *Cuscuta decipiens*, in its original delimitation, is polyphyletic and was thus recircumscribed. In contrast to previous taxonomic treatments of *C. californica* s. l., phylogenetic relationships in conjunction with morphological data support the delimitation of three species: *C. brachycalyx*, *C. californica*, and *C. occidentalis*.

***Keywords*—**Conservation, ITS, new species, parasitic plants, *rbcL*, SEM, Taxonomy, *trnL–F*, 26S rDNA.

A recent taxonomic treatment of the *Cuscuta salina-californica* complex from the area covered by the *Flora of North America* (Costea et al. 2006a) expanded subsect. *Californicae* to include subsect. *Subinclusae*, both circumscribed by Yuncker (1932). This taxonomic fusion, based initially on morphological characters, was subsequently validated by molecular phylogenetic studies of *Cuscuta* subg. *Grammica* (Stefanović et al. 2007; Stefanović and Costea 2008). Based on noncoding sequences (*trnL–F* and ITS), these studies indicated the presence of 15 well-supported major clades. A major infrageneric group that includes the species of the *Cuscuta salina-californica* complex (Costea et al. 2006a), informally labeled as "clade A" by Stefanović et al. (2007), will be examined in more detail and referred to here as the *C. californica* complex. Members of this group are distributed in western North America, from British Columbia to Baja California, mostly west of the Rocky Mountains, but with a couple of species reaching the southwestern U. S. A. (Nevada, Arizona, New Mexico, and Texas) and the adjacent Mexican states. One additional species, *C. decipiens*, traditionally placed in subsection *Racemosae* (Yuncker 1932, 1965), formed a sister lineage to all the remaining members of clade A (Stefanović et al. 2007).

Cuscuta californica s. l. comprises taxa characterized by a complete reduction of the infrastaminal scales. Historically, these taxa were placed by Yuncker (1932) in subsection *Californicae*, but the delimitation of species in this group has proven to be especially problematic, as illustrated by the multitude of taxonomic treatments available. Yuncker (1932) recognized three species: *C. brachycalyx, C. californica*, and *C. occidentalis*. Beliz (1993) accepted only one species, a broadly defined *C. californica*, in which she also included *C. suksdorfii*. Finally, Costea et al. (2006a) proposed two species based on morphology, *C. californica* (including *C. brachycalyx*) and *C. occidentalis*. In view of these disagreements, we have studied numerous additional collections in an attempt to reach a solution based on the phylogeny of the subgroup and the complex as a whole. In the process, a better resolution on the relationships of *C. californica* s. l. was achieved, and one new species from New Mexico and Texas, *C. draconella*, was discovered. The aims of this study are to: 1) recover the phylogeny of the entire clade based on plastid *trnL–F* and *rbcL*, and nuclear ITS and 26S rDNA sequences, 2) update the taxonomy of *C. californica* s. l., and 3) describe and place the new species in the *C. californica* complex phylogeny.

Material and Methods

***Taxon Sampling and Outgroup Selection*—**We have studied specimens from over 100 herbaria in connection with the upcoming treatments of *Cuscuta* for the second edition of *The Jepson Manual* and *Flora of North America* projects. Collections were identified to species and the morphology examined using light microscopy. Because the micromorphology of the complex had already been examined in detail and reported in a previous study (Costea et al. 2006a), only the problematic taxa (*C. californica* and *C. brachycalyx*), the new species, *C. draconella*, as well as its closest relative *C. decipiens*, were investigated using scanning electron microscopy (SEM). Sampling for SEM included a total of 19 specimens, for which voucher information is provided in the taxonomic treatment under "representative specimens examined". In addition, the SEM photographs of pollen from the "*C. californica* s. l." collections cited in Costea et al. (2006a) were reexamined in the light of the current results. A set of 41 specimens, representing nine ingroup species, was used for the molecular phylogenetic analyses (Appendix 1). Taking into account the difficulties in defining many of these species morphologically, efforts were made to sample multiple accessions, particularly for those species spanning large biogeographical ranges and/or those with variable morphology. As a result, all ingroup species are represented by two to seven individuals in the molecular analyses. Based on our previous, more inclusive, phylogenetic analyses of *Cuscuta* subg. *Grammica* (Stefanović et al. 2007; Stefanović and Costea 2008), we selected four species, *C. campestris, C. glabrior, C. gronovii*, and *C. suaveolens*, to serve as successively more distant outgroups (Appendix 1).

***Morphology and Micromorphology*—**Descriptions are based on herbarium material. We examined the basic morphology of rehydrated flowers and capsules under a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 6.8 software (MIS Inc., Villa Park, Ilinois). Flowers of *C. draconella* were treated with an aqueous solution of neutral red 0.1% (Vogel 1990) for 20 min, and multicellular protuberances were examined with a Nikon Eclipse 50i compound microscope. Hundreds of photographs that illustrate details of the floral and fruit morphology for all the species are available on the *Digital Atlas of Cuscuta* (Costea 2007-onwards).

Micromorphological measurements and pictures were taken at 10 kV using a Hitachi S-570 scanning electron microscope. Herbarium samples were coated with 30 nm gold using an Emitech K 550 sputter coater. The terminology regarding the micromorphology of flowers, seeds capsules, and pollen follows Costea et al. (2006b). The conservation status was assessed using NatureServe (2008) ranks and criteria.

***Molecular Methods*—**In addition to the DNA samples used in previous studies (Stefanović et al. 2007; Stefanović and Costea 2008), 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 *trnL–F* 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 cloning, amplicon purification, and sequencing procedures followed the protocols detailed in Stefanović et al. (2007). Sequences generated in this study are deposited in GenBank (accession numbers EU883435-EU883530, see Appendix 1).

Phylogenetic Analyses—Sequence alignments for all four regions were performed manually using the program Se-Al version 2.0a11 (Rambaut 2002). For the three nonprotein coding regions (i.e. all except *rbcL*), a number of gaps had to be introduced in the alignment. The gaps were scored automatically using SeqState version 1.32 (Müller 2005), coded as simple indels (Simmons and Ochoterena 2000), and appended to the sequence matrix as binary characters. Phylogenetic analyses were conducted under parsimony and Bayesian optimality criteria.

Parsimony searches, along with accompanying clade support estimations, were conducted for each matrix separately as well as the ptDNA, nrDNA, and combined dataset. Under this criterion, nucleotide characters were treated as unordered and all changes, including gap characters, were equally weighted. The heuristic searches for most parsimonious (MP) trees were performed with PAUP* version 4.0b10 (Swofford 2002), each involving 1,000 replicates with stepwise random taxon addition, tree bisection-reconnection (TBR) branch swapping, and MULTREES option on. Relative support for clades was inferred by nonparametric bootstrapping (Felsenstein 1985) as implemented in PAUP* using 500 heuristic bootstrap replicates, each with 20 random addition cycles, TBR branch swapping, and MULTREES option off (DeBry and Olmstead 2000). Nodes receiving bootstrap (BS) values < 70%, 70–85, and > 85% were considered weakly, moderately, and strongly supported, respectively. Conflict between datasets was evaluated by visual inspection, looking for the presence of strongly supported yet conflicting topologies from individual data partitions.

Bayesian phylogenetic inferences were performed using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003) on the ptDNA, nrDNA, and combined datasets. Modeltest ver. 3.7 (Posada and Crandall 1998) was used to determine the model of sequence evolution that best fit the data by the hierarchical likelihood ratio test (hLRT), starting with the parsimony-derived tree rather than the neighbor-joining default. The transition model (TIM) of DNA substitution, with variable base frequencies, variable transition rates, yet equal transversion rates, and with rate variation among nucleotides following a discrete gamma distribution (TIM + G), was selected as the best-fit for the data sets. Each Bayesian analysis consisted of two runs of one million generations from a random starting tree using the default priors and four Markov chains sampled every 100 generations. Convergence of the chains was determined by examining the plot of all parameter values and the –lnL against generation using Tracer version 1.3 (Rambaut and Drummond 2004). Stationarity was assumed when all parameter values and the –lnL had stabilized. Burn-in trees were discarded and the remaining trees and their associated parameters were saved. Because no significant differences between two runs were detected (for each of three separate Bayesian analyses), the reported topologies and posterior probabilities (PP) are based on trees from pooled runs. Only the nodes receiving ≥ 0.95 PP were considered statistically significantly supported (Rannala and Yang 1996).

Results

General Morphology and Micromorphology—The micromorphology of *C. decipiens* and *C. draconella* was examined for the first time. Floral morphology is diverse within the *C. californica* complex, which explains why Yuncker (1932) classified the species recognized here in three subsections: *Californicae*, *Subinclusae,* and *Racemosae*. Inflexed corolla lobes, present only in *C. decipiens* and *C. draconella* (Fig. 1H), are reminiscent of the *C. pentagona* complex, which is the closest infrageneric group ("clade B" in Stefanović et al. 2007). The obtuse calyx lobes of *C. decipiens* and some *C. draconella* populations, also seem to reflect the phylogenetic affinities with the *C. pentagona* complex.

Infrastaminal scales in this complex are more variable than in any other clade of *Cuscuta* subg. *Grammica*: from well developed in *C. draconella* and *C. decipiens*, reduced to fimbriate ridges in *C. salina* var. *major*, bifid in *C. suksdorfii*, or completely reduced in the subgroup of *C. californica*. Pollen is uniform, as in the *C. pentagona* complex. The tectum is predominantly imperforate or sometimes perforate. The additional collections of *C. californica* and *C. brachycalyx* studied failed to reveal any micromorphological differences. The pollen, calyx, corolla, ovary, capsule, and seed surface are similar in these two species, and in *C. occidentalis*. However, this did not come as a surprise because the entire infrageneric group, as well as other North American clades of *Cuscuta* subg. *Grammica*, exhibit relatively little micromorphological variation at the species level (Costea et al. 2006a,b,c; Costea et al. 2008).

Cuscuta draconella is the only member of the *C. californica* complex that has multicellular protuberances on the calyx lobes (Fig. 1 B–G). These formations develop early on bracts and calyx lobes of floral buds, and they are fully formed when the reproductive structures are not yet mature. They are fleshy, conical, or dome-like structures that bear apparently normal stomata at their apex (Fig. 1F). Neutral red produced no staining, therefore, they likely do not have a secretory function. These developmental/histochemical data suggest that these formations are not directly associated with the reproductive biology of the plant, but rather that they have a different role. The presence of raised stomata on specialized structures on the calyces of a desert parasitic plant is remarkable, and their physiological function and adaptive significance deserve further attention.

Sequences and Alignments—Characteristics of sequence alignments obtained from the four regions targeted in our study (individually and in different combinations) are summarized in Table 1. No size variation was found in the sequenced portion of the *rbcL* open reading frame and alignment posed no problem. Although the remaining three noncoding regions exhibited length variation, the alignments were also straightforward and the assessment of primary homology was unambiguous throughout the entire length of these matrices. This is in contrast to the higher-level phylogenetic study of *Cuscuta* subg. *Grammica* (Stefanovic´ et al. 2007; Stefanovic´ and Costea 2008) in which large portions of the *trnL–F* could not be aligned across major clades, and these consequently had to be excluded from the analyses. Despite repeated attempts (including efforts to amplify the fragments in two parts), sequence data could not be obtained for some of the regions from several individuals, presumably due to the poor quality or limited quantity of the DNA extracted from some older herbarium specimens. Missing data accounts for 5.7%, 6.3%, 14.7%, and 8% of *trnL–F*, ITS, *rbcL*, and 26S rDNA matrix cells, respectively. Missing sequences are indicated by asterisks in Appendix 1. Alignments in the Nexus format were deposited in TreeBASE (study number S2126).

Tree Topologies—Several preliminary phylogenetic analyses were conducted to explore the distribution of phylogenetic signal in the different individual matrices, with and without coded gaps. Statistics of MP trees derived from these separate analyses are summarized in Table 1. Clades recovered in each analysis were congruent with the tree structure recov-

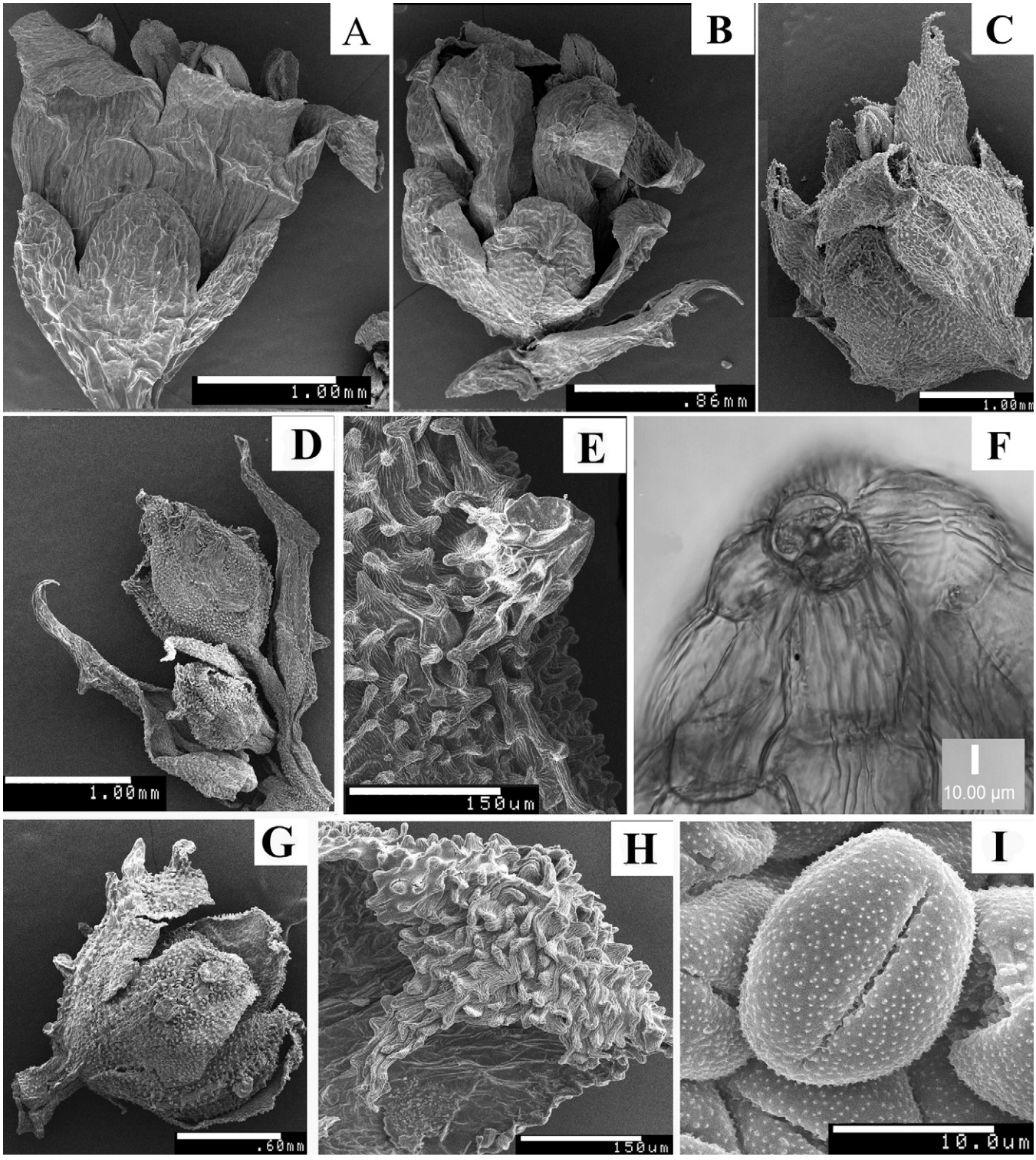

Fig. 1. Morphological features of *Cuscuta decipiens* and *C. draconella*. A. *Cuscuta decipiens* flower (*Henrickson 13394*, MEXU). B–I, *C. draconella*: B. Flower of nonpapillate form (*Tharp 46072*, GH). C. Flower of papillate form. D. Bracts with multicellular protuberances and developing cyme. E. Multicellular protuberance (SEM). F. Stomata at the top of a multicellular projection (light microscopy). G. Calyx. H. Inflexed, cucullate corolla lobe apex (*Spellenberg and Mahrt 10497*, NMC). I. Pollen (*Tharp 46072*, GH).

ered using data from the other matrices. Being present on the same organellar genome, *trnL–F* 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 phylogenetic results for the combined ptDNA data and the combined nrDNA data (Fig. 2); the trees from individual matrix analyses are not shown. Bayesian analyses of both the ptDNA and nrDNA data achieved apparent stationarity at no later than 100,000 generations. The relationships inferred through the Bayesian approach are topologically congruent with those derived under the parsimony criterion (Fig. 2).

The products of gene sequence analyses are gene phylogenies, which infer relationships between genes or genomes.

TABLE 1. Summary descriptions for sequences included in, and maximum parsimony trees derived from, individual and combined analyses of *Cuscuta californica* complex and its close outgroups selected from *Cuscuta* subg. *Grammica*. [1]Including coded gaps; [2]Including only OTUs for which all sequences are available. CI = consistency index (excluding parsimony uninformative characters); df = degrees of freedom; nrDNA = nuclear ribosomal data combined; OTU = operational taxonomic unit; ptDNA = plastid data combined; RI = retention index

	trnL–F	*rbcL*	ITS	26S rDNA	ptDNA	nrDNA	Combined
Number of OTUs included	43	40	43	42	44	45	45
Sequence characteristics:							
Aligned length	513	1340	626	858	1853	1484	3337
Number of gaps coded as binary characters	38	0	20	4	38	24	62
Variable sites[1]	143	211	228	112	354	340	694
Parsimony informative sites[1]	109	132	160	83	241	244	485
Mean AT content (%)	62	57	49	45	58[2]	47[2]	53[2]
Base frequency homogeneity (χ^2/df/*P*)	22.8/126/1.0	11.3/117/1.0	13.0/126/1.0	3.8/123/1.0	14.0/114/1.0[2]	8.5/117/1.0[2]	12.0/108/1.0[2]
Tree characteristics:							
Number of trees	90	8537	462	24	>100000	9057	2318
Length	183	279	325	147	466	474	945
CI/RI	0.83/0.96	0.81/0.95	0.77/0.94	0.80/0.94	0.81/0.95	0.77/0.94	0.79/0.94

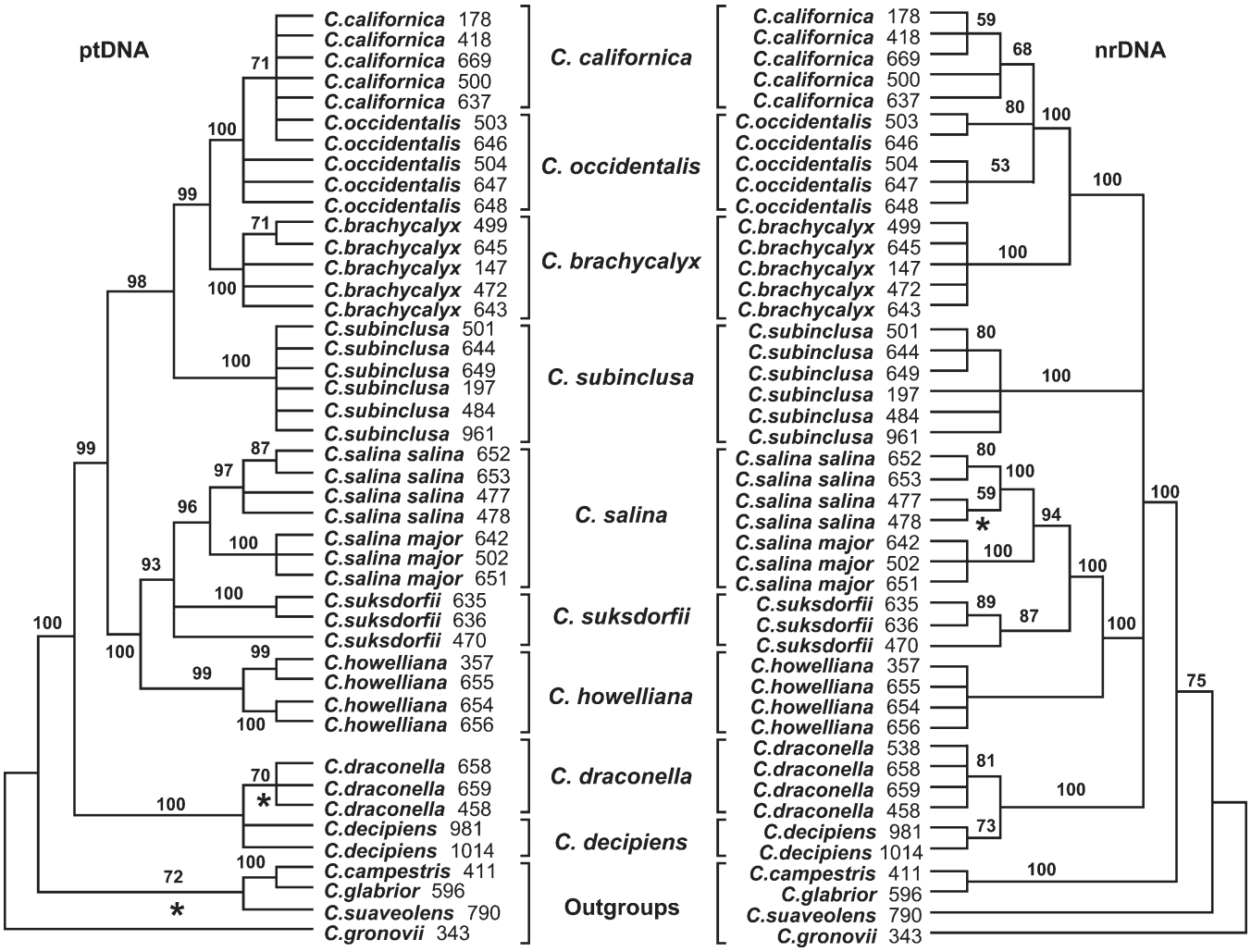

FIG. 2. Strict consensus trees derived from maximum parsimony analyses of plastid DNA data (ptDNA; *trnL–F* plus *rbcL*) and nuclear ribosomal DNA data (nrDNA; ITS plus 26S rDNA) from the *Cuscuta californica* complex. The lineages corresponding to nine species currently circumscribed within this group are specified. The trees are rooted using closely related species from *Cuscuta* subg. *Grammica* as outgroups. Bootstrap values are indicated for nodes supported at ≥ 50%. Asterisk indicates branches with Bayesian posterior probabilities < 0.95; all other branches have posterior probability ≥ 0.95. Numbers following species names correspond to DNA isolates (see Appendix 1).

These gene trees do not necessarily have to agree with the true evolutionary pathways of the taxa under investigation due to natural phenomena such as introgression, gene duplication, and lineage sorting (Doyle 1992; Sang and Zhong 2000). Instances of reticulate evolution in plants can be detected through careful analyses of discordance among different unlinked gene trees (Rieseberg and Soltis 1991; Rieseberg 1995; Sang and Zhong 2000). Five such cases were described recently within several major lineages of *Cuscuta* subg. *Grammica*, and were interpreted as results of five independent hybridization events (Stefanović and Costea 2008). However, the trees resulting from separate analyses of the ptDNA and nrDNA datasets in this study are completely congruent (Fig. 2), showing no indication of hybridization/introgression occurring (given the present taxonomic sampling and molecular markers analyzed). Because there was no conflict between the histories reflected by the two genomes, we conducted a combined analysis (total-evidence approach) that also benefits from the greater resolution that the larger dataset can provide.

The parsimony analysis using the total-evidence approach resulted in 2,318 MP trees, each 945 steps in length (Table 1). The strict consensus of these equally parsimonious trees is presented in Fig. 3A. Both runs of the Bayesian analysis on this same data set (with gaps excluded), each initiated from a random starting tree, converged on similar –lnL scores and reached an asymptotic plateau at no later than 100,000 generations. The majority-rule consensus tree calculated from the posterior distribution (excluding burn-in trees) with mean branch lengths is shown in Fig. 3B. This tree is entirely congruent with the one resulting from the parsimony analysis.

All of the analyses conducted here show the *C. californica* complex to be a strongly supported monophyletic group (100% BS; 1.00 PP). Within this complex, four major lineages can be delimited based on a combination of their individual strong support (100% BS; 1.00 PP) and molecular distinctiveness, as evidenced by the long branches subtending them (Fig. 3B). The first lineage comprises three morphologically very similar species, *C. brachycalyx*, *C. californica*, and *C. occidentalis*. The results reveal that reciprocal monophyly between two of these

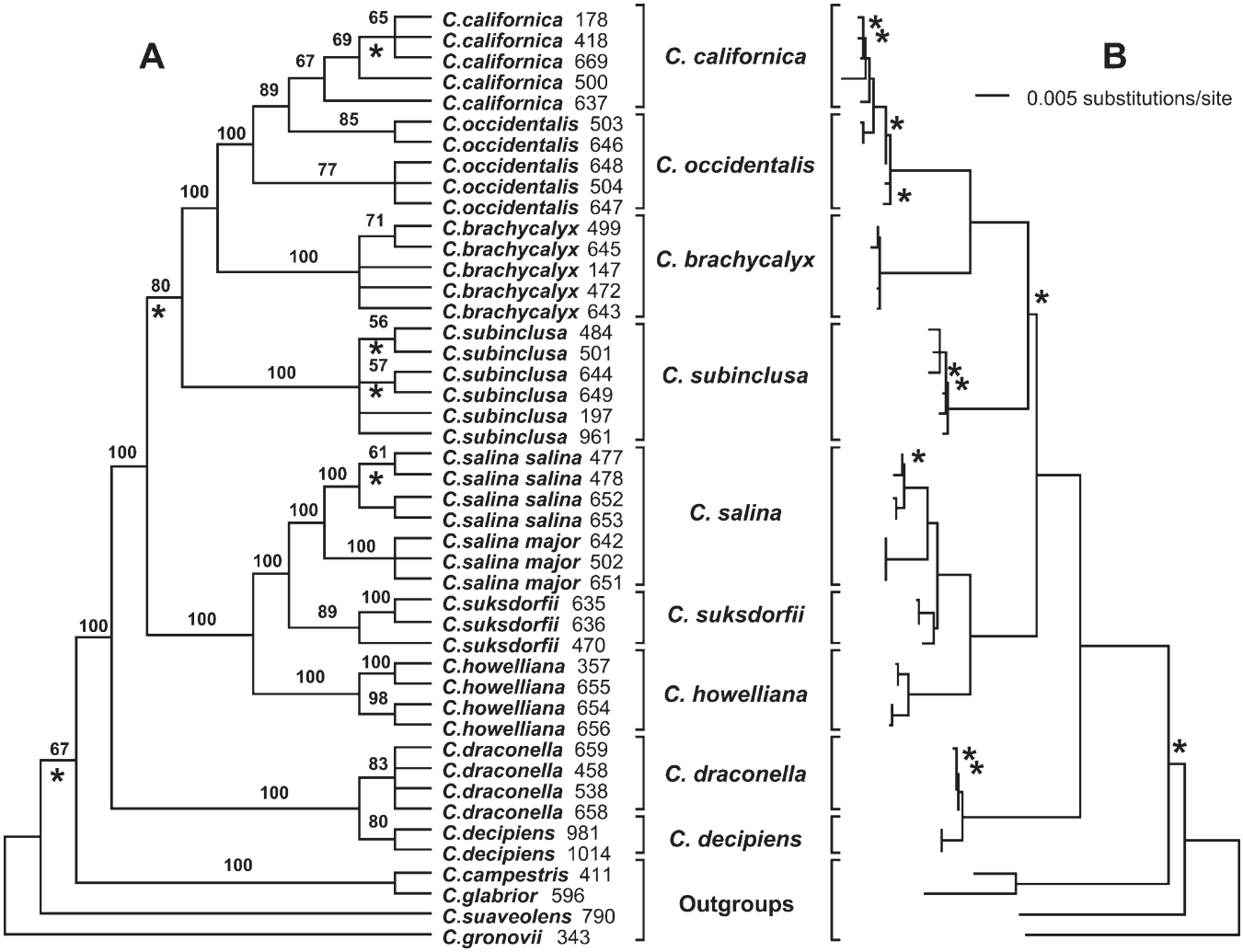

FIG. 3. Phylogenetic relationships among species of the *Cuscuta californica* complex recovered from the combined ptDNA and nrDNA data analyses. The lineages corresponding to nine species currently circumscribed within this complex are specified. The trees are rooted using closely related species from *Cuscuta* subg. *Grammica* as outgroups. Asterisk indicates branches with Bayesian posterior probability < 0.95; all other branches have posterior probabilities ≥ 0.95. A. The strict consensus of 2,318 equally parsimonious trees (L = 945; CI = 0.79; RI = 0.94) including both the sequence data and gaps coded as binary characters. Bootstrap values are indicated for nodes supported at ≥ 50%. Numbers following species names correspond to DNA isolates (see Appendix 1). B. Majority-rule consensus tree (excluding burn-in trees) from the Bayesian analysis of combined sequence data under the TIM + G model of DNA evolution. Branch lengths are proportional to the mean number of substitutions per site. Terminal taxon names have been removed for simplicity.

speciesshasnotyetbeenachieved,withmonophyletic*C.californica* nested within representatives of *C. occidentalis*. Morphologically closely allied yet quite distinct using molecular data, *C. brachycalyx* is found to be sister to the *C. californica* plus *C. occidentalis* clade. The second lineage consists of a single species, *C. subinclusa*. Plastid-derived data place this species in a sister-group position to the previous lineage with high support (Fig. 2; 98% BS; ≥ 0.95 PP). This position is also recovered in total-evidence analyses but only with moderate support (Fig. 3; 80% BS; < 0.95 PP). The third lineage includes three species, *C. howelliana*, *C. salina*, and *C. suksdorfii*, all three of which are strongly supported as monophyletic. The typical variety and var. *major* of *C. salina* (variety *papillata* was not sampled; Yuncker 1965) are monophyletic and sister to one another, which is consistent with recognizing them as two distinct species. Finally, the remaining two species form the fourth major lineage within the *C. californica* complex. One of those, *C. draconella* from New Mexico and western Texas (U. S. A.), is described here and the other one is closely related *C. decipiens*, a species from Mexico. These two species together are strongly supported as the sister group to the rest of the complex (Fig. 3).

Discussion

Disentangling Cuscuta californica, C. brachycalyx, and C. occidentalis—The results of our phylogenetic analyses are consistent with taxonomically recognizing one, two, or three species within *C. californica* s. l. The one-species option which recognizes *C. californica* (the earliest binomial), as including *C. occidentalis* and *C. brachycalyx*, may provide an easier identification escape, but it does not reflect the variation patterns, and it is inconsistent with the treatment of other species from across different *Cuscuta* subg. *Grammica* clades. Defining two sister species, *C. californica* (including *C. occidentalis*) and *C. brachycalyx*, is not practical because morphologically *C. occidentalis* is usually easier to distinguish from *C. californica* than from *C. brachycalyx*. The most significant morphologic feature that separates *C. brachycalyx* from both *C. californica* and *C. occidentalis* is a calyx 1/2–1/4 as long as the corolla tube. Costea et al. (2006a) considered *C. brachycalyx* conspecific with *C. californica* because in addition to the other similarities, the flowers of some specimens exhibited considerable variation in the calyx/corolla tube ratio, from flowers with a calyx about equaling the corolla tube, to flowers with a calyx shorter than 1/2 the length of the corolla tube. Based on the molecular evidence (Figs. 2–3) we now know that such collections pertain to *C. brachycalyx*. While in all three species the calyx is almost fully developed at the beginning of anthesis, the corolla continues to grow even after fertilization in *C. brachycalyx* (Costea et al. 2006a, Fig. 1a–c). This differential developmental pattern alters the calyx/corolla tube ratios to such an extent that at the beginning of anthesis, the flowers of *C. brachycalyx* are similar to those of *C. californica* (Costea et al. 2006a, Fig. 1a). However, if flowers are examined when the corolla lobes are fully spread or when they become reflexed, the calyx/corolla tube ratio, the corolla tube/lobe ratio, and the overall flower size and shape are consistent and provide reliable discriminators. In short, accepting the three species formula proposed originally by Yuncker (1932) is not only feasible, but in our view it also represents the best taxonomic solution. The plants with shorter staminal filaments recognized as variety *apodanthera* of either *C. californica* (Yuncker 1921; Costea et al. 2006a) or *C. brachycalyx* (Yuncker 1932) are within the range of variation of the latter and cannot be separated. Updated descriptions of *C. californica* and *C. brachycalyx* are provided in the taxonomic treatment; for *C. occidentalis* and the other members of the *C. californica* complex, see Costea et al. (2006a).

Delimitation of C. decipiens and C. draconella—*Cuscuta decipiens* as circumscribed by Yuncker (1921, 1932, 1965) is polyphyletic because the author included under this binomial two distantly related taxa: one with white flowers from Zacatecas (Mexico) that corresponds to the holotype, and one with reddish flowers from Coahuila and Zacatecas [*Purpus 4873* (US!, GH!) and *Kirkwood 50* (MO!), Yuncker 1921, 1932]. Based on both ptDNA and nrDNA the "reddish-flowered" form should not be included in *C. decipiens*. Instead, this plant belongs to "clade B" (see Stefanović et al. 2007) where it shares close relationships with *C. runyonii* and *C. glabrior* (Costea and Stefanović, unpubl. data). The identity of this unknown taxon from Coahuila and Zacatecas, Mexico will be dealt with elsewhere.

We found *C. decipiens* only in Zacatecas. The collections known as "*C. decipiens*" from Texas belong to the newly described *C. draconella*, and thus *C. decipiens* does not occur in the U.S.A. Morphologically, *C. draconella* is the most divergent member of the *C. californica* complex because of the presence of fleshy multicellular protuberances on the bracts and calyx. *Cuscuta draconella* additionally differs from *C. decipiens* as indicated in the identification key and the taxonomic treatment. Despite its apparent genetic homogeneity (Fig. 3B), this new species is morphologically variable. The collections from New Mexico (Figs. 4D–F fig4 have densely papillate bracts, peduncles and flowers, the calyx lobes are membranous, more acute, and each provided with more numerous (1–3) multicellular protuberances, while corolla lobes are evidently

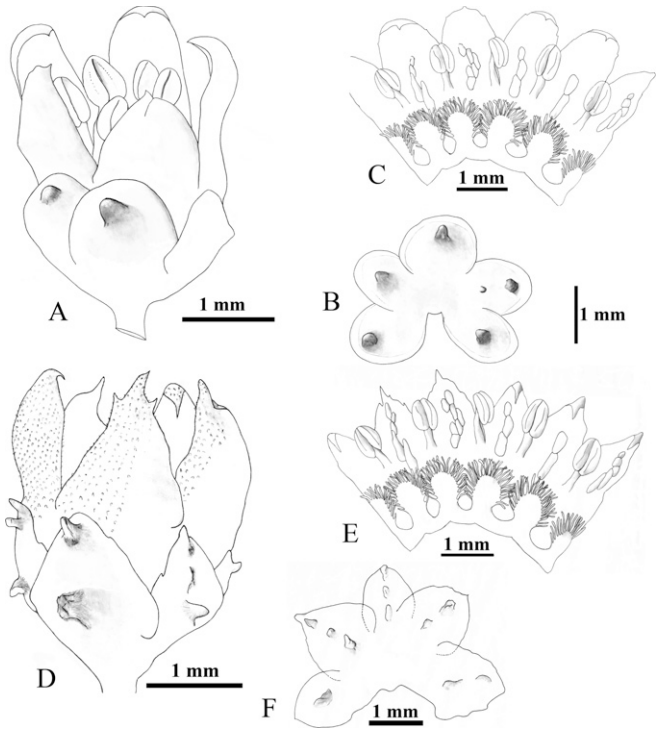

Fig. 4. *Cuscuta draconella* Costea and Stefanović, sp. nov. A–C, Non papillate form (*Tharp 46072*, GH): A. flower. B. Dissected calyx, dorsal side. C. Dissected corolla (opened, ventral side). D–F: Papillate form (*Spellenberg and Mahrt 10497*, NMC): D. Flower. E. Dissected corolla (opened, ventral side). F. Dissected calyx, dorsal side.

1(–3)-cuspidate (Figs. 1, 4). The plants from Trans-Pecos, Texas lack papillae and resemble *C. decipiens*. Their flowers have rounded, more fleshy calyx lobes, each with 1(–2) multicellular protuberances, and the corolla lobes are truncate, short cuspidate or mucronate (Figs. 1, 4). Similar papillate forms in the *C. californica* complex (e.g., *C. californica*) have been distinguished from non-papillate ones at a varietal level even in the absence of molecular support. Such a separation is potentially feasible in *C. draconella* as well, but because the species is known only from six collections (two non-papillate and four papillate plants), we postpone it until more material can be studied.

Taxonomic Treatment

Key to Species of *Cuscuta californica* Complex

1. Infrastaminal scales present, fimbriate 2
   2. Corolla lobe apices inflexed 3
      3. 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*, sp. nov.
      3. 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*
   2. Corolla lobes apices not inflexed 4
      4. Flowers 5–7(–9) mm long; calyx ca. 1/2 of the corolla tube, with lobes overlapping at base; corolla lobes 1/4–1/3 as long as the tube; anthers 0.8–2.0 mm long ..... *C. subinclusa*
      4. Flowers 2.8–5.0(–6.0) mm long; calyx ca. equaling or somewhat longer than corolla tube, with nonoverlapping lobes; corolla lobes ± equaling the tube; anthers 0.3–0.7 mm long 5
         5. Flowers 5-merous; calyx and corolla lobes acute to acuminate; capsules elliptical-ovate, ± thickened around the interstylar aperture, with 1–2 seeds ..... *C. salina*
         5. Flowers 4- and 5-merous; at least some calyx and corolla lobes in the same flower long-attenuate; capsules globose to slightly depressed, not thickened apically, with 1–4 seeds ..... *C. howelliana*
1. Infrastaminal scales completely absent, reduced to ridges, or represented by lateral, dentate wings 6
   6. Flowers 4–5-merous; calyx and corolla lobes long acuminate; infrastaminal scales bifid or represented by lateral, dentate wings; withered corolla surrounding capsule in the lower half ..... *C. suksdorfii*
   6. Flowers 5-merous; calyx and corolla lobes not long acuminate; infrastaminal scales completely absent or reduced to ridges; withered corolla completely enveloping the capsule or leaving only its top visible 7
      7. Styles 0.5–1.0(–1.5) mm long; anthers 0.25–0.5 mm long, broadly-elliptic; capsule surrounded by corolla (visible top) ..... *C. occidentalis*
      7. Styles 1.2–3.0 mm long; anthers 0.7–1.1 mm long, oblong to linear; capsule enclosed by corolla (top not or barely visible) 8
         8. Calyx length 1/2–1/4 of the corolla tube; corolla lobes shorter than to equaling the tube; filaments 0.2–0.6 mm long ..... *C. brachycalyx*
         8. Calyx length 3/4 to equaling the corolla; corolla lobes equaling or longer than corolla tube; filaments 0.6–1.1 mm long ..... *C. californica*

Cuscuta californica Hook. & Arn., Bot. Beechey Voy., 364. 1839 (non Choisy 1842).—TYPE: U.S.A. California. *Douglas s.n.* (K!). For more information on typification, synonymy and infraspecific variation see Costea et al. (2006a).

Inflorescences loose to dense paniculate cymes of 3–20 flowers, confluent; pedicels (0.5–) 1.0–2.5(–3.0) mm long; one bract at the base of the cymes and another (or not) at the base of the pedicels, membranous, ovate to lanceolate, 0.7–1.6 × 0.3–6 mm, margins entire, apex acute to acuminate, sometimes ± recurved. Flowers 5-merous, 3–5(–5.5) mm long, fleshy; papillae sometimes present on the pedicels, receptacle, calyx and corolla; laticifers isolated, elongated present in the corolla and capsules; calyx 1.5–2.2 mm long, golden yellow when dried, finely reticulate and shiny, turbinate-campanulate, ± angled, 3/4 to ca. equaling the corolla tube length, divided 1/2–2/3 to the base, tube 0.4–0.7 mm long, lobes 0.8–2 mm long, equal, triangular-ovate to lanceolate, overlapping at base, acute to acuminate, margins entire; corolla 3–5 mm long, white when fresh, creamy when dried, the tube 1.6–2.4 mm long, cylindric-campanulate to obconic, lobes 2.0–2.6 mm long, narrowly lanceolate, equaling or longer than the corolla tube, initially erect, later reflexed, not overlapping at the base, apex acute, not inflexed; stamens exserted when the flowers are completely open, anthers oblong to linear, 0.6–1 × 0.35–0.5 mm, filaments 0.6–1 mm long; infrastaminal scales absent or reduced to ridges; ovary ovoid to obovoid, not thickened and enlarged apically into a collar, styles evenly filiform, 1.2–2.2 mm long, ca. as long or longer than the ovary. Pollen as in *C. brachycalyx* (see Costea et al. 2006a). Capsules globose or ovoid-conic, 1.5–2.2 × 1.2–2.5 mm, sometimes apically pointed, indehiscent, entirely surrounded but not capped by the withered corolla with patent or reflexed lobes; interstylar aperture may be somewhat visible. Seeds as in Costea et al. (2006a). Infraspecific variation described in Costea et al. (2006a), minus *C. californica* var. *apodanthera*.

Phenology—Flowering March to September.

Host Ecology—Grows at 50–3,000 m elevation on numerous herbs and shrubs from various habitats: sandy desert areas, chaparral, coastal sage scrub, grasslands, *Pinus ponderosa* forests, and roadsides.

Distribution—U.S.A.: Arizona, California, Nevada, Oregon, Utah, Washington; Mexico: Baja California.

Conservation Status—G4G5 status ("Apparently Secure" to "Secure").

Representative Specimens Examined—MEXICO. Baja California: near Rancho El Ciprés, near 30°23′N 115°38′W, elevation 475 m, host: *Eriogonum fasciculatum*, 2 Jun 1963, *Thorne 31943* (RSA).

U.S.A. California. Inyo Co.: 2 mi S of Pleasant Valley campground beside Owens River, elevation 1,280 m, 16 June 1993, *Helmkamp* s.n. (RSA, UCR). Plumas Co.: S side of Pacific Crest Trail, N of Mount Etna, T22N R10E, SW 1/4 Section 23, elevation 2,290 m, host *Phacelia mutabilis*, 22 July 1994, *Ahart 7506* (CHSC, JEPS). Riverside Co.: Santa Ana Mountains, head of San Juan Creek, host *Adenoma fasciculatum*, 26 Jul 1962, *Wheeler*

8177 (CAS, RSA). San Diego Co.: Walker Canyon Ecological Reserve, 32°66′14″N 116 °23′39″W, elevation 951 m, host: *Eriogonum fasciculatum*, 4 May 2004, *Rebman et al. 10044* (SD). For (10) more specimens see Costea et al. (2006a, p., 193, *C. californica* var. *californica* minus the collections indicated as "brachycalyx" or "some flowers brachycalyx-like").

Cuscuta brachycalyx (Yunck.) Yunck., Mem. Torrey Bot. Club 18: 159. 1932.—TYPE: U.S.A. California: Near Hanford, dry soil on *Centromadia pungens*, 21 Jun 1901, *Kearney 52* (holotype: NY!; isotype: US!).

Cuscuta californica Hook. & Arn. var. *brachycalyx* Yunck., Illinois Biol. Monogr. 6, nos. 2, 3: 62, Fig. 45, 75. 1921.

Cuscuta brachycalyx var. *apodanthera* (Yunck.) Yunck., Mem. Torrey Bot. Club 18: 159. 1932.

Cuscuta californica var. *apodanthera* Yunck., Illinois Biol. Monogr. 6: 152. 1921.—TYPE: U.S.A. California: Yosemite Valley, 7–12 Jul 1896, *Jepson 80a* (holotype: JEPS!, fragment NY!).

Inflorescences dense to loose, paniculate cymes of 1–9 flowers, usually confluent in larger inflorescences; pedicels 1–6 mm long; one bract at the base of cymes and another (or not) at the base of the pedicels, membranous, lanceolate, 0.9–1.6 × 0.3–0.5 mm, margins entire, apex acute to acuminate. Flowers 5-merous, 4.5–6.0 mm long, fleshy; papillae absent; laticifers isolated, elongated, present in the corolla and capsules; calyx 1.5–2.0 mm long, usually together with the receptacle fleshy, brown when dried, not reticulate and shiny, campanulate-cupulate, not angled, 1/2–1/3 the length of the corolla tube, divided ca. 2/3 to the base, tube 0.3–0.5 mm long, lobes 0.8–1.2 mm long, equal, triangular-ovate, slightly overlapping at base, margins entire, acute; corolla 4.4–6.0 mm long, white when fresh, creamy brown when dried, the tube 2.0–3.5 mm long, initially cylindric-campanulate becoming gradually urceolate and saccate between stamen attachment points; lobes 1.5–2.6 mm long, triangular to lanceolate, shorter than to equaling the corolla tube, initially erect, later reflexed, not overlapping at the base, apex acute, not inflexed; stamens exserted when the flowers are completely open, anthers oblong to linear, 0.7–1 × 0.3–0.5 mm, filaments 0.3–0.6 mm long; infrastaminal scales absent; styles evenly filiform, 1.2–3.0 mm long, ca. as long or longer than the ovary, which is spherical to obovoid, not thickened nor enlarged into a collar apically. Pollen as in *C. californica* (see Costea et al. 2006a). Capsules globose to obovoid, 1.6–2.3 × 1.8–2.5 mm, indehiscent, surrounded and capped by the withered, white-papery corolla whose tube is ± narrowed above the top of the capsule and distally bearing the stamen and style remnants; corolla lobes at this stage patent or reflexed; interstylar aperture not visible. Seeds as in *C. californica* (see Costea et al. 2006a).

Phenology—Flowering June to September.

Host Ecology—Grows at 200–2,500 m on numerous herbs from chaparral, grasslands, *Pinus ponderosa,* and *Abies magnifica* forests.

Distribution—U.S.A.: California and Oregon.

Conservation Status—G4G5 status ["Apparently Secure" to "Secure"].

Representative Specimens Examined—U.S.A. California. Butte Co.: along Hurleton Swedes Flat Road, 1.5 mi S of Hurleton, T19N R5E, NE 1/4 Section 26, elevation 487 m, hosts: *Calycadenia multiglandulosa* and *Brodiaea californica* var. *californica*, 19 Jul 1998, *Ahart 8048* (CHSC, JEPS). Plumas Co.: ca. 1/8 mi N of intersection of Lumpkin Ridge Road and the road to Tamarack Flat, 39º44′32.9″N 121 º01′29.5W, elevation 1743 m, host: *Apocynum androsaemifolium*, 18 Jul 2002, *Ahart 9856* (CHSC, JEPS). Tehama Co.: burned area on the E side of road M2, ca. 9 mi W of Paskenta, T24N R7W, W border, Section 34, elevation 762 m, host: *Trichostema laxum*, 8 June 2001, *Ahart 8771* (CHSC, JEPS). Mariposa Co.: Yosemite National Park, N slope of Merced River Canyon, on N side of Hwy 140, ca. 1.5 mi W of the Arch Rock Entrance Station, elevation 870 m, host: *Lupinus formosanus* var. *formosanus*, 16 June 2004, *Colwell and Coulter 04–31* (YM, TRTE, WLU). Oregon. Klamath Co.: Bear Wallow, near Klamath Falls, 24 Sep 1952, *McLeod s.n.* (ORE). For three more specimens see Costea et al. (2006a, pp: 193), cited as "brachycalyx" or "some flowers brachycalyx-like" under *C. californica* var. *californica*.

Cuscuta draconella Costea and Stefanović, sp. nov.—TYPE: U.S.A. Texas: El Paso Co., Hueco Mountains, 31 mi E of El Paso, 25 Jul 1946, *E. C. Tharp 46072* (holotype: TEX!; isotypes: IND, GH!, K!).

Cuscutae decipienti similis, sed 1–2 bracteis, 2.4–3.5 × 0.4–1.2 mm in pediculorum basi; calice angulari maximeque dispertito, cum excedentibus lobulis, 1–3(–5) protuberantibus multicellularibus proditis; infrastaminalibus scalis filamentis staminalibus curtioribus.

Stems filiform, pale orange. Inflorescences dense, glomerulate clusters of (1–)2–5 subsessile flowers; pedicels 0.1–0.8 mm long; bracts one at the base of the cymose clusters and 1–2 at the base of the pedicels, membranous, ovate-triangular to linear, 2.4–3.5 × 0.4–1.2 mm, with 1–3(–5) horn- or dome-like multicellular protuberances along the midveins, margins entire, acute, apex cuspidate to long attenuate, ± recurved. Flowers 5-merous, 2.5–3.6(–4) mm long, fleshy; papillae absent or present 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; calyx 1.4–1.7 mm long, membranous, reticulate and shiny or ± fleshy, golden yellow to brown when dried, campanulate, ± angled, equaling corolla tube, divided 1/2–2/3 to the base, tube 0.4–0.8 mm long, lobes 0.8–1.3 mm long, slightly unequal, triangular ovate, broadly ovate to subrotund, with 1–2(–5) horn- or dome-like, multicellular protuberances, 0.1–0.3 mm long, distributed along the midveins; apices subacute, rounded or obtuse, broadly overlapping at base; margins membranous, irregularly serrulate to entire, or denticulate-papillose. Corolla 2.0–3.5 mm long, white when fresh, creamy-yellow when dried, the tube 1.2–1.6 mm long, campanulate, lobes 1.3–1.6 mm long, triangular-ovate, equaling the corolla tube, slightly spreading to reflexed, margins overlapping at the base, entire or irregularly denticulate, apex ± cucullate, acute or truncate, cuspidate (sometimes 2–3-cuspidate) or mucronate, inflexed, stamens becoming exserted only when corolla lobes are reflexed, shorter than the lobes, anthers broadly elliptical, 0.5–0.8 × 0.4–0.5 mm; filaments 0.4–0.8 mm long; infrastaminal scales 0.7–1 mm long, spatulate to obovate, ca. 3/4 the length of the corolla tube (not reaching filaments), deeply fimbriate, fimbriae 0.2–0.3 mm long; styles distinct, evenly stoutish, 0.5–1.2 mm long, shorter to ca. as long as the ovary; ovary obovoid, apically thickened and enlarged into a collar at the style bases. Pollen tricolpate 17–19(–21) μm long, subsphaerical to prolate, rounded at the poles, tectum imperforate or with a few

small, scattered puncta, 200–350 nm in diameter; exine granulate. Capsules indehiscent [no mature capsules and seeds were examined]. Fig. 4.

Phenology—Flowering from August to September.

Host Ecology—Grows at ca. 1,600 m on in rocky arroyos, on herbaceous species from genera such as *Atriplex, Gutierrezia,* and *Thelysperma*.

Distribution—U.S.A. New Mexico: Catron, Soccoro and Dona Ana Counties. Texas: El Paso Co.

Conservation Status—Based on the few herbarium collections available, we propose a G2 status ["Imperiled—At high risk of extinction due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors", NatureServe 2008].

Etymology—The specific epithet derives from the Latin "Draco", dragon, alluding to the appearance given sometimes by the multicellular protuberances on the bracts and calyces.

Representative Specimens Examined—U.S.A. New Mexico: Doña Ana Co., White Sands Missile Range, San Augustin Mts., ca. 17 km NE of Las Cruces, 1.5 km N of US 70 and 2 km E of San Augustin Pass, Black Prince Arroyo; T21S, R4E, SW corner Sec 28; UTM 355700/3909000; 1,660 m; 16 Aug 1990, *Spellenberg & Mahrt 10497* (NMC, NY, UC). Catron Co.: E of Mogollon along Hwy 78 (T10S, R12E, Sec.32), 9 Aug 1977, *Wagner 3395* (UNM). Socorro Co.: extreme SE corner of county on White Sands Missile Range 25 mi SE of Stallion Range Center on Range Rd., 1/8 mi E of Ben Site, 23 Jul 1988, *Herman 462* (NMC, NY); Mocking Bird Pass, 0.25 mi NW of the old mine S of the Rd.; Township 8 South; Range 5 East, SE quarter section 31; Tularosa Grazing District. Sandy flat drainage wash in alluvial fan, 5,300 ft, 7 Aug 1944, *Dunn 3114* (UC). Texas: El Paso Co., on west side of Blackbrush Gap, flats, 6 Aug 1941, *Warnock 20997* (LL).

Cuscuta decipiens Yunck., Illinois Biol. Monogr. 6: 145. 1921.—TYPE: MEXICO. Zacatecas: Hacienda de Cedros, summer 1908, *F. E. Lloyd 193* (holotype US!).

Stems slender, orange-yellow. Inflorescences dense, paniculate clusters of 2–9 flowers, often confluent; pedicels 0.5–3 mm long; one bract or none at the base of the cymes, generally absent at the base of the pedicels, ovate to lanceolate, 0.9–1.1 × 0.5–0.7 mm, without multicellular protuberances, margins entire, apex acute. Flowers 5-merous, 3–4 mm long, somewhat fleshy; papillae absent; laticifers present in the calyx, corolla, ovary/capsule, isolated or in rows, ovoid to elongated; calyx 1.8–2.3 mm long, fleshy when fresh, membranous, ± reticulate and shiny when dry, golden-yellow to brown, campanulate, not angled, ca. 3/4 the length of the corolla tube, divided ca. 1/2 the length, tube 0.9–1.15 mm long, lobes 0.9–1.15 mm long, bases not overlapping, ovate, not carinate or provided with multicellular protuberances, margins entire, apex obtuse; corolla 3.0–3.8 mm long, white when fresh, creamy-white when dried, tube campanulate, 1.5–2.0 mm long, lobes 1.5–1.8 mm long, ca. equaling the tube in length, ovate, spreading, sparsely denticulate distally, apex cucullate, acute to cuspidate, inflexed; stamens not exserted, shorter than the corolla lobes; anthers broadly elliptic to ovate, 0.5–0.7 × 0.4–0.5 mm, filaments 0.4–0.6 mm long; infrastaminal scales 1.5–1.9 mm long, reaching the filament bases, oblong-spatulate, uniformly densely fringed, fimbria 0.2–0.4 mm long; styles evenly filiform, 0.4–0.8 mm, shorter than the ovary; stigmas capitate, globose. Pollen as in *C. draconella*. Capsules indehiscent, globose-ovoid, 1.8–2.4 × 1–1.6 mm, thickened and ± enlarged around the small interstylar aperture, not translucent, surrounded by the withered corolla. Seeds 1(–2) per capsule, dorsoventrally compressed, ovate to broadly-elliptic, 1.5–1.9 × 1–1.4 mm, hilum area lateral.

Phenology—Flowering from July to October.

Host Ecology—Grows at 1,000–2,500 m on species of *Croton*, *Chenopodium*, *Flourensia*, and *Salsola*.

Distribution—MEXICO: Zacatecas.

Conservation Status—Because *C. decipiens* is known only from the collections mentioned below, we propose a G2 status (see *C. draconella* above).

Representative Specimens Examined—MEXICO. Zacatecas: Chihuahuan Desert, 12.5 mi NNE of Rancho Hidalgo, ca. 27 mi NNW of Camacho, elevation 1990 m, 24°47′N 102°14′W, parasitic on *Croton*, 2 Sep 1971, *Henrickson 6362* (CSLA, RSA); ca. 144.5 km NE of Zacatecas, along Hwy 54 to Saltillo, 23°52′N 101°44′W, elevation 1,950 m, parasitic on *Salsola* and *Chenopodium*, 19 Oct 2001, *Henrickson 22781* (CSLA, RSA); ca. 8 (air) mi NE of Estacion Camacho, 2 mi NE of La Palmilla towards Pico de Teyra, 24°32′N 102°16′W, elevation 1,646 m, on *Flourensia cernua*, 23 Sep 1973, *Henrickson 13394* (MEXU, RSA); Cedros, 25 Nov 1907, *Lloyd 28* (MO).

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Appendix 1. Taxa, authorities, DNA extraction numbers, sources of plant material from which DNA was extracted, and GenBank accession numbers for sequences used in this study. DNA extraction numbers are indicated on the phylogenetic trees following species names. GenBank accession numbers are given in the following order: *trnL–F*, *rbcL*, ITS, and 26S rDNA (newly generated sequences are indicated in bold). The symbol "***" indicates sequences not obtained. Abbreviations of herbaria in which the vouchers are deposited follow Index Herbariorum.

Cuscuta brachycalyx Yunck.: **147**, *Stefanović 98-59* (TRTE), EF194486, **EU883440**, EF194696, ***; **472**, *Stefanović 04-140/AC-04-31* (TRTE/YM), EF194484, **EU883441**, EF194699, **EU883489**; **499**, *Ahart 9856* (JEPS), EF194487, **EU883442**, EF194697, **EU883490**; **643**, *Colwell AC 04-305* (YM/WLU), EF194485, **EU883443**, EF194700, **EU883491**; **645**, *Ahart 2971* (NY), EF194488, **EU883444**, EF194698, E**U883492**. ***Cuscuta californica*** Hook. & Arn.: **178**, *Colwell AC s.n.* (no voucher), **EU883435**, **EU883445**, **EU883480**, **EU883493**; **418**, *Stefanović 00-59* (TRTE), EF194480, **EU883446**, EF194692, **EU883494**; **500**, *Boyd 9839* (JEPS), EF194478, **EU883447**, **EU883481**, **EU883495**; **637**, *Pinzl 7238a* (NY), EF194475, **EU883448**, EF194688, **EU883496**; **669**, *White 5033* (ASU), EF194479, **EU883449**, EF194691, **EU883497**. ***Cuscuta decipiens*** Yunck.: **981**, *Henrickson 13394* (MEXU), EF194509, ***, ***, **EU883498**; **1014**, *Henrickson 22781* (TEX), EF194510, **EU883450**, EF194718, **EU883499**. ***C. draconella*** Costea & Stefanović: **458**, *Tharp 46072* (IND), EF194508, ***, **EU883482**, **EU883500; 538**, *Wagner 3359* (UNM), ***, ***, **EU883483**, ***; **658**, *Herman 462* (NMC), **EU883436**, **EU883451**, **EU883484**, **EU883500**; **659**, *Mahrt 10497* (NMC), **EU883437**, **EU883452**, **EU883485**, **EU883501**. ***Cuscuta howelliana*** Rubtzoff: **357**, *Tank s.n.* (no voucher), EF194506, **EU883453**, EF194716, **EU883502**; **654**, *Oswald & Ahart 7978* (JEPS), EF194504, **EU883454**, ***, **EU883503**; **655**, *Ahart 8044* (JEPS), EF194507, **EU883455**, EF194717, **EU883504**; **656**, *Reino & Alava 6809* (JEPS), EF194505, **EU883456**, EF194715, **EU883505**. ***C. occidentalis*** Millsp.: **503**, *Ertter 7326* (NY), EF194477, ***, EF194690, **EU883506**; **504**, *Tiehm 12257* (NY), EF194481, **EU883457**, EF194693, **EU883507**; **646**, *Ahart 9116* (JEPS), EF194476, **EU883458**, EF194689, **EU883508**; **647**, *Tiehm 14108* (NY), EF194482, **EU883459**, EF194694, **EU883509**; **648**, *Schoolcraft et al. 2220* (NY), EF194483, **EU883460**, EF194695, **EU883510**. ***Cuscuta salina*** Engelm. var. ***salina***: **477**, *Tiehm 12744* (ASU), EF194492, **EU883464**, EF194704, **EU883514**; **478**, *Tiehm 13405* (ASU), EF194493, **EU883465**, EF194705, **EU883515**; **652**, *Hammond 10349* (NY), EF194495, **EU883466**, EF194707, **EU883516**; **653**, *Felger & Fenn s.n.* (NY), EF194496, **EU883467**, EF194708, **EU883517**. ***Cuscuta salina*** Engelm. var. ***major*** Yunck.: **502**, *Standley 777* (NY), EF194499, **EU883461**, EF194710, **EU883511**; **642**, *Halse 4961* (NY), EF194498, **EU883462**, EF194709, **EU883512**; **651**, *Kennedy & Ganders 4947* (UBC), EF194500, **EU883463**, EF194711, **EU883513**. ***Cuscuta subinclusa*** Durand & Hilg.: **197**, *Munz & Balls 17942* (WTU), EF194489, **EU883468**, EF194703, **EU883518**; **484**, *Keil 14274-1* (ASU), **EU883438**, ***, **EU883486**, ***; **501**, *Raz & Boyd 15* (NY), EF194491, **EU883469**, EF194701, **EU883520**; **644**, *Anderson 3248* (NY), EF194490, E**U883470**, EF194702, **EU883521**; **649**, *Ahart 7638* (JEPS), ***, **EU883471**, **EU883487**, **EU883522**; **961**, *Sanders et al. 17902* (RSA), **EU883439**, **EU883472**, **EU883488**, **EU883523**. ***Cuscuta suksdorfii*** Yunck.: **470**, *Colwell AC-04-159* (YM/TRTE), EF194503, **EU883473**, EF194714, **EU883524**; **635**, *Ahart 9885* (JEPS), EF194501, **EU883474**, EF194712, **EU883525**; **636**, *Ahart 3949* (JEPS), EF194502, **EU883475**, EF194713, **EU883526**.

Outgroups: ***Cuscuta campestris*** Yunck.: **411**, *Stefanović 03-103* (TRTE), EF194450, **EU883476**, EF194663, **EU883527**. ***Cuscuta glabrior*** (Engelm.) Yunck.: **596**, *Palmer 723* (GH), EF194470, **EU883477**, EF194684, **EU883528**. ***Cuscuta suaveolens*** Ser.: **790**, *Paget 2579* (MEL), EF194441, **EU883478**, EF194652, **EU883529**. ***Cuscuta gronovii*** Willd.: **343**, *Stefanović 02-03* (TRTE), EF194418, **EU883479**, EF194637, **EU883530**.