

Evolutionary history and taxonomy of the *Cuscuta umbellata* complex (Convolvulaceae): Evidence of extensive hybridization from discordant nuclear and plastid phylogenies

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Abstract The *Cuscuta umbellata* complex is one of the 15 major clades recently circumscribed in *C.* subg. *Grammica*. Most of its members occur in North America and the Caribbean (*C. desmouliniana*, *C. lacerata*, *C. leptantha*, *C. liliputana*, *C. odontolepis*, *C. polyanthemus*, *C. tuberculata*, *C. umbellata*), but three species (*C. acuta*, *C. membranacea*, *C. umbellata*) grow in South America, and one (*C. hyalina*) is found as a native species in India, Pakistan and Eastern to South Africa. Basic morphology, scanning electron microscopy and sequence data from the nuclear internal transcribed spacer (ITS) and the plastid *trnL-F* region were used to reconstruct the phylogeny, gain a better understanding of the evolutionary history, and determine species boundaries. Our results show that in its currently accepted delimitation *C. umbellata* is polyphyletic. Discordances between phylogenies derived from plastid and nuclear data strongly suggest that at least four independent hybridization events have occurred in the evolution of this species group, rendering relationships among its members more complex than previously thought. One of these reticulation events involves *C. umbellata* var. *reflexa*, a taxon that has been considered synonymous to *C. umbellata* var. *umbellata* in the last decades. This hybrid is morphologically intermediate but distinct from its putative parents, *C. odontolepis* or *C. acuta* on the maternal side, and *C. umbellata* (var. *umbellata*) on the paternal side, which supports its treatment as a new species, *C. legitima*. *Cuscuta umbellata* is further redefined to exclude *C. umbellata* var. *dubia*, which is merged into *C. desmouliniana*. A new classification is provided, together with an identification key, descriptions, illustrations, and geographical distributions for the twelve species of the clade.

Keywords Convolvulaceae; *Cuscuta*; hybridization; ITS; molecular phylogeny; morphology; taxonomy; *trnL-F*

■ INTRODUCTION

With more than 200 species and over 70 varieties *Cuscuta* L. (dodders) is one of the most diverse and challenging groups of parasitic plants. The genus is nearly cosmopolitan, but the highest diversity of species (ca. 140–160) is encountered in the Americas (Yuncker, 1932; García & Martín, 2007; Stefanović & al., 2007). Dodders are important both economically and ecologically. A few species are among the most damaging pests worldwide, being capable of producing considerable losses to agricultural crops (Parker & Riches, 1993; Holm & al., 1997; Costea & Tardif, 2006). Surprisingly, however, numerous other species in this genus are presumed extinct or require conservation measures (Costea & Stefanović, 2009a).

Almost eight decades after Truman G. Yuncker's monograph (Yuncker, 1932), systematics of *Cuscuta* is receiving a renewed interest. Two of the three accepted subgenera, *C.* subg. *Cuscuta* and subg. *Grammica*, have been recently the subject of broad-scale phylogenetic studies (García & Martín, 2007; Stefanović & al., 2007). In *C.* subg. *Grammica*, the largest and most complicated infrageneric group, 15 major lineages have been circumscribed (Stefanović & al., 2007), with little correspondence to Yuncker's sections and subsections. In parallel, a series of focused systematic studies have been initiated to investigate these clades at species level. To date, a total of five major *Grammica* clades have been examined: four that

comprise mostly species from the territory covered by *Flora of North America* (Costea & al., 2006a–c; Costea & Stefanović, 2009b; Costea & al., 2009), and one with predominantly Mexican dodders (Costea & al., 2008).

Our present study continues this series by investigating “clade L” (Stefanović & al., 2007), referred to here as the “*Cuscuta umbellata* complex” in the absence of a formal section name (to be published with a new infrageneric classification of the genus; Costea & al., in prep.). The core of this group is represented by species of the former *C.* subsect. *Umbellatae* in which Yuncker (1932, 1965) included nine species characterized by umbellate inflorescences and dehiscent capsules: *C. umbellata*, *C. deltoidea*, *C. desmouliniana*, *C. fasciculata*, *C. gracillima*, *C. hyalina*, *C. lacerata*, *C. macvaughii*, *C. saccharata*, and *C. serruloba*. However, recent molecular results (Stefanović & al., 2007; Stefanović & Costea, 2008) have shown that the composition of the clade is radically different. Five other species previously included by Yuncker (1932) in various sections and subsections of *C.* subg. *Grammica* are also part of the *C. umbellata* complex (Stefanović & al., 2007; Stefanović & Costea, 2008). Two of these, *C. acuta* and *C. membranacea*, have indehiscent capsules (previously included in *C.* sect. *Eugrammica* subsect. *Acutae*; Yuncker, 1932; Hunziker, 1949), while the rest have circumscissile capsules: *C. odontolepis* (formerly in *C.* sect. *Eugrammica* subsect. *Odontolepisae*; Yuncker 1932), *C. tuberculata*, *C. leptantha*, and *C. polyanthemus* (formerly

in *C. sect. Eugrammica* subsect. *Leptanthae*; Yuncker, 1932). In addition, *C. lilliputana*, a new species that is nested within this group, has been recently described (Stefanović & Costea, 2008). In contrast, *C. gracillima*, *C. sidarum* (= *C. saccharata*), *C. deltoidea* (= *C. serruloba*) do not belong to the *C. umbellata* clade as previously thought by Yuncker (1932, 1965), but form a separate group (Stefanović & al., 2007; Costea & al., 2008).

Most of the members of the *C. umbellata* complex are known to occur in southwestern U.S.A. and Mexico, but three species (*C. umbellata*, *C. acuta*, *C. membranacea*) grow in South America, and another one (*C. hyalina*) can be found in India, Pakistan and Africa. Recent phylogenetic studies have clearly indicated that the boundaries of some species (e.g., *C. umbellata* and *C. desmouliniana*) must be reconsidered (Stefanović & al., 2007; Stefanović & Costea, 2008). These studies have also revealed discordant nuclear and plastid phylogenies which suggested that at least two of the species, *C. lilliputana* and *C. desmouliniana*, likely have a hybrid origin (Stefanović & Costea, 2008). These cases of reticulation, together with the disjunct distribution of the taxa, have shown that the evolutionary history of the *C. umbellata* clade is much more complex than previously thought. In view of these interesting preliminary findings based on relatively limited sampling within the *C. umbellata* complex, we have studied numerous herbarium specimens that have accumulated worldwide since Yuncker's monographs (Yuncker, 1932, 1965). The aims of this study are to (1) recover the evolutionary history of the *C. umbellata* complex based on nuclear ITS and plastid *trnL-F* sequences and further investigate the extent of reticulate evolution known to occur in this group; (2) investigate the morphology and micromorphology of the taxa involved; and (3) provide a new classification of the *C. umbellata* complex with the description of a new species, *C. legitima*.

■ MATERIALS AND METHODS

Taxon sampling. — We have studied specimens from over 100 herbaria in connection with the upcoming treatments of *Cuscuta* for *Flora of North America* Project, *Flora Neotropica*, and a future monograph of the genus. A subset of 34 accessions, representing eleven ingroup species of the *C. umbellata* complex, was used for the molecular phylogenetic analyses (Appendix 1). Efforts were made to sample multiple accessions, particularly for those species spanning large biogeographical ranges (e.g., *C. hyalina*) and/or those with variable morphology (e.g., *C. umbellata*). As a result, two to nine individuals are included in the molecular analyses for all but one rare species, *C. membranacea*, known only from its type locality. In addition, several taxa (*C. lacerata*, *C. fasciculata*, *C. hyalina* var. *nubiana*, *C. umbellata* var. *dubia*) are known only from their type specimens (Yuncker, 1921, 1932), and *C. umbellata* var. *desertorum* from two historical collections (Engelmann, 1859; Yuncker, 1932). Hence, these taxa could not be sampled for the molecular analyses. Based on our previous, more inclusive phylogenetic analyses of *Cuscuta* subg. *Grammica* (Stefanović & al., 2007; Stefanović & Costea, 2008), we

selected two species from the *C. gracillima* clade as outgroup (Appendix 1).

Morphology and micromorphology. — Descriptions are based on herbarium material (Appendix 2). 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 7.0 software (MIS Inc., Villa Park, Illinois, U.S.A.). Micromorphological measurements and pictures were taken at 10 kV using a Hitachi SU1510 scanning electron microscope. Herbarium samples (Appendix 2) 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 & al. (2006a). Hundreds of photographs that illustrate details of the floral parts, pollen and fruit morphology for all the species (including the types) are available on the *Digital Atlas of Cuscuta* (Costea, 2007-onwards). The geographical distribution of taxa, phenology, elevation and host ranges are based on observation made from herbarium specimens.

Molecular techniques and alignments. — To infer phylogenetic relationships among species of the *C. umbellata* complex, sequences for the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) as well as *trnL-F* intron/spacer region from the plastid genome (ptDNA) were obtained. In addition to the DNA samples used in previous studies (Stefanović & al., 2007; Stefanović & Costea, 2008), total genomic DNA was isolated from newly obtained specimens as well. DNA extractions, polymerase chain reaction (PCR) reagents and conditions, amplicon purifications, cloning, as well as sequencing procedures followed the protocols detailed in Stefanović & al. (2007). Initial sequencing of nuclear and plastid amplicons was done directly. However, in the cases where significant polymorphism was detected, the PCR product was cloned and multiple clones per individual were sequenced. Sequences generated in this study are deposited in GenBank (accession numbers HM748863–HM748905; see Appendix 1). Sequences were aligned manually using Se-Al v.2.0a11 (Rambaut, 2002).

Phylogenetic analyses. — Phylogenetic analyses were conducted under parsimony and Bayesian optimality criteria; summary descriptions of these analyses, for individual as well as combined datasets, are provided in Table 1.

Under the parsimony criterion, nucleotide characters were treated as unordered and all changes were equally weighted. Depending on the number of operational taxonomic units (OTUs) included, different search strategies were employed for the different matrices, using PAUP* v.4.0b10 (Swofford, 2002). For the ITS matrix, searches for most parsimonious (MP) trees were performed using a two-stage strategy. First, the analyses involved 10,000 replicates with stepwise random taxon addition, tree bisection-reconnection (TBR) branch swapping saving no more than 10 trees per replicate, and MULTREES off. The second round of analyses was performed on all trees in memory with the same settings except with MULTREES on. Both stages were conducted to completion or until one million trees were found. For the *trnL-F* matrix, a full heuristic search was performed, involving 1000 replicates with stepwise

random taxon addition, TBR branch swapping, and MULTREES option on. Given the relatively moderate number of terminal units included in the combined dataset, we performed a Branch-and-Bound search, therefore ensuring recovery of all MP trees. In all three cases, support for clades was inferred by nonparametric bootstrapping (Felsenstein, 1985), using 500 heuristic bootstrap replicates, each with 20 random addition cycles, TBR branch swapping, and MULTREES option off (DeBry & Olmstead, 2000). Nodes receiving bootstrap (BS) values <60%, 60%–75%, and >75% were considered weakly, moderately, and strongly supported, respectively.

Bayesian phylogenetic inferences were performed using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). Model-Test v.3.7 (Posada & Crandall, 1998) was used to determine the model of sequence evolution that best fit the data by the Akaike Information Criterion (AIC), starting with the parsimony-derived tree rather than the neighbor-joining default. The Tamura-Nei (TrN) model of DNA substitution (Tamura & Nei, 1993), with rate variation among nucleotides following a discrete gamma distribution (TrN+G), was selected as the best-fit for the ITS sets. For the *trnL-F* matrix, the F81 (Felsenstein, 1981) model was selected. Each Bayesian analysis consisted initially of two runs of one million generations from a random starting tree using the default priors and four Markov chains

sampled every 100 generations. If needed, the run lengths were increased until the standard deviation of split frequencies between two runs was well below 0.01 (see Table 1 for details on MrBayes settings and number of generations used for each of three analyses). Convergence of the chains was determined by examining the plot of all parameter values and the $-\ln L$ against generation using Tracer v.1.3 (Rambaut & Drummond, 2004). Stationarity was assumed when all parameter values and $-\ln L$ 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 the three separate Bayesian analyses; Table 1), 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 & Yang, 1996).

Topological incongruence and alternative hypothesis testing.— Conflict between datasets was first evaluated by visual inspection, by searching for the presence of conflicting and strongly supported topologies from individual matrices. For all the cases where such conflicts were found, reciprocally constrained topologies were constructed using MacClade v.4.06 (Maddison & Maddison, 2003) and their cost in parsimony was assessed using PAUP* (Swofford, 2002). In

Table 1. Summary descriptions for sequences included in, phylogenetic analyses conducted on, and trees derived from, individual and combined datasets of the *Cuscuta umbellata* complex.

	ITS (nuclear)	<i>trnL-F</i> (plastid)	Combined
Number of OTUs included	69	37	25
Sequence characteristics:			
Aligned length	643	543	1207
Variable sites	253	45	191
Parsimony informative sites	140	40	158
Mean AT content (%)	47	64	54
Parsimony search conditions:			
Algorithm	Two-stage heuristic	Full heuristic	Branch-and-Bound
RSA/branch swapping/MULTREES	10,000/TBR/off; Memory/TBR/on	1000/TBR/on	na/na/on
MP tree characteristics:			
Number of trees	>1,000,000	1454	2100
Length	376	48	251
CI/RI	0.795/0.947	0.979/0.996	0.873/0.956
Bayesian search conditions:			
Model of DNA evolution (MrBayes settings used)	TrN + G (nst = 6; rates = gamma)	F81 (nst = 2; rates = equal)	Combined (partitioned)
Number of generations (number of runs)	4×10^6 (2)	1×10^6 (2)	2×10^6 (2)
Burn-in (%)	20	20	20
Bayesian tree characteristics:			
Mean $-\ln L$	-3509.959	-1116.633	-3115.534
Number of trees retained	64,000	16,000	32,000

CI, consistency index (excluding parsimony uninformative characters); df, degrees of freedom; nst, number of substitution states; OTU, operational taxonomic unit; RI, retention index; RSA, random sequence addition; TBR, tree bisection and reconnection.

this fashion, for each case of the strongly supported incongruence between the two datasets, one randomly chosen MP tree representing topological results obtained from nuclear data was imposed on plastid data and vice versa. To evaluate the significance among these alternative phylogenetic hypotheses, we implemented the one-tailed Shimodaira-Hasegawa tests (SH tests; Shimodaira & Hasegawa, 1999; Goldman & al., 2000) in PAUP*. The test distributions were obtained using the re-estimated log likelihoods (RELL; Kishino & Hasegawa, 1989) with 10,000 bootstrap replicates.

■ RESULTS

General morphology and micromorphology. — Although the clade of *C. umbellata* is relatively easy to distinguish from other major groups of *Cuscuta* (see Stefanović & al., 2007), most of its species are notoriously difficult to separate from each other. The overall morphology of this clade reflects its phylogenetic affinities with the *C. gracillima* clade (“clade N” in Stefanović & al., 2007). The loose, umbellate inflorescence encountered in most species, the shape of the calyx lobes as well as the morphology of the capsules are relatively similar to the species of the *C. gracillima* complex (Costea & al., 2008). However, unlike in the latter group, the stems of species in the *C. umbellata* clade are persistent at maturity and inflorescences do not emerge directly from the host’s stems (Costea & al., 2008).

Papillae are present on the perianth of some species, both on the calyx and corolla (*C. liliputana*, *C. leptantha*, *C. desmouliniana*; Fig. 1D, G, I), or only on the corolla (*C. odontolepis*, *C. tuberculata*, *C. umbellata*; Fig. 1A, E). *Cuscuta desmouliniana*, *C. tuberculata* and sometimes *C. liliputana* are the members of this clade that have multicellular protuberances with stomata on the bracts and calyx lobes (Fig. 1G–H). Similar structures with an unknown role have been also reported from *C. draconella* in the *C. californica* clade (Costea & Stefanović, 2009b). Infrastaminal scales with laticifers in the fimbriae are present in most species (Fig. 1B–C), except for *C. hyalina* in which scales are reduced or absent. The pollen is relatively uniform among species, comparable to that of *C. indecora* and *C. gracillima* clades (Costea & al., 2006b, 2008). Pollen grains are 3(–4)-zonocolpate, subspheroidal to prolate with perforate or imperforate tectum (for images see Costea, 2007 onwards; for descriptions see Welsh & al., 2010). In most species, capsules dehisce by a circular line at the base of the fruit. The capsules of the Caribbean form of *C. umbellata* var. *umbellata* dehisce late by a more or less irregular line (also found at the base of the fruit). The fruit is indehiscent in *C. acuta* and *C. membranacea*, although the capsule may tear irregularly at the base if pressure is applied. The seeds are angled; the seed coat cells are alveolate when dry and papillose when hydrated, 20–55 μm in diameter. The hilum region is terminal and round, and the vascular scar of the funiculum is short, vertical.

Sequences and alignments. — Summary descriptions for sequences obtained from ITS and *trnL-F* regions are presented in Table 1. Sequences newly generated for this study

were incorporated together with the relevant portions of the alignments used in our previous analyses (Stefanović & al., 2007; Stefanović & Costea, 2008). Although these two non-coding regions exhibited length variation, the alignments among the ingroup taxa were straightforward throughout the entire length of these matrices and were used in their entirety for phylogenetic analyses. This is in contrast to the higher-level phylogenetic study of *Cuscuta* subg. *Grammica* (Stefanović & al., 2007; Stefanović & Costea, 2008) in which large portions of *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 one or the other region from a few individuals, presumably due to the poor quality or limited quantity of the DNA extracted from some older herbarium specimens.

Unconstrained analyses and overall levels of support. — Preliminary phylogenetic analyses were conducted on individual matrices with the inclusion of the outgroup taxa (trees not shown). Those analyses indicated that the first split within the *C. umbellata* group occurs between the *C. leptantha/C. polyanthemos* clade on one side, and the remainder of this complex on the other, in agreement with our previous broad-scale results (“clade L” in Stefanović & al., 2007; Stefanović & Costea, 2008). Taking this into account, in all subsequent analyses we used *C. leptantha* and *C. polyanthemos* as functional outgroup (Figs. 2–4), allowing for the full usage of all available nuclear and plastid data. Summary descriptions of trees derived from individual and combined datasets are presented in Table 1. For all these three analyses, the strict consensus of equally parsimonious trees (not shown) resulted in relationships that were topologically identical or nearly identical to the respective results derived under the Bayesian criterion (Figs. 2–3).

Four major clades labeled A–D were resolved within the *Cuscuta umbellata* complex with nuclear ITS sequences (Fig. 2, left). All of these clades have branches with substantial length subtending them and have received strong bootstrap support (97%–100%) as well as significant posterior probabilities (≥ 0.95). Clade A groups all the accessions/clones of *C. umbellata*, *C. hyalina*, *C. membranacea*, *C. liliputana*, and *C. desmouliniana*. In addition, this lineage contains some but not all the clones derived from the *C. legitima* accessions. In contrast to the strong support for this clade, the relationships within it remained mostly unresolved and unsupported, with a couple of exceptions. Namely, all the members of *C. hyalina* are found grouped together and sister to the sole representative of *C. membranacea*. Both of these results received strong support (98% BS; ≥ 0.95 PP). Clade B consists of all the representatives of *C. acuta* and *C. odontolepis* plus the remainder of the clones obtained from *C. legitima* accessions. Similarly to the situation described above for clade A, the relationships within clade B are mainly unresolved as well. Moderate support was observed only for a clade grouping all the *C. acuta* clones (52% BS; ≥ 0.95 PP), while the representatives of the other two species are found interspersed among each other. Clade C contains exclusively *C. tuberculata* individuals, and clade D groups together two

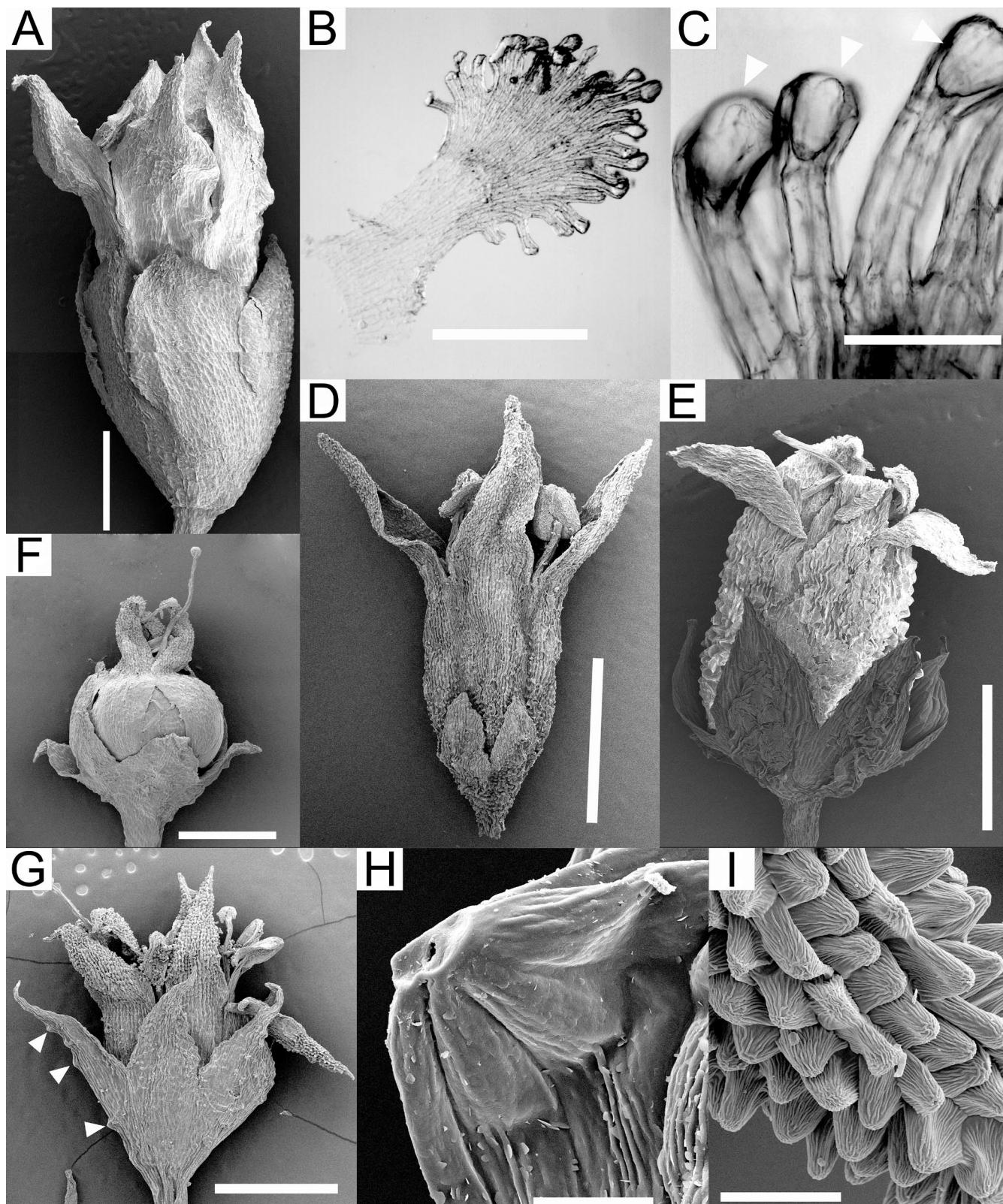


Fig. 1. Morphological and micromorphological features of species from the *Cuscuta umbellata* complex. **A**, *Cuscuta odontolepis* flower; **B**, infrastaminal scale of *C. umbellata* (var. *umbellata*); **C**, laticifers (arrowheads) in the infrastaminal scales of *C. umbellata* (var. *umbellata*); **D**, *C. leptantha* flower; **E**, *C. tuberculata* flower; **F**, capsule and persistent corolla in *C. desmouliniana*; **G**, flower of *C. desmouliniana* with multicellular protuberances on the calyx (arrowheads); **H**, multicellular protuberance with stomata; **I**, papillae on the corolla of *C. desmouliniana*. Bars: A, D–G, 1 mm; B, 0.5 mm; C, 100 μ m; H, 30 μ m; I, 60 μ m.

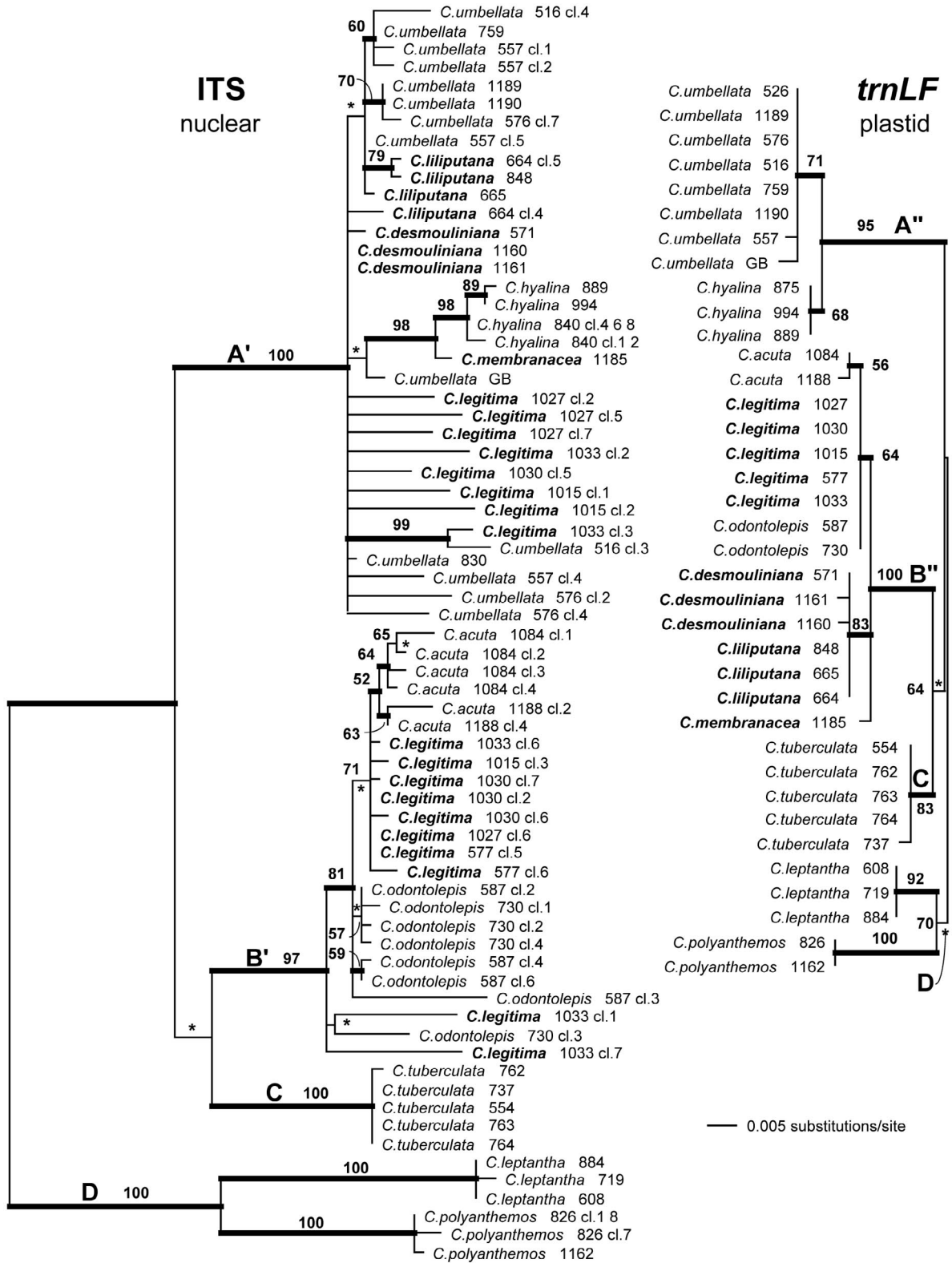


Fig. 2. Phylogenetic relationships among species of the *Cuscuta umbellata* complex derived from separate Bayesian analyses of nuclear and plastid sequences. Majority-rule consensus trees with mean branch lengths are drawn at the same scale for both phylograms. Four major lineages are labeled A–D. Prime and double-prime symbols indicate clades exhibiting substantial topological incongruence between nuclear and plastid results. Species with conflicting positions are depicted in bold. Parsimony bootstrap values are indicated for nodes supported $\geq 50\%$. Asterisks indicate branches with Bayesian posterior probability < 0.95 ; all other branches have posterior probability ≥ 0.95 (thick lines). Numbers following species names correspond to DNA accessions (see Appendix 1); in addition, for the ITS data different clones are labeled, if applicable.

remaining species from this complex, *C. leptantha* and *C. polyanthemus*; all these results received maximum support (100% BS; ≥ 0.95 PP).

Analyses of plastid *trnL-F* matrix also recovered four major, well-defined, and well-supported lineages (A–D; Fig. 2, right). However, the composition of two of those lineages, clades A and B, differs substantially compared to that obtained from the nuclear matrix. With plastid data, clade A contains only individuals of *C. umbellata* and *C. hyalina*. Members of these two species are reciprocally monophyletic and both are moderately supported (71% and 68% BS, respectively; ≥ 0.95 PP for both clades). Similarly to the ITS results, clade B contains *C. acuta* and *C. odontolepis*. However, in addition to these two species, and unlike in the results obtained with nuclear data, all the individuals of *C. membranacea*, *C. liliputana*, *C. desmouliniana*, and *C. legitima* are also confined to clade B, with strong support (100% BS; ≥ 0.95 PP). Relationships within clade B are only weakly supported with the exception of the *C. liliputana/desmouliniana* subclade (83% BS; ≥ 0.95 PP). The remaining two major groups, clades C and D, are identical in composition between the nuclear and plastid matrices, and consist of *C. tuberculata* and *C. leptantha/polyanthemus* individuals, respectively.

The combined analyses were conducted on a dataset in which nuclear and plastid sequences were concatenated but the accessions with strongly supported conflicting positions

in individual analyses excluded. Not surprisingly, the same basic underlying tree structure containing four major clades was recovered (Fig. 3). In addition, the combined data provided some support for the backbone relationships among these four lineages. Clades B and C were found sister to each other with stronger support (60% BS; ≥ 0.95 PP) than in individual analyses. Together, these two clades are sister to clade A. As previously indicated, the preliminary analyses including the outgroup placed *C. leptantha* and *C. polyanthemus* (i.e., clade D) as sisters to the rest of the *C. umbellata* complex, with strong support (100% BS; ≥ 0.95 PP; trees not shown).

Tests of alternative tree topologies. — The analyses of separate nuclear and plastid matrices produced trees of remarkably similar topologies, with the exception of four striking and strongly supported conflicts (Figs. 2 and 4) whose topological discordances span across two major clades, A and B. According to the nuclear data, *C. membranacea*, *C. liliputana*, *C. desmouliniana* as well as a number of clones from *C. legitima* accessions belong to the strongly supported clade A. In contrast, the plastid haplotypes place all these four species within clade B. Using nuclear data yet enforcing *trnL-F* results on these species and constraining them individually or in combination to clade B, with *C. acuta* and *C. odontolepis*, produced trees 17–22 steps longer than the optimal trees. All these length differences were deemed strongly significant and were rejected based on the SH tests (Table 2). Similarly, constraining these species to group in a clade with *C. umbellata* and *C. hyalina* (following the ITS results) with plastid data yielded trees 5–6 steps longer. Despite the relatively small length penalty, these results were also rejected as significantly worse solutions by the SH tests (Table 2).

DISCUSSION

Evidence for hybridization in the *Cuscuta umbellata* complex and alternative explanations for the observed plastid-nuclear discordance.

— Instances of reticulate evolution in plants can be detected through detailed analyses of discordance among different unlinked gene trees (Rieseberg, 1995; Sang & Zhong, 2000). When the ptDNA tree is compared with an independently derived phylogenetic tree (from morphology or other molecular data), conflicting position of a taxon between phylogenies may be taken as evidence for the hybrid origin of this taxon (Sang & Zhong, 2000; an illustration of this principle is depicted in Fig. 4). We present here evidence for four cases of strongly supported yet conflicting phylogenetic signals between ITS and *trnL-F* sequence data for four species of the *Cuscuta umbellata* complex. Two of these cases, *C. desmouliniana* and *C. liliputana*, were already described and discussed in detail in our previous broad-scale assessment of hybridization in *Cuscuta* subg. *Grammica* (Stefanović & Costea, 2008). The other two putative cases of hybridization involving *C. membranacea* and *C. legitima* are documented here for the first time.

In addition to hybridization, strongly conflicting gene trees can result from several other biological phenomena (e.g., Maddison, 1997; Wendel & Doyle, 1998), as discussed in detail for the *Cuscuta* cases by Stefanović & Costea (2008). While

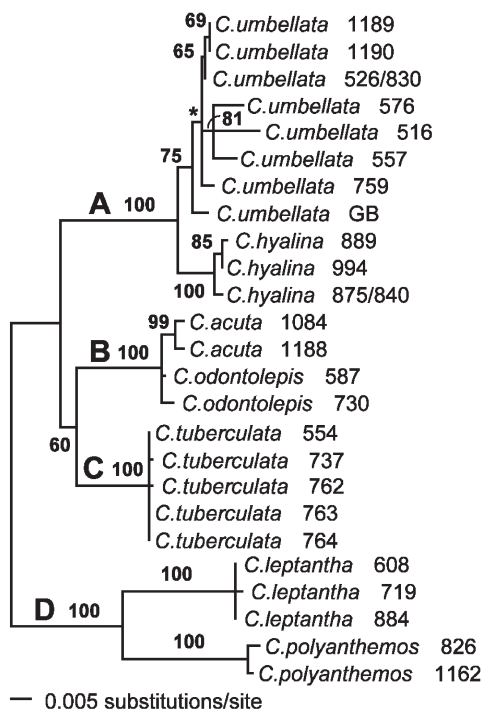


Fig. 3. Majority-rule consensus tree with mean branch lengths from the Bayesian analysis of combined nuclear (ITS) and plastid (*trnL-F*) data showing the backbone relationships among species of the *Cuscuta umbellata* complex. Four major lineages are labeled A–D. Bootstrap values are indicated for nodes supported $\geq 50\%$. The asterisk indicates a branch with posterior probability < 0.95 ; all other branches have posterior probability ≥ 0.95 . Numbers following species names correspond to DNA accessions (see Appendix 1).

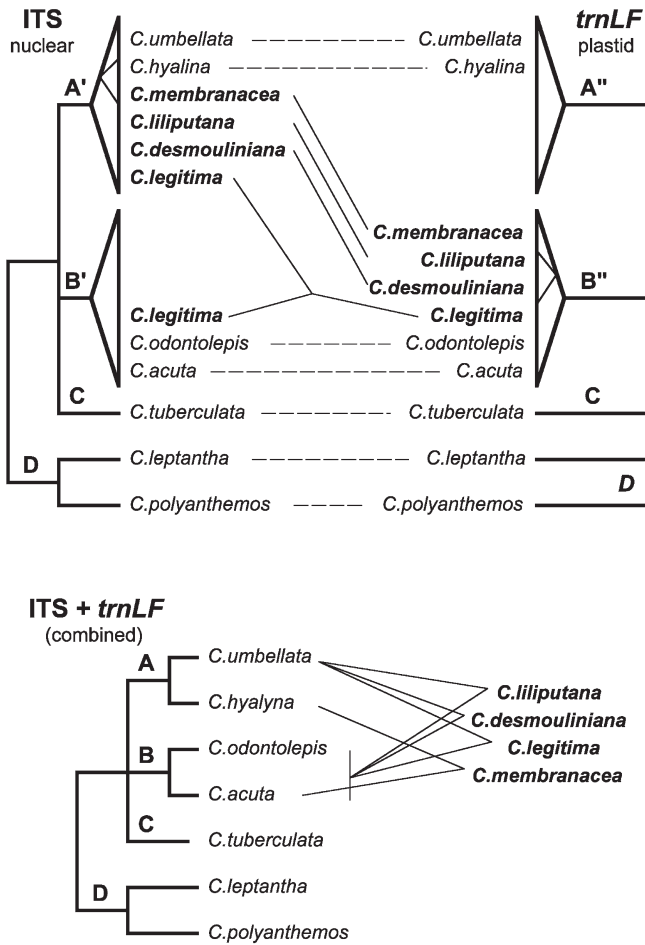


Fig. 4. Schematic overview of phylogenetic relationships within the *Cuscuta umbellata* complex deduced from separate and combined analyses of nuclear and plastid sequences. Four major lineages are labeled A–D. For simplicity, only the strongly supported backbone nodes are shown as resolved. Solid lines illustrate the conflicting topologies between nuclear and plastid data indicative of hybrid origin of involved species (in bold). Dashed lines connect species whose topology is congruent between the two datasets. The combined topology depicts inferred parental species of putative hybrid taxa.

a disproportionately large number of the reported horizontal gene transfer (HGT) events involve parasitic plants (Davis & Wurdack, 2004; Mower & al., 2004; Nickrent & al., 2004; Davis & al., 2005), the discordances discussed here are at lower phylogenetic levels, where hybridization is expected to occur, and they involve nrDNA and ptDNA, for which there are virtually no known cases of HGT in land plants despite extensive amounts of available data (Rice & Palmer, 2006).

Paralogy (i.e., gene duplication followed by differential deletion) is also not likely to be the cause for the topological discrepancy between plastid and nuclear phylogenies detected in our study. Although nrDNA is present in multiple copies in plants, it generally evolves in unison through the process of concerted evolution (Zimmer & al., 1980; Buckler & al., 1997). However, despite our intensive cloning efforts, ITS sequences from putative hybrids either were not different within a given species or showed only limited amount of polymorphism. When present, the paralogous sequences were most closely related to each other, consistent with either relatively recent duplication events or minor DNA polymerase errors rather than with the divergent ancestral paralogs (Stefanović & al., 2007; Stefanović & Costea, 2008). The only significant departure from this was found in the *C. legitima* case. In this species, almost all accessions yielded two substantially distinct sets of clones, phylogenetically segregated into two clades (A and B in Figs. 2 and 4). The presence of two ribotypes is interpreted here as an additional evidence for the hybrid origin of this species. The additive pattern observed in nrDNA arrays of *C. legitima* is likely due to a recent hybridization event following which concerted evolution did not have time to homogenize towards one of the parental types (e.g., Sang & al., 1995 in *Paeonia*; Ainouche & Bayer, 1997 in *Bromus*; reviewed by Álvarez & Wendel, 2003). On the other side, the *trnL-F* sequences used here are located in the large single-copy region of *Cuscuta* plastids (Funk & al., 2007; McNeal & al., 2007) and hence are likely to be orthologous. No polymorphism for this ptDNA region was observed within any individual and very little, if any, polymorphism was seen among different individuals from the same species.

Lineage sorting represents potentially the strongest alternative explanation but for the cases presented here we still

Table 2. Results of the Shimodaira-Hasegawa (SH) tests for comparison between highly supported yet incongruent topologies recovered from nuclear and plastid datasets of the *Cuscuta umbellata* species complex. Probabilities below 0.05 (i.e., tree topology rejected as significantly worse) are indicated in bold.

Dataset	Constrained topology	Length	Length difference	SH test
Nuclear (ITS)	Optimal tree (Figs. 2, 4; left)	376	Best	1.000
	<i>C. membranacea</i> constrained to clade B	394	18	0.001
	<i>C. legitima</i> constrained to clade B	398	22	<0.001
	<i>C. liliputana</i> and <i>C. desmouliniana</i> constrained to clade B	393	17	0.006
	<hr/>			
Plastid (<i>trnL-F</i>)	Optimal tree (Figs. 2, 4; right)	48	Best	1.000
	<i>C. membranacea</i> constrained to clade A	53	5	0.025
	<i>C. legitima</i> constrained to clade A	54	6	0.014
	<i>C. liliputana</i> and <i>C. desmouliniana</i> constrained to clade A	53	5	0.025

favor hybridization for a number of reasons. First, because the plastid genome is uniparentally inherited and haploid, the plastid haplotype tree has a substantially higher probability of shorter coalescence time, leading to the relatively rapid elimination of any polymorphism (Moore, 1995). Second, like the majority of *Cuscuta* species (Yuncker, 1932), the four species of putative hybrid origin included in our study have relatively narrow geographic distributions. Of these, *C. membranacea* is the only species represented by a single individual because it is known only from its type locality. By contrast, each of the other three putative hybrids are represented by multiple individuals (3–5), spanning their respective distribution ranges. Yet, in all cases, the results were identical (or nearly so) among all the individuals included. Third, perhaps as a result of the multiple hybridization events, hybrids and their putative parental species are so closely allied that their morphological intermediacy is readily apparent (see below for details).

Phylogenetic analyses of additional, independently inherited sequence data, such as low-copy nuclear genes, as well as critically needed cytological information (the chromosome number is known only from *C. hyalina*—Vij & al., 1974) will help to further support the extent and importance of hybridization in the evolution of *Cuscuta*. However, in light of currently available molecular phylogenetic evidence for hybrid origins we discuss below the delineation of species within this complex.

Basis for species delimitation. — Due to the taxonomic difficulty of this clade, neither morphological nor molecular data alone allowed a corroboration of taxon boundaries. In some instances we had to make a decision based on one type of data alone. For example, in the cases where taxa were known from historical collections only (e.g., *C. lacerata*, *C. fasciculata*, *C. umbellata* var. *desertorum*), and DNA could not be extracted, a conclusion had to be reached solely based on morphology. In contrast, the evolutionary relationships and putative cases of hybridization inferred from molecular data lead us to maintain some species in the absence of a clear morphological distinctiveness. This is exemplified by the case of *C. membranacea* and *C. acuta*, two species from South America that are not only very similar morphologically to one another, but also difficult to separate from the morphotype of *C. umbellata* var. *umbellata* that grows on the Cape Verde islands, the Caribbean Islands and the N to NE coast of South America (see below).

Redefinition of *Cuscuta umbellata* and *C. desmouliniana*. — The delimitation of *C. umbellata* represents the prerequisite for the taxonomy of the entire clade. Kunth's protologue (Bonpland & al., 1818), and later Choisy (1841) referred to a plant collected from central Mexico by Humboldt and Bonpland. Subsequently, Engelmann (1859) expanded *C. umbellata* to include other forms "from many localities along the United States and Mexican boundary line from northern Mexico, and from the Antilles". He also included here as a variety ("β?") *C. desertorum*, described on a herbarium specimen by Martius from Brazil, expanding therefore the geographical distribution of *C. umbellata* to South America (Engelmann, 1859). Yuncker (1921) increased even more the complexity of *C. umbellata* by adding two more varieties: *C. umbellata* var. *reflexa* from southern U.S.A. and northern Mexico and *C. umbellata* var.

dubia from Sonora. In this study, we show that *C. umbellata* circumscribed with four varieties is polyphyletic and that only Engelmann's delimitation (1859) reflects the reconstructed phylogenetic relationships among taxa.

Cuscuta umbellata var. *reflexa* was described as a variety of *C. californica* from Texas by Coulter (1890) and was later transferred to *C. umbellata* by Yuncker (1921), who maintained this combination until 1965 when he reconsidered and merged it with the type variety (Yuncker, 1965). Consequently, subsequent North American overviews (e.g., Kartesz, 1999; USDA-NRCS, 2010) did not differentiate between the two entities, and *C. umbellata* var. *reflexa* has been generally considered synonymous to the type variety. However, our results have determined that *C. umbellata* var. *umbellata* and var. *reflexa* segregate in different clades of the complex and have different evolutionary histories (Figs. 2 and 4). In addition, *C. umbellata* var. *reflexa* differs from var. *umbellata* in larger flowers with acuminate calyx and corolla lobes (Fig. 5). Based on its molecular and morphologic distinction, *C. umbellata* var. *reflexa* is redefined as a species, and since the binomial *C. reflexa* is not available (*C. reflexa* Roxb., Pl. Coromandel 2: 3, pl. 104. 1798), we prefer to describe it as a new species, *C. legitima* (Fig. 5A–D).

Cuscuta umbellata var. *dubia* was described by Yuncker (1921, 1932, 1965) from a single, poor specimen collected in Sonora and is characterized by a calyx with revolute lobe bases and more or less angled sinuses. Revolute bases of calyx lobes can also be observed in typical *C. desmouliniana*, but the angled feature is not as conspicuous because the calyx lobes are usually narrower. Molecular data together with other morphological features (e.g., infrastaminal scales shorter than the corolla tube, papillae on both sides of corolla lobes, and the presence of stomata on the calyx) firmly indicate that *C. umbellata* var. *dubia* is within the variation range of *C. desmouliniana*, where we transfer it without further recognition at infraspecific level.

We could not reach a final decision about the taxonomic identity of *C. umbellata* var. *desertorum* described by Engelmann from Brazil (Piauí and Ceara) because of the poor quality of the only two herbarium specimens available (Appendix 2). Morphologically, this taxon appears to be quite similar to the *C. umbellata* plants encountered in Cape Verde islands, the Caribbean Archipelago, and N to NE littoral of South America, which are slightly different from those growing in Mexico and the U.S.A. This Atlantic form of *C. umbellata* has few-flowered, loose inflorescences, and often plants become dark-brownish upon drying (the U.S.-Mexican *C. umbellata* has many-flowered, dense inflorescences and plants commonly remain straw-yellow when dried). The only difference between the Atlantic form and *C. umbellata* var. *desertorum* resides in the more reduced, with fewer fimbria or rarely bifid infrastaminal scales encountered in the latter. Engelmann himself mentioned that a specimen of *C. umbellata* from Antigua (*Wullschlagel* 352, MO) was very similar to *C. umbellata* var. *desertorum* (Engelmann, 1859). In view of this unresolved issue, we have not distinguished a new variety of *C. umbellata* from the Pacific, and we maintained *C. umbellata* var. *desertorum* until more plants can be collected and studied from Brazil.

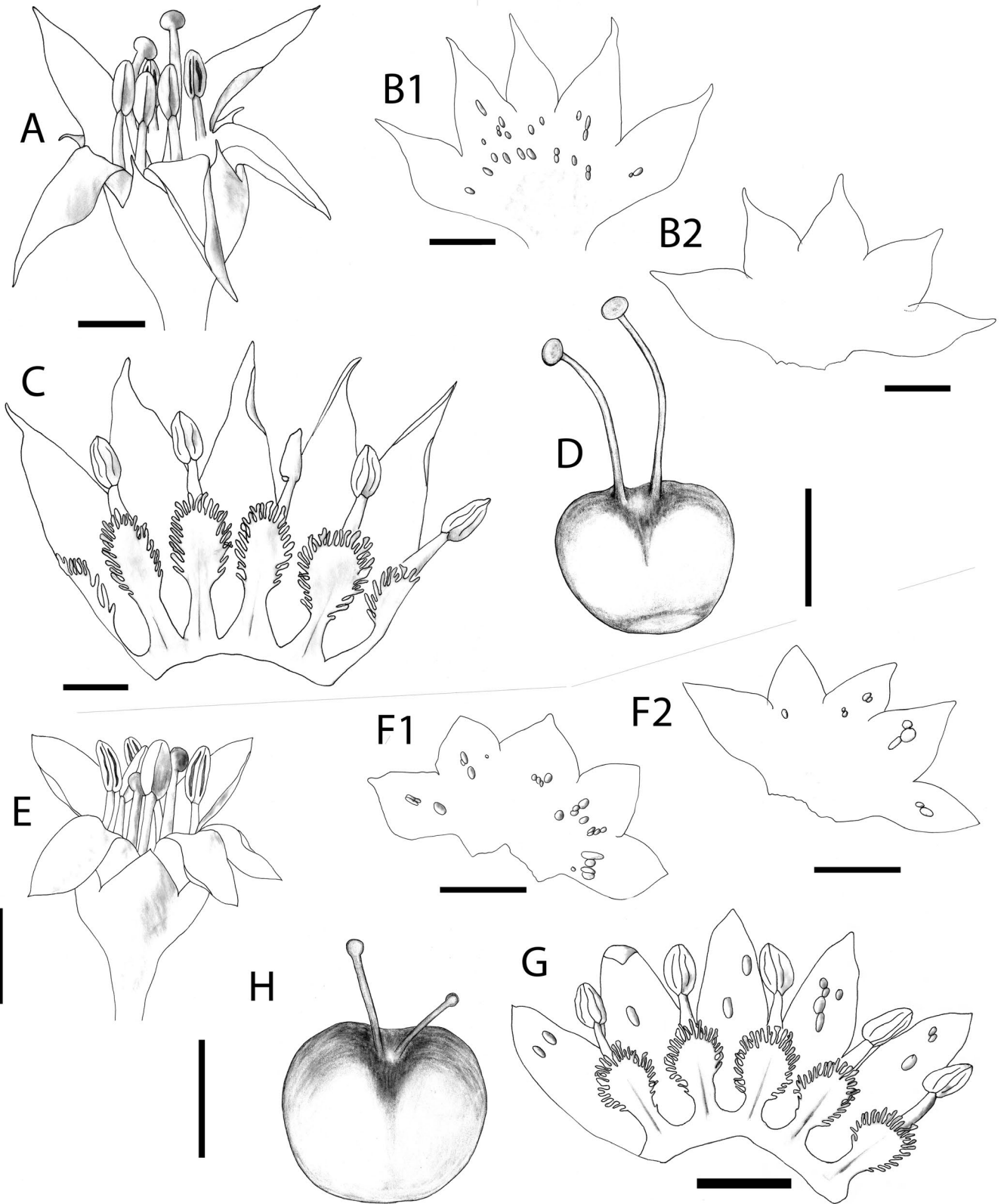


Fig. 5. A–D, *Cuscuta legitima*: A, Flower; B1–B2, calyx variation; C, corolla dissected; D, gynoecium. E–H, *C. umbellata* (var. *umbellata*): E, Flower; F1–F2, calyx variation; G, corolla dissected; H, gynoecium. Bars: 1 mm.

Late and occasionally irregular dehiscence of capsules is another subtle morphological difference that distinguishes the Atlantic form of *C. umbellata* from those that grow in Mexico and the U.S.A., in which capsules dehisce by a regular circular line even when they are still immature. The late dehiscence of capsules represents also the only character that separates the Atlantic *C. umbellata* from the morphologically very similar *C. acuta* and *C. membranacea* (see below). The decision to maintain these three species distinct is based on the evolutionary relationships observed among them (Figs. 2–3) and the complex reticulation patterns inferred (Fig. 4).

Cuscuta fasciculata, known from a single specimen (Yuncker, 1932), is morphologically identical to typical *C. umbellata*, and the former name is therefore considered a heterotypic synonym.

***Cuscuta acuta* and *C. membranacea*.** — Since its description in 1859, *C. acuta* has been largely considered endemic to Galapagos Islands (Engelmann, 1859; Yuncker, 1921, 1932; Hunziker, 1949). Austin (1982) reported first *C. acuta* from mainland Ecuador and observed that “*C. acuta* is very similar to *C. membranacea* [...] and perhaps a single species is involved” (Austin, 1982). The doubt about the distinctiveness of the two species was prompted by the fact that the mainland Ecuador collection cited by Austin as a voucher of *C. acuta* (*Asplund 5136*, S, US) had been identified by Yuncker as “*C. membranacea*” (S) or “*C. membranacea* vel. aff.” (US). As pointed out by Yuncker’s identification (keep in mind that *C. membranacea* was described by Yuncker, 1939), these *C. acuta* plants are morphologically different from the “typical” *C. acuta* found in the Galapagos in that they exhibit some common features with *C. membranacea*. Similarly to *C. membranacea*, these dodders display a globose capsule with a small interstyler aperture and erect styles (*C. acuta* has a globose-depressed capsule with a relatively large interstyler aperture and divergent styles). Notwithstanding their apparent intermediacy, these mainland Ecuadorian *C. acuta* plants are slightly different morphologically from both *C. membranacea* and the “typical” *C. acuta* in their larger flowers, which remind more of *C. legitima*. We have found additional specimens of this continental *C. acuta* from Peru, where it has been generally identified as “*C. umbellata*”. The difficulty to distinguish *C. acuta* and *C. membranacea* morphologically certainly makes the idea of a single species appealing, but this approach is unsupported by molecular data. *Cuscuta membranacea* is morphologically so close to *C. acuta* because it is most likely a hybrid species, and *C. acuta* is the putative maternal progenitor (see the plastid haplotype tree; Fig. 2, right; Fig. 4).

■ TAXONOMIC TREATMENT

Identification Key for species of the *Cuscuta umbellata* clade

- 1. Capsules indehiscent 2
- 1. Capsules dehiscent, irregularly dehiscent at the base or opening late. 3

- 2. Flowers 2.5–3.6(–4.0) mm; calyx 1.6–2.3 mm; infrastaminal scales uniformly dense-fringed; styles slightly subulate at the base 1. *C. acuta*
- 2. Flowers 2.0–2.8 mm; calyx 1.2–1.6 mm; infrastaminal scales distally fringed; styles evenly filiform 8. *C. membranacea*
- 3. Calyx and corolla lobes lacerate. 4. *C. lacerata*
- 3. Calyx and corolla lobes entire 4
- 4. Infrastaminal scales absent or represented by scarcely dentate ridges 3. *C. hyalina*
- 4. Infrastaminal scales present, well developed, rarely bifid or with a few fimbria 5
- 5. Corolla tube cylindrical. 6
- 5. Corolla tube campanulate. 10
- 6. Inflorescences dense, paniculiform-glomerulate; calyx lobes basally overlapping; capsules 2.9–4.0 × 3.0–3.5 mm, not translucent; seeds 1.00–1.25 × 0.65–0.80 mm 9. *C. odontolepis*
- 6. Inflorescence loose, umbelliform or racemiform; calyx lobes not basally overlapping; capsules 1.3–2.2 × 1.5–2.3 mm, translucent; seeds 0.6–0.9 × 0.3–0.8 mm 7
- 7. Flowers 5.0–7.5 mm; corolla lobes ca. 1/2 the tube 10. *C. polyanthemus*
- 7. Flowers 2.5–4.5(–5.0) mm; corolla lobes equaling the tube 8
- 8. Flowers 5-merous; calyx lobes carinate; corolla lobes erect. 11. *C. tuberculata*
- 8. Flowers (3–)4-merous; calyx lobes not carinate; corolla lobes spreading to reflexed. 9
- 9. Calyx equaling corolla tube; infrastaminal scales bridged at 0.1–0.3 mm 7. *C. liliputana*
- 9. Calyx 1/3–1/2 of the corolla tube; infrastaminal bridged at 0.4–0.8 mm 6. *C. leptantha*
- 10. Infrastaminal scales ca. 3/4 of the corolla tube 2. *C. desmouliniana*
- 10. Infrastaminal scales equaling or slightly longer than the corolla tube 11
- 11. Flowers 4.0–5.5(–6.0) mm; calyx lobes acuminate 5. *C. legitima*
- 11. Flowers 2–3 mm; calyx lobes obtuse to acute 12. *C. umbellata*

1. *Cuscuta acuta* Engelm. in Trans. Acad. Sci. St. Louis 1: 497. 1859 – Type: Ecuador, Galapagos Islands, Chatham [San Cristobal] Island, 1853, *Andersson s.n.* (holotype: K; isotypes: GH, MO, IT).

Stems slender, yellow-orange. *Inflorescences* dense-umbelliform, confluent; pedicels 0.6–3.0 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 1.5–2.8 mm long, triangular-ovate, margins entire, apex acuminate. *Flowers* 5-merous, 2.5–3.6(–4.0) mm, membranous, white when fresh, creamy-brown when dried; papillae absent, laticifers evident in the bracts, calyx, corolla, tips of infrastaminal scale fimbriae, and ovary, isolated or in rows, ovoid to elongate; calyx 1.6–2.3(–2.6) mm, straw-yellow to brown, not reticulate or shiny, campanulate, longer than corolla tube, divided ca. 2/3 the length, tube 0.4–0.8 mm, lobes (unequal) 0.7–1.5 mm,

not basally overlapping, ovate-triangular, not carinate, margins entire, apex acuminate; *corolla* 1.8–3.3(–3.8) mm, tube 0.9–1.7 mm, campanulate, lobes 0.9–1.9 mm, initially erect, later reflexed, ca. as long or slightly longer than the tube, ovate-lanceolate, margins entire, apex acute to acuminate, straight; *stamens* exerted, shorter than the lobes, anthers 0.33–0.40 × 0.20–0.25 mm, broadly ovate to oblong, filaments 0.4–0.7 mm; *infrastaminal scales* extremely thin, 0.9–1.7 mm long, equaling the tube, bridged at 0.15–0.30 mm, obovate to oblong, uniformly dense-fringed, fimbriae 0.15–0.30 mm; *styles* 0.4–1.1 mm, shorter or equaling the ovary, slightly subulate at the base, filiform in the rest. *Capsules* indehiscent, 1.7–2.5 × 0.9–1.4 mm, globose-depressed, thickened around the moderate interstyler aperture, translucent, surrounded by the withered corolla. *Seeds* 4 per capsule, 0.7–1.2 × 0.7–1.0 mm, subround to round.

Distribution and ecology. – Galapagos Islands and the Pacific Coast of Ecuador and Peru; flowering Jan.–July; elevation 40–160 m; hosts: *Alternanthera*, *Coldenia*, *Boerhavia*, *Euphorbia*, *Ipomoea*, *Pectis*, *Portulaca*, *Rhynchosia* and *Tribulus*.

2. *Cuscuta desmouliniana* Yunck. in Illinois Biol. Monogr. 6(2–3): 40. 1921 ≡ *C. desmouliniana* Yuncker var. *attenuiloba* Yunck. in Illinois Biol. Monogr. 6 (2–3): 41. 1921 – Type: Mexico. Sonora, hills near Altar, 26 Aug 1884, Pringle 105 (holotype: NY; isotypes: G, GH, IND, MEXU, MO, NY, US). Yuncker (1921: 41) mentioned that “[t]his specimen [Pringle 105] seems to be a mixture of the following two distinguishable varieties [*typica*’ and *attenuiloba*’].” Figure 1F–I.

= *Cuscuta umbellata* var. *dubia* Yunck. in Illinois Biol. Monogr. 6(2–3): 43. 1921 – Type: Mexico. Sonora, Guayamas, 22 Feb 1904, Palmer 1209 (holotype: US).

Stems slender, yellow-orange. *Inflorescences* loose, umbellate, often confluent; pedicels 1–5 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.6–1.0 mm long, ovate-lanceolate, margins entire, apex acute. *Flowers* 5-merous, 2–3 mm, membranous, white when fresh, creamy-white when dried, papillae usually present on the pedicels, calyx, abaxial and adaxial epidermis of corolla lobes, and sometimes on the ovary/capsule; laticifers not visible or hardly so in the midveins of corolla lobes, elongate; *calyx* 0.6–1.2 mm, brownish-yellow, ± reticulate or shiny, campanulate, equaling or somewhat longer than the corolla tube, divided 1/3–1/2 the length, tube 0.25–0.50 mm, lobes 0.50–0.76 mm, not overlapping, triangular-ovate to lanceolate, weakly to distinctly carinate, with small dome-like multicellular projections on the midveins, margins irregular, ± revolute at the base and forming angled sinuses especially when lobes are triangular ovate, apex acute to acuminate somewhat reflexed; *corolla* 1.5–2.9 mm, tube narrow-campanulate, 0.8–1.5 mm, lobes 1.0–1.5 mm, initially erect, later spreading or reflexed, slightly longer than the tube, lanceolate, margins entire to irregular, sometimes involute upon drying and appearing very narrow, apex acute, ± incurved; *stamens* short-exserted, shorter than corolla lobes, anthers 0.4–0.6 × 0.2–0.3 mm, ovate to oblong, filaments 0.4–0.7 mm; *infrastaminal scales* 0.6–1.0 mm long, ca. 3/4 of the corolla tube, bridged at 0.1–0.2 mm, oblong to spatulate,

short-fringed, fimbriae 0.05–0.15 mm; *styles* 1.2–2.1 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.2–2.0 × 0.9–1.7 mm, globose to globose-depressed, slightly thickened and risen, or with a few protuberances around the inconspicuous interstyler aperture, translucent, capped by the withered corolla. *Seeds* 2–4 per capsule, 0.75–0.90 × 0.70–0.80 mm, subrotund to broadly elliptic.

Distribution and ecology. – Mexico: Baja California and Sonora; flowering Aug.–Sep.; Dec.–Mar.; elevation 30–300 m; hosts: usually on *Chamaesyce*, rarely on *Boerhavia* or *Pectis*.

3. *Cuscuta hyalina* Roth, Nov. Pl. Sp.: 100. 1821 – Type: India “orientale,” Heyne s.n. (holotype: B, apparently destroyed; isotype: K).

= *C. epitribulum* Schinz in Bull. Herb. Boissier, sér. 2, 1: 880. 1901 – Type: South West Africa, Namibia, Okomita, Dinter 506 (holotype: Z).

Stems slender, yellow-orange. *Inflorescences* dense to loose, umbelliform, confluent; pedicels 2–4 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 2.0–3.6 mm long, narrow triangular lanceolate, margins entire, apex long-acuminate. *Flowers* 5-merous, 2.5–4.2 mm, membranous, creamy-white when fresh, creamy-yellow when dried; papillae absent, laticifers evident in the bracts, calyx, corolla lobes, and ovary, isolated, ovoid to elongate; *calyx* 2.0–3.2 mm, straw-yellow, not reticulate, slightly shiny, campanulate, much longer than corolla tube, divided 1/2–2/3 the length, tube 0.9–1.4 mm, lobes 1.5–2.0 mm, not basally overlapping, triangular-lanceolate, not carinate, margins entire, apex acuminate, ± reflexed; *corolla* 2.3–4.0 mm, tube 1.0–1.4 mm, campanulate, lobes 1.5–2.5 mm, initially erect, later reflexed, longer than the tube, triangular-lanceolate, margins entire, apex acuminate, straight; *stamens* exerted, shorter than the lobes, anthers 0.4–0.6 × 0.3–0.4 mm, elliptic, filaments 0.5–0.7 mm; *infrastaminal scales* absent or represented by scarcely dentate ridges; *styles* 0.9–2.0 mm, equaling or longer than the ovary, evenly filiform. *Capsules* circumscissile, 2.0–3.0 × 2.0–2.5 mm, globose, thickened and slightly risen around the inconspicuous interstyler aperture, translucent, surrounded by the withered corolla. *Seeds* 2–4 per capsule, 1.3–1.5 × 0.9–1.1 mm, elliptic.

Note. – *Cuscuta hyalina* var. *nubiana* Yunck. in Mem. Torrey Bot. Club 18(2): 236. 1932 [Type: Sudan, Gef. bei Suakin. Nubische Küste, Jun 1864, Schweinfurth 964 (isotype: K)] has flowers with scales occasionally represented by ridges.

Distribution and ecology. – Asia: Pakistan and India; Africa: Ethiopia, Sudan, Botswana, Zimbabwe, Uganda, Kenya, Ruanda, Burundi, South Africa, Namibia; flowering July–Nov.; Dec.–Mar.; 700–1500 m; hosts: *Cyperus bulbosus*, *Portulaca* sp., *Tribulus terrestris*, and *Zaleya pentandra*.

4. *Cuscuta lacerata* Yunck. in Illinois Biol. Monogr. 6 (2–3): 44. 1921 – Type: Mexico. Oaxaca, Cuicatlan, 15 Jul 1895, L.E. Smith 406 (holotype: GH).

Stems slender, yellow-orange. *Inflorescences* loose, umbellate, often confluent; pedicels 1.5–4.0 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.6–1.2 mm long, lanceolate, margins entire or irregularly dentate, apex

acuminate. *Flowers* 5-merous, 3.0–4.4 mm, membranous, white when fresh, creamy-white when dried, papillae absent; laticifers visible in the calyx and corolla lobes, isolated, ovoid to elongate; *calyx* 1.8–2.4 mm, yellow, \pm reticulate or shiny, campanulate, longer than the corolla tube, divided 1/4–1/3 the length, tube 0.3–0.6 mm, lobes 1.5–1.8 mm, not overlapping, lanceolate, not carinate, not forming angled sinuses, margins with a few irregular teeth (especially toward apex), apex long acuminate, reflexed; *corolla* 2.8–4.2 mm, tube 1.0–1.4 mm, campanulate, lobes 2.0–1.6 mm, initially erect, later spreading or reflexed, longer than the tube, linear, margins with a few large, irregular teeth, sometimes involute upon drying and appearing very narrow, apex long-acuminate, capillary; *stamens* exerted, shorter than corolla lobes, anthers 0.5–0.6 \times 0.2–0.3 mm, ovate to oblong, filaments 0.6–1.0 mm; *infrastaminal scales* 1.0–1.6 mm long, equaling or longer than corolla tube, bridged at 0.16–0.25 mm, oblong-spathulate, medium-fringed, fimbriae 0.12–0.25 mm; *styles* 1.8–2.4 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.2–1.6 \times 1.0–1.7 mm, globose, with a ring of protuberances around the inconspicuous interstyler aperture, translucent, capped by the withered corolla. *Seeds* 1–4 per capsule, 0.9–1.0 \times 0.8–0.9 mm, angled, subrotund.

Distribution and ecology. – Known only from the type collection from Cuicatlan, Mexico; flowering July; elevation and host unknown.

5. *Cuscuta legitima* Costea & Stefanović, sp. nov. – Type: Mexico. Sonora: Northwest side of Río Yaqui at MEX 15 near Esperanza, ca. 9 km north of Ciudad Obregón, 27°35'45" N 109°56' W, ca. 40 m elevation, locally common parasite on *Boerhavia coccinea* (Nyctaginaceae), flowers white, stems yellow, 10 Sep 1994, *Van Devender 94-458 & al.* (holotype: ARIZ; isotypes: ASU, MEXU, UC, UCR, WLU). Figure 5A–D.

= *Cuscuta californica* var. *reflexa* J.M. Coulter in Contr. U.S. Natl. Herb. 1: 45. 1890; 2: 295. 1892 \equiv *Cuscuta umbellata* var. *reflexa* (J.M. Coulter) Yunck. in Illinois Biol. Monogr. 6(2–3): 42. 1921 – Type: U.S.A. Texas, Roma, 1889, *Nealley 338* (holotype: US; isotype: GH).

Cuscutae umbellatae similis, sed flores 4.0–5.5(–6.0) mm longi; calyx 2.5–3.2 mm longus, lobis acuminatibus; corolla 3.8–5.2(–5.6) mm longa. *Cuscutae acutae* et *C. membranacea* similis, sed floribus majoribus et capsulae dehiscentibus.

Stems slender, yellow-orange. *Inflorescences* dense to loose, umbelliform, confluent; pedicels 2–10 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 2.0–3.6 mm long, broadly triangular-ovate, margins entire, apex acuminate. *Flowers* 5-merous, 4.0–5.5(–6.0) mm, membranous, white when fresh, creamy-white when dried; papillae absent, laticifers evident in the bracts, calyx, corolla, tips of infrastaminal scale fimbriae, and ovary, isolated, ovoid; *calyx* 2.5–3.2 mm, straw-yellow, finely reticulate, slightly shiny, campanulate, longer than corolla tube, divided ca. 2/3 the length, tube 0.6–1.0 mm, lobes 1.5–2.2 mm, not basally overlapping, ovate-lanceolate, not carinate, margins entire, apex acuminate; *corolla* 3.8–5.2(–5.6) mm, tube 1.6–2.1 mm, campanulate, lobes 1.8–3.0 mm, initially erect,

later reflexed, longer than the tube, linear-lanceolate, margins entire, apex acuminate, straight; *stamens* exerted, shorter than the lobes, anthers 0.50–0.70 \times 0.24–0.36 mm, elliptic to oblong, filaments 0.6–1.0 mm; *infrastaminal scales* 1.8–2.2 mm long, equaling or slightly longer than the tube, bridged at 0.2–0.4 mm, spathulate to obovate, uniformly dense-fringed, fimbriae 0.2–0.5 mm; *styles* 0.9–2.5 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 2–3 \times 1–2 mm, depressed, irregularly thickened and slightly risen around the inconspicuous interstyler aperture, translucent, surrounded or capped by the withered corolla. *Seeds* 2–4 per capsule, 0.9–1.2 \times 0.8–0.9 mm, broadly elliptic to subround.

Distribution and ecology. – U.S.A. and Mexico; flowering Aug.–Nov.; elevation 40–1200 m; hosts: *Allionia*, *Amaranthus*, *Boerhavia*, *Chamaesaracha*, *Evolvulus*, *Kallstroemia*, *Salsola*, *Solanum*, *Tidestromia*, *Trianthema*, *Tribulus*.

6. *Cuscuta leptantha* Engelm. in Trans. Acad. Sci. St. Louis 1: 489. 1859 – Type: U.S.A. Texas, Oct 1849, *Wright 522* (holotype: MO; isotype: US). Figure 1D.

= *Cuscuta palmeri* S. Watson in Proc. Amer. Acad. Arts 24: 64. 1889 – Type: Mexico, Baja California, 1887, *Palmer 544* (holotype: NY; isotypes: US, GH).

Stems slender, yellow-orange. *Inflorescences* loose, umbellate, confluent; pedicels (1–)2–7 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.75–1.00 mm long, triangular ovate, margins entire, apex acute. *Flowers* 4-merous, 3.5–4.5(–5.0) mm, membranous, white when fresh, creamy-white when dried, papillae usually present on the pedicels and perianth; laticifers not visible; *calyx* 1.5–1.8 mm, straw-yellow, not reticulate or shiny, campanulate, 1/3–1/2 of the corolla tube, divided ca. 1/2 the length, the tube 0.5–0.8 mm, lobes 0.8–1.0 mm, not basally overlapping, triangular-ovate, not carinate, margins entire, apex acute; *corolla* 3–4 mm, tube 1.5–2.5 mm, cylindrical, lobes 1.5–2.0 mm, initially erect, later spreading or reflexed, as long as the tube, lanceolate, margins entire often involute upon drying and corolla lobes appearing narrow, apex acute, \pm cucullate; *stamens* short-exserted, shorter than corolla lobes, anthers 0.40–0.60 \times 0.35–0.45 mm, subround to broadly elliptic, filaments 0.3–0.6 mm; *infrastaminal scales* 1.3–2.1 mm long, ca. 1/2 of the corolla tube, bridged at 0.4–0.8 mm, oblong, uniformly short-fringed, fimbriae 0.05–0.15 mm; *styles* 1.2–2.1 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.5–2.0 \times 1.6–1.9 mm, globose, slightly thickened and risen or with a few protuberances around the inconspicuous interstyler aperture, translucent, capped by the withered corolla. *Seeds* 2–4 per capsule, 0.75–0.90 \times 0.70–0.80 mm, angled, subrotund to broadly elliptic.

Distribution and ecology. – U.S.A.: Texas, New Mexico; Mexico: Baja California, Sonora, Sinaloa; flowering Nov.–May; elevation 10–125 m; host: *Chamaesyce* sp.

7. *Cuscuta liliputana* Costea & Stefanović in Botany 86(8): 802. 2008 – Type: U.S.A. New Mexico, Sierra Co., 3 mi S of Hillsboro, 5500 ft, 9 Sep 1904, *O.B. Metcalfe 1290* (holotype: UNM; isotypes: ARIZ, MO, NMC, NY, UNM, WLU).

Stems slender, yellow to pale orange. *Inflorescences* loose, umbelliform; pedicels (1–)2–3(–5) mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.7–1.0 mm long, ovate-lanceolate, margins entire, apex acute. *Flowers* (3–)4-merous, 2.8–4.0 mm, fleshy, white when fresh, creamy when dried; papillae usually present on pedicels, calyx and corolla; laticifers hardly visible only in the midveins of the corolla lobes, elongate; *calyx* 1.3–1.7 mm, straw-yellow, somewhat reticulate and shiny, equaling the corolla tube, divided ca. 3/4 the length, tube 0.3–0.7 mm, cylindric, lobes 1.00–1.35 mm, not basally overlapping, ovate-triangular, not carinate but sometimes with multicellular protuberances bearing stomata on the midveins, apex acute to acuminate, margins entire; *corolla* 3.0–3.6 mm, tube 1.5–2.0 mm, cylindric, lobes 1.30–1.65 mm, initially erect, later spreading and reflexed, equaling the tube, lanceolate, margins entire, apex acute straight; *stamens* exerted, shorter than the lobes, anthers 0.35–0.50 × 0.20–0.35 mm, broadly to narrow elliptic, filaments 0.5–0.8 mm; *infrastaminal scales* 0.6–0.8 mm long, 1/4–1/2 of the corolla tube, bridged at 0.1–0.3 mm, truncate to slightly obovate, distally fringed, fimbriae 0.10–0.18 mm; *styles* 0.8–2.5 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.50–2.20 × 0.75–1.50 mm, globose to globose-depressed, thicken and slightly risen, or with 2–4 protuberances around the small interstylar aperture, translucent, capped by the withered corolla. *Seeds* 2–4 per capsule, 0.80–1.15 × 0.70–0.85 mm, subrotund to broadly elliptic.

Distribution and ecology. – U.S.A.: Southern New Mexico, Arizona, and SW Texas; flowering July–Nov.; Nov.–Feb.; elevation 30–1700 m; host: *Chamaesyce* sp.

8. *Cuscuta membranacea* Yunck. in Lilloa 4: 452. 1939 – Type: Argentina. Departamento Trancas, Tucumán, Tapia, 600 m, [the host is *Amaranthus muricatus*], 29 Nov 1918, Schreiter 983 (holotype: LIL).

Stems slender, orange. *Inflorescences* dense, umbelliform; pedicels 1–3 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 1.6–2.6 mm long, triangular-ovate, margins entire, apex acute to acuminate. *Flowers* (4–)5-merous, 2.0–2.8 mm, membranous, white when fresh, creamy-brown when dried; papillae absent, laticifers evident in the bracts, calyx, corolla, and ovary, isolated ovoid to elongate; *calyx* 1.2–1.6 mm, straw-yellow to brown, not reticulate or shiny, campanulate, longer than corolla tube, divided 1/3–1/2 the length, tube 0.4–0.8 mm, lobes [unequal] 0.7–1.2 mm, not basally overlapping, ovate-triangular, not carinate, margins entire, apex acute to apiculate; *corolla* 1.5–2.5 mm, tube 0.9–1.3 mm, campanulate, lobes 0.7–1.3 mm, initially erect, later reflexed, ca. as long as the tube, triangular-lanceolate, margins entire, apex acute to acuminate, initially cucullate, later straight; *stamens* exerted, shorter than the lobes, anthers 0.3–0.5 × 0.2–0.3 mm, broadly ovate to elliptic, filaments 0.4–0.7 mm; *infrastaminal scales* extremely thin, 0.9–1.4 mm long, equaling or longer than the tube, bridged at 0.15–0.30 mm, oblong, distally fringed, fimbriae 0.10–0.25 mm; *styles* 0.4–1.0 mm, shorter than the ovary, evenly filiform. *Capsules* indehiscent, 1.9–2.5 × 0.9–2.0 mm, globose with irregular thickenings raised around the small interstylar aperture, translucent, surrounded by the withered corolla.

Seeds 2–4 per capsule, 0.90–1.26 × 0.80–1.10 mm, subround to broadly elliptic.

Distribution and ecology. – Argentina; flowering: Nov.–Mar.; elevation 500–1575 m; hosts: *Amaranthus*, *Boerhavia*, *Gomphrena*, *Kallstroemia*, *Nicotiana*, *Portulaca*.

9. *Cuscuta odontolepis* Engelm. in Trans. Acad. Sci. St. Louis 1: 486. 1859 – Type: U.S.A. Arizona, Santa Rita Mts., south of Tucson, 1851–1852, Wright 1624 (holotype: MO; isotypes: GH, K, NY). Figure 1A.

Stems slender, yellowish. *Inflorescences* dense, paniculiform-glomerulate; pedicels to 1 mm; bracts 1 at the base of cymes and 0–1 at the base of pedicels/flowers, 2–3 mm long, subround to broadly ovate, margins entire, apex acute to short acuminate. *Flowers* 5-merous, 4.5–5.0 mm, membranous, white when fresh, creamy-white when dried; papillae present on the bracts, calyx and corolla lobes; laticifers poorly visible only in the corolla lobes, isolated, elongated; *calyx* 2.0–2.5 mm, straw-yellow, finely reticulate, not shiny, campanulate, 1/2–3/4 as long as the corolla tube, divided ca. 2/3, tube 0.5–0.9 mm, lobes 1.3–1.5 mm, ovate-triangular, outer 2 lobes auriculate, basally overlapping, not carinate, margins entire, apex acute to short acuminate; *corolla* 3.5–4.5 mm, tube 2.2–2.8 mm, cylindric, lobes 1.6–2.0 mm, initially erect, later reflexed, ovate-triangular, margins entire, basally overlapping, apex acute to short acuminate, straight; *stamens* barely exerted, shorter than corolla lobes, anthers 0.70–1.10 × 0.25–3.00 mm, oblong, filaments 0.3–0.7 mm; *infrastaminal scales* 2.0–2.5 mm long, 1/2 to equaling the corolla tube, bridged at 0.25–0.50 mm, oblong-spathulate to obovate, rounded, fringed in the distal 1/2, fimbriae 0.2–0.3 mm; *styles* 2.8–4.0 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, 2.9–4.0 × 3.0–3.5 mm, globose to globose-depressed, thickened and raised around the inconspicuous interstylar aperture, translucent, loosely surrounded and capped by the withered corolla. *Seeds* 3–4 per capsule, 1.00–1.25 × 0.65–0.80 mm, broadly elliptic.

Distribution and ecology. – U.S.A.: Arizona; Mexico: Chihuahua and Sonora; flowering Aug.–Oct.; elevation 900–1500 m; host: *Amaranthus* sp.

10. *Cuscuta polyanthemus* Schaffner ex Yunck. in Illinois Biol. Monogr. 6(2–3): 46. 1921 – Type: Mexico. Sinaloa, Culiacán, Schaffner s.n. (holotype: NY).

Stems slender, yellow. *Inflorescences* loose, corymbiform or umbellate, often confluent; pedicels 4–15(–20 mm); bracts 1 at the base of clusters, 0.8–1.2 mm long, ovate triangular to lanceolate, margins entire, apex acute. *Flowers* 5-merous, 5.0–7.5 mm, membranous, white both when fresh and dry, papillae present on the corolla lobes; laticifers not visible; *calyx* 2.0–2.5 mm, straw-yellow, not reticulate or shiny, cylindric campanulate, 1/4–1/3 of the corolla tube, divided ca. 1/3 the length, the tube 0.4–0.8 mm, lobes 1.5–2.0 mm, not basally overlapping, triangular-ovate to lanceolate, not carinate but with small protuberances on the midveins, margins entire, apex acute; *corolla* 5–7 mm, tube 4–5 mm, cylindric, lobes 2.0–2.5 mm, initially erect, later spreading or reflexed, 1/2 as long as the tube, triangular lanceolate, margins entire, apex acute to

acuminate; *stamens* short-exserted, shorter than corolla lobes, anthers 0.60–1.00 × 0.35–0.45 mm, oblong elliptic, filaments 0.5–0.8 mm; *infrastaminal scales* 2.0–2.5 mm long, bridged at 0.25–0.40 mm, 1/3–1/2 of the corolla tube, oblong, sparsely short-fringed, fimbriae 0.05–0.20 mm; *styles* 4–5 mm, much longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.0–2.0 × 0.8–1.2 mm, globose, thickened and risen around the inconspicuous interstylar aperture, translucent, capped by the withered corolla. *Seeds* 2–3 per capsule, 1.00–1.20 × 0.70–0.85 mm, subrotund to broadly ovate.

Distribution and ecology. – Mexico: Sonora and Sinaloa; flowering Aug.–Sep.; elevation ca. 635 m; host: *Chamaesyce* sp.

11. *Cuscuta tuberculata* Brandege in Univ. Calif. Publ. Bot. 3: 389. 1909 – Type: Mexico, 6 Mar 1889, *Brandegee s.n.* (holotype: UC). Figure 1E.

Stems filiform, yellow-orange. *Inflorescences* loose, umbelliform or racemiform, confluent; pedicels 2–3(–5) mm; bracts 1 at the base of clusters, usually absent at the base of peduncles, 0.50–0.75 mm long, ovate-lanceolate, margins entire, apex acute. *Flowers* 5-merous, 2.5–4.0 mm, membranous, white-creamy when fresh, creamy when dried; papillae present especially at the base of the corolla tube, laticifers barely visible in the corolla, isolated, ovoid to elongated; *calyx* 0.5–1.5 mm, yellow, not or finely reticulate, ± glossy, campanulate-angular, 1/3–1/2 as long as the corolla tube, divided almost to the base, tube 0.2–0.5 mm, lobes 1.0–1.3 mm, not basally overlapping, triangular to lanceolate, carinate and with multicellular protuberances bearing stomata on the midveins, margins entire, acute to acuminate; *corolla* 2.0–3.5 mm, tube 1.5–2.2 mm, cylindrical, lobes 1.2–2.0 mm, erect, about equaling the tube, triangular lanceolate, margins entire, apex acute, straight; *stamens* barely exserted, shorter to almost equaling corolla lobes, anthers 0.50–0.80 × 0.25–0.30 mm, ovate to oblong, filaments 0.4–0.7 mm; *infrastaminal scales* 0.5–1.0 mm long, ca. 1/2 the length of the corolla tube, bridged at 0.3–0.5 mm, ovate, uniformly short-fringed, fimbriae 0.05–0.15 mm; *styles* 1.5–3.0 mm, longer than the ovary, evenly filiform. *Capsules* circumscissile, globose, 1.3–2.2 × 1.0–2.3 mm, slightly thickened and risen around the small interstylar aperture, translucent, capped by the withered corolla. *Seeds* usually 4 per capsule, 0.6–0.9 × 0.3–0.5 mm, elliptic-oblong.

Distribution and ecology. – U.S.A.: Arizona and New Mexico; Mexico: Baja California and Sonora; flowering Aug.–Nov.; elevation 70–700 m; host usually *Boerhavia*, rarely *Amaranthus* and genera of Euphorbiaceae.

12. *Cuscuta umbellata* Kunth, Nov. Gen. Sp. Pl. 3 [folio]: 95. 1818 – Type: [Mexico.] *Crescit in Nova Hispania, inter Querretaro et Salamanca, Humboldt s.n.* (lectotype: MO, designated by Yuncker, 1932; isolectotype: P). Figures 1B–C and 5E–H.

= *C. fasciculata* Yunck. in Mem. Torrey Bot. Club 18: 240. 1932 – Type: U.S.A. New Mexico, Santa Fe, 26 Jul 1918, *Bro. Bertraud 48* (holotype: US; isotype: UNM).

Stems slender, yellow-orange. *Inflorescences* dense to loose, umbelliform, confluent; pedicels 2–10 mm; bracts 1

at the base of clusters, usually absent at the base of pedicels, 0.5–2.0 mm long, triangular-ovate, margins entire, apex acute. *Flowers* 5-merous, 2–3 mm, membranous, white when fresh, creamy-white or dark brown when dried; papillae sometimes present but only on the adaxial face of corolla lobes; laticifers evident in the bracts, calyx, corolla, tips of infrastaminal scale fimbriae, and ovary, isolated, ovoid; *calyx* 0.8–1.4 mm, straw-yellow, finely reticulate, slightly shiny, campanulate, equaling the corolla tube, divided ca. 2/3 the length, tube 0.25–0.60 mm, lobes 0.5–0.9 mm, not basally overlapping, broadly triangular-ovate, not carinate, margins entire, apex obtuse to acute, initially cucullate, later straight; *corolla* 2.0–2.5 mm, tube 0.6–1.2 mm, campanulate, lobes 0.8–1.5 mm, initially erect, later reflexed, equaling or slightly longer than the tube, oblong to lanceolate, margins entire, apex obtuse to acute, straight; *stamens* exserted, shorter than the lobes, anthers 0.40–0.60 × 0.24–0.30 mm, elliptic to oblong, filaments 0.4–0.7 mm; *infrastaminal scales* 0.8–1.2 mm long, equaling or slightly longer than the tube, bridged at ca. 0.1 mm, subspathulate to obovate, uniformly dense-fringed, fimbriae 0.15–0.32 mm; *styles* 0.8–1.7 mm, equaling or longer than the ovary, evenly filiform. *Capsules* circumscissile, 1.0–2.5 × 0.5–1.2 mm, depressed, irregularly thickened and slightly risen around the inconspicuous interstylar aperture, translucent, surrounded or capped by the withered corolla. *Seeds* 4 per capsule, 0.80–1.20 × 0.65–0.80 mm, broadly elliptic to subround.

Note. – *Cuscuta umbellata* var. *desertorum* Engelm. in Trans. Acad. Sci. St. Louis 1(3): 488. 1859, differs in having more reduced infrastaminal scales, with fewer fimbriae (rarely bifid, see the holotype morphology gallery in Costea, 2007 onwards).

Distribution and ecology. – North and Central America: U.S.A., Mexico, Panama; Caribbean: Cuba, Haiti, Jamaica, Turks and Caicos, Virgin Islands; South America: Venezuela, Guyana, Suriname, Brazil; Cape Verde. Flowering June–Dec.; Dec.–Mar.; elevation 10–2700 m; sometimes on saline soils; hosts: *Acleisanthes*, *Alternanthera*, *Allionia*, *Amaranthus*, *Atriplex*, *Boerhavia*, *Gilia*, *Iresine*, *Kallstroemia*, *Phyloxerus*, *Sesuvium*, *Salsola*, *Selinocarpus*, *Suaeda*, *Tidestromia*, *Trianthema*, *Tribulus*.

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Appendix 1. Taxa, DNA accession 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 in the main text following species names. GenBank accession numbers are given in the following order: *trnL-F*, ITS (if applicable, multiple clones are separated by forward slash). Sequences newly generated for this study are indicated in bold. A dash indicates the sequence was not obtained. Abbreviations of herbaria in which the vouchers are deposited follow *Index Herbariorum*.

Cuscuta acuta: 1084, Fosberg 44965 (US), EF194330, EF194565/HM748867/HM748868/HM748869; 1188, Ferreyra & al. 10665 (USM), HM748863, HM748870/HM748871. *C. desmouliniana*: 571, Porter 224 (GH), EU288341, EU288359; 1160, Sanders 12674 (UCR), HM748864, HM748872; 1161, Wider 06-368 (WLU), EU288342, EU288360. *C. hyalina*: 840, Bosch 25022 (BOL), –, EF194561/EU288365; 875, Hardy & de Winter 1392 (PRE), EF194318, –, 889, Parvati s.n. (RSA), EF194319, EF194562; 994, Mkhanno 45 (ARIZ), EF194320, HM748873. *C. legitima* (\equiv *C. umbellata* var. *reflexa*): 577, Spellenberg & Zucker 12966 (NMC), EF194325, EF194566/EU288370; 1015, Van Devender 94-458 (TEX), EF194326, HM748874/HM748875/HM748876; 1027, Austin & Austin 7585 (ASU), EF194327, HM748877/HM748878/HM748879/HM748880; 1030, Van Devender & al. 94-458 (ASU), EF194328, HM748881/HM748882/HM748883/HM748884; 1033, Daniel 2445 (ASU), EF194329, HM748885/HM748886/HM748887/HM748888/HM748889. *C. leptantha*: 608, Wiggins 20889 (MICH), EF194322, EF194569; 719, Wiggins 14668 (GH), EF194323, EF194570; 884, Fritsch & Fritsch 1337 (RSA), EF194324, EF194571. *C. liliputana*: 664, Sivinski 5689 (NY), EU288343, EU288363/EU288364; 665, Neese s.n. (NY), EU288344, EU288362; 848, Metcalfe 1290 (NY), EU288345, EU288361. *C. membranacea*: 1185, Hunziker 4693 (MO), HM748865, HM748890. *C. odontolepis*: 587, White 2730 (GH), EF194331, EF194563/HM748891/HM748892/HM748893; 730, Hartman 52 (GH), EF194332, EF194564/HM748894/HM748895/HM748896. *C. polyanthemos*: 826, Robles 123 (XAL), EF194321, EF194572/EU288366; 1162, Van Devender 2006-809 (WLU), HM748866, HM748897. *C. tuberculata*: 554, de la Luz 8543 (ARIZ), EF194334, EF194568; 737, Wiggins 15153 (GH), EF194335, EU288367; 762, Daniel & Butterwick 4341 (NY), EF194333, EF194567; 763, Stevens & Fairhurst 2052 (MICH), EF194336, EU288368; 764, Carter & Kellogg 3085 (GH), EF194337, HM748898. *C. umbellata* (var. *umbellata*): 516, Fletcher 5857 (UNM), EF194315, EF194558/HM748899; 526, Ward & Spellenberg 81-167 (ASU), EU288346, –, 557, Blankenhorn 216 (ARIZ), EF194317, EF194560/HM748900/HM748901/HM748902; 576, Silversmith s.n. (NMC), EU288347, HM748903/HM748904/HM748905; 759, Bleakey 4662 (NMC), EF194316, EF194559; 830, Nee & Taylor 29575 (XAL), –, EU288369; 1189, Carranza 7045 (WLU); 1190, Carranza 7191 (WLU); GB, Medina s.n. (MA), AJ428053, EF192271. **Outgroup**: *C. serruloba* Yunck.: 977, Orcutt 4457 (MEXU), EF194313, EF194555. *C. vandevenderi* Costea & Stefanović: 1058, Gentry & al. 19423 (US), EU426964, EU426958.

Appendix 2. Herbarium vouchers used for taxa description and examined for micromorphology. Species accession code: country, region, locality, elevation (m. a.s.l.), date, collector(s), herbarium acronym.

Cuscuta acuta, ECUADOR. Galapagos, Hood Island, Gardner Bay, 20 Apr 1932, Howell 8688 (B, CAS); James Island, Sullivan Bay, 13 Jun 1932, Howell 10048 (B, CAS, G, GH, K, MO, NY); Tower Island, 16 Jun 1932, Howell 10140 (CAS, G, GH, NY); 18 Apr 1923, Wheeler & al. 21 (GH, NY); Culpepper Island, 25–30 Jan 1964, Hendrickson 5 (CAS, GH); Isabella Island, ca. 4 km W of Puerto Villamil, 50 m, 23 Feb 1965, Wiens 3821 (CAS). Prov. Guayas. La Libertad, 26 Feb 1939, Asplund 5136 (G, NY, UPS, US, S). Prov. Manabi. Bahia de Caraquez, 15 Feb 1981, Sparre 19700 (S). PERU. Dept. Piura. Jalara, 1926, Haught 154a (GH, NY, US). *C. desmouliniana*, MEXICO. Baja California. Near San Bruno, 7 Nov 1946, Wiggins 11394 (DS, RSA); 25.5 mi S of Santa Rosalia, 7 Feb 1960, Porter 224 (CAS, DS, G, MEXU); Bahia de la Concepcion, 18 Oct 1962, Wiggins & Wiggins 17968 (CAS, DS, MEXU). Sonora. Mpio. Caborca: 35.2 km W of Caborca on road to Desemboque, 30°44'35"N 112°26'32"W, 63 m, 16 Jan 2002, Van Devender & Reina-G. 2002-23 (WLU). Mpio. Guaymas: San Carlos, 27°57'42"N 111°03'43"W, ca. 35 m, 26 Dec 2000, Reina-G. & Van Devender 2000-917 (CAS, US, WLU); 5 mi E of Bahia Kino, 19 Oct 1963, Felger 9046 (ARIZ); Guayamas, 22 Feb 1904, Palmer 1209 (type of *C. umbellata* var. *ubia*: US). Mpio. Hermosillo: Isla Tiburón, ca. 12 mi, S from Tecamate, 28°57'20"N 112°24.5', ca. 280 m, [no date], Felger 76-T14 & al. (ARIZ). Mpio. Huatabampo: 1.9 km W of Tierra y Libertad, 26°33'00"N 109°12'45"W, 25 m, Friedman & Zittere 213-95 (ARIZ). Mpio. Soyopa: Arroyo Los Garambullos, 1.5 km east of Tónichi; 28°34'10"N 109°33'00"W, 180 m, 15 Sep 1998, Van Devender & al. 98-1120 (ARIZ, WLU); 4 Sep 1996, Van Devender & al. 96-360 (ARIZ, NMC, WLU). *C. hyalina* var. *hyalina*, INDIA. Delhi, 8 Aug 1954, Mkhanno 45 (ARIZ); Sep 1960, Parvati s.n. (RSA); NAMIBIA. Windhoek, March 1931, Bosch 25022 (BOLUS). SOUTH AFRICA. Walvisbay Distr., Hardy & de Winter 1392 (PRE). TANGANYIKA. Musoma Distr.: Mugungu River, Banagi, 1371 m, Greenway 9965 (PRE). UGANDA. Karamoja District: near Amud, 1 Jun 1939, Thomas 2989 (K). ZIMBABWE. Chimanimani, Birchenough Bridge, 700 m, 17 Dec 1952, Chase 4741 (K). *C. lacerata* [the type]. *C. legitima* (\equiv *C. umbellata* var. *reflexa*), U.S.A. Arizona. Cochise Co.: San Pedro Riparian National Conservation Area, 31°47.667'N, 110°12.519', 1218 m, 19 Oct 2003, Makings 1673 (ASU, CAS, NY). Maricopa Co.: ca. 80 km W of Phoenix, 365 m, 18 Aug 1999, Spellenberg & Zucker 12966 (NMC). Pima Co.: Cabeza Prieta National Wildlife Refuge, 32°07'N 113°05'W, 365 m, 15 Sep 1992, Felger & Gierlach 92-740 (ARIZ, CAS); Tucson, Highland Avenue, 750 m, 20 Aug 1953, Parker 8309 (CAS, MO). Yuma Co.: 0.25 mi intersection of Mohawk Valley Blvd. and Avenue 36E, 32°43.916'N 114°0.259'W, 75 m, 7 Jun 2003, Northam s.n. (MO). Kansas. Hamilton Co.: 1 mi S of Coolidge, 23 Sep 1972, McGregor 24751 (NY). New Mexico. Dona Ana Co.: College Ranch ca. 15 mi N of Las Cruces, 5 Sep 1970, Spellenberg & Spellenberg 2379 (NMC). Texas. Brewster Co.: Big Bend National Forest, 22 Jul 1957, Correll & Johnston 18334 (UC); Starr Co.: Fort Ringgold, 45 m, 13 Jul 1941, Runyon 2727 (UC). MEXICO. Baja California. 9 mi E of La Paz, 25 Nov 1959, Wiggins 15613 (ARIZ, CAS); ca. 23.5 mi N from Pozo Grande, 100 m, 28 Oct 1959, Thomas 8373 (DS, ARIZ, MEXU); Loreto, 23 Oct 1930, Jones 27348 (CAS, MO); La Paz, 29 Oct 1969, Thomas 8414 (CAS, MEXU). Chihuahua. 13 Km E of Guzman, 31°10'N 107°23'W, 1130 m, 22 Aug 1972, Chiang & al. 8798

Appendix 2. Continued.

(CAS). **Coahuila**. Mpio. Cuatro Ciénegas and Ocampo: Loma Prieta, 27°09'50" N 102°16'30"W, 1000 m, 2 Oct 1976, *Wendt & al.* 1862 (MEXU). **Sonora**. Mpio. Agua Prieta: S edge of Agua Prieta, 31°18'21"N 109°34'55"W, 1204 m, 13 Sep 2006, *Van Devender & Reina-G.* 2006-757 (HCIB, MO, TEX, WLU). Mpio. Álamos: Capitahuasa, 26°45'35"N 108°55'W, 160 m, 25 Sep 1993, *Van Devender & al.* 93-1123 (ARIZ, UC, UCR). Mpio. Cajeme: Ciudad Obregón, 29 Sep 1933, *Gentry* 272 (ARIZ, MICH); Cerro La Antena, 27°27'45"N 109°46'20"W, 200 m, 19 Sep 1994, *Van Devender & Yetman* 94-603, (ARIZ, ASU, MEXU, UC, USON); NW side of Río Yaqui, ca. 9 km N of Ciudad Obregón; 27°35'45"N 109°56'W, 40 m, 10 Sep 1994, *Van Devender & al.* 94-458 (ARIZ, ASU, MEXU, UC, UCR). Mpio. Hermosillo: 20 mi S of Hermosillo, 28 Oct 1926, *Jones s.n.* (MO); 27 mi W of Hermosillo, on road to Kino Bay, 28 Aug 1941, *Wiggins & Rollins* 133 (ARIZ, DS, MO). Mpio. Navojoa: San José de Masiaca; 26°45'N 109°14'30"W, 70 m, 22 Sep 1994, *Van Devender & Yetman* 94-710, 94-711 (ARIZ, MEXU, UC). Mpio. Puerto Peñasco: MacDougal Crater, 8 Sep 1964, *Felger* 10488 & *Lincoln* (ARIZ); 0.5 km E of MacDougal Crater, 8 Sep 1964, *Felger* 10432A, 10435, 10436 (ARIZ); W Pinacate, 6 Nov 1982, *Equihua s.n.* (ARIZ); Sykes Crater, NW of Pinacate Region, 155 m, 8 Dec 1970, *Burke & al.* 20035 (ARIZ); ca. 1 Km SW Papago Tanks, 28 Sep 1964, *Felger & Lincoln* 10608 (ARIZ); Rancho Grijalva (Rancho Guadalupe Victoria), 32°00'35"N 113°34'25"W, 225 m, 9 Nov 1982, *Ezcurra s.n.* (ARIZ). Mpio. Soyopa: Tónichi, 28°35'55"N 109°33'50"W, 200 m, 17 Aug 2006, *Van Devender & Reina-G.* 2006-627 (ARIZ, NMC, WLU); 3.5 km S of Tónichi, ca. 28°34'03"N 109°33'25"W, 220 m, 17 Aug 2006, *Van Devender & Reina-G.* 2006-638 (WLU); Arroyo los Conejos, 28°35'39"N 109°35'33"W, 225 m, 16 Aug 2006, *Reina-G. & Van Devender* 2006-586 (MEXU, WLU); *Reina-G. & Van Devender* 2006-606, 2006-612 (WLU). **Tamaulipas**. vicinity of Victoria, ca. 320 m, May 1–Jun 13 1907, *Palmer* 441 (K, MO, NY). **C. leptantha**, U.S.A. Texas. Karnes Co.: 0.3 mi NW of Falls City, 5 Oct 1952, *Johnson* 1032 (BRIT, NY). **MEXICO. Baja California**. 1/2 mi N of fork of Rd to Rancho San Pedro, ca. 24°51'N 111°04'W, 225 m, 15 Nov 1959, *Wiggins* 15478 (DS, MEXU); ca. 3 mi S of Santa Rosalia, 24 May 1959, *Thomas* 7971 (MEXU); 5.8 mi from La Paz, 30 Dec 1956, *Porter* 123 (G, MEXU); Cape Region, near 24°11'N 110°12'W, 4 Jan 1959, *Moran* 6882 (CAS, DS, K, RSA, SD). **SONORA**. Mpio. Hermosillo: ca. 1.5 mi E of Santa Rosa, 15 Feb 1965, *Felger & al.* 12575 (ARIZ); 4 mi by road NW of Rancho Noche Buena, 14 May 1966, *Felger & al.* 14035 (ARIZ); ca. 1 mi E of 19 mi by road S of Desemboque, ca. 29°20'N 112°14'W, 18 Feb 1968, *Felger & al. s.n.* (ARIZ); 3.7 mi S of Punta Chueca, 13 Apr 1980, *Bowers & McLaughlin* 1966 (ARIZ). Playa Esthela, 28°52'28"N 112°01'20", 50 m, 31 Dec 2000, *Van Devender & Reina-G.* 2000-933 (WLU). Mpio. Pitiquire: 19.8 mi S of Desemboque Río San Ignacio, 14 May 1966, *Felger & Bezy* 14080 (ARIZ). **C. liliputana**, see Stefanović & Costea, 2008. **C. membranacea**, ARGENTINA. Provincia de la Rioja, Depto. de Capital, La Ramadita, 25 Km of Rioja, 17 Feb 1944, *Hunziker* 4823 (S, US); 17 Feb 1944, *Hunziker* 4833 (S, US); 9 Mar 1944, *Hunziker* 4695 (S). Provincia La Salta, Depto. de la Pima, 2 Feb 1941, *Hunziker* 1149 (NY). **C. odontolepis**, MEXICO. Chihuahua. Nabogame, 12 Km NW of Yepachic, 28°30'N 108°30'W, 1800 m, 23 Oct 1986, *Laferrriere* 318 (MEXU). **Sonora**. Mpio. Arispe: 5 Km of NW Bacanuchi, 30°39'22"N 110°15'52"W, 1880 m, 22 Nov 1997, *Flores* 5143 (IEB, USON). Mpio. Arivechi: Arroyo Bámori, 5 km S Bámori, 28°49'15"N 109°10'24"W, 536 m, 15 Sep 2006, *Van Devender & Reina-G.* 2006-869 (ARIZ, USON, WLU). Mpio. Cucurpe: Palm Canyon, 30°29'N 111°46'W, 1300 m, 2 Oct 1976, *Van Devender & al. s.n.* (ARIZ). Mpio. Fronteras: 1387 m, 25 Sep 1890, *Hartman* 52 (K, US); S edge of Esqueda on SON 17, 30°42'41"N 109°35'15"W, 1215 m, 13 Aug 2006, *Van Devender & Reina-G.* 2006-467 (ARIZ, MEXU, WLU). **C. polyanthemus**, MEXICO. Sinaloa. 22.6 mi S of Culiacan, 140 m, 17 March 1955, *Wiggins* 13153 (CAS, SD). **Sonora**. Mpio. Quiriego: 31 mi NW of Quiriego on Rd to Cajeme, 6 Mar 1933, *Wiggins* 6457 (CAS). Mpio. Moctezuma: 18.9 km SSE of junction with Moctezuma-Huásabas Hwy on road to Tepache, 29°39'N 44°N 109°37'13"W, 635 m, 14 Sep 2006, *Van Devender & Reina-G.* 2006-809 (WLU). **C. tuberculata**, U.S.A. Arizona. Maricopa Co.: South Mts., T1S R3E NW1/2 Sec. 20, 580 m, 15 Sep 1985, *Daniel & Butterwick* 4341 (CAS). Pinal Co.: Picacho Pass, 10 Sep 1971, *Beauchamp* 3112 (SD). Yuma Co.: Mohawk, 17 Sep 1929, *Jones* 24949 (CAS, UC). Yavapai Co.: 3 mi S of Yarnell, 26 Aug 1989, *Austin & Austin* 7587 (RSA, ASU). **MEXICO. Sonora**. Mpio. Álamos: Mocúzari (Adolfo Ruiz Cortinez) Dam on the Río Mayo, WNW of Álamos, 27°13'10"N 109°06'30"W, 120 m, 16 Oct 1992, *Van Devender & Van Devender* 92-1386 (ARIZ, ASU, CAS, UCR). Mpio. Hermosillo: 8 mi W of Hermosillo, 27 Aug 1941, *Wiggins & Rollins* 98 (ARIZ, DS, MO); ca. 25 km W of Hermosillo on Rd. to Bahía de Kino, 29°01'29"N 111°08'33"W, 10 Aug 2001, *Reina-G. & Van Devender* 2001-624 (ARIZ, MEXU, USON, WLU). Mpio. La Colorada: 36 Km, SE of Hermosillo on MEX 16, 28°49'54"N 110°39'25"W, 317 m, 15 Aug 2006, *Van Devender & Reina-G.* 2006-552 (HCIB, USON, WLU); 4.7 Km E of Tecoripa on MEX 16, 28°37'04"N 109°54'25"W, 410 m, 16 Aug 2006, *Reina-G. & Van Devender* 2006-559 (ARIZ, CAS, WLU). Mpio. General Plutarco Elias Calles: 2.7 mi W of Sonoyta on Mex Hwy 2, 14 Sep 1986, *Felger* 86-315 (ARIZ). Mpio. Moctezuma: 14.1 km SSE of Moctezuma on road to Tepache, 29°40'53"N 109°38'00"W, 607 m, 14 Aug 2006, *Reina-G. & Van Devender* 2006-544 (MO, TEX, WLU). Mpio. Opodepe: Querobabi, 30°03'14"N 111°01'39"W, 680 m, 20 Aug 2001, *Reina-G. & Van Devender* 2001-730 (ASU, HCIB, NMC, WLU). Mpio. Soyopa: Arroyo Los Garambullos, 0.5 km SE of Río Yaqui bridge on MEX 16, 3.3 km S, 1.5 km E of Tónichi, 28°34'10"N 109°33'00"W, 180 m, 15 Sep 1998, *Van Devender & al.* 98-1111 (ARIZ, WLU). Mpio. Puerto Peñasco: Pinacate Region, Sykes Crater, 400 m, 8 Dec 1970, *Burke & al.* 19998 (ARIZ). **C. umbellata** var. *umbellata, U.S.A. Arizona. Apache Co.: Hubbell Treading Post National Historic Site, UTM 12S: 630137E, 3951920N, 1920 m, 19 Sep 2002, *Roth s.n.* (NMC, BRIT). Colorado. Fremont Co.: 28 Jul 1813, *Brandegee* 407 (UC). Otero Co.: Fowler, R-59W T-22s, 1320 m, 10 Sep 1980, *McIntyre & Anderson* 75 (MO). **New Mexico**. Dona Ana Co.: S edge of Las Cruces, 7 Jun 1981, *Ward & Spellenberg* 81-167 (NMC, NY, MO, TEX). McKinley Co.: ca. 33 mi N of Milan, 35°38'950"N 107°52'141"W, 2145 m, 20 Sep 2002, *Bleakley* 4662 (NMC). San Miguel Co.: head of Cuevas Canyon, 20 mi ESE of Las Vegas, 1850–1920 m, *Hill & Levandoski* 11952 (MO). Santa Fe Co.: ca. 10 mi NW of Santa Fe, 35°45'59.8"N 106°02'13.4"W, 11 Oct 2002, *Cox s.n.* (NMC, BRIT). Torrance Co.: ca. 10 mi W of Mountainair, T3N R5E Sec NW1/4, 1950 m, 14 Sep 2002, *Sivinski & al.* 5669 (NMC). Texas. Culberson Co.: 36 mi N of Van Horn, 27 Jul 1952, *Webster* 4527 (BRIT); 13 Oct 1985, *Spellenberg s.n.* (NMC, UC). El Paso Co.: 1 mi N of El Paso, 23 Sep 1944, *Barkley* 14535 (BRIT, K); 11 Sep 1988, *Worthington* 17336 (CHSC, UNM); just W of Ft. Bliss, 1100 m, 12 Oct 1950, *Dunn* 7208 (NMC). **MEXICO. Coahuila**. Cañon de Agua, 3.5 mi NNW of Cuatro Ciénegas, 14 Aug 1967, *Minkley & Pinkava* 3864 (ASU). Chihuahua. Near Chihuahua, 31 Aug 1887, *Pringle* 783 (G, MO, MEXU); Camino de Aldama to Río Conchos, 25 Aug 1966, *Robert s.n.* (MEXU). **Distrito Federal**. Between Santa María Astahuacán and Santa Cruz Meyehualco, 2250 m, 1 Jun 1966, *Rzedowski* 22418 (IEB, MEXU). **Durango**. Mpio. De Gómez Palacio: Cerro San Ignacio, 17 Jul 1984, *Pacheco* 9 (MEXU); 26 Km WSW of Torreón, 25°27'N 103°42'W, 1225 m, *Illis & Lasseigne* 96 (MEXU). **Guerrero**. Mpio. Coahuayutla de Guerrero: 5.46 km N of La Corva, 18°32'38"N 101°50'28", 20 Oct 1999, *Soto* 17626 (MEXU). **Guanajuato**. Mpio. de Yuridia: Yuridia Lake, 1850 m, 29 Aug 1970, *Rzedowski* 27592 (IEB); 3 km al NW of Cuitzeo on Hwy to Salamanca, 1850 m, 18 Aug 1986, *Rzedowski* 40388 (IEB). **Estado de Mexico**. Mpio. de Tultepec: 2 Km of Salinas, 2250 m, 23 Aug 1963, *Rzedowski* 17099 (IEB, MEXU). **Jalisco**. Ca. 4.5 mi from Zacoalco on Rd to Acatlán, 16 Sep 1969, *Dieterle* 3471 (MICH, MEXU). **Michoacan**. Mpio. de Santa Clara: La Lagunita, San Gregorio, 2700 m, 4 Dec 1986, *Barriga* 3422 (IEB). Mpio. Huaniqueo: 1.8 Km of SW Tendeapacua, 2050 m, 7 Oct 1992, *Silva-Sáenz* 351 (EBUM, IEB). Mpio. de Patzcuaro: Cerro del Frijol, 2550 m, 10 Dec 1985, *Escobedo* 760 (IEB). **Nuevo Leon**. El Manantial, 26°23'N 100°55'W, 560 m, 22 Aug 1984, *Carranza & al.* 2640 (MEXU). **Oaxaca**. Mpio. de Santa María Tecomavaca: 3 mi S of Tecomavaca, 550 m, 12–13 Aug 1976, *Webster* 20792 (MEXU, MO, UC). Mpio. San Juan Bautista Cuicatlán: 10.2 Km al NE of Chilar, 17°47'21"N 96°59'31", 665 m, 1 Oct 2002, *Soto* 24009 (MEXU). **Queretaro**. Mpio. de Peñamiller: 1 km SW of Higuierillas, 1400 m, 12 Aug 1989, *Zamudio* 3698 (IEB). **San Luis Potosí**. Mpio. de Tierra Nueva: 5 Km al NNW of Tierra Nueva, 1750 m, 9 Jun 1959, *Rzedowski* 10786 (MEXU). **Sonora**. Mpio. General Plutarco Elias Calles: Quitovac, 2 Sep 1980, *Nabhan & Rea* 167 (ARIZ); 0.5 km E of Río Sonoyta, 4 Oct 1985, *Felger & Van Houten* 85-940 (ARIZ). **Puebla**. Mpio. Tehuacan: near Tehuacan, 1675 m, 24 Dec 1896, *Pringle* 6297 (G, MEXU, MO, US). Mpio. San José Miahuatlán: 18°13'N 97°13', 950 m, 4 Nov 1993, *Salinas & al.* 7610 (MEXU). **Tamaulipas**. Mpio. San Carlos: 24°16.8'N 98°59.4'W, 360 m, 27 Nov 1998, *Martinez* 5030 (MEXU). **Veracruz**. Close to the border with Puebla on Rd to Xalapa, 12 Jul 1969, *Ramos* 295 (MEXU). **PANAMA**. Distr. de Parita: Sarigua, 1 Km of Linon Harbour, 9 Oct 1984, *Caballero & Sandoval* 57 (MO). **ANTIGUA AND BARBUDA**. Antigua Island, 1857, *Wulfschlagel* 352 (MO). **PUERTO RICO**. Guanica, 11–12 Mar 1913, *Britton & Shafer* 1866 (GH, MO, NY); Mona Island, ca. 1 Km N of the lighthouse, 25 Jan 1992, *Proctor & al.* 47591 (UPRRP). **CUBA**. 1860–1864, *Wright* 3107 (K, GH, MO, NY, S). Prov. Oriente: Santiago, 22 Jun 1914, *Ekman* 1419 (S). **HAITI**. Massif de la Selle, 21 Jul 1926, *Ekman* 6714 (K, S). **JAMAICA**. Parish Kingston: Palisades, 15 Feb 1966, *Adams* 12882 (MO); Georges Lane, back of Institute of Jamaica, 24 Jul 1957, *Proctor* 16497 (GH). **TURKS & CAICOS**. Grad Turk: North Wells, 12 Jun 1974, *Proctor & Gillis* 34044 (B, GH); 28 Nov 1977, *Correll* 49198 (GH, MO). South Caicos, vicinity of Cockburn Harbour, 17 Jun 1954, *Proctor* 8819 (GH). **VIRGIN ISLANDS**. Anegada, 2 Aug 1970, *D'Arcy* 4904 (MO). **GUYANA**. Georgetown, 29 Oct 1919, *Hitchcock* 16364 (GH, NY, S). **SURINAME**. Nickerie, 21 Feb 1951, *Geyskes* 30 (GH); just S. of Braamspunt, 18 Nov 1960, *Boxtel* 2109 (NY). **VENEZUELA**. La Guaira, 18 Mar 1940, *Tamayo* 1247 (NY, US). **CAPE VERDE**. *Medina s.n.* (MA). **C. umbellata** var. *desertorum*. **BRAZIL**. Prov. Piauh, *Martius s.n.* (the holotype, MO); Prov. Ceara, *Gardner* 2425 (K).*