Systematics of “horned” dodders: phylogenetic relationships, taxonomy, and two new species within the *Cuscuta chapalana* complex (Convolvulaceae)

Mihai Costea, Ignacio García Ruiz, and Saša Stefanović

Abstract: The *Cuscuta chapalana* complex (Convolvulaceae) is a recently circumscribed clade within the subgenus *Grammica* that includes several little-known species from Mexico and Central and northern South America characterized by the presence of peculiar subapical multicelullar appendages on the corolla and often on the calyx lobes. Basic morphology, scanning electron microscopy, and DNA sequence data from the plastid *trnL–F* region and the 26S rDNA and internal transcribed spacer nuclear regions were used to investigate the phylogenetic relationships within the group and to test the species limits. Multicellular appendages are horn-like or tubular in shape and bear one or more stomata at their tips; hence the vernacular name “horned” dodders. Eight lineages were reconstructed; two of them, both from Mexico, were described as new species: ***Cuscuta bonafortunae*** Costea & I. García, sp. nov., and ***Cuscuta carnosa*** Costea & Stefanović, sp. nov. *Cuscuta pringlei* is redefined as a variety of *Cuscuta strobilacea*. A taxonomic treatment with an identification key, descriptions, and illustrations is provided.

Key words: Cuscuta, dodders, molecular phylogeny, ITS, 26S, *trnL–F*, SEM, new species, systematics.

Résumé : Le complexe *Cuscuta chapalana* (Convolvulaceae) constitue un clade récemment circonscrit récement circonscrit dedans le sous-genre *Grammica* incluant plusieurs espèces peu connues du Mexique, du centre et du nord de l’Amérique du Sud, caractérisées par la présence d’appendices subapicales multicellulaires particulières sur la corolle, et souvent sur les lobes du calice. A fin d’examiner les relations phylogénétiques dans ce groupe et vérifier les limites des espèces, les auteurs ont utilisé les données morphologiques générales, la microscopie électronique à balayage et les séquences de l’ADN provenant de la région plastidique *trnL–F* et des régions nucléaires de 26S rADN et de l’espaceur interne transcrit (ITS). Les appendices multicellulaires prennent la forme d’une corne ou d’un tube, et portent un ou plusieurs stomates à leur apex, d’où le nom vernaculaire de cuscute cornue. Ils ont reconstruit huit lignées; ils décrivent deux d’entre elles, toutes deux du Mexique, comme espèces nouvelles : ***Cuscuta bonafortunae*** Costea & I. García, sp. nov. et ***Cuscuta carnosa*** Costea & Stefanović, sp. nov. On redéfinit le *Cuscuta pringlei* comme une variété du *Cuscuta strobilacea*. Les auteurs fournissent un traitement taxonomique avec une clé d’identification, des descriptions et des illustrations.

Mots-clés : Cuscuta, cuscute, phylogénie moléculaire, ITS, 26S, *trnL–F*, nouvelles espèces, systématique.

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Introduction

Cuscuta L. (dodders) is one of the most diverse and challenging groups of parasitic plants. The genus is cosmopolitan and includes over 200 species and 60 nonautonymic varieties, but the highest diversity of species (ca. 140) is encountered in the Americas (Yuncker 1932; García and Martín 2007; Stefanović et al. 2007). Dodders are important both economically and ecologically. A few species can produce considerable losses to agricultural crops (Parker and Riches 1993; Costea and Tardif 2006). The majority of *Cuscuta* species, however, act as keystone species in their natural ecosystems (reviewed by Press and Phoenix 2005). In addition, numerous dodders require conservation measures, and some are presumed extinct (Costea and Stefanović 2009*a*).

Almost eight decades after Truman G. Yuncker’s monograph (Yuncker 1932), the systematics of *Cuscuta* (dodders) is receiving renewed interest. Two of the three accepted subgenera, *Cuscuta* and *Grammica*, have recently been the subject of broadscale phylogenetic studies (García and Martín 2007; Stefanović et al. 2007). In the subgenus *Grammica*, the largest and most complicated infrageneric group, 15 major lineages have been circumscribed (Stefanović et al. 2007), with little correspondence to Yuncker’s sections and subsec-

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tions. Subsequently, a series of focused systematic studies have been initiated to investigate these clades at a species level. To date, six major *Grammica* clades have been examined: four that consist of mostly species from the territory covered by the Flora of North America (Costea et al. 2005, 2006*a*, 2006*b*, 2006*c*, 2009; Costea and Stefanović 2009*b*) and two with predominantly Mexican dodders (Costea et al. 2008; Costea and Stefanović 2010).

Our present study continues this series by investigating a group of little-known species corresponding to clade K of Stefanović et al. (2007). In the absence of a formal sectional name, which will be published with a new infrageneric classification of the genus (M. Costea et al., unpublished data), we here refer to this clade as the *Cuscuta chapalana* complex. This group includes the species of the former subsection Ceratophorae (section Cleistogrammica), in which Yuncker (1932, 1965) grouped four species, *Cuscuta blepharolepis* (not examined in this study), *C. chapalana*, *Cuscuta erosa*, and *Cuscuta boldinghii*, characterized by a deeply divided calyx with variously denticulate lobes and gynoecia with subulate styles. Recent molecular results have shown that three other species, *Cuscuta strobilacea*, *Cuscuta mexicana*, and *Cuscuta costaricensis*, previously included by Yuncker (1932, 1965) in other subsections of the subgenus *Grammica*, are also a part of the *C. chapalana* complex (Stefanović et al. 2007; Stefanović and Costea 2008).

Species of this clade are distributed mostly in Mexico; however, *C. erosa* is also found in southern Arizona; *C. costaricensis* and *C. strobilacea* reach Central America (Costa Rica and Guatemala), and *C. boldinghii* expands to the Caribbean and Central and northern South America. Most of the species were originally described by Yuncker from scarce herbarium material. Among them, *C. chapalana*, *C. mexicana*, and *Cuscuta ortegana* were known only from their type collections, while *C. strobilacea* and *C. boldinghii* were represented by a few specimens (Yuncker 1932; Carranza 2008). To build on this taxonomic foundation, we included numerous additional collections in an attempt to test species limits based on their evolutionary relationships. The objectives of this study were to (*i*) recover the evolutionary history of the *C. chapalana* clade based on plastid (*trnL–F*) and nuclear (internal transcribed spacer (ITS), 26S rDNA) sequences; (*ii*) investigate the morphology and micromorphology of the taxa involved; and (*iii*) provide a new classification with the description of two new species, *Cuscuta bonafortunae* and *Cuscuta carnosa*.

Material and methods

Taxon sampling

Specimens from over 100 herbaria were studied in connection with the upcoming treatments of *Cuscuta* for the Flora of North America Project, Flora Mesoamericana, Flora Neotropica, and a future monograph of the genus. A subset of 21 accessions, representing nine ingroup taxa, including two new species described here as *C. bonafortunae* and *C. carnosa*, was used for the molecular phylogenetic analyses (Appendix A). Efforts were made to sample multiple accessions, including for the species previously known only from their type collections (e.g., *C. chapalana* and *C. mexicana*). As a result, one to four individuals are included in the molecular analyses for all but two species, *C. blepharolepis* and *C. ortegana*, which we could not sample for the molecular analyses. *Cuscuta blepharolepis* is known only from the type specimen (BM, NY). Although we found additional herbarium collections for *C. ortegana*, their quantity and quality did not permit DNA extraction.

Based on our previous broader phylogenetic analyses of *Cuscuta* subgenus *Grammica* (Stefanović et al. 2007; Stefanović and Costea 2008), we selected *Cuscuta corymbosa* var. *stylosa* (clade J) and *Cuscuta americana* (clade I) as outgroup taxa (Appendix A).

Morphology and micromorphology

Descriptions are based on rehydrated herbarium material (Appendix B) and were corroborated whenever possible by fresh flowers collected in the field and preserved in formalin–acid–alcohol (Ruzin 1999). 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 7.2 software (MIS Inc., Villa Park, Ill.). For scanning electron microscopy, we used hexamethydisilazane as an alternative to critical point drying (method modified from Bray et al. 1993). Rehydrated herbarium samples (Appendix B) were dehydrated using an ethanol series (70%, 80%, 95%, and 100%; each step 1 h), immersed for 1 h in 1:1 *v*/*v* ethanol–hexamethydisilazane, and passed through an overnight change of 100% hexamethydisilazane. Samples were air dried and coated with 30 nm gold particles using an Emitech K 550 sputter coater (Emitech Ltd., Ashford, UK). Examination, measurements, and pictures were taken at 10 kV using a Hitachi SU1510 variable pressure scanning electron microscope (Hitachi Canada Ltd., Mississauga, Ont.). Pollen data had already been provided by Welsh et al. (2010) for all the species except *C. mexicana*, *C. bonafortunae*, and *C. carnosa*. Here, we studied the pollen of these species and increased the sampling for all the other species (Appendix B).

The terminology regarding the micromorphology of flowers and seeds follows Costea et al. (2006*a*); pollen terminology uses Welsh et al. (2010). Hundreds of photographs that illustrate details of the floral parts and pollen and fruit morphology for all the species, including the types, are available in the Digital Atlas of Cuscuta (Costea 2007–onwards). The geographical distribution of taxa, phenology, elevation, and host ranges are based on observation made in the field and from herbarium specimens.

Molecular methods and alignments

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 cetyltrimethylammonium bromide method (Doyle and Doyle 1987) and purified using Wizard minicolumns (Promega Corporation, Madison, Wis.). DNA fragments for three 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). The ITS region of nuclear ribosomal DNA (nrDNA) containing ITS1, 5.8S, and ITS2 (here called ITS) was obtained using primers described by Baldwin (1992). To amplify a ca. 950 bp portion at the 5″end of the nuclear large subunit ribosomal DNA (26S rDNA), primers described by Kuzoff et al. (1998) were used. PCR reagents and conditions as well as amplicon purification and sequencing procedures followed the protocols detailed in Stefanović et al. (2007). Sequences newly generated in this study are deposited in GenBank (accession Nos. JN234778-JN234818; see Appendix A). Sequences were aligned manually using Se-Al version 2.0a11 (Rambaut 2002).

Phylogenetic analyses

Phylogenetic analyses were conducted using PAUP* version 4.0b10 (Swofford 2002) under both parsimony and maximum likelihood criteria.

Given the moderate number of terminal units, the parsimony searches were conducted with a branch-and-bound algorithm, ensuring recovery of all the most parsimonious trees. Matrix characters were treated as unordered (Fitch 1971), and all changes were equally weighted.

ModelTest version 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 starting with the parsimony-derived tree rather than the neighbor-joining default. The Hasegawa–Kishino–Yano (HKY) model of DNA substitution (Hasegawa et al. 1985), with rate variation among nucleotides following a discrete gamma distribution (HKY + G), was selected as the best fit for the plastid-derived *trnL–F* matrix. The Tamura–Nei (TrN) model of DNA substitution (Tamura and Nei 1993), with rate variation among nucleotides following a discrete gamma distribution (TrN + G), was selected as the best fit for both nuclear-derived data sets (ITS and 26S rDNA) as well as for the combined data. The full heuristic searches for maximum likelihood trees were performed using corresponding models of DNA evolution, each involving 100 replicates with stepwise random taxon addition, tree bisection–reconnection branch swapping, and MULTREES option on.

Under both criteria, the support for clades was inferred by nonparametric bootstrapping (Felsenstein 1985) using 200 heuristic bootstrap pseudoreplicates, tree bisection–reconnection branch swapping, and MULTREES option on. Nodes receiving bootstrap (BS) values <70%, 70%–85%, and >85% were considered weakly, moderately, and strongly supported, respectively. Potential conflict between data sets was evaluated by visual inspection, looking for the presence of strongly supported but conflicting topologies from individual data partitions.

Results

General morphology and micromorphology

The deeply divided calyx, and especially the characteristic subapical multicellular appendages present on the corolla and (or) calyx lobes, distinguish the *C. chapalana* clade from other major groups of subgenus *Grammica*. Multicellular protuberances have evolved multiple times in subgenus *Grammica*; however, in the *C. chapalana* clade, they attained a degree of morphological distinctiveness that is not encountered in other clades. First, in the *C. chapalana* clade, appendages develop on the bracts, calyx, and corolla lobes, and they have a characteristic subapical position (Figs. 1*a*–1*h*). In other *Grammica* clades, multicellular protuberances usually develop only on the bracts and calyx, and they are irregularly distributed along the midveins. Second, the morphology of the appendages in the *C. chapalana* clade is unique; namely, they are narrow conical, tubular, or horn shaped (Figs. 1*a*–1*h*), and hence the vernacular name used for these species is “horned dodders”. In other groups, the shape of the multicellular protuberances can be dome-like (*C. dragonella*, clade A; *C. desmouliniana*, clade L) or crest-like (*C. cotijana*, clade G; *C. chinensis*, clade H; *C. tuberculata*, clade L; for *Grammica* clades, see Stefanović et al. 2007). However, as for the species from other clades, the calyx and corolla appendages in the *C. chapalana* clade begin to develop early in the bud, and they are fully formed when reproductive structures are not yet mature. Calyx and corolla appendages are fleshy; they bear one or more stomata at their apex (Figs. 1*f* and 1*h*), and their physiological function is still unknown.

Based on the presence and morphology of the corolla appendages, we are confident that *C. ortegana* belongs to the *C. chapalana* clade even if we could not include it in the molecular analyses. Moreover, the morphology of the flowers indicates that among other species of this clade, *C. ortegana* is likely the most closely allied to *C. costaricensis*. These are the only two species within the *C. chapalana* complex that are morphologically reminiscent of the *C. umbellata* clade, one of the major *Cuscuta* subgenus *Grammica* groups that share evolutionary affinities with the horned dodders (Stefanović et al. 2007; Costea and Stefanović 2010). *Cuscuta costaricensis* and *C. ortegana* have membranous flowers that maintain their cream-white color when dried; styles are thin, and in general they exhibit the same shape of calyx and corolla lobes as the members of the *C. umbellata* clade. The remaining species in the *C. chapalana* clade have fleshy flowers that tend to become dark brown after they dry; styles are either subulate or thick and cylindrical; perianth parts have a different morphology (see identification key and descriptions).

Capsules are dehiscent in all the species. The subulate styles present in several species of the *C. chapalana* clade (*C. boldinghii*, *C. bonafortunae*, *C. chapalana*, and *C. erosa*) are a feature that evolved in *Cuscuta* in only two other clades from subgenus *Grammica* (clades G and O; Stefanović et al. 2007).

Pollen grains are 3(–4)-zonocolpate, subspheroidal to prolate; the tectum is more diverse than in the *C. umbellata* clade and is imperforate, perforate, or microreticulate. No additional pollen variation was encountered for previously studied species (Welsh et al. 2010; for pollen data and images, see Costea 2007–onwards).

Sequences and alignments

Summary descriptions for sequences obtained from *trnL–F*, ITS, and 26S rDNA 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 et al. 2007; Stefanović and Costea 2008). Although these three noncoding regions exhibited length variation, the alignments among the ingroup taxa

Fig. 1. Micromorphology of the *Cuscuta chapalana* complex. (*a–c*) *Cuscuta chapalana*: (*a*) calyx lobe appendage; (*b*) flower; (*c*) corolla lobe appendage. (*d–h*) *Cuscuta bonafortunae*: (*d*) flower; (*e–f*) calyx appendages; (*g–h*) corolla appendages. Note the stomata indicated by small arrowheads. (*i*) Infrastaminal scales with long, branched fimbriae in *C. mexicana* morphotype from Sierra de Manantlan. (*j–k*) *Cuscuta carnosa*: (*j*) thick infrastaminal scales fimbriae; (*k*) perforate pollen tectum. Scale bars = 0.5 mm (*a*, *e*, *g*); 1 mm (*b*, *d*); 100 µm (*c*); 50 µm (*f*, *h*); 1 mm (*i*); 0.2 mm (*j*); 2.5 µm (*k*).

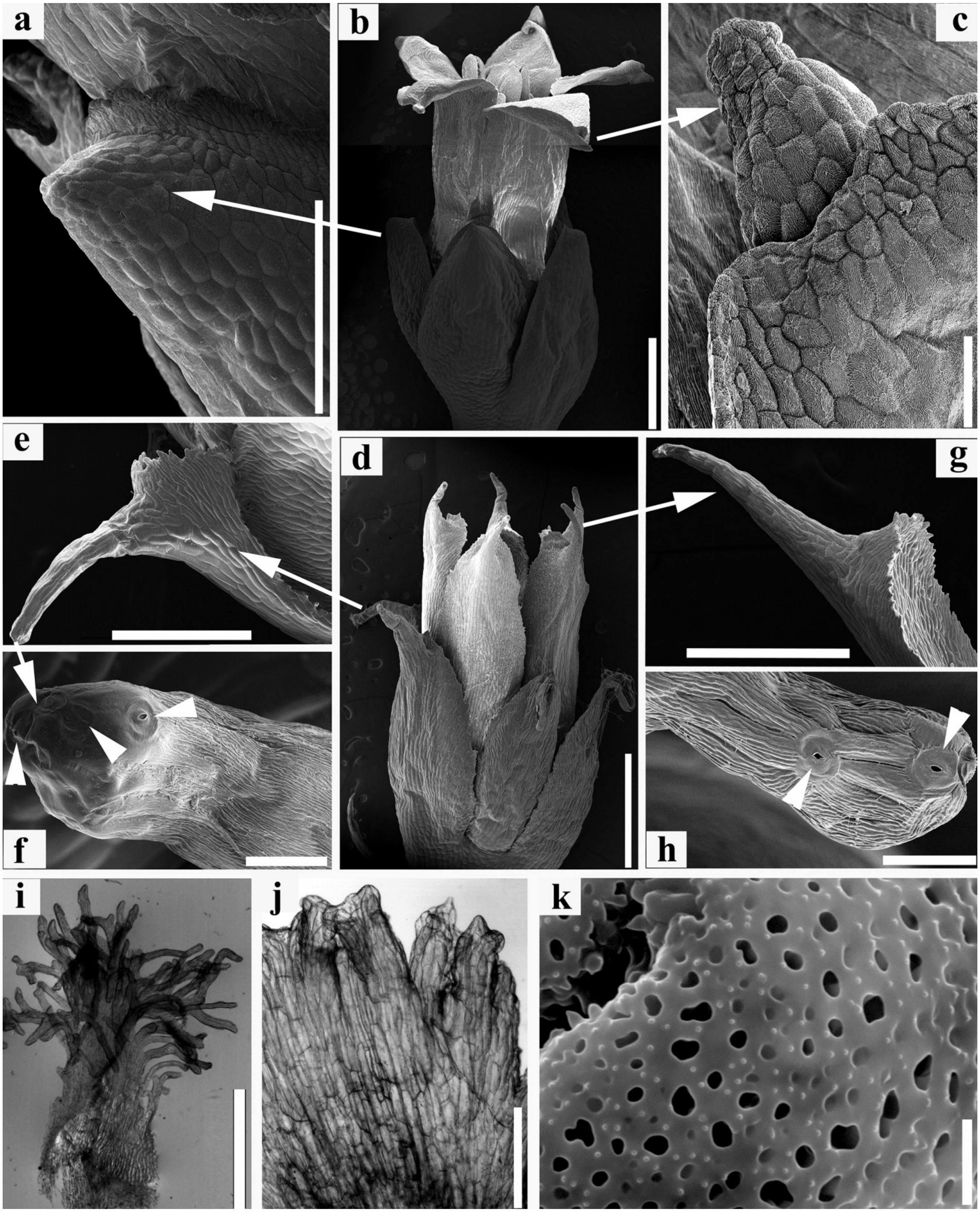


Table 1. Summary descriptions for sequences included in and trees derived from individual and combined data sets of the *Cuscuta chapalana* complex.

	trnL–F (plastid)	ITS (nuclear)	26S rDNA (nuclear)	Combined
No. of OTUs included	17	22	21	23
Sequence characteristics				
Aligned length	618	622	864	2104
Variable sites	96	205	112	413
Parsimony-informative sites	53	132	63	248
Mean AT content (%)	63	50	45	50
MP search				
No. of trees	2	1	3	27
Length	124	314	148	519
CI	0.895	0.799	0.851	0.826
RI	0.916	0.866	0.902	0.880
ML search				
Model of DNA evolution	HKY + G	TrN + G	TrN + G	TrN + G
No. of trees	1	1	1	1
–ln *L*	1440.6096	2428.303	2056.2397	6063.1182

Note: CI, consistency index (excluding parsimony-uninformative characters); HKY + G, Hasegawa–Kishino–Yano model of DNA substitution plus discrete gamma distribution; TrN + G, Tamura–Nei model of DNA substitution plus discrete gamma distribution; –ln *L*, ln likelihood; MP search, most parsimonious search; ML search, maximum likelihood search; OTU, operational taxonomic unit; RI, retention index.

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* subgenus *Grammica* (Stefanović et al. 2007; Stefanović 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 one or the other region from a few individuals, presumably because of the poor quality or limited quantity of the DNA extracted from some older herbarium specimens. In addition, we failed to obtain any amplicons for the plastid region (*trnL–F*) in *C. boldinghii* and *C. mexicana*. The simple explanation of poor DNA quality could be excluded as unlikely in some of these cases because the very same extractions were used successfully to amplify the nuclear ribosomal regions. Furthermore, multiple attempts to amplify smaller fragments using different combinations of internal and (or) alternative primers were also unsuccessful. Consistent with our previously reported results (Stefanović et al. 2007; Stefanović and Costea 2008), these data indicate that the *trnL–F* region either experienced a significant acceleration in substitution, and thus attained sequence divergence at priming sites used in PCR, or it was altogether lost from the plastid genome of these species. Missing sequences are indicated by an en dash in Appendix A.

Phylogenetic analyses

Initial phylogenetic analyses were conducted on individual *trnL–F*, ITS, and 26S rDNA matrices. For all three of these analyses, the strict consensuses of equally parsimonious trees (not shown) resulted in relationships that were topologically identical or nearly identical to the respective results derived under the maximum likelihood criterion (Fig. 2). Also, clades recovered in each analysis were congruent with the tree structure recovered using data from the other matrices. Because there were no strongly supported but conflicting topologies from individual data partitions, we proceeded with a combined analysis. This total-evidence approach benefits from the most complete taxon sampling as well as greater resolution than the larger data set can provide. The maximum likelihood analysis using the total-evidence approach resulted in a single best tree; the phylogram illustrating the inferred relationships as well as branch lengths is shown in Fig. 3. This tree is entirely congruent with the strict consensus tree resulting from the parsimony analysis (Table 1; tree not shown).

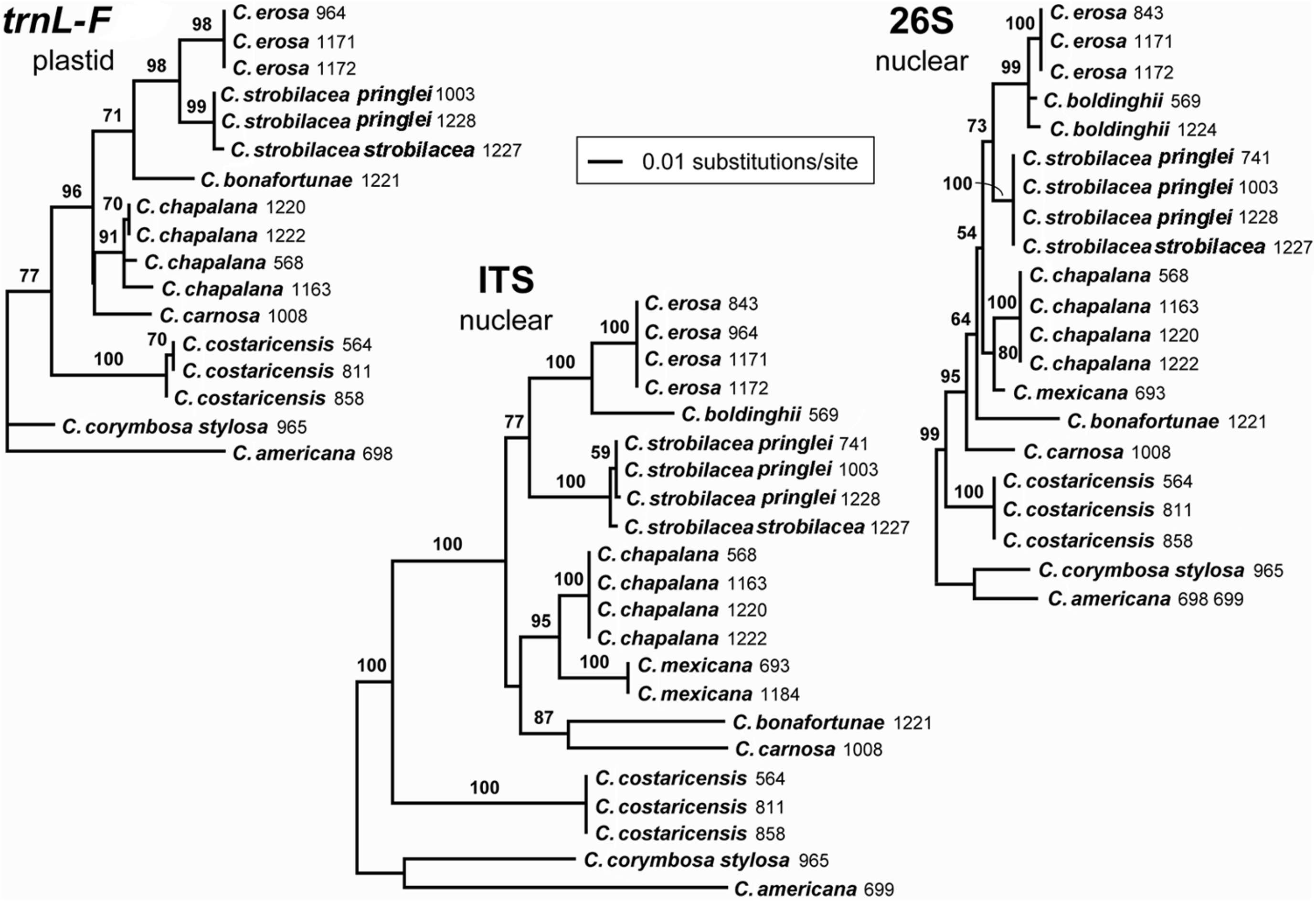
The topology resulting from the combined data sets revealed that the *C. chapalana* species complex is monophyletic and strongly supported as such (100% BS; Fig. 3). The first split within the *C. chapalana* group occurs between the *C. costaricensis* clade on one side, and the remainder of this complex on the other side. Both of these results are in agreement with our previous broadscale results (clade K; Stefanović et al. 2007; Stefanović and Costea 2008). Within the larger clade, three major subclades were recovered. The first two subclades, both strongly supported (100% BS; Fig. 3), consist of three (*C. erosa*, *C. boldinghii*, and *C. strobilacea*) and two (*C. chapalana* and *C. mexicana*) previously described species, respectively. The third subclade contains a single representative, a molecular placeholder, for each of the two lineages described in this study as new species, *C. bonafortunae* and *C. carnosa*. The internal support for the sister group relationship between these two species varied in individual analyses (Fig. 2), resulting in only a moderate support in the combined analysis (75% BS; Fig. 3). While some resolution for the backbone relationships among these three subclades is recovered, the support remains week (<50% BS; Fig. 3).

Discussion

Placement of *Cuscuta blepharolepis*

Cuscuta blepharolepis, an African species included by

Fig. 2. Phylogenetic relationships among species of the *Cuscuta chapalana* complex obtained from maximum likelihood analyses of individual plastid (*trnL–F*) and nuclear [internal transcribed spacer (ITS), 26S rDNA] data sets. Closely related species *C. corymbosa* var. *stylosa* and *C. americana* are used as outgroups. Branch lengths are drawn at the same scale for all three phylograms. Maximum likelihood bootstrap values are indicated for nodes supported ≥50%. Numbers following species names correspond to DNA accessions (see Appendix A).



Yuncker (1932) in subsection Ceratophorae, most likely does not belong to the *C. chapalana* species complex. Based on Yuncker's description and line drawings, *C. blepharolepis* lacks the characteristic subapical multicellular appendages found on the corolla and (or) calyx lobes of most species in this group. Furthermore, the subulate stiles and deeply divided calyx lobes described for *C. blepharolepis* are similar to those of some species from clades G and O of subgenus *Grammica* (Stefanović et al. 2007). These latter New World clades include known cases of long-distance dispersal to Australia or Africa (e.g., *C. victoriana* and *C. tasmanica* to Australia in clade G, and *C. kilimanjari* to Africa in clade O; Stefanović et al. 2007). Therefore, it is possible that *C. blepharolepis* may belong to one of these clades rather than to the *C. chapalana* complex. However, the exact phylogenetic position of this species remains questionable, and to solve this problem, additional and more recent specimens than the type collected by Welwitsch in 1856–1857 (BM) are needed for detailed morphological examination as well as DNA extraction.

Species variation and delimitation

Detailed morphological examination as well as the phylogenetic relationships interred from molecular data (Figs. 2 and 3) confirm the distinctiveness of the species treated by Yuncker (1932) in his monograph, including those that were known only for the type collections. In addition, the two new species described here, *C. bonafortunae* and *C. carnosa*, are quite distinct from both morphological and molecular points of view. *Cuscuta bonafortunae* (Figs. 1*d*–1*h* and 4) is most similar morphologically to *C. boldinghii* and *C. chapalana*; from the former it differs in the corolla lobes that are three to four times longer than the tube and the short infrastaminal scales; from the latter, in the short corolla tube without longitudinal concavities (see the identification key and descriptions). *Cuscuta carnosa* is reminiscent morphologically of *C. mexicana* from which it can be distinguished by the very fleshy flowers and corolla lobes without appendages (Figs. 1*j* and 5; see identification key and descriptions).

Given the scarcity of previously known specimens for the *C. chapalana* species complex (e.g., Yuncker 1932; Carranza 2008), it was not a surprise that the new herbarium vouchers we found and examined revealed additional morphological variation. *Cuscuta chapalana*, for example, was described by Yuncker (1932) as having 3–4 mm long flowers, with a calyx shorter than to equal the length of the corolla tube. First, the size of the flowers in this species can normally reach 5–6 mm. Second, infrastaminal scales in C. *chapalana* can vary from truncate and almost entire (Yuncker 1932) to bifid

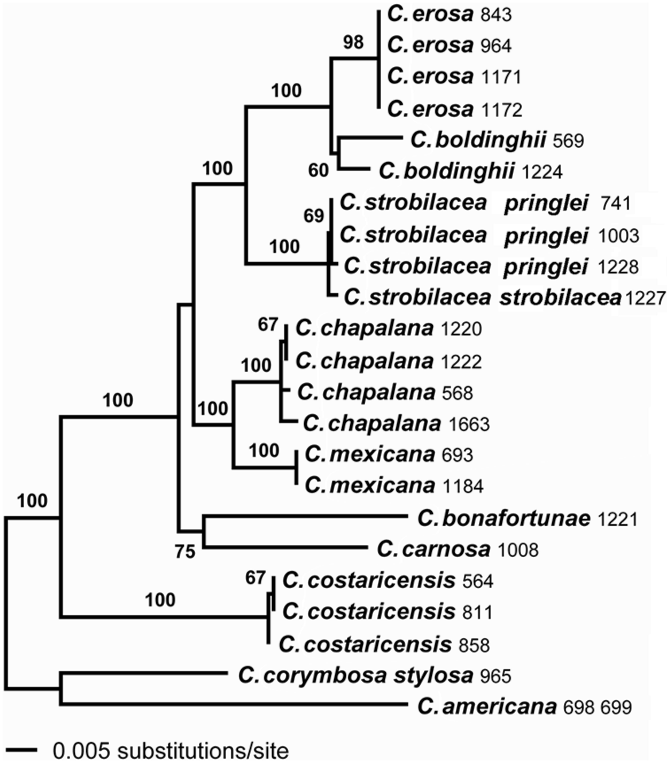


Fig. 3. Phylogenetic relationships among species of the *Cuscuta chapalana* complex obtained from maximum likelihood analyses of combined plastid and nuclear data sets (*trnL–F*, internal transcribed spacer, 26S rDNA) under the TrN + G model of DNA evolution. Closely related species *C. corymbosa* var. *stylosa* and *C. americana* are used as outgroups. Maximum likelihood bootstrap values are indicated for nodes supported ≥50%. Numbers following species names correspond to DNA accessions (see Appendix A).

or even fimbriatae. In particular, we discovered in Jalisco, Mexico, a morphotype of *C. chapalana* with 6–7 mm long flowers and a corolla tube that is two to three times longer than the calyx. Similarly, *C. mexicana*, a species included by Yuncker in subsection Tinctoriae (Yuncker 1932), is also more variable than initially thought. Most notably, a morphotype from Sierra de Manantlan (Jalisco, Mexico) has infrastaminal scales with dendritically branched, multiseriate fimbriae up to 0.4–0.8 mm long, which are the longest ever encountered in any *Cuscuta* species (Fig. 1*i*). The recognition of these morphotypes as varieties is premature at this point, but it may be possible in the future after the examination of additional material using faster-evolving molecular markers and after gaining a better understanding of their biogeography.

Yuncker described *Cuscuta pringlei* in 1921, but later he reassessed and considered this species to be a synonym of *C. strobilacea*, an earlier binomial of Liebmann (Yuncker (1932, 1965). Our study confirms that *C. strobilacea* and *C. pringlei* are conspecific, but a closer examination of their types, geographical distribution, and morphological variation patterns revealed new data that strongly suggest that two parapatric varieties can be recognized, albeit with weak molecular support for their separation (Fig. 3). The type variety occurs in Guerrero, Michoacán, Veracruz, Oaxaca (Mexico), El Salvador, and Honduras. It has acute calyx and corolla lobes, and subapical appendages are present both on the corolla and calyx lobes (Fig. 6, *a*1–*a*2; identification key). The other variety corresponds to *C. pringlei*, and it grows in Baja California, Chiapas, Durango, Jalisco, Morelos, and Nayarit (Mexico). Its calyx and corolla lobes are rounded, and subapical appendages are present only in the calyx lobes (Fig. 6, *b*1–*b*3; identification key). Similar discrete variations in the shape of the calyx and (or) corolla lobes are commonly recognized at a varietal level in species from other clades of subgenus *Grammica*; for example, *Cuscuta indecora* var. *longisepala* Yunck.; *Cuscuta platyloba* var. *triangulata* Yunck.; and *Cuscuta xanthochortos* var. *lanceolata* Mart. Consequently, a new nomenclatural combination and the variety status are proposed for *C. pringlei* in the taxonomic treatment.

Taxonomic treatment

1. *Cuscuta boldinghii* Urban, Repert. Spec. Nov. 16: 38. 1919

TYPE: Netherlands Antilles, Bonaire 1909–1910, *Boldingh 7379*.

HOLOTYPE: at B was apparently destroyed during the Second World War.

ISOTYPES: K, NY, U.

= *Cuscuta ceratophora* Yunck., Illinois Biol. Monogr. 6(2–3): 28. 1921

TYPE: Mexico, Guerrero–Michoacán, 8 October 1898, *Langlassé 438*.

HOLOTYPE: US.

ISOTYPES: F, GH, K, NY, P.

DESCRIPTION: STEMS slender, yellow-orange. INFLORESCENCES glomerulate or dense-paniculiform, globose-isolated or confluent; pedicels 0.2–0.6 mm; bracts 1 at the base of clusters, 0–2 at the base of pedicels, 0.75–1.8 mm long, ovate to lanceolate resembling sepals, margins entire, apex acuminate to attenuate. FLOWERS 5-merous, 2.5–4 mm, membranous, creamy when fresh, brown when dried; papillae absent; laticifers not visible; calyx 2.3–2.8 mm, brownish, not reticulate, shiny, campanulate, ca. as long as the corolla tube, divided 1/2–2/3 the length, tube 0.6–1.1 mm, lobes 1.3–1.8 mm, overlapping, ovate, oblong to obovate, not carinate, margins entire or finely serrulate-denticulate, apex acute or obtuse with a subapical horn-like projection, 0.3–0.6 mm long, prolonging beyond the apex; corolla 2.2–3.2 mm, tube 1.2–1.6 mm, campanulate, lobes 1.2–1.8 mm, ca. as long as the tube, spreading to reflexed, ovate to lanceolate, margins entire to irregular denticulate, apex obtuse but with a subapical horn-like projection 0.3–0.7 mm (like the calyx lobes), straight; stamens exserted, shorter than corolla lobes, 0.4–0.5 mm × 0.2–0.3 mm, anthers ovate to elliptic, filaments 0.5–0.9 mm; INFRASTAMINAL SCALES 1.2–1.6 mm long, equaling corolla tube, bridged at 0.5–0.7 mm, oblong to broadly ovate, rounded, sparsely short-fringed, fimbriae 0.04–0.15 mm; styles 0.9–2 mm, longer than the ovary, stout and subulate, wider at the base and tapering toward the stigma. CAPSULES circumscissile, 1.8–2.3 mm × 1–2 mm, globose to slightly depressed, not thickened or risen around the small interstylar aperture, not translucent or becoming translucent very late, capped by the withered corolla. SEEDS 2–4 per capsule, 0.75–1.1 mm × 0.7–0.9 mm, angled, subround, ovate to broadly elliptic, seed coat cells alveolate–papillate.

Fig. 4. *Cuscuta bonafortunae*, sp. nov: (*a*) flower; (*b*1) dissected calyx; (*b*2) calyx lobe detail; (*c*) corolla after removal of calyx; (*d*) dissected corolla showing infrastaminal scales and stamens. Note the short corolla tube and the infrastaminal scales, bifid or with a few fimbriae. Scale bars = 1 mm.

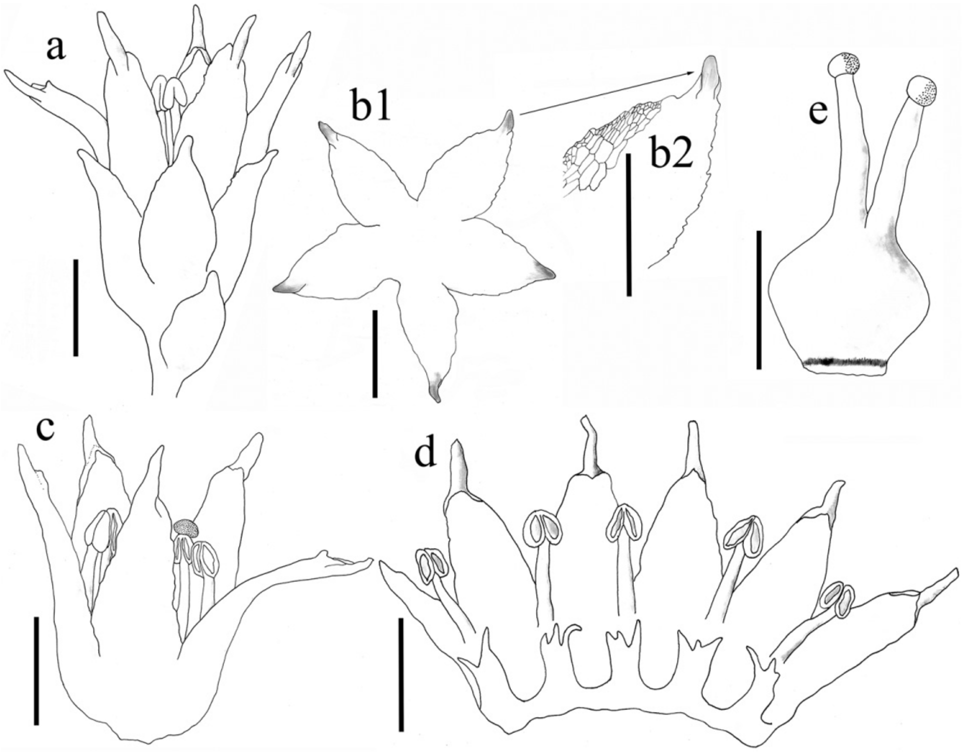


Fig. 5. *Cuscuta carnosa*, sp. nov: (*a*) flower; (*b*) dissected calyx; (*c*) undissected calyx; (*d*) dissected corolla showing infrastaminal scales and stamens; (*e*) gynoecium. Scale bars = 1 mm.

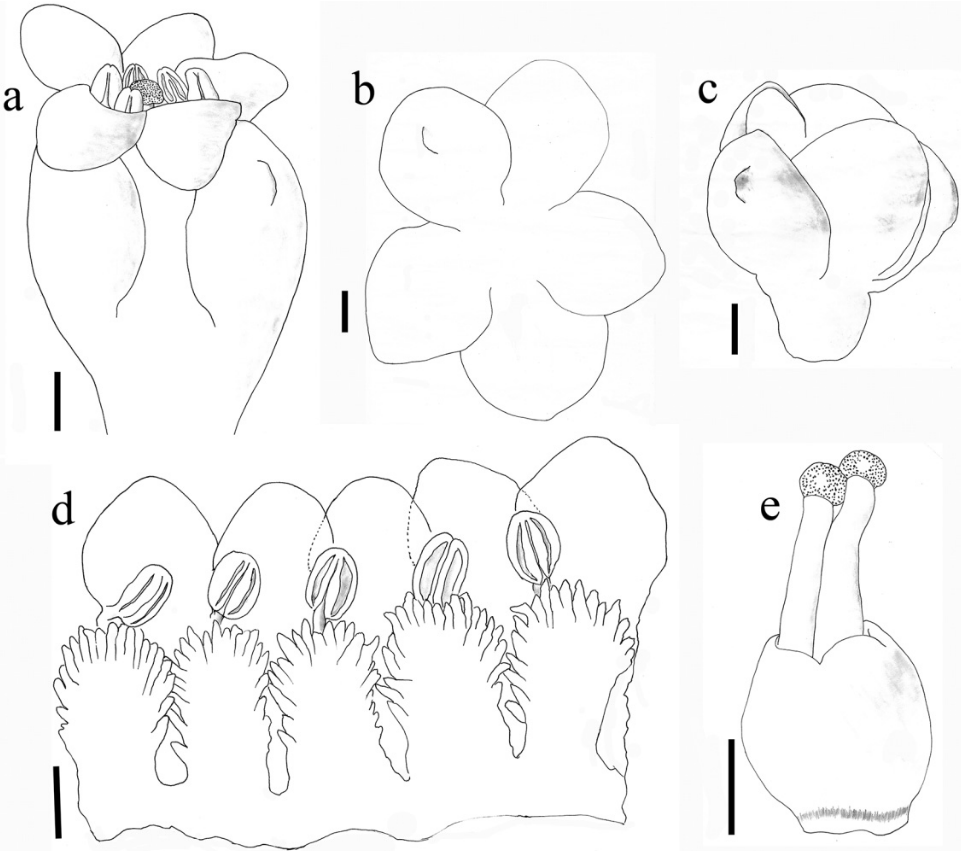
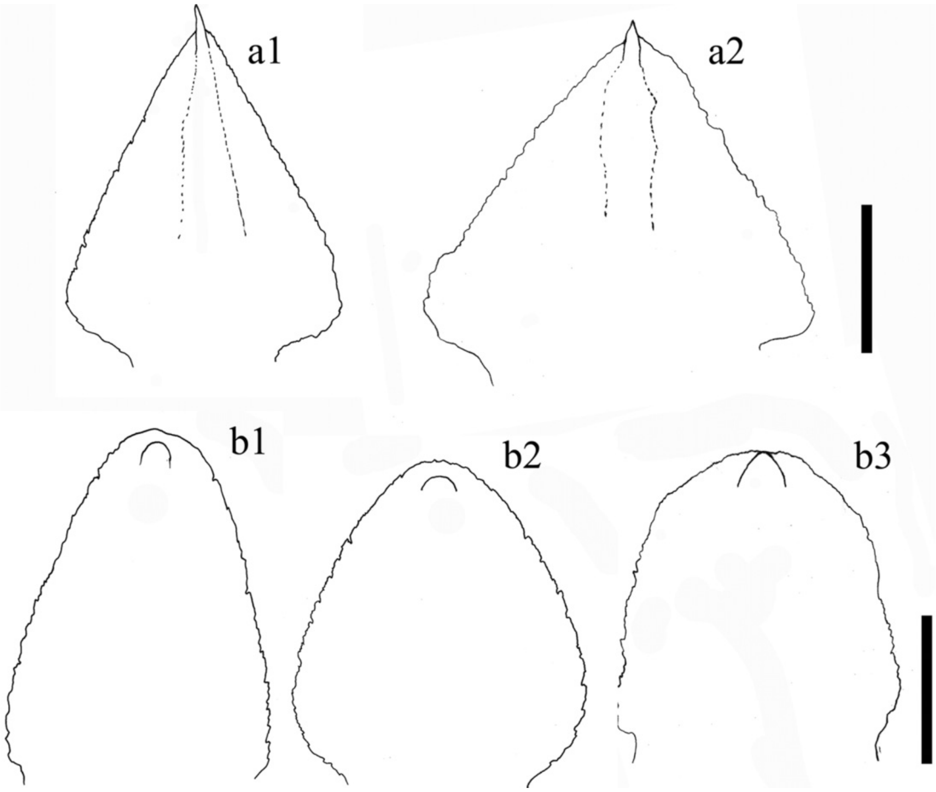


Fig. 6. Variation of calyx lobe shape in varieties of *Cuscuta strobilacea*. (*a*1–*a*2) *C. strobilacea* var. *strobilacea*; (*b*1–*b*3) *C. strobilacea* var. *pringlei*. Scale bars = 1 mm.



Identification key for species of *Cuscuta chapalana* clade

1*a*. Each flower subtended by 0–2 bracts 3
1*b*. Each flower subtended by 5–7 bracts 2

2*a*. Bracts and calyx lobes acute (Fig. 6, *a*1–*a*2); corolla lobes triangular-lanceolate with a subapical appendage . . . . . *C. strobilacea* var. *strobilacea*
2*b*. Bracts and calyx lobes rounded (Fig. 6, *b*1–*b*3); corolla lobes ovate to oblong, rounded without a subapical appendage . . . . . *C. strobilacea* var. *pringlei*

3*a*. Corolla lobes without multicellular appendages (Fig. 5) . . . . . 3. *C. carnosa*, sp. nov.
3*b*. Each corolla lobe with a subapical horn-like appendage (Fig. 1) 4

4*a*. Each calyx lobe with a subapical horn-like appendage (Fig. 1) 5
4*b*. Calyx lobes without multicellular appendages 8

5*a*. Corolla tube at maturity with 5 basal longitudinal concavities (Fig. 1*b*) . . . . . 4. *C. chapalana*
5*b*. Corolla tube without concavities 7

6*a*. Corolla lobes 3–4 times longer than the tube; infrastaminal scales bifid or with a few fimbriae (Fig. 4) . . . . . 2. *C. bonafortunae*, sp. nov.
6*b*. Corolla lobes approximately ca. as long as the tube; infrastaminal scales broadly ovate, oblong to almost truncate, densely fringed 7

7*a*. Calyx lobes orbicular to oblong-obovate, apex nearly truncate not exceeded by the subapical dome-like appendage; seeds 0.94–1.45 mm × 0.8–1.38 mm . . . . . 6. *C. erosa*
7*b*. Calyx lobes ovate, oblong to slightly spathulate, apex obtuse to acute, exceeded by the apical horn-like appendage; seeds 0.75–1.1 mm × 0.7–0.9 mm . . . . . 1. *C. boldinghii*

8*a*. Calyx fleshy, not reticulate, 1/2–3/4 as long as the corolla tube . . . . . 7. *C. mexicana*
8*b*. Calyx membranous, reticulate, equal in length to corolla tube 9

9*a*. Corolla cylindrical; infrastaminal scales 1/2–2/3 as long as corolla tube . . . . . 8. *C. ortegana*
9*b*. Corolla campanulate; infrastaminal scales equal in length to corolla tube . . . . . 5. *C. costaricensis*

DISTRIBUTION AND ECOLOGY: North America (Mexico, Guatemala, Honduras, and Costa Rica), West Indies, and South America (Venezuela). Flowering May–November, –January; elevation 5–1000 m; hosts: *Acalypha*, *Aeschynomene*, *Blechnum*, *Borreria*, *Bouchea*, *Dalea*, *Desmodium*, *Dicliptera*, *Euphorbia*, *Hamelia*, *Phyllanthus*, *Salvia*, *Tephrosia*, *Wedelia*.

2. ***Cuscuta bonafortunae*** Costea & I. García, sp. nov. (Figs. 1*d*–1*h* and 4)

TYPE: Mexico, Michoacán, Mpio. Zamora: Libramiento Sur-Sureste de Zamora, Michoacán; cerca del entronque de la Carr. Libre Zamora-Morelia, y salida libramiento hacia Jiquilpan aprox. a 500 m al W. 19°57″N, 102°15.125″W; 1740 m; Hierba parásita en manchón, de tallos no muy largos y de 20–30 cm sobre el suelo sobre varias herbáceas, *Salvia*, *Bouchea*, etc. escasa. Cerca del matorral subtropical; 11 septiembre 2009, *García Ruiz 8290*.

HOLOTYPE: CIMI.

ISOTYPES: GH, IEB, MEXU, MO, NY, US, WLU.

Cuscuta boldinghii *et* C. chapalana *maxime simile, sed lobis corollae tubo 3–4plo longioribus; ab C. boldinghii differt infrastaminalibus scalis curtioribus; ab C. chapalana differt corolla tubo 0.6–0.8 mm longi, campanulato, sine sulci longitudinaribus.*

DESCRIPTION: STEMS slender, orange. INFLORESCENCES dense, glomerulate; pedicels 0.2–1 mm; bracts 1–2 at the base of clusters and 0–1 at the base of pedicels, 0.8–1.7 mm long, ovate-lanceolate, margins entire, apex acuminate. FLOWERS 5-merous, 3–4 mm, fleshy, white when fresh, creamy-white when dried, papillae absent; laticifers not visible; CALYX 1.5–2.1 mm, brownish-yellow, not reticulate or shiny, campanulate, longer than the corolla tube, divided to ca. 1/3 the length, tube 0.4–0.7 mm, lobes 1.4–1.8 mm, slightly overlapping, triangular-ovate to lanceolate, not carinate, with a subterminal dorsal horn-like projection, 0.2–0.6 mm (Figs. 1*d*–1*e*); margins membranous, irregular, sparsely denticulate, apex acute to acuminate slightly reflexed; COROLLA 2.5–3 mm, tube campanulate, 0.6–0.8 mm, lobes 2–2.4 mm, initially erect, later spreading or reflexed, 3–4 times longer than the tube, lanceolate to linear, margins entire, apex acute with a subterminal horn-like projection, 0.4–0.8 mm (Figs. 1*g*–1*h*); STAMENS exerted when corolla lobes are reflexed, shorter than the latter, anthers 0.3–0.4 mm × 0.25–0.3 mm, subround to broadly ovate; POLLEN GRAINS prolate, 20–24 µm, imperforate (when puncta are present, their diameter is 50–200 nm); filaments 0.6–1 mm; INFRASTAMINAL SCALES 0.6–8 mm long, ca. equaling the corolla tube, bridged at 0.25–0.3 mm, oblong, bifid or with a few fimbriae 0.05–0.2 mm; STYLES 0.8–1.3 mm, equaling to slightly longer than the ovary, subulate. CAPSULES circumscissile, 1.8–2.5 mm × 1.2–2 mm, globose to slightly depressed, not thickened or risen around the relatively large interstylar aperture, translucent, not capped by the withered corolla. SEEDS 2–3 per capsule, 0.8–1.2 mm × 0.7–0.9 mm, angled, subround to broadly elliptic, seed coat cells alveolate–papillate.

ETYMOLOGY: Specific epithet comes from the Latin “bonus” and “fortuna” meaning “of good luck” alluding both to the chance of encountering the new species at the end of a journey through Mexico in August 2009, and the good fortune that prevented potentially tragic consequences after an accident that happened when we collected the plants.

DISTRIBUTION AND ECOLOGY: Mexico: Guanajuato and Michoacán; flowering August–October; elevation 1900–2000 m; hosts: parasitic on low herbaceous plants: *Bouchea*, *Porophylllum*, *Salvia*, *Simsia*.

3. ***Cuscuta carnosa*** Costea & Stefanović, sp. nov. (Fig. 5)

TYPE: Mexico, Durango, Mpio. El Saldo, Sierra Madre Occidental, along Hwy. 40 from 1 to 4.6 miles north of the state line and 1.6 to 5.2 miles south of Revolcaderos, ca. 3–4 miles north of El Palmito (approx. 105°50″W, 23°36″N). Humid pine and oak forest on steep northeast-facing slopes. A white-flowered parasite on *Salvia*; elevation 6600 ft; 27 March 1984; *Sanders et al. 4940*.

HOLOTYPE: UCR; fragment WLU.

Cuscutae mexicanae *similis sed floribus carnosis, calyx 3.5–4.5 mm longus; corolla 5–6 mm longa, lobis non appendiculatae; infrastaminales scalae cum fimbriis crasae.*

DESCRIPTION: STEMS coarse, orange. INFLORESCENCES dense, glomerulate; pedicels 0.5–2 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 3–4 mm long, broadly ovate, margins entire, apex rounded. FLOWERS 5-merous, 5–7 mm, very fleshy, white when fresh, creamy-white or brownish when dried, papillae absent; laticifers not visible; CALYX 3.5–4.5 mm, brownish-yellow, not reticulate or shiny, cupulate to sub-globose, shorter than the corolla tube, divided to 1/3–1/4 the length, tube 0.5–1 mm, lobes 2.6–3.8 mm, overlapping, broadly ovate to round, some lobes carinate or with a dorsal dome-like projection, 0.1–0.2 mm; margins membranous, entire, apex rounded; COROLLA 5–6 mm, tube ovoid to urceolate, 3–3.8 mm, lobes 1.5–2.2 mm, initially erect, later spreading, shorter than the tube, broadly ovate to round, margins entire, apex rounded without a subterminal horn-like projection; STAMENS not exerted, anthers 0.7–1 × 0.6–8 mm, elliptic to broadly elliptic, filaments 0.1–0.2 mm; POLLEN grains prolate spheroidal to prolate, 22–30 µm, tectum perforate, diameter of puncta 0.2–0.8 µm (Fig. 1*k*; corresponds to tectum perforatum 2 of Welsh et al. 2010]; INFRASTAMINAL SCALES 2.8–3.3 mm long, ca. equaling the corolla tube, bridged at 0.8–1.4 mm, oblong to obovate, very thick, fimbriae 0.05–0.3 mm, very thick (Fig. 1*j*); STYLES 1.5–2 mm, equaling the ovary, thick, cylindrical. CAPSULES circumscissile, 2.5–3 × 3–6 mm, ovoid, not thickened, but risen in a collar around the inconspicuous interstylar aperture, pericarp thick, not translucent, capped by the withered corolla. Mature seeds not seen.

ETYMOLOGY: The specific epithet alludes to the thick, fleshy texture of all the floral parts including the infrastaminal scales (from Latin “*carnis*” = flesh, meat).

DISTRIBUTION AND ECOLOGY: Mexico. Durango: Sierra Madre Occidental; flowering March; elevation 2000 m; host *Salvia* sp. Although *C. carnosa* is known only from one herbarium collection, we are fully confident of its validity because the type specimen has numerous mature flowers, which allowed both a thorough morphological investigation and the inclusion in the molecular analysis. A search at the type collection site in the Sierra Madre Occidental Mountains in February 2010 failed to recover the species, which indicates that, similarly to other dodders, *C. carnosa* is probably a rare species.

4. *Cuscuta chapalana* Yunck., Illinois Biol. Monogr. 6(2–3): 28. 1921 (Figs. 1*a*–1*c*)

TYPE: Mexico, Jalisco, Mountains near Lake Chapala, 18 Nov 1893, *Pringle 5349*.

HOLOTYPE: US, a fragment at NY.

ISOTYPES: GH, MEXU.

DESCRIPTION: STEMS slender to medium, orange. INFLORESCENCES dense, glomerulate-paniculate often confluent; pedicels 0.2–1 mm; bracts 1–2 at the base of clusters and 0–1 at the base of pedicels, 0.8–1.7 mm long, ovate, margins entire, apex acute. FLOWERS 5-merous, 4–7.2 mm (Fig. 1*b*), fleshy, white when fresh, creamy-white when dried, papillae absent; laticifers not visible; CALYX 2.4–3 mm, brownish-yellow, not reticulate or shiny, narrow-campanulate to tubular, 1/2–3/4 of the corolla tube, divided to ca. 1/3 the length, tube 0.6–1.4 mm, lobes 2–2.6 mm, slightly overlapping, ovate to lanceolate, not carinate, with a subterminal dorsal horn-like projection, 0.1–0.3 mm (Fig. 1*a*); margins membranous, irregular, entire to sparsely denticulate, apex obtuse to acute; COROLLA 3.8–7 mm, tube cylindrical, 2.5–5 mm, lobes 1.2–2.5 mm, initially erect, later spreading or reflexed, 2–3 times shorter than the tube, lanceolate to linear, margins entire, apex acute with a subterminal horn-like projection, 0.2–0.5 mm (Fig. 1*c*); STAMENS exerted when corolla lobes are reflexed, shorter than the latter, anthers 0.7–0.9 mm × (0.3) 0.4–0.6 mm, ovate to oblong, filaments 0.1–3 mm; INFRASTAMINAL SCALES 1.5–2.4 mm long, ca. 1/2 the corolla tube, bridged at 0.2–0.3 mm, linear, bifid or with a few fimbriae, 0.05–0.2 mm; STYLES 2–3.8 mm, longer than the ovary, subulate. CAPSULES circumscissile, 1.6–4 mm × 1.5–2 mm, depressed globose, not thickened or risen around the inconspicuous interstylar aperture, become translucent very late, capped by the withered corolla. SEEDS 1–3 per capsule, 1.4–1.6 mm × 1.1–1.25 mm, angled, elliptic to broadly elliptic, seed coat cells alveolate–papillate.

DISTRIBUTION AND ECOLOGY: Mexico: Michoacán and Jalisco; flowering September–January; elevation 1500–2340 m; hosts: *Bidens*, *Mirabilis*, *Montanoa*, *Ricinus*, *Salvia*, *Sida*, *Stevia*, *Tithonia*.

5. *Cuscuta costaricensis* Yunck., Mem. Torrey Bot. Club 18: 227. 1932

TYPE: Mexico: Durango, Santiago Papasquiaro, August 1896, *Palmer 412*.

HOLOTYPE: US, fragment in B.

ISOTYPES: B, GH, K, MO.

DESCRIPTION: STEMS slender to medium, yellow or orange. INFLORESCENCES dense, glomerulate, often confluent; pedicels 0–1.5 mm; bracts 1 at the base of clusters, 0–1 at the base of pedicels, 3–3.5 mm long, broadly triangular (broader than long), margins entire, apex cuspidate. FLOWERS 5-merous, 4.2–5.5 mm, membranous, white when fresh, creamy-white when dried; papillae present on the calyx and corolla lobes; laticifers visible in the corolla lobes, anthers and sometimes in the infrastaminal scales; CALYX 3.2–3.5 mm, straw-yellow, reticulate, not shiny, campanulate, equaling the corolla tube, divided 2/3–3/4, tube 1–1.5 mm, lobes 1.5–2.1 mm, basally overlapping, broadly ovate-triangular, not carinate, margins entire, apex cuspidate; COROLLA 3.5–4.5 mm, tube 2–3 mm, campanulate, lobes 1.5–2 mm, erect to reflexed, 1/2–1/3 the tube, ovate, overlapping at base, margins entire, apex rounded or obtuse but appearing cuspidate because of a subterminal dorsal cusp, 0.1–0.3 mm long prolonging beyond the apex; STAMENS barely exserted, shorter than corolla lobes, anthers 0.5–7 mm × 0.45–0.55 mm, elliptic, filaments 0.3–0.6 mm; INFRASTAMINAL SCALES 2–2.8 mm long, reaching filament bases, bridged at 0.4–0.6 mm, oblong-obovate, dense and long fringed, fimbriae 0.2–0.4 mm; STYLES 3–3.5 mm, longer than the ovary, evenly filiform. CAPSULES circumscissile, 2.5–4 mm × 2–3.1 mm, depressed globose, thickened at the apex with large interstylar aperture, translucent, loosely surrounded and capped by the withered corolla. SEEDS 3–4 per capsule, 1–1.2 mm × 0.6–0.8 mm, angled, broadly elliptic, seed coat cells alveolate–papillate.

DISTRIBUTION AND ECOLOGY: Mexico, Guatemala, Costa Rica. Flowering August–September; elevation 1000–2100 m; hosts: *Amaranthus*, *Anoda*, *Cologania*, *Desmodium*, *Heterosperma*, *Melampodium*, *Milleria*, *Salvia*, *Simsia*, *Tagetes*, *Xanthocephalum*.

6. *Cuscuta erosa* Yunck., Illinois Biol. Monogr. 6 (2–3): 26. 1921

TYPE: Mexico, Sonora, 1869, *Palmer s.n.*

HOLOTYPE: US.

DESCRIPTION: STEMS medium, yellow-creamy to purple. INFLORESCENCES loose to moderately dense, paniculiform or corymbiform; pedicels 1.5–6 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.8–1.9 mm long, ovate-triangular to lanceolate, margins entire to serrulate-denticulate, apex obtuse to acute, sometimes with a subapical horn-like projection. FLOWERS 5-merous, 3.5–4.5 mm, membranous, creamy to reddish-brown both when fresh and dried; papillae absent; laticifers not visible; CALYX 1.5–2.2 mm, yellow, finely reticulate, shiny, cupulate, 3/4 to almost equaling corolla tube, divided 1/2–2/3 of the length, tube 0.5–0.8 mm, lobes 1.2–1.6 mm, basally overlapping, oblong-obovate to orbicular, unevenly carinate, margins membranous and minutely erose or denticulate, apex nearly truncate with a dorsal subapiacal dome-like projection, not exceeding the apex; COROLLA 3–4 mm, tube 1.5–2.2 mm, campanulate, sometimes with horizontal ridges between stamen attachments, lobes 1.2–1.6 mm, erect to spreading or reflexed, ovate-oblong, margins entire to denticulate, apex obtuse, cucullate, often with a dorsal subapical horn-like appendage, 0.1–0.2 mm long; STAMENS exserted, shorter than the corolla lobes, anthers 0.7–1 mm × 0.4–0.5 mm, ovate to oblong, filaments 0.4–1 mm; INFRASTAMINAL SCALES 1.5–2 mm long, 3/4 to almost equaling corolla tube, bridged at 0.4–0.6 mm, oblong to almost truncate, dense and long fringed, fimbriae 0.2–0.4 mm; styles 1.8–3.2 mm, longer than the ovary, thick and ± subulate, wider at the base and tapering toward the stigma. CAPSULES circumscissile, 2–2.5 mm × 2.2–2.5 mm, globose, thickened but not risen around the inconspicuous interstylar aperture, not translucent, carrying the withered corolla about the middle or at the top. SEEDS 1–4 per capsule, 0.94–1.45 mm × 0.8–1.38 mm, angled, subround to ovate, seed coat cells alveolate–papillate.

DISTRIBUTION AND ECOLOGY: USA: Arizona; Mexico: Baja California, Sonora, Sinaloa. Flowering August–October; elevation 400–1300 m; hosts: *Abutilon*, *Amaranthus*, *Ambrosia*, *Anisacanthus*, *Bidens*, *Carlowrightia*, *Euphorbia*, *Gom-*

phrena, *Hymenoclea*, *Ipomoea*, *Jatropha*, *Justicia*, *Kallstroemia*, *Merremia*, *Mimosa*, *Ruella*, *Russelia*, *Sphinctospermum*, *Talinum*, *Tephrosia*.

7. *Cuscuta mexicana* Yunck., Mem. Torrey Bot. Club 18: 215. 1932

TYPE: Mexico: Durango, Sianori, 800 m, February 1924, *Ortega 5363*.

HOLOTYPE: US.

ISOTYPES: GH, K, MEXU.

DESCRIPTION: STEMS medium, orange. INFLORESCENCES dense, glomerulate; pedicels 0.5–2 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 1.5–2.6 mm long, broadly ovate, margins entire, apex acute. FLOWERS 5-merous, 4–6 mm, fleshy, white when fresh, creamy-white or brownish when dried, papillae absent; laticifers not visible; CALYX 2.2–3 mm, brownish-yellow, not reticulate or shiny, cupulate, 1/2–3/4 as long as the corolla tube, divided to ca. 1/3 the length, tube 0.6–1 mm, lobes 1.5–2 mm, overlapping, broadly ovate to elliptic, sometimes slightly carinate; margins membranous, entire to irregularly crenulate, apex rounded; COROLLA 4–5 mm, tube cylindrical to ovoid, 2.5–3 mm, lobes 1.5–2 mm, initially erect, later spreading, somewhat shorter than the tube, broadly ovate, margins entire irregularly crenulate, apex obuse, ± cucullate, without subterminal horn-like projection, 0.2–0.2 mm; STAMENS not exerted or only slightly so, anthers 0.7–1 mm × 0.4–0.6 mm, elliptic, filaments 0.4–0.6 mm; POLLEN grains prolate spheroidal to prolate, 21–25 µm, tectum perforate, diameter of puncta 0.2–0.8 µm (corresponds to TP2 type) of Welsh et al. 2010); INFRASTAMINAL SCALES 1.6–2.8 mm long, 3/4 to ca. equaling the corolla tube, bridged at 0.3–0.5 mm, oblong to obovate, fimbriae vary from 1-seriate, unbranched, 0.2–0.4 mm to 3–4-seriate, dendritically branched and 0.4–0.8 mm (Fig. 1*i*); STYLES 1.8–3 mm, longer to equaling the ovary, thick, cylindrical. CAPSULES circumscissile, ovoid, 3.3–4 mm × 2.8–3.3 mm, thickened but not risen around the inconspicuous interstylar aperture, not translucent, enveloped by the withered corolla. SEEDS 1–2 per capsule, 1.8–2.1 mm × 1.8–2.1 mm, angled to spherical, subround to round, seed coat cells alveolate–papillate.

DISTRIBUTION AND ECOLOGY: Mexico: Durango and Jalisco, 800–2000 m; hosts were not recorded in any of the herbarium specimens and could not be identified based only on the stems and leaves.

8. *Cuscuta ortegana* Yunck., Mem. Torrey Bot. Club 18: 232, 1932

TYPE: Mexico, Durango, La Bajada, Tamazula, 300 m, 1921, *Ortega 4255*.

HOLOTYPE: US.

DESCRIPTION: STEMS slender to medium, yellow or orange. INFLORESCENCES dense, glomerulate, often confluent; pedicels 0.4–1.5 mm; bracts 1–2 at the base of clusters, 0–1 at the base of pedicels, 2.5–3 mm long, broadly triangular (broader than long), margins entire, apex long-cuspidate. FLOWERS 5-merous, 4.2–6 mm, membranous, white when fresh, creamy-white when dried; papillae present or absent on the calyx and corolla; laticifers visible in the corolla lobes, anthers and infrastaminal scales; CALYX 3.2–4 mm, straw-yellow, reticulate, not shiny, campanulate, equaling the corolla tube, divided ca. 1/3, tube 0.8–1.2 mm, lobes 2.2–3 mm, basally overlapping, broadly ovate-triangular, not carinate, margins entire, apex long-cuspidate; COROLLA 4–5 mm, tube 3–3.3 mm, cylindrical, lobes 1.5–2 mm, erect to reflexed, 1/2–2/3 the tube, ovate, overlapping at base, margins entire, apex ± acute, cucullate, with a subterminal dorsal cusp, 0.25–0.4 mm long; STAMENS not or barely exserted, shorter than corolla lobes, anthers 0.4–0.55 mm × 0.3–0.4 mm, elliptic, filaments 0.2–0.3 mm; INFRASTAMINAL SCALES 2–2.4 mm long, 1/2–2/3 as long as the tube, bridged at 0.4–0.7 mm, oblong to obovate, dense fringed, fimbriae 0.2–0.4 mm; STYLES 2.5–3.5 mm, longer than the ovary, evenly filiform. CAPSULES circumscissile, 2–3.3 mm × 1.8–2.2 mm, depressed globose, thickened at the apex with large interstylar aperture, translucent or not, loosely surrounded and capped by the withered corolla. SEEDS 1–2 per capsule, 1–1.25 mm × 0.9–1.1 mm, angled, subround to round, seed coat cells alveolate–papillate.

DISTRIBUTION AND ECOLOGY: Mexico: Durango, Jalisco, Michoacán; elevation 1000–2000 m; hosts were not recorded for any of the collections and are impossible to identify based on the fragments present in herbaria.

9. *Cuscuta strobilacea*, Liebm., Förh. Skand. Naturf. Möte 1844: 194 (–195). 1847. (Fig. 6)

TYPE: Mexico, Veracruz, Mirador 2/1842, *Liebmann 12361*.

LECTOTYPE: here designated, C.

DESCRIPTION: STEMS medium, yellow to orange. INFLORESCENCES dense, paniculate-glomerulate, often confluent; pedicels 0.2–1 mm; bracts 2–5 at the base of clusters and 5–7 at the base of pedicels, spiraled and resembling the sepals, 1.5–2.7 mm long, triangular or broadly ovate, margins membranous, finely erose, apex rounded to acute. FLOWERS 5-merous, 4–6 mm, fleshy, white when fresh, brownish when dried, papillae absent; laticifers not visible; CALYX 2.–2.8 mm, brownish to reticulate and shiny, cupulate, equaling or longer than the corolla tube, divided to 1/4–1/5 the length, tube 0.3–0.5 mm, lobes 1.7–2.5 mm, overlapping, broadly ovate to triangular, sometimes slightly carinate; margins membranous, finely erose, apex rounded or acute (Fig. 6); ± cucullate, with a subterminal dome-like or cusp, 0.05–0.3 mm long; COROLLA 3.6–5.5 mm, tube narrow-campanulate, 1.8–3 mm, lobes 1.5–2.5 mm, initially erect, later spreading, ± equaling the tube or slightly shorter, ovate to oblong-lanceolate, margins entire to finely erose, apex obuse or acute, slightly cucullate, with or without subterminal horn-like projection, 0.2–0.3 mm; STAMENS exerted, anthers 0.7–1 mm × 0.5–0.7 mm, oblong to elliptic, filaments 0.6–0.9 mm; INFRASTAMINAL SCALES 1.8–2.8 mm long, equaling the corolla tube, bridged at 1–1.2 mm, ovate to broadly elliptic, fimbriae 0.3–0.4 mm (some branched); STYLES 1.2–2.5 mm, equaling to longer than the ovary, thick, cylindrical. CAPSULES ovoid 3–3.8 mm × 2.2–2.8 mm, thickened and risen around the inconspicuous interstylar aperture, not translucent, capped by the withered corolla. SEEDS 2–4 per capsule, 1.3–1.6 mm × 1.1–1.3 mm, angled, broadly oblong to subround, seed coat cells alveolate–papillate.

NOTE: Three other specimens at C bear the same label information as the lectotype but have different collection numbers and are considered syntypes: *Liebmann 12362*, *12364*, *12371* (C). Although the labels of these type collections contain as a locality only "Mirador", which could not be found on the current maps of Veracruz, "Dep. Veracruz" is clearly stated in the protologue. In addition, according to Friis (2000), who retraced Liebmann's exploration in Mexico, "Mirador" is the name of a hacienda located in Veracruz near Orizaba, at an elevation of about 1000 m.

Cuscuta strobilacea var. ***strobilacea***

DISTRIBUTION AND ECOLOGY: Mexico (Jalisco, Guerrero, Michoacán, Oaxaca, and Veracruz), El Salvador, and Honduras. Flowering December–March; elevation 200–1500 m; hosts: *Aeschynomene*, *Bouganvillea*, *Ficus*, *Triumfetta*. Figure 6, *a*1–*a*2.

Cuscuta strobilacea var. ***pringlei*** *(Yunck.) Costea & I. García, comb. et stat. nov.*

BASIONYM: *Cuscuta pringlei* Yunck., Illinois Biol. Monogr. 6(2–3): 29. 1921.

TYPE: Mexico, Jalisco. Hillsides near Guadalajara, 10 October 1889, *Pringle 2472*.

HOLOTYPE: US.

ISOTYPES: F, G, GOET, K, NY, LL, MEXU, MO, P, UPS.

DISTRIBUTION AND ECOLOGY: Mexico: Baja California, Chiapas, Durango, Morelos, and Nayarit. Flowering October–February; elevation 1000–2000 m; hosts: *Calliandra*, *Dalea*, *Eriosema*, *Mimosa* (hosts are frequently identified only as "Fabaceae" in the labels of herbarium specimens). Figure 6, *b*1–*b*3.

NOTE: The line drawing that Yuncker (1932) used for *C. strobilacea* represents in fact *C. strobilacea* var. *pringlei*.

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Appendix A

Taxa, DNA accession Nos., sources of plant material from which DNA was extracted, and GenBank accession Nos. for sequences used in this study are listed below.

DNA extraction numbers are indicated on the phylogenetic trees in the main text following the species names. GenBank accession Nos. are given in the following order: *trnL–F*, ITS, 26S rDNA. Sequences newly generated for this study are indicated in bold. An en dash (–) indicates that the sequence was not obtained. Abbreviations of herbaria in which the vouchers are deposited follow Index Herbariorum.

Cuscuta boldinghii: **569**, *Breedlove 37373* (NY), –, EF194575, **JN234778**; **1224**, *Carranza & Silva 7448* (WLU), –, –, **JN234779**. ***C. bonafortunae***: **1221**, *García Ruiz 8290* (WLU/CIMI), **JN234799**, **JN234809**, **JN234780**. ***C. carnosa***: **1008**, *Sanders et al. 4940* (TEX/LL), **JN234800**, **JN234810**, **JN234781**. ***C. chapalana***: **568**, *McVaugh 22042* (MICH), EF194338, EF194578, **JN234782**; **1163**, *Carranza & Medina 7297* (IEB, WLU), **JN234801**, **JN234811**, **JN234783**; **1220**, *García Ruiz & Machuca 8169* (WLU/CIMI), **JN234802**, **JN234812**, **JN234784**; **1222**, *García Ruiz et al. 8064* (CIMI, WLU), **JN234803**, **JN234813**, **JN234785**. ***C. costaricensis***: **564**, *Chazaro et al. 7527* (MICH), EF194340, EF194580, **JN234786**; **811**, *Chazaro 7537* (XAL), EF194341, EF194581, **JN234787**; **858**, *Gonzalez 145* (NY), EF194342, EF194582, **JN234788**. ***C. erosa***: **843**, *Kearney & Peebles 14988* (NY), –, EF194573, **JN234789**; **964**, *Lehto & Lehto L49371* (ASU), **JN234804**, EF194574, –; **1171**, *van Devender et al. 2004-1199* (WLU), **JN234805**, **JN234814**, **JN234790**; **1172**, *Reina et al. 2001-748* (ARIZ, WLU), **JN234806**, **JN234815**, **JN234791**. ***C. mexicana***: **693**, *McVaugh 26593* (MICH), –, EF194579, **JN234792**; **1184**, *Gentry & Jardel 73521* (MO), –, **JN234816**, –. ***C. strobilacea var. strobilacea***: **1227**, *García Ruiz 8333* (CIMI, WLU), **JN234807**, **JN234817**, **JN234793**. ***C. strobilacea var. pringlei***: **741**, *Gentry 5291* (GH), –, EF194576, **JN234794**; **1003**, *Gentry 5291* (MEXU), EF194339, EF194577, **JN234795**; **1228**, *García Ruiz et al. 8274* (CIMI, WLU), **JN234808**, **JN234818**, **JN234796**. **Outgroups**: ***C. corymbosa Ruiz & Pav. var. stylosa Engelm.***: **965**, *Rzedowski 28752* (ASU), EF194348, EF194587, **JN234797**. ***C. americana L.***: **698**, *Garneau et al. 1470* (TRT), EF194363, –, –; **699**, *Buswell 6231* (NY), –, EF194597, **JN234798**.

Appendix B

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

1. *Cuscuta boldinghii*. **NORTH AMERICA**. **MEXICO**. **Baja California**. Miraflores, 28 February 1928, *Jones 24368* (RSA). **Chiapas**. Mpio. de Acala: 12–14 km south of Hwy. 190 near Tuxtla along road to La Angostura, 550 m, 9 September 1974, *Breedlove 37373* (MEXU, MO). **Jalisco**. Mpio de La Huerta: 8 km east of Chamela, 30–50 m, 8–10 December 1970, *McVaugh 25140* (MICH). **Guerrero**. Mpio. Galeana: San Luis, 14 m, 19 October 1937, *Hinton 10867* (K). **Michoacán**. Mpio. Apatzingan: 4–5 km east of Apatzingan on road Apatzingan-Cuatro Caminos, 320 m, 6 September 2007, *García Ruiz 7782* (CIMI, WLU). Mpio. de Huetamo: ca. 4.5 km southeast of de La Estancia, 18°40′00″ N, 100°51′00″W, 800 m, 9 September 2007, *Ramírez-Amezcua & Steinmann* 1158 (IEB, WLU). Mpio. de Lázaro Cárdenas: ca. 2.5 km from Lazaro Cardenas on the Hwy. Playa Azul, 10 m, 4 February 2008, *Carranza & Silva 7448* (IEB, WLU). **Sinaloa**. Mpio. Culiacán: close to Tamazula, 15 February 1988, *Vega & Hernández 2630* (MEXU). **Sonora**. Mpio. Álamos: Güirocoba crossing of Río Cuchujaqui, 12.3 km (by air) south–southeast of Álamos, 26°56′15″N, 108°53″W, 260 m, 28 January 1992, *Van Devender 92–31 et al.* (ARIZ, UC). Mpio. Huatabampo: 2.3 km northeast of Las Bocas, 26°37′53″N, 109°19′36″W, 20 m, 22 Sep 1994, *Van Devender & Yetman 94–692* (ARIZ, ASU, UC, UCR). **State of Mexico**. Mpio. Temascaltepec: Bejucos, 610 m, 19 September 1933, *Hinton 4776B* (G, K, MEXU, US). **Tabasco**. Mpio. Cárdenas, 24 June 1985, *Rodríguez & Curiel 3593*

(XAL). **Tamaulipas**. Rancho el Cielito, Valle del Rio Salinas, 25 September 1984, *McDonald 896* (IEB). **Veracruz.** Mpio. Actopan: Actopan, 19°30″N, 96°37″W, 500–600 m, 29 June 2001, *Provance 3403* (UCR). Mpio. Yecuatla: 19° 52′, 96°46″W, 25 May 1981, *Gutiérrez 141* (IBUG). **Yucatan**. Mpio. Valladolid, Xuilub, 20°26″W, 87°59″N, 25m, 23 November 1989, *Mogensen 1231* (AAU). **GUATEMALA**. Dept. Sololá: along Río Bravo below Finca Mocá, 800–1000 m, *Steyermark 48051* (F). Dept. Santa Rosa: region of Platanares between Taxisco and Guazacapán, 220 m, 3 December 1940, *Standley 79151* (F). **HONDURAS**. Dept. Morazán: Zamorano, 800 m, 4 September 1945, *Rodiguez 3281* (F). Dept. de Yoro: near Progreso, 30 m, 24 January 1928, *Standley 55040* (F). **NICARAGUA**. Dept. Chinandega: vicinity of Chichigalpa, 90 m, 12–15 July 1947, *Standley 11166* (F, NY, US). Dept. Managua: vicinity of Escuela Nacional de Agricultura, 12 km east of Managua, 16 January 1969, *Seymour 2238* (GH). Dept. Masaya, northeast part of Volcano Masaya, 30 October 1977, *Neill 2857* (MO). **COSTA RICA**. 4 km south of Punta Arenas, 20 August 1938, *Morrison 8775* (G, GH, K, US); Punta Arenas, 9°23″ N, 84°09″W, 10 m, 16 May 1990, *Grayum 9850* (MO). **WEST INDIES**. **BONAIRE**. Along road., north of BOPEC, 27 February 1999, *Proosdij 859* (GH, U). **CURACAO**. 14 January 1885, *Suringar s.n.* (B). **BARBADOS**. Groves Agricultural Station, 15 August 1979, *Adams & Chinnery 14518* (BAR, MO, TRIN). **GRENADA**. Saint Andrew Parish, roadside near Grenville, 25 January 1951, *Hunnewell 19549* (GH). **HAITI**. Massif de la Hotte, close to Dame Marie, on the beach, 1 August 1928, *Ekman 10455* (G, GH, K, NY, S). **PUERTO RICO**. Ramos Island, 12 November 1983, *Liogier et al. 34662* (UPRRP). **SOUTH AMERICA**. **Venezuala**. Vicinity of Maracay and Caracas 1930–1934, *Vogl 971* (NY); east of San Fernando de Apure, 100 m, 3 December 1955, *Wurdack & Monachino 39796* (NY).

2. *Cuscuta bonafortunae*. **MEXICO**. **Guanajuato**. Mpio. Santiago de Maravatío: close to Ojo de Agua, 1900 m, 15 October 1989, *Rzedowski 49127* (IEB). **Michoacán.** Mpio. Zamora, same location as the type, 11 September 2010, *García Ruiz & García 8375* (CIMI, WLU); 16 October 2010, *García Ruiz 8391* (CIMI, WLU).

3. *Cuscuta carnosa*. **MEXICO**. **Durango**. Mpio. El Saldo, Sierra Madre Occidental, elevation 6600 feet; 27 March 1984; *Sanders et al. 4940* (UCR).

4. *Cuscuta chapalana*. **MEXICO**. **Jalisco**. Mpio. Ojuelos de Jalisco: Guadalupe Victoria, 21°43′20″N, 101°38′55″, 2200 m, 11 October 1998, *Carrillo-Reyes et al. 468* (IBUG); Rancho “Las Papas de Arriba”, 4.5 km northeast of Guadalupe Victoria, 21°43′48″N, 101°39′48″W, 2260 m, 14 October 2000, *García & Harker 438* (IBUG); El Carrizo (Las Azucenas), 20°17′7.2″N, 103°29′9.3″W, 2084 m, 8 November 2008, *García Ruiz & Machuca 8169* (CIMI, WLU). **Michoacán**. Mpio. Huirmaba: Huiramba, 2200 m, 5 September 1986, *Escobedo 1223* (IEB, WLU). Mpio. de Jiquilpan: Jiquilpan, 19°59′17.9″N, 102°42′17.2″W, 1550 m, 1 November 2007, *García Ruiz 7942*; same location, 14 December 2007, *García Ruiz et al. 8024* (CIMI, WLU). Mpio. de Morelia: 5 km north of Indaparapeo, 2100 m, 8 November 1987, *Rzedowski 41290* (IEB, WLU). South of Morelia, on the western part of Cerro Verde, 2260 m, 22 December 2006, *Carranza & Medina 7293* (IEB, WLU). Morphotype with long corolla tube: **Jalisco**. Mpio. Jocotepec: north face of Cerro Viejo, 2200 m, 17 January 1987, *Chazaro et al. 4408* (IBUG, XAL); Barranca de Sayula southeast de San Pedro Tesistán, November–December 1993, *Machuca 7026* (MICH, XAL); same location, 1859 m, 9 February 2003, *Machuca 9099* (CIMI, IBUG). Mpio. Tlajomulco: between Potrerillos and Trojes, southeast face of Cerro Viejo, 20°20′ 29.3″N, 103°21′6.3″W, 1785 m, 19 December 2007, *García Ruiz et al. 8064* (CIMI, WLU).

5. *Cuscuta costaricensis*. **MEXICO**. **Chihuahua**. Mojarachic (Munèrachic?), 2103 m, 18 September 1989, *Knobloch 5837* (US). **Durango**. Mpio. de Canelas: E of Canelas, 1400 m, 16 March 1986, *Vizcarra 243* (MEXU). Mpio. Mezquital: 5 km north of Temoaya, 23 September 1982, 1350 m, *Fernández 1175* (IEB, MEXU). Mpio. Nombre de Dios: San José de la Parrilla, ca. 4 km west of 23°43′99″N, 104°8′99″ W, 2150 m, 25 October 1983, *Gonzáles 2758* (MEXU). **Guanajuato**. Mpio. San Miguel de Allende: surroundings of Rancho Viejo 1900 m, 25 September 1994, *Rzedowski 52675* (CAS, IEB); 5 km north of Comonfort, 14 September 1946, *Hernández et al. 2323* (MEXU); Laguna de Yuria, 29 August 1970, 1850 m, *Rzedowski 27592* (MEXU). Mpio. Santiago Maravatio: east of Ojo de Agua de la Hierba Buena, 20°08′ 37″N, 101°01′19″W, 1870 m, 11 September 2007, *Carranza 7293* (IEB, WLU). **Jalisco**. Mpio. La Manzanilla: La Rosa Amarilla, 20°05′49.6″N, 103°09′26.9″W, 2022 m, 18 December 2007, *García Ruiz 8052* (CIMI, WLU); Mpio. Tuxcueca: La Tachica, 20°09′08″N, 103°15′16″W, 2030 m, 1 October 2000, *Machuca 8497* (CIMI). **Michoacán**. Mpio. de Coeneo: deviation to Matugeo, 2250 m, 29 November 1985, *Escobedo 730* (IEB, WLU). Mpio. De Jiménez: Cerro La Alberca 2000, 20 November 1991, *Pérez-Calix & García 2576* (IEB, WLU). Mpio. Jiquilpan: ca. 1 km north of Los Tábanos and 5–6 km west of Jiquilpan, on road to Colima, 2100 m, 30 September 2010, *García Ruiz 8388* (CIMI, WLU). Mpio. Los Reyes de Salgado: Barranca de Los Chorros del Varal, ca. 14–15 km east–southeast of Los Reyes, 900 m, 21 October 2010, *García Ruiz & Cortes 8405* (CIMI, WLU). Mpio. Sahuayo: Barranca La Gloria, west of Sahuayo, 1700 m, 18 October 2007, *García Ruiz et al. 7910* (CIMI, WLU). **Sonora**. Mpio. Álamos: Rancho Santa Bárbara, 42.3 km east–northeast of Álamos, 27°07′08″N, 108° 43′18″W, 1250 m, 2 October 2006, *Reina-G. 2006-1049 et al.* (ARIZ, WLU). Mpio. Yécora: ca. 2 km northwest of Yécora on old road to Santa Rosa, 28°22′33″N, 108°56′24″W, 1560 m, 5 September 1996, *Wiens 96-125 et al.* (WLU); Río Yepachic near junction with Arroyo Hondo, 28°27′10″N, 108°32′15″W, 1380 m, 27 September 1998, *Van Devender & Reina-G. 98-1789* (ARIZ, WLU); Yécora, 28°21′48″N, 108°55′56″W, 1556 m, 16 September 2006, *Reina-G. & Van Devender 2006-888* (ARIZ, USON, WLU). **State of Mexico**. Mpio. Temascaltepec: Vigas, 1080 m, 16 November 1932, *Hinton 2604* (MEXU, MO). **GUATEMALA**. Volcano Santa María de Jesús, eastern slope, 24 October 1976, *Stuessy & Gardner 4343* (MEXU). Mpio. de Amatitlán: Amatitlán, laguna, 1110 m, [date illegible], *Morales Ruano 1327* (F). Dept. Guatemala, [no day or month] 1939, *Aguilar 149* (F). **COSTA RICA**. Curridabat, November 1856, *Hoffman 463* (B); San Francisco de Guadalupe, 1100 m, October 1912, *Conduz 17397* (G); Cartago: Ochomogo, 1532 m, November 1896, *Conduz 10873* (K).

6. *Cuscuta erosa*. **USA**. **Arizona**. Pima Co.: Baboquivari Mountains, 20 September 1920, *Harrison 5823* (ARIZ); 30 September 1934, *Kearney & Peebles 10377* (CAS, RSA, UC); same location, 1065–1360 m, 1 September 1940, *Kearney & Peebles 14988* (ARIZ, CAS, RSA). Santa Cruz Co.: Santa Rita Mountains, Florida Canyon, 7 October 1937, *Kearney & Peebles 10574* (K); ridge top west of Fresno Canyon, 1270 m, *McLaughlin & Lewis 8504* (ARIZ). **MEXICO**. **Baja California**. Sierra de Guadalupe Region, San Borjitas archeological area, 26°22″N, 112°52″W, 390 m, 20 September 1997, *Rebman et al. 4275* (SD, UCR). **Sinaloa**. La Noria, 245 m, 10 October 1925, *Mexia 235* (MO). **Sonora**. Mpio. Agua Prieta: ca. 7.5 km (by air) southwest of Agua Prieta, 31°15′34″N, 109°36′34″W, 1233 m, 3 October 2004, *Van Devender et al. 2004-1199* (WLU). Mpio. Arizpe: ca. 3 km south–southwest of Arizpe on SON 89, 30°19′37″N, 110°11′33″W, ca. 920 m, 18 August 2001, *Sánchez et al. NF-172* (WLU). Mpio. Baviacora: southwest edge of Mazocahui on SON 117 to Ures, 29°47′56″N, 109°40′36″W, 620 m, 14 August 2006, *Reina-G. & Van Devender 2006-475* (ARIZ, ASU, MO, USON, WLU). Mpio. Cucurpe: Cucurpe; 30°19′46″N, 110°42′18″W, 880 m, 22 August 2001, *Reina-G. & Van Devender 2001-748* (ARIZ, HCIB, WLU). Mpio. Cumpas: Cumpas, 29°59′47″N, 109°46′33″W, 13 August 2006, *Van Devender & Reina-G. 2006-462* (WLU). Mpio. La Colorada: 4 miles east of Willard, between Hermosillo and Colorada, 5 September 1941, *Wiggins & Rollins 288* (ARIZ, CAS, DS); *Van Devender & Reina-G. 2006-55* (ARIZ, USON, WLU). Mpio. Moctezuma: 18.9 km south–southeast of junction with Moctezuma-Huásabas Hwy. on road to Tepache, 29°39′44″N, 109°37′13″W, 635 m, 14 September 2006, *Van Devender & Reina-G. 2006-856* (WLU). Mpio. Yécora: Curea, 28°18′42″N, 109°16′42″W, 490 m, 17 September 1998, *Reina-G. et al. 98-1251* (WLU); 2.7 km west–northwest of Tepoca on MEX 16, 28°27′36″N, 109°15′48″W, 750 m, 30 August 2000, *Van Devender et al. 2000-526* (ARIZ, WLU).

7. *Cuscuta mexicana*. **MEXICO**. **Jalisco**. Sierra de Manantlán, Biosphere Reserve, Las Joyas section 1950 m, 21 March 1991, *Gentry & Jardel 73521* (MO); 3–4 km west to Las Joyas, "2000 m or above", 7 February 1983, *McVaugh 26593* (MICH). Mpio. Autlan: vicinity of Puerto San Campus, 1 km east of El Zarzamoro, 19°35′16″N, 104°14′52″W, 2000 m, 16 May 1990, *Cuevas & Núñez 3834* (IEB, ZEA).

8. *Cuscuta ortegana*. **MEXICO**. **Jalisco**. Mpio. Tepatitlán de Morelos: Crucero Rd between Pegueros and Arandas, 20°42′47″N, 102°42′21″W, 1900 m, 10 October 1996, *Rodríguez & Castro 777* (MEXU). **Michoacán**. Mpio. Coalcomán de Vázquez Pallares, Aquila, 16 January 1948, *Hinton et al. 16294* (K, MICH). **State of Mexico**. Mpio. Temascaltepec, (Plan de?) Vigas, 1080 m, 16 November 1932, *Hinton 2604* (K).

9. *Cuscuta strobilacea* var. *strobilacea*. **MEXICO**. Jalisco. Mpio. Mazamitla: Mazamitla, por la Entrada de San José de Gracia, 2200 m, *García Ruiz et al. 8411* (CIMI, WLU). **Guerrero**. Mpio. de Arcelia: outskirts of Arcelia, 18°20″N, 100°18″W, 350 m, 11 January 1992, *Prather & Soule 1202* (LL, TEX, MEXU); 1.2 km northeast of Achotla, 18°08′45″N, 100°10′07″W, 800 m, 3 February 2005, *Steimann & Porter 4858* (IEB). **Michoacán**. Mpio. Jiquilpan: Jiquilpan, Colegio Colón, 1530 m, 12 March 2008, *García Ruiz 8071* (CIMI, WLU); same location, 4 March 2010, *García Ruiz 8333* (CIMI, WLU). **Oaxaca**. Along dirt road to Chayuco, 12 km from Hwy. 200, 220 m, 29 January 1983, *Miller & Tenorio 527* (MO). **Veracruz**. Mpio. Soteapan: Soteapan, 420 m, 12 January 2000, *Leonti 363* (MEXU). **EL SALVADOR**. Mpio. de Candelaria de la Frontera: ca. 6 km north of Candelaria de la Frontera, 14°08′30″N, 89°40′09″W, 1300 m, 9 December 1994, *Linares & Martínez 2138* (MEXU). **HONDURAS**. **Dept. Cortés**: along Rio Lindo N of Lake Yojoa, 500–600 m, 9–12 April 1951, *Morton 7809* (F, US). *Cuscuta strobilacea* var. *pringlei*. **MEXICO**. Baja California. Loreto, Cayuca Ranch, 23 October 1930, *Jones s. n.* (NY). **Chiapas**. Mpio. de Ixtapa: near the Zinacantántan Paraje of Muctajoc, 1065 m, 29 October 1981, *Breedlove & Davidse 54000* (CAS); along Hwy. 195 between Chiapa de Corzo and Pichucalco, 7.9 miles north of Bochil, 17°03″N, 92°51″W, 1990 m, 17 February 1987, *Croat & Hannon 65094* (MO). **Durango**. Sierra Tres Picos, 1066 m, 20 December 1939, *Gentry 5291* (ARIZ, CAS, GH, NY). La Barranca, Guadalajara, 23 November 1930, *Jones 97347* (CAS, MICH, MO, RSA). **Morelos**. Along Hwy. 115D between Cuautla and Cuernavaca, northwest of Cuautla, 18°59″N, 99°06″W, 1960 m, 24 February 1987, *Croat & Hannon 65757* (MEXU, MO). **Nayarit**. San Blas, 9 November 1920, *Lehto 24253A* (ASU); Mpio. Tepic, ca. 5 km east–northeast of San Andrés, 21°35′31.1″N, 104°51′35.8″W, 693 m, *García Ruiz et al. 8274* (CIMI, WLU).