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More Problems Despite Bigger Flowers: Systematics of *Cuscuta tinctoria* Clade (subgenus *Grammica*, Convolvulaceae) with Description of Six New Species

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Abstract—*Cuscuta tinctoria* clade, the second largest infrageneric group of subgenus *Grammica*, includes 14 species that are centered in Mexico and adjacent regions, but also two species that are found in Australia, presumably as a result of long-distance dispersal. Flowers, pollen, and stigmas are among the largest in *Cuscuta*, with plants being xenogamous or facultatively xenogamous. In this clade, the convergent evolution of morphological traits, especially those associated with the calyx and gynoeceum/capsule, has obscured the identity of some species and has hindered previous efforts to determine their limits. 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. Overall, species were grouped in five subclades. Based on their morphological and molecular similarity, *C. tinctoria*, *C. aurea*, and *C. floribunda* are best treated as a single species, with the latter two taxa being retained as varieties of the former. Our results also show that in their currently accepted delimitation, *C. rugosiceps* and *C. tinctoria* are polyphyletic, the former including one new species, *C. volcanica*, and the latter two new species, *C. timida* and *C. tolteca*. In addition, three other new species are described: *C. iguanella* and *C. insolita*, both with multicellular protuberances on the calyx and/or corolla lobes, and *C. montana*, with broader than long calyx lobes. A taxonomic treatment that includes an identification key, descriptions, geographical distribution, ecological data, and illustrations for all taxa is provided.

Keywords—Evolution, floristics, geographical distribution, morphology, parasitic, phenology, phylogeny.

Cuscuta L. (dodders) is one of the most economically important groups of parasitic plants because infestation by some of its species can result in significant yield losses in a variety of crops (Parker and Riches 1993; Costea and Tardif 2006). Such species are listed as noxious/invasive weeds in the legislation of most countries, and commercial seed/crop shipments found to contain *Cuscuta* seeds at the border are subject to quarantine (Costea and Tardif 2006). In addition, some traditional medicinal *Cuscuta* species from Asia have been recently investigated for their immunostimulating, antioxidating, and antibacterial properties, as well as for their beneficial effects on the reproductive system (e.g. Bao et al. 2002; Gupta et al. 2003; Pal et al. 2006). From an ecological point of view, dodders are keystone species (reviewed by Press and Phoenix 2005), and many of them are endangered requiring conservation measures (Costea and Stefanović 2009a).

Eight decades after Truman G. Yuncker's monograph (Yuncker 1932), the systematics of *Cuscuta* is undergoing an extensive revision. The genus includes ca. 200 species and more than 60 varieties with subcosmopolitan distribution (Yuncker 1932; García and Martín 2007; Stefanović et al. 2007; Costea 2007-onward). Two of the three accepted subgenera, *Cuscuta* and *Grammica* (Lour.) Yunck., have been the subject of broad-scale phylogenetic studies (García and Martín 2007; Stefanović et al. 2007). In subgenus *Grammica*, the largest and most complex infrageneric group, 15 major lineages have been circumscribed (Stefanović et al. 2007). Subsequently, a series of focused systematic studies have been initiated to investigate these clades at a species level. To date, eight major *Grammica* clades have been examined in detail: four that comprise mostly species from the territory covered by the *Flora of North America* (Costea et al. 2005; Costea et al. 2006a,b,c; Costea and Stefanović 2009b; Costea et al. 2009) and four with predominantly Mexican

dodders (Costea et al. 2008a; Costea and Stefanović 2010; Costea et al. 2011 a,b).

Our present study continues the series with the *Cuscuta tinctoria* species complex (clade G, Stefanović et al. 2007), one of the most species rich infrageneric groups of subg. *Grammica* (second only to clade O from South America). This complex includes all the species grouped by Yuncker (1932) in subsect. *Subulatae* Engelm. (*C. jalapensis*, *C. mitrifomis*, *C. rugosiceps*, *C. lindsayi*, *C. woodsonii*), and also, as reported by Stefanović et al. (2007), species from five other subsections of subg. *Grammica*: *Tinctoriae* Yunck. (*C. aurea* and *C. tinctoria*), *Odontolepisae* Yunck. (*C. purpusii*), *Americanae* Yunck. (*C. floribunda*), *Lobostigmae* Engelm. (*C. tasmanica*) and *Platycarpae* Engelm. (*C. victoriana*). In addition, a new species belonging to this clade, *C. cotijana*, was recently described (Costea et al. 2008b). Most of the species of this group are distributed in Southern U. S. A., Mexico and Central America; however, *C. victoriana* and *C. tasmanica* are found in Australia, strongly implying a long-distance dispersal event (Stefanović et al. 2007).

Some of the species of this clade, e.g. *C. jalapensis*, *C. mitrifomis*, and *C. tinctoria*, are among the most common and often weedy dodders in Mexico. The remaining species (e.g. *C. aurea*, *C. cotijana*, *C. floribunda*, *C. lindsayi*, *C. purpusii*, *C. rugosiceps*, and *C. woodsonii*) are relatively rare and little known from different points of view: systematics, biology, ecology, and conservation status. The fact that Yuncker (1932) placed the species of this clade in six different subsections suggests a considerable range of morphological heterogeneity. Flowers, pollen and stigma are among the largest in *Cuscuta* (Welsh et al. 2010; Wright et al. 2011), and plants are xenogamous or facultatively xenogamous (Wright et al. 2012). Although previous floristic treatments of Mexican *Cuscuta* have not highlighted any taxonomic problems (e.g. Ortega-Rubio 2005;

Carranza 2008), our previous studies within subg. *Grammica* (Stefanović et al. 2007) revealed that despite their larger flowers, this clade is among the least known taxonomically in this subgenus, with poorly defined taxa, polyphyletic or unknown species, being in great need of a systematic reappraisal. To build on our preliminary observations, we have sampled numerous additional collections in an attempt to test species limits based on their evolutionary relationships. The objectives of this study are to 1) recover the evolutionary history of the *C. tinctoria* clade based on plastid (*trnL-F*) and nuclear (ITS) sequences; 2) investigate the morphology and micromorphology of the taxa involved and reveal patterns of convergent evolution; 3) revise the taxonomy of the clade, and 4) compile the data about ecology, host range, phenology, and geographical distribution using both the herbarium specimens, and our personal observations in the field during the last seven years.

MATERIAL AND METHODS

Taxon Sampling and Outgroup Selection—We studied specimens from over 100 herbaria in connection with the upcoming treatments of *Cuscuta* for the *Flora of North America* project, *Flora Neotropica*, and a future monograph of the genus (Appendix 2). A subset of 57 accessions, representing 16 ingroup species of the *C. tinctoria* complex, was used for the molecular phylogenetic study (Appendix 1). Efforts were made to sample multiple accessions, particularly for those species spanning large biogeographical ranges (e.g. *C. jalapensis*) and those with variable morphology (e.g. *C. tinctoria* with its three varieties). As a result, two to 13 individuals are included in the molecular analyses for all taxa except for *C. insolita* and *C. timida*, both of which are only represented by a single individual. While *C. insolita* is a potentially extirpated species known only from its type locality, *C. timida* is available from only a limited number of collections. Based on our previous broad phylogenetic analyses of *Cuscuta* subg. *Grammica* (Stefanović et al. 2007; Stefanović and Costea 2008), we selected three species (*C. haughtii*, *C. applanata*, and *C. americana*) with its three closely related groups (clades F, H, and I, respectively) as outgroups (Appendix 1).

Molecular Techniques and Alignments—To infer phylogenetic relationships among species of the *C. tinctoria* complex, sequences for the *trnL-F* intron/spacer region from the plastid genome (ptDNA) as well as from the internal transcribed spacer (ITS) region of nuclear ribo-

somal DNA (nrDNA) were obtained. In addition to the DNA samples used in previous studies (Stefanović et al. 2007; Stefanović and Costea 2008), total genomic DNA was isolated from newly obtained specimens by the modified CTAB method (Doyle and Doyle 1987) and purified using Wizard® minicolumns (Promega, Madison, Wisconsin). DNA extractions, polymerase chain reaction (PCR) reagents and conditions, amplicon purifications, cloning, as well as sequencing procedures followed the protocols detailed in Stefanović et al. (2007). Initial sequencing of plastid and nuclear 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 KC485354–KC485422; Appendix 1).

Phylogenetic Analyses—Sequence alignments were performed manually using the program Se-Al version 2.0a11 (Rambaut 2002). A number of gaps had to be introduced in the alignments. The gaps were scored automatically using SeqState version 1.32 (Müller 2005), coded as simple indels (Simmons and Ochoterena 2000), and appended to the sequence matrix as binary characters. Phylogenetic analyses were conducted under parsimony and Bayesian optimality criteria; summary descriptions of these analyses, for individual as well as combined datasets, are provided in Table 1.

For parsimony, nucleotide characters were treated as unordered and all the changes, including gap characters, were equally weighted. The heuristic searches for most parsimonious (MP) trees were performed with PAUP* version 4.0b10 (Swofford 2002), 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. Relative support for clades was inferred by nonparametric bootstrapping (Felsenstein 1985) as implemented in PAUP*, using 500 heuristic bootstrap replicates, each with 20 random addition cycles, TBR branch swapping, and MULTREES option off (DeBry and Olmstead 2000). Nodes receiving bootstrap (BS) values <60%, 60–75, and >75% were considered weakly, moderately, and strongly supported, respectively.

Bayesian phylogenetic inferences were performed using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). Modeltest v.3.7 (Posada and Crandall 1998) was used to determine the model of sequence evolution that best fit the data by the hierarchical likelihood ratio test (hLRT), starting with the parsimony-derived tree (see Table 1 for models selected). Initially, each Bayesian analysis consisted of two runs of three million generations from a random starting tree using the default priors and four Markov chains sampled every 300 generations. If needed, the run lengths were increased until the standard

TABLE 1. Summary descriptions for sequences included in, phylogenetic analyses conducted on, and trees derived from, individual and combined datasets of *Cuscuta tinctoria* complex. ¹Including coded gaps; ²Including only OTUs for which all sequences are available. CI = consistency index (excluding parsimony uninformative characters); G = rate variation among nucleotides following a discrete gamma distribution; K81 = The Kimura 3-parameter model of DNA substitution (Kimura, 1981); MP = most parsimonious; nst = number of substitution states; OTU = operational taxonomic unit; RI = retention index; TrN = The Tamura-Nei model of DNA substitution (Tamura and Nei, 1993).

	<i>trnL-F</i> (plastid)	ITS (nuclear)	Combined
Number of OTUs included	60	67	60
Number of accessions	59	53	60
Sequence characteristics:			
Aligned (analysed) length	604 (570)	651 (641) ¹	1,255 (1,211) ¹
Variable sites	145	240	362
Parsimony informative sites	98	140	231
Mean AT content (%)	63.4	52.1	57.1 ²
MP tree characteristics:			
Number of trees	>1 × 10 ⁶	>1 × 10 ⁶	>1 × 10 ⁶
Length	206	368	545
CI/RI	0.811/0.949	0.813/0.911	0.802/0.925
Bayesian search conditions:			
Model of DNA evolution (MrBayes settings used)	K81 + G (nst = 6; rates = gamma)	TrN + G (nst = 6; rates = gamma)	Combined (partitioned)
Number of generation (number of runs)	3 × 10 ⁶ (2)	3 × 10 ⁶ (2)	4 × 10 ⁶ (2)
Sampling frequency; Burn-in (%)	300; 20	300; 20	300; 20
Bayesian tree characteristics:			
Mean -lnL	2,035.741	2,986.363	4,877.869
Number of trees retained	16,000	16,000	21,334

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 and Drummond 2004). Stationarity was assumed when all parameter values and the $-\ln L$ 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 significantly supported (Rannala and Yang 1996).

Conflict between datasets was first evaluated by visual inspection, by searching for the presence of conflicting and strongly supported topologies from individual matrices. For one instance where such conflict was found, reciprocally constrained topologies were constructed and their cost in parsimony was assessed using PAUP* (Swofford 2002). One randomly chosen MP tree representing topological results obtained from plastid data was imposed on nuclear data and vice versa. To evaluate the significance among these alternative phylogenetic hypotheses, we implemented the one-tailed Shimodaira-Hasegawa tests (SH tests; Shimodaira and Hasegawa 1999; Goldman et al. 2000) in PAUP*. The test distributions were obtained using the re-estimated log likelihoods (RELL; Kishino and Hasegawa 1989) with 10,000 bootstrap replicates.

Morphology and Micromorphology—Descriptions are based on rehydrated herbarium material (Appendix 2) and corroborated whenever possible by fresh flowers collected in the field and preserved in Formalin–Acid–Alcohol (FAA; Ruzin 1999). We examined the basic morphology of fixed and rehydrated flowers and capsules under a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 7.4 software (MIS Inc., Villa Park, Illinois). The fleshy flowers of most species become dark-brown or even blackish after pressing and drying. Their rehydration requires boiling for a few minutes in a solution of 50% ETOH, then discarding the solution and repeating the operation one or two times to remove some of the dark pigments that accumulate in the flower tissues. Because of these difficulties, it would be important that for the species of this clade to also collect spirit samples together with herbarium specimens. For scanning electron microscopy (SEM), we used hexamethyldisilazane (HMDS) as an alternative for critical dry point (Costea et al. 2011a,b). Rehydrated herbarium samples (Appendix 2) were dehydrated using a series of ethanol (70%, 80%, 95% and 100%; each step one hour), immersed for 1 hr in 1:1 ethanol and HMDS, and passed through an overnight change of 100% HMDS. Samples were air dried and coated with 30 nm of gold using an Emitech K 550 sputter coater. Examination, measurements and pictures were taken at 10 kV using a Hitachi SU1510 variable pressure scanning electron microscope. Welsh et al. (2010) provided a comprehensive survey of *Cuscuta* pollen morphology and its evolution. Considering the taxonomic problems of this group, in addition to examining the new species, we increased the sampling and reexamined the previously studied species (Appendix 2). The terminology regarding the micromorphology of flowers and seeds follows Costea et al. (2006a); pollen and stigma terminology uses Welsh et al. (2010) and Wright et al. (2011), respectively. 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 in the field and from herbarium specimens.

RESULTS

Sequences and Alignments—Summary descriptions for sequences obtained from *trnL-F* and ITS 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 two non-coding regions exhibited length variation, the alignments among the ingroup taxa were straightforward. However, to accommodate inclusion of outgroups, small

fractions of alignments were excluded from phylogenetic analyses (Table 1). This is in contrast to the higher-level phylogenetic study of *Cuscuta* subg. *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 several individuals, presumably due to the poor quality or limited quantity of the DNA extracted from some older herbarium specimens. Missing sequences are indicated by dash in Appendix 1. Alignments in the Nexus format were deposited in TreeBASE (study number TB2:S13806).

Individual and Combined Phylogenies—Several preliminary phylogenetic analyses were conducted using parsimony to explore the distribution of phylogenetic signal in the different individual matrices, with and without coded gaps. Neither resolution nor support were affected in a substantial way by the inclusion of gaps (results not shown). 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. 1, 2). All of the analyses conducted here show the *Cuscuta tinctoria* complex to be a strongly supported monophyletic group (100% BS; ≥ 0.95 PP), in agreement with our previous broad-scale results (clade G; Stefanović et al. 2007; Stefanović and Costea 2008).

Within the *C. tinctoria* complex, five major subclades labeled A–E were recovered with plastid *trnL-F* sequences (Fig. 1, left). All of these groups have branches with substantial length subtending them and are moderately to strongly supported (71–100% BS; ≥ 0.95 PP). Subclade A consists of two reciprocally monophyletic species, *C. tinctoria* and *C. purpusii*. As defined here, *C. tinctoria* includes all accessions previously attributed to three species: *C. tinctoria*, *C. aurea*, and *C. floribunda*. This new circumscription of *C. tinctoria* is both strongly supported and molecularly quite distinct, as evidenced by the length of the branch subtending it (Fig. 1). Within this species, three haplotypes are recovered, consistent with the recognition of three varieties. Subclade B includes representatives of *C. volcanica*, *C. montana*, *C. tolteca*, *C. timida*, and *C. woodsonii*. In contrast to the strong support for this clade, the relationships within this lineage remained mostly unresolved and unsupported, with one exception. Namely, all the members of the newly described *C. volcanica* are found grouped together and closely related to representatives of *C. montana* and *C. tolteca*. This relationship received strong support (78% BS; ≥ 0.95 PP). Subclade C consists of representatives of *C. rugosiceps*, *C. jalapensis*, *C. cotijana*, *C. mitriformis*, *C. iguanella*, and *C. insolita*. This subclade is moderately supported, as are the backbone relationship within it, with bootstrap values ranging from 71–73%. Noteworthy here is that one individual identified as *C. mitriformis* (accession 815) showed levels of polymorphism that are unusual for plastid DNA, requiring cloning of its *trnL-F* amplicon prior to sequencing. Two distinct haplotypes were recovered, both strongly supported as part of a group with representatives of *C. rugosiceps* and

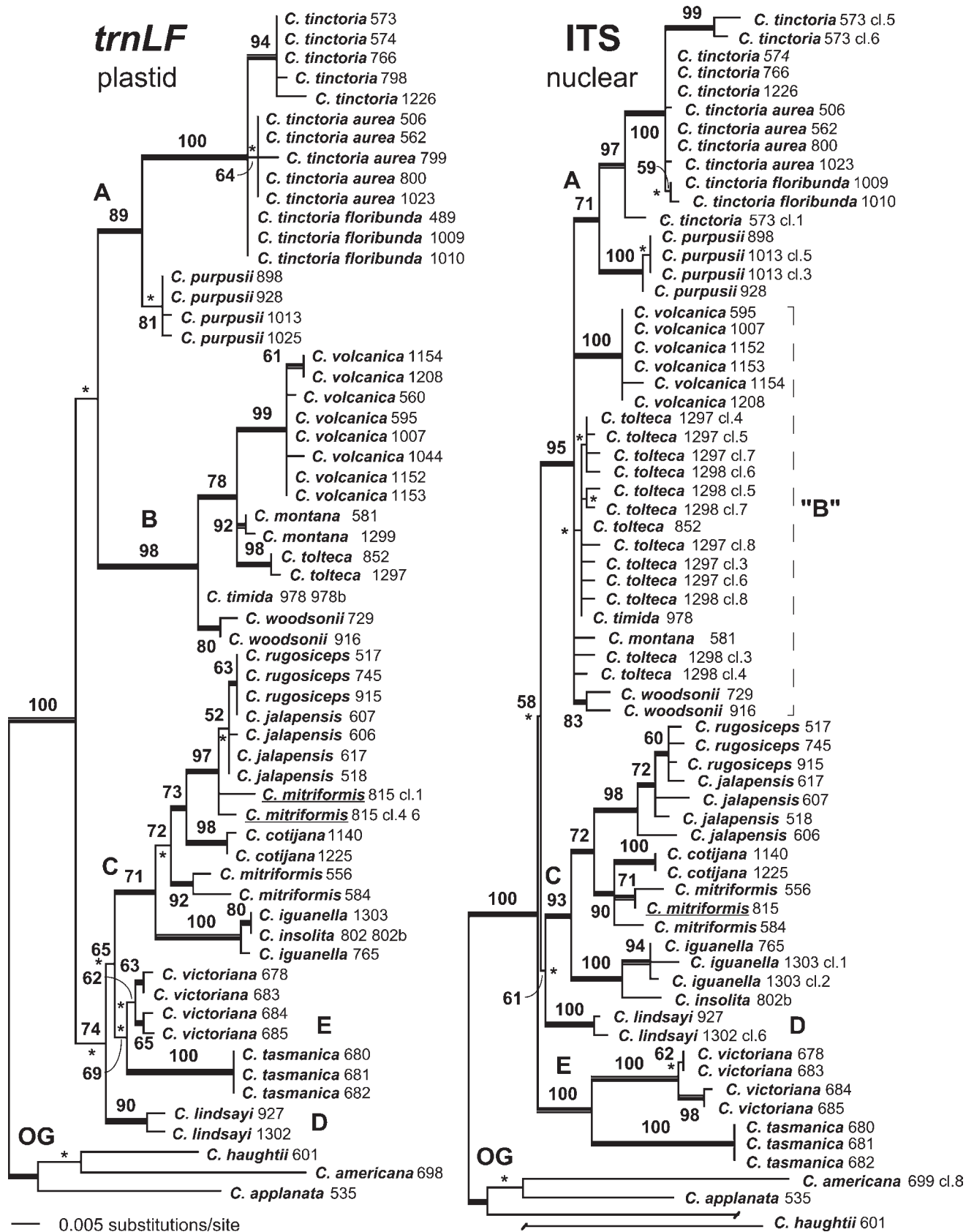


FIG. 1. Phylogenetic relationships among species of the *Cuscuta tinctoria* complex derived from separate Bayesian analyses of plastid and nuclear sequences. Majority-rule consensus trees with mean branch lengths are drawn at the same scale for both phylograms. Five major lineages are labeled A–E. Trees are rooted using three outgroup (OG) species from closely related clades. Individual with confliction position is underlined. 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 extractions (see Appendix 1); in addition, for the ITS data different clones are labeled, when applicable.

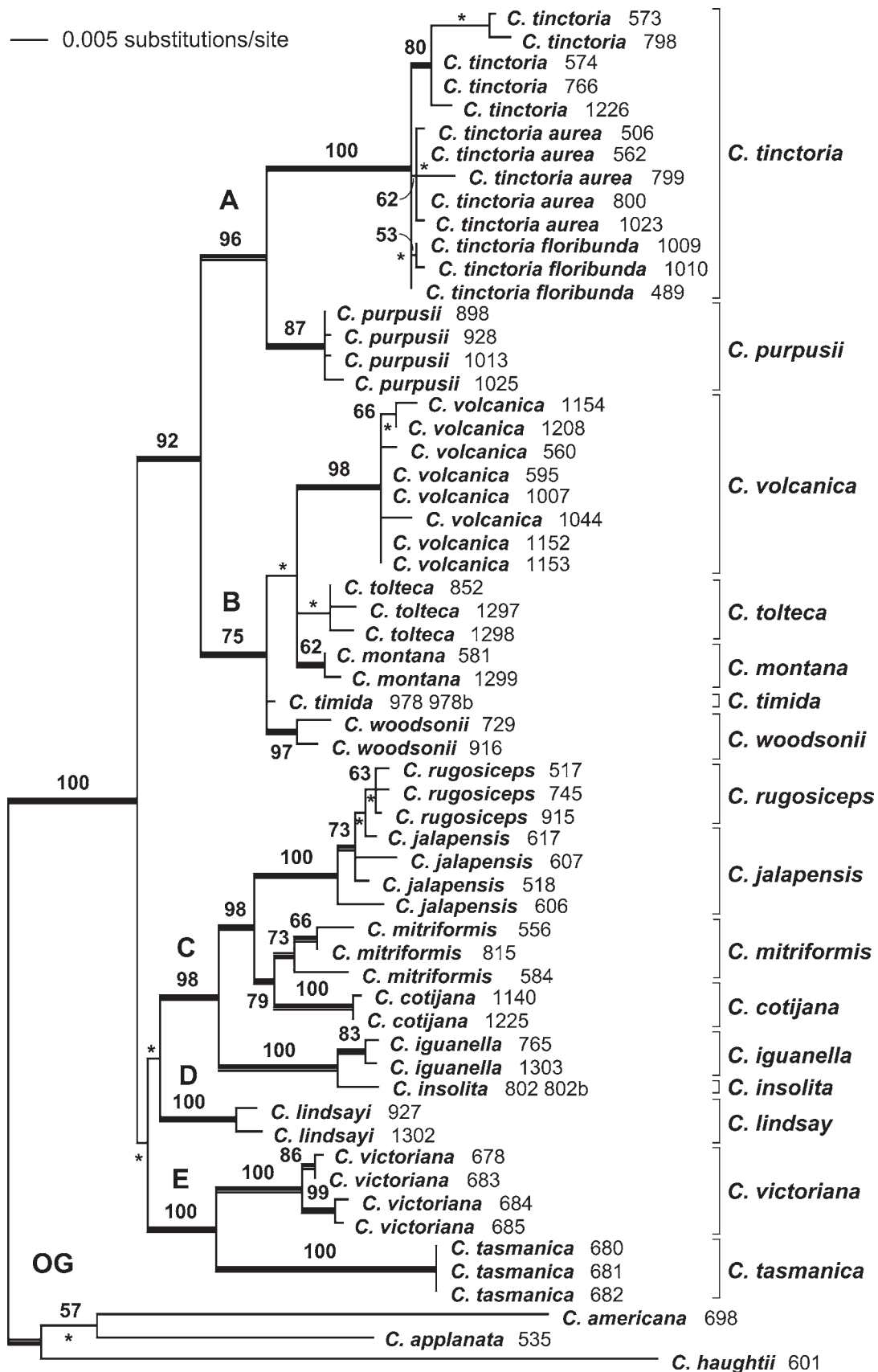


FIG. 2. Majority-rule consensus tree with mean branch lengths from the Bayesian analysis of combined plastid (*trnL-F*) and nuclear (ITS) data showing the backbone relationships among species of *Cuscuta tinctoria* complex. Five major lineages are labeled A–E. Trees are rooted using three outgroup (OG) species from closely related clades. Parsimony bootstrap values are indicated for nodes supported $\geq 50\%$. Asterisk indicates a branch with posterior probability < 0.95 ; all other branches have posterior probability ≥ 0.95 (thick lines). Numbers following species names correspond to DNA extractions (see Appendix 1).

C. jalapensis, instead of other members of *C. mitrifomis* (Fig. 1, left; underlined). Subclade D contains exclusively *C. lindsayi* individuals with strong support (90% BS; ≥ 0.95 PP). Finally, subclade E groups together with two remaining species from this species complex, *C. tasmanica* and *C. victoriana*, albeit their sister group relationship is only weakly supported based on plastid data (62% BS; < 0.95 PP). These two species occur in Australia and exhibit a striking disjunct distribution compared to an otherwise almost exclusively Mexican species complex, as documented previously (Stefanović et al. 2007).

Four of the same major well-defined and well-supported groups were recovered by analysing the nuclear ITS matrix (subclades A, C–E; Fig. 1, right), each with identical species composition to those discussed above for the plastid matrix. While subclade A received somewhat weaker bootstrap value (71%), the support for the other three subclades (C–E) was significantly improved in comparison to the plastid phylogeny. However, members of the fifth group, subclade B, did not cluster together as expected based on *trnL-F* data. Instead, all of its accessions/clones were found as an unresolved polytomy (labeled as “B”; Fig. 1, right), grouped together with subclade A (95% BS; ≥ 0.95 PP).

The analyses of separate plastid and nuclear matrices produced trees of overall remarkably similar topologies and complementary levels of support, with the exception of one major conflict confined within subclade C (Fig. 1; underlined). According to the nuclear data, all three sampled individuals of *C. mitrifomis* are closely related to each other and together with accessions of *C. cotijana* belong to a strongly supported group (90% BS; ≥ 0.95 PP), sister to the *C. rugosiceps/C. jalapensis* lineage. In contrast, the plastid tree resolves *C. cotijana* and *C. mitrifomis* as successive sisters to *C. rugosiceps/C. jalapensis*, and places one individual of *C. mitrifomis* (accession 815; underlined in Fig. 1) as part of this lineage with strong support (97% BS; ≥ 0.95 PP). Using nuclear data yet enforcing *trnL-F* results on these species and constraining *C. mitrifomis* accession 815 with *C. rugosiceps* and *C. jalapensis*, produced trees of 372 steps. While these trees are four steps longer than the optimal trees (Table 1), this length difference was not deemed sufficiently significant and could not be rejected based on the SH tests ($p = 0.07$). Constraining this accession to group in a clade with *C. mitrifomis* (following the ITS results) with plastid data yielded trees of 211 steps. Despite the similarly small length penalty (five additional steps), these results were rejected as significantly worse solutions by the SH tests, but only marginally so ($p = 0.03$). Instances where taxa show conflicting position independent phylogenies may be taken as evidence for the hybrid origin of those taxa (Sang and Zhong 2000). This process is well documented in plants generally (e.g. Rieseberg 1995; Sang and Zhong 2000) and genus *Cuscuta* in particular (e.g. Stefanović and Costea 2008; Costea and Stefanović 2010). However, a nearest neighbour interchange (NNI) swap, a simple topological change due to rooting, can account for differences seen between these two topologies and could explain why one of the SH tests have failed to find the significance in observed length differences between the optimal and constrained trees. Taken all of these elements together, we deem that the evidence for hybridization is not strong enough in this

instance. Also, biological phenomena other than reticulation, such as random sorting of ancestral polymorphism or lineage sorting, could provide an explanation for the observed topological discrepancy (Sang and Zhong 2000; Stefanović and Costea 2008).

The combined analyses were conducted on a data set in which plastid and nuclear sequences were concatenated but the *trnL-F* sequence for *C. mitrifomis* accession with strongly supported conflicting positions in individual analyses excluded. Not surprisingly, the same basic underlying tree structure containing five major subclades was recovered (Fig. 2). In addition, owing to complementary nature of two matrices with respect to their resolution and support, the total-evidence approach provided additional support for the backbone relationships among these five lineages. Subclades A and B were sister to each other (92% BS; ≥ 0.95 PP). Together, these two clades are sister to the remainder of the *C. tinctoria* complex, but no additional support was gained there (Fig. 2).

General Morphology and Micromorphology—With the exception of the *Cuscuta grandiflora* complex (clade O) from S America, flowers of *C. tinctoria* group are in general at least two times larger than in other clades of subg. *Grammica*; however, *C. victoriana* and *C. tinctoria* var. *aurea* are relatively small-flowered. Also, flower morphology of this group appears to have been affected by convergent evolution more than in other subg. *Grammica* clades. Calyx and corolla lobes are commonly rounded, and often their margins overlap to different degrees (Fig. 3). Calyx lobes width versus their length (e.g. lobes wider than long versus about as wide as long) was considered by Yuncker (1932, 1965) to be an important separation character. We found that species from three of the five major subclades, for example, *C. tinctoria* (subclade A), *C. montana*, *C. tolteca*, *C. timida* (subclade B), and *C. rugosiceps*, *C. cotijana* (subclade C), have evolved calyx lobes that are broader than long (Fig. 3). The latter calyx lobes have also commonly distinctly auriculate margin bases. A carena on the outer two calyx lobes also evolved multiple times (Fig. 3; *C. cotijana*, *C. iguanella*, *C. rugosiceps*, *C. volcanica*, and *C. montana*). One or two bracts at the base of the each flower that resemble the calyx lobes have evolved in *C. rugosiceps*, *C. montana*, *C. tolteca* (Fig. 4K), and *C. timida*. Overlapping and auriculate corolla lobes were thought by Yuncker (1939, 1965) to be unique to *C. woodsonii*, while “lobes not obviously auriculate” were in his view characteristic to *C. jalapensis* and *C. mitrifomis*. In fact, the majority of species from across all subclades exhibit different degrees of overlapping corolla lobes with more or less lobed or auriculate bases.

Multicellular protuberances on the calyx and/or corolla lobes evolved only in three species confined to subclade C: *C. cotijana*, *C. insolita*, and *C. iguanella* (Fig. 3). In the former species, the protuberances are confined to the outer two calyx lobes, while in the latter two they are also present on the corolla lobes (Fig. 4). The morphology of these structures varies from isolated conical, horn-like or cylindrical (*C. cotijana* and *C. insolita*; Fig. 4 A–E), to extensive crest-like formations (*C. iguanella*; Fig. 4 G–J). Multicellular protuberances begin to develop early in the bud, and bear one or several distal stomata. Similar structures have also evolved in other clades of subg. *Grammica* (Costea and Stefanović 2009b, 2010; Costea et al. 2011a,b) but their physiological function is unknown.

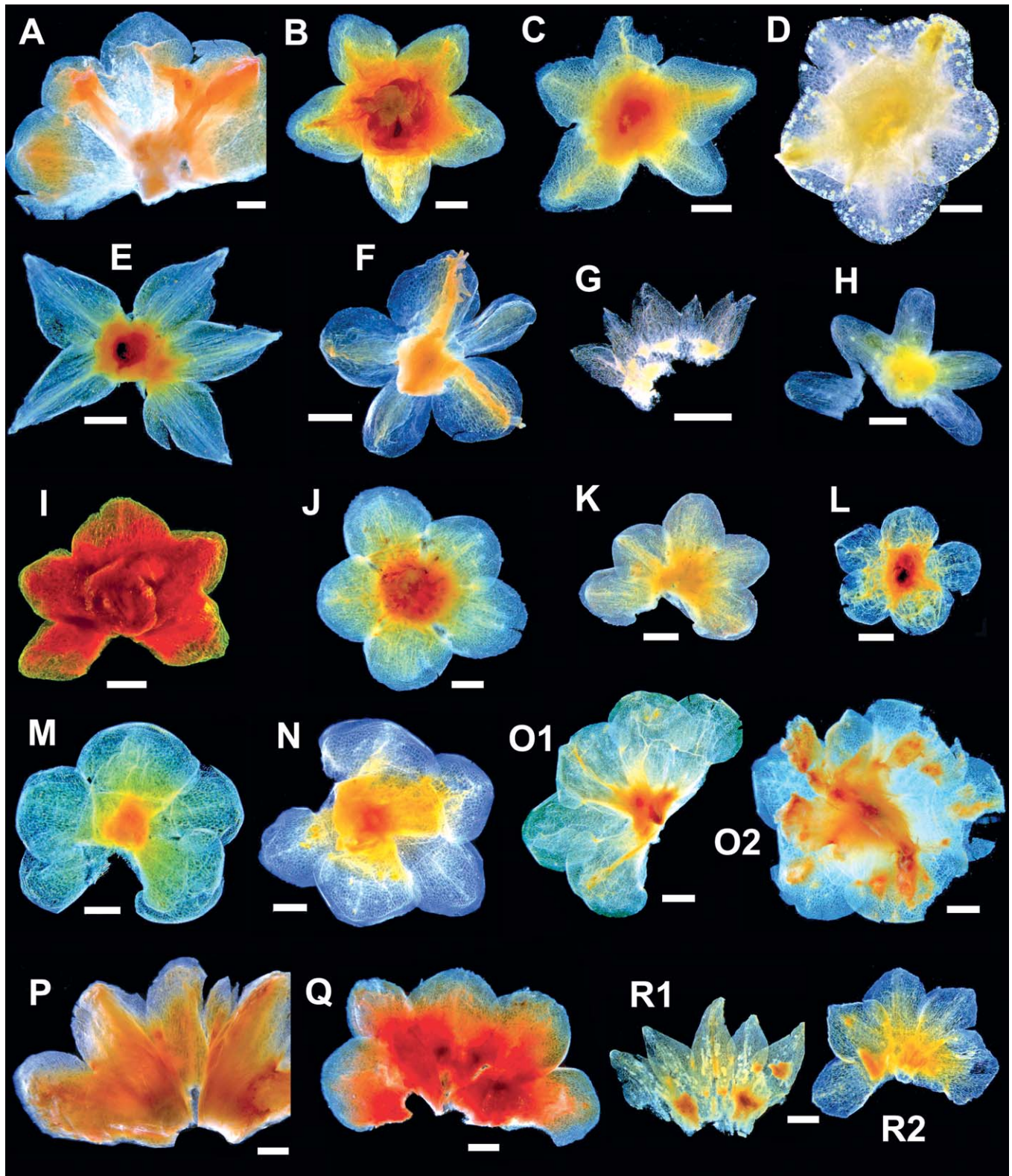


FIG. 3. Morphology of dissected calyx for the *Cuscuta tinctoria* complex. A. *Cuscuta rugosiceps*. B. *C. jalapensis*. C. *C. mitriformis*. D. *C. cotijana*. E. *C. insolita*. F. *C. iguanella*. G. *C. victoriana*. H. *C. tasmanica*. I. *C. lindsayi*. J. *C. tinctoria* var. *tinctoria*. K. *C. tinctoria* var. *floribunda*. L. *C. tinctoria* var. *aurea*. M. *C. tolteca*. N. *C. timida*. O1–O2. *C. montana*. P. *C. volcanica*. Q. *C. woodsonii*. R1–R2. *C. purpusii*. Scale bars = 1 mm.

Morphology of the styles (Fig. 5) has also been affected by convergent evolution. Historically, Yuncker (1932, 1965) distinguished only subulate and cylindrical styles, and deemed the former feature significant enough to define

subject. *Subulatae* based on it. However, this simplistic distinction can be a source of confusion because it does not acknowledge that the gynoecium morphology changes significantly across the timespan from anthesis to fruiting in

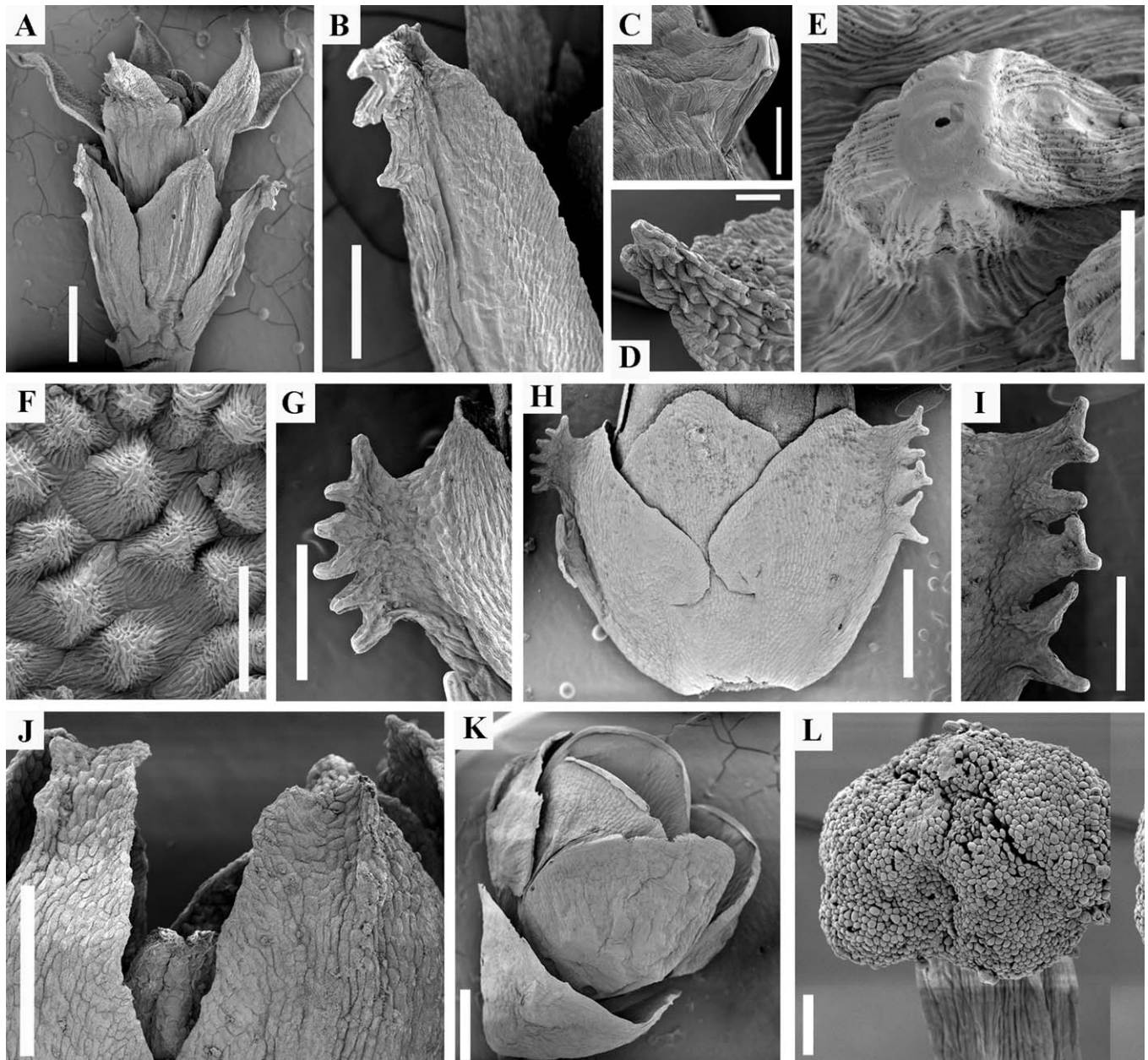


FIG. 4. Morphology of multicellular protuberances for the *Cuscuta tinctoria* complex. A–I. *Cuscuta insolita*. A. flower. B. Calyx lobe. C. Multicellular protuberances on calyx. D. Subterminal multicellular protuberance on corolla lobe. E. Stomata of multicellular protuberance. F. Corolla papillae. G–I. Crest-like multicellular protuberances on calyx lobes of *C. iguanella*. J. Multicellular protuberances on corolla lobes of *C. iguanella*. K. *C. tolteca*, bract and calyx. L. *C. montana*, lobed stigma. Scale bars A, H, K = 1 mm; B, G, I, J = 0.5 mm; C, L = 100 μ m; D = 200 μ m; E, F = 50 μ m.

some species. At the flowering stage, strictly subulate styles do not exist in any of the species. At anthesis, the styles with an enlarged base are actually conical (Fig. 5 A1, B1). At fruiting stage, however, as the capsules develop and the pericarp dries, the conical styles can become subulate (i.e. flattened laterally, with a more or less triangular base) in some species (Fig. 5 B2). Thus strictly subulate styles can be observed only at capsule stage, and only in certain species. The distinction between conical and subulate styles is a developmental one, but it has an evolutionary significance. Conical styles are encountered in three subclades (B, C, and D; Fig. 5), while distinctly subulate styles have evolved only in one group of species in subclade C (*C. cotijana*, *C. mitriformis*, *C. jalapensis*,

C. rugosiceps; Fig. 5). Cylindrical styles (both at anthesis and at fruiting stages) are the norm in subgenera *Cuscuta* and *Grammica*, and can be considered the ancestral condition. In *Cuscuta tinctoria* complex, cylindrical styles are present in species of all clades (Fig. 5), although in some species they are thin [e.g. 0.13–0.3 mm in diameter; *C. tinctoria* (Fig. 5 F) and *C. purpusii* (Fig. 5 G1–G2)] and in thick in others [e.g. 0.4–0.9 mm in diameter; *C. montana* (Fig. 5 K1–K2) and *C. volcanica* (Fig. 5 J1–J2)]. The species with thick, cylindrical styles may also have more or less conical styles, which can potentially lead to confusions during flowering stage with the species having subulate styles. The enlargement of the style base can be seen as a convergent trend that has culminated with the evolution

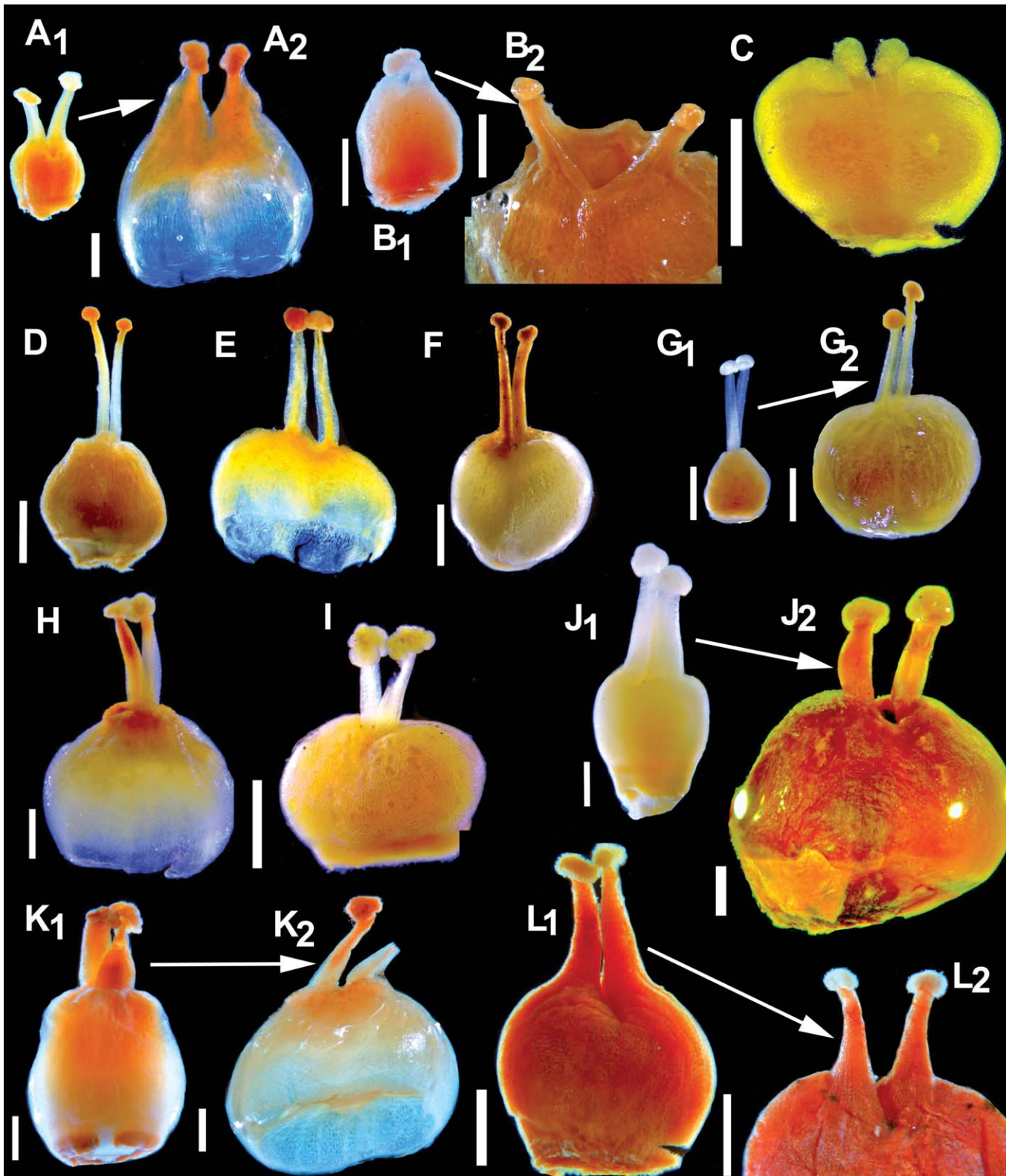


FIG. 5. Morphology of styles at anthesis and/or fruiting stages for the *Cuscuta tinctoria* complex. A1–A2. *Cuscuta rugosiceps*: conical styles at anthesis (A1) become subulate at capsule stage (A2). B1–B2. *C. mitrifomis*: gynoecium (B1) and capsule (B2). C. *C. victoriana*, gynoecium. D. *C. insolita*, capsule. E. *C. iguanella*, capsule. F. *C. tinctoria* var. *tinctoria*. G1–G2. *C. purpusii*: cylindrical styles at anthesis (G1) remain cylindrical at capsule stage (G2). H. *C. timida*, capsule. I. *C. tolteca*, capsule. J1–J2. *C. volcanica*: conical styles at anthesis (J1) become cylindrical to conical at capsule stage (J2). K1–K2. *C. montana*: gynoecium (K1) and capsule (K2). L1–L2. *C. woodsonii*: gynoecium (L1) and capsule (L2). Scale bars = 1 mm.

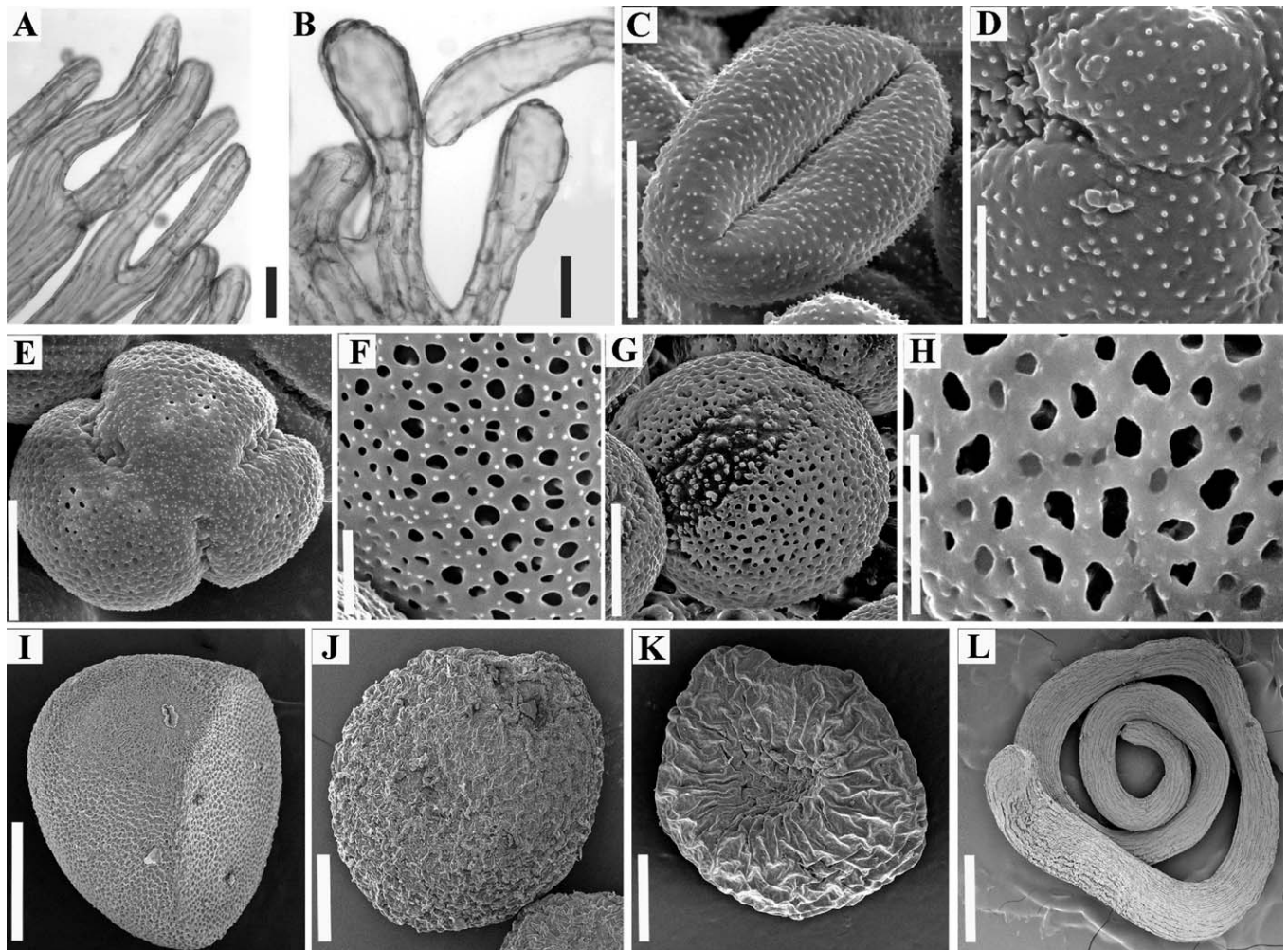


FIG. 6. Morphology of infrastaminal fimbriae, pollen and seeds for the *Cuscuta tinctoria* complex. A. Cylindrical infrastaminal scale fimbriae of *C. insolita*. B. Club-shaped infrastaminal scale fimbriae of *C. timida*. C–D. Pollen grains with imperforate tectum (*C. insolita*). E–F. Pollen grains with perforate tectum (*C. mitriformis*). G–H. Pollen grain with microreticulate tectum (*C. volcanica*). I. Seed of *C. insolita*. J–K. Seed of *C. rugosiceps*. J. Hydrated. K. Dry. L. Embryo (*C. woodsonii*). Scale bars. A–B = 100 μ m; C, E, G = 10 μ m; D, F, H = 3 μ m; I–L = 0.5 mm.

of subulate styles in the capsules of one group of species. Stigmas are large, head-like, entire or lobed (Fig. 4L; Fig. 5). The higher pollen/ovule ratios and xenogamy observed in the species of this clade (Wright et al. 2012) correlate with the thicker styles and larger, lobed stigmas, which can be explained by the fact that stigmas must retain the pollen grains, while styles are the arena for pollen tube competition. However, the reproductive advantage of styles enlarged at the base (including subulate in fruit) is unknown.

Infrastaminal scale fimbriae belong to *Cuscuta* type (Riviere et al. 2013), with a terminal distal laticifer. While in most species, fimbriae are cylindrical (Fig. 6A), in *C. rugosiceps*, *C. timida*, and *C. toteca* they are club-shaped (Fig. 6B). Pollen is 3(–4)–zonocolpate, varying from oblate, spheroidal to prolate, with suprategal ornamentations that are conical and acute. The largest pollen grains are encountered in the group of species with subulate styles (27–33 μ m long; *C. cotijana*, *C. mitriformis*, *C. jalapensis*, *C. rugosiceps*). Tectum micromorphology is diverse, imperforate, perforate to microreticulate (Fig. 6 C–H), but with no apparent trend within this species complex.

Capsules are indehiscent in all the species except in *C. victoriana* and *C. tasmanica*. Capsules with subulate styles have commonly large interstyler apertures, while capsules with conical or cylindrical styles have small or inconspicuous interstyler apertures. Seeds are larger than 1.3 mm (commonly double the size of species from other clades of subg. *Grammica*). Although the seed coat cells are commonly dome-like when seeds are hydrated (Fig. 6I), in some species (e.g. *C. cotijana*, *C. mitriformis*, *C. jalapensis*, *C. rugosiceps*) the seed coat does not become alveolate when the seeds dry out, but wrinkles in a characteristic radial pattern (Fig. 6 J–K). Embryo is coiled 2–3 times (Fig. 6L).

DISCUSSION

Our results did not confirm the circumscription of some of Yuncker's taxa (1932). The great number of subsections in which Yuncker (1932) placed the species of this clade reflects appropriately the extent of morphological diversity, but at the same time it generates a false image of its species distinctiveness. It would be expected, for example,

that *C. floribunda*, the only species of this group included by Yuncker in subsect. *Americanae* (1932), to be sharply differentiated morphologically from the other species; however, that is not the case. With the exception of the Australian species (*C. victoriana* and *C. tasmanica*), which are quite distinct morphologically, most of the American species are remarkably similar, and their evolutionary affinities are not always apparent based on morphology because of the marked convergent evolution in the morphology of calyx and styles (see above). The taxonomic changes we propose are extensive and reflect the complexity of these evolutionary relationships. In essence, we found that both *C. floribunda* and *C. aurea* are in fact varieties of *C. tinctoria*. On the other hand, *C. rugosiceps* and *C. tinctoria* in their current delimitation are polyphyletic, including one or two new species, respectively (see below).

Cuscuta rugosiceps* and *C. volcanica—A closer examination of the three specimens cited by Yuncker (1921, 1932) under *C. rugosiceps* revealed that one of them belongs to an unknown species. *Cuscuta rugosiceps* shares close affinities with *C. mitriformis*, *C. cotijana*, and especially with *C. jalapensis* (Figs. 1, 2, 3, 5). Morphologically, these four species have in common the conical styles (Fig. 5), which at capsule stage become subulate, flattened laterally and spread apart to reveal a large interstyler aperture (e.g. Fig. 5 B1–B2). The specimen from Colima vulcano (“M. E. 347”, Yuncker 1921, 1932) has also thick and slightly conical styles, but these do not become subulate at fruiting stage, and the interstyler aperture is small (Fig. 5 J1–J2). In addition, the calyx lobes are oblong to broadly elliptic in this specimen, and not broader than long as they are in *C. rugosiceps*. A number of such specimens, including those from Colima vulcano, were placed by the molecular analysis into another subclade (B) that comprises, among other species, *C. woodsonii* (Figs. 1, 2). We recognize these plants as a new species, *C. volcanica*, which is quite common at elevations over 2,000 m in the Transverse Neovolcanic Belt from Colima, Jalisco, and Michoacán.

Cuscuta rugosiceps* and *C. montana—Several herbarium specimens collected from Sierra Madre Occidental of Durango (see Appendix 2) had been initially thought to be “*C. rugosiceps*” because their calyx and corolla have a similar morphology as the latter species, and their styles are thick and slightly conical at anthesis (compare *C. rugosiceps* and *C. montana* in Figs. 3 and 5). However, the molecular analysis placed these specimens in subclade B, while *C. rugosiceps* belongs to subclade A (Figs. 1, 2). A closer morphological examination of these specimens showed that although very similar because of convergent evolution, the Durango plants have styles that do not become subulate at the capsules stage (as they do in *C. rugosiceps*), remaining more or less conical (Figs. 5A2, 5K2). In addition, their seed coat does not form the characteristic radial pattern observed in *C. rugosiceps* (Fig. 6K), being alveolate when dry and papillate when hydrated, as in the majority of *Cuscuta* species. These plants from Sierra Madre Occidental are described as a new species, *C. montana*.

Cuscuta floribunda* and *C. aurea* are Varieties of *C. tinctoria—Neither *C. aurea* nor *C. floribunda* have been mentioned by any floristic or taxonomic reference after the earlier monographs (*C. aurea*, Yuncker 1921, 1932, 1965;

C. floribunda, Engelmann 1859; Yuncker 1932, 1965). While *C. aurea* is obviously a smaller flowered form of *C. tinctoria* (Yuncker 1932, 1965), the identity of *C. floribunda* has been problematic because Yuncker included this taxon in the same group of species as *C. americana* (subsect. *Americanae*, Yuncker 1921, 1932, 1965). *Cuscuta floribunda* was described by Bonpland et al. (1818) from a plant collected by Bonpland at Puente de Ixtla (currently located in the state of Morelos, Mexico) during the itinerary from Acapulco to Mexico City in April 1803 (Sprague 1924). Engelmann (1859) cited a Bonpland specimen from the Willdenow Herbarium (W3159). Although the original collection in Berlin was apparently destroyed during the Second World War, a fragment of this latter collection is available at MO. The specimen consists from three dissected corollas, two calyces, four gynoecia, and four seeds mounted on a small piece of paper. Yuncker’s description of *C. floribunda* from 1921 is based on this specimen. A decade later, however, Yuncker (1932) cited the Bonpland specimen, plus another collection, *Kerber 248* (Maltrata), and in this description of *C. floribunda*, he amalgamated characteristics pertaining to both specimens, thus altering the previous delimitation. A closer analysis of both specimens, and of the protologue of *C. floribunda* revealed that *Kerber 248* belongs to another unknown species (*C. timida*, see below). According to the protologue, the inflorescence of *C. floribunda* is corymbiform and flowers are pedicellate (Bonpland et al. 1818), which together with the flower fragments dissected by Engelmann leave no doubt that this taxon is closely allied to *C. tinctoria*, as it was also observed by the latter author (Engelmann 1859). Based on both its morphology and molecular data (Figs. 1, 2), *C. floribunda* is in fact a variety of *C. tinctoria*, as it is also *C. aurea*. In contrast to *C. tinctoria*, *C. floribunda* has a longer and narrower corolla tube, with the calyx ca. 1/2–2/3 of the length of the corolla tube. *Cuscuta aurea* has slightly smaller flowers (see description of *C. tinctoria* varieties). While the morphological separation of var. *floribunda* usually poses no problems, var. *aurea* is sometimes more difficult to distinguish from var. *tinctoria* because of the overlapping sizes of the different flower parts (see descriptions). We have not performed a morphometric analysis because too few specimens are available for var. *aurea* and var. *floribunda*. However, we considered important to maintain these forms as varieties because they represent a good example of incipient speciation in *Cuscuta*. The three varieties overlap in their general geographic distribution in the States of Mexico and Guerrero; var. *tinctoria* and var. *floribunda* in Michoacán and Morelos, and var. *tinctoria* and var. *aurea* in the States of Mexico, Querétaro, and Puebla. Yet, the tree varieties were very rarely collected within the same Municipio of a given individual state, and never from the same locality (see Appendix 2).

***Cuscuta tinctoria* is Polyphyletic and Includes Two New Species**—Yuncker incorporated within the normal variation of *C. tinctoria* (subclade A) plants characterized by the presence of a large, orbicular bract at the base of the flowers (Yuncker 1921, 1932, 1965; see the iconography from 1921 and the numerous annotated herbarium specimens from different herbaria). Such plants have also larger and sessile flowers (flowers of *C. tinctoria* are pedicellate). Furthermore, molecular results placed unambiguously the bracteate plants within the *C. woodsonii-volcanica* subclade (subclade B;

Figs. 1, 2), and indicated that they represent a complex of forms rather than a unique lineage. Two new species with floral bracts, *C. tolteca* and *C. timida*, were revealed both by the morphological and molecular studies, but their phylogenetic relationships remain unresolved (Fig. 2). Their morphological distinctiveness is not always sharp because of the marked convergent evolution within the subclades A and B. Thus, *C. tolteca* and *C. timida* resemble *C. tinctoria* (subclade A) because of their cylindrical styles (Fig. 5) and apparently similar calyx morphology (Fig. 3). *Cuscuta tolteca* is most likely the plant that Yuncker (1921) described as *C. tinctoria* var. *kellermaniana*, which was known to the author only from the type specimen. Although the type specimen is in poor condition, the characteristic bract

at the base flowers is clearly present. In addition, we have found another specimen in a slightly better condition collected close to the type locality of var. *kellermaniana* in Guatemala (Kellerman 4812, US), which is *C. tolteca*. Considering the poor quality of the type, and to eliminate any possible confusion with *C. tinctoria*, we prefer to describe this plant as a new species, *C. tolteca*, which occurs in central and south Mexico (Guanajuato, Hidalgo, Querétaro, Veracruz) and Guatemala. The second species, *C. timida* resembles *C. tolteca* but has a longer corolla tube (calyx ca. 1/3–1/2 as long as corolla), and the capsule that becomes narrowed distally, at the base of the styles. The specimen Kerber 248, erroneously considered to be *C. floribunda* (Yuncker 1932, see above), is in fact *C. timida*.

TAXONOMIC TREATMENT

Key to Species of the *Cuscuta tinctoria* Clade—

1. Capsules indehiscent; Australia 2
 2. Pedicels 4–12 mm; flowers 2.5–5 mm long; styles 0.8–1.6 mm; capsules globose to ovate *C. tasmanica*
 2. Pedicels 0.5–2.5 mm; flowers 1.5–2.5 mm; styles 0.1–0.3 mm; capsules depressed-globose *C. victoriana*
1. Capsules circumscissile; North and Central America 3
 3. Styles cylindrical both at the anthesis and capsule stages 4
 4. Calyx lobes with multicellular protuberances 5
 5. Inflorescence glomerulate; pedicels absent; calyx lobes round to 1.5 times broader than long with rounded apex *C. iguanella*
 5. Inflorescence corymbiform; pedicels 1–3 mm; calyx lobes ovate with acute apex *C. insolita*
 4. Calyx lobes without multicellular protuberances 6
 6. Each flower with a bract at the base (not to be mistaken with the bract(s) present at the base of clusters) 7
 7. Outer two calyx lobes carinate; infrastaminal scale fimbriae cylindrical; capsules 4–5.5 × 3–3.5 mm *C. montana* (in part)
 7. Calyx lobes not carinate; infrastaminal scale fimbriae club-like; capsules 2.5–4 mm 8
 8. Calyx equalling corolla tube; styles 0.5–1 mm; capsules not narrowed apically *C. tolteca*
 8. Calyx 1/2–3/4 as long as corolla tube; styles 1.5–3 mm; capsules narrowed apically *C. timida*
 6. Flowers without a bract at the base (but 1–2 bracts present at the base of the clusters) 9
 9. Infrastaminal scales shorter than corolla tube, obovate to spatulate *C. lindsayi*
 9. Infrastaminal scales equalling or longer than corolla tube, ovate to oblong 10
 10. Flowers 7–9 mm; styles 0.4–1 mm thick; capsules 5–6 × 3–4 mm *C. volcanica* (in part)
 10. Flowers 2.8–7 mm; styles 0.15–0.3 mm thick; capsules 2–3.5 × 1.8–2.5 mm 11
 11. Calyx lobes round to 1.75 times broader than long; corolla lobes apex rounded *C. tinctoria*
 11. Calyx lobes ovate-lanceolate to ovate-triangular; corolla lobes apex obtuse to subacute *C. purpusii*
 3. Styles enlarged at the base, conical at anthesis; in some species they become subulate at capsule stage 12
 12. Calyx lobes with multicellular protuberances *C. cotijana*
 12. Calyx lobes without multicellular protuberances 13
 13. At least some of the calyx lobes are wider than long 14
 14. Styles becoming subulate in fruit; capsules with large interstyler aperture surrounded by withered corolla at the base; dry seeds with a radial pattern of wrinkling *C. rugosiceps*
 14. Styles remain conical in fruit; capsules with small interstyler aperture, capped by the corolla; dry seeds alveolate *C. montana* (in part)
 13. None of the calyx lobes are wider than long 15
 15. Styles subulate in fruit; capsules with large interstyler apertures 16
 16. Calyx equalling corolla tube; corolla campanulate *C. mitriformis*
 16. Calyx ca. 1/2 of the corolla tube; corolla cylindrical *C. jalapensis*
 15. Styles conical in fruit; capsules with inconspicuous interstyler apertures 17
 17. Flowers 6–7 mm long; calyx lobes not carinate; capsules surrounded by withered corolla at the base *C. woodsonii*
 17. Flowers 7–9 mm long; calyx lobes carinate; capsules surrounded and capped by withered corolla *C. volcanica* (in part)

1. ***Cuscuta cotijana*** Costea & I. García, *Brittonia* 60(3): 235 (–239, Figs. 1, 2). 2008.—TYPE: MEXICO. Michoacán, Los Gallineros, ca. 1,900 m, 19 Apr 1991, *García Ruiz & Olmos* 3289 (holotype: CIMI; isotypes: IEB, IBUG, NY, UCR, WLU).

After its publication in 2008, more specimens of this species have been collected and examined (Appendix 2); however, the protologue from Costea et al. (2008b) does not need to be amended.

Distribution and Ecology—*Cuscuta cotijana* was previously known only from Sierra de Cotija in Michoacán, Mexico (Costea et al. 2008b) but we have also collected it more recently in Colima (see Appendix 2). The species

grows in tropical deciduous and mesic oak-pine forests with a degree of disturbance, at 1,300–2,050 m elevation. Hosts are both herbaceous and woody plants from genera such as: *Acalypha*, *Alnus*, *Baccharis*, *Bidens*, *Crotalaria*, *Dicliptera*, *Eupatorium*, *Fuchsia*, *Podachaenium*, *Ricinus*, *Rhyncosia*, *Salix*, *Salvia*, *Solanum*, *Vernonia*, and *Vitis*. Flowering takes place in Aug–Mar. Field work we have conducted in Sierra de Cotija in Feb 2013 has revealed that the species has become quite rare (only one population was found) as a result of increased deforestation and expansion of the avocado plantations in the region. Villagers from Los Amoles indicated that the species is destroyed when found because it is believed to be detrimental to the avocado trees.

2. *Cuscuta iguanella* Costea & I. García, sp. nov.—TYPE: MEXICO. Jalisco, wooded hills near Guadalajara. Flowers fragrant, 2 Sep 1893, *Pringle 4529* (holotype: MEXU; isotypes: F!, GH!, K!, NY!, MO!, S!, US!).

Most similar to *C. toteca* from which it differs in the narrower, carinate calyx lobes with crest-like multicellular protuberances, longer styles, stigmas not lobed, and smaller seeds.

Stems medium, pale yellow or whitish. Inflorescences dense, glomerulate, often confluent; pedicels absent; bracts 1–2 at the base of clusters, 1 at the base of each flower, 2–3.5 × 2–3 mm, ovate to broadly-deltoid, rounded to subacute, carinate and with crest-like multicellular protuberances; margins entire. Flowers 5-merous, 4–5.5 mm long, thick, white when fresh, creamy-yellow when dried; papillae absent; laticifers visible in the calyx and corolla lobes, elongated, arranged in rows; multicellular protuberances present on bracts, calyx and corolla lobes; calyx 2.2–3 mm long, straw-yellow, more or less reticulate, ± glossy, campanulate, equalling corolla tube, divided 1/4–1/3 the length, tube 0.5–0.8 mm long, lobes 1.8–2.2 mm long, broadly overlapping, round to 1.5 times broader than long, outer 2 lobes carinate and cristate with multicellular protuberances, 0.3–0.5 mm long on the midveins, margins entire, apex rounded; corolla 3.8–5.3 mm long, tube 2–2.5 mm long, campanulate, lobes 2.1–2.5 mm long, initially erect, later reflexed, equalling the tube, ovate, overlapping, margin entire, apex rounded, straight; multicellular protuberances are dorsal, subterminal, less obvious than on the calyx, 0.1–0.15 mm long, crest-like or conical; stamens exerted, shorter than corolla lobes, anthers 0.7–1.1 mm long, broadly-elliptic to ovate, filaments 0.6–0.8 mm long; pollen tricolpate, 19–23 μm long, sphaerical to prolate, tectum imperforate or with a few small, scattered puncta, 0.2–0.3 μm in diameter; infrastaminal scales 2.1–2.7 mm long, equalling to longer than corolla tube, oblong to ovate, bridged at 0.9–1.3 mm, uniformly dense-fringed, fimbriae 0.2–0.4 mm long, cylindrical; styles 1.2–2 mm long, 0.2–0.3 mm thick, sometimes with multicellular protuberances, longer than the ovary, cylindrical; stigmas not lobed. Capsules circumscissile, 2–4 × 1.8–2.5 mm, ovoid to globose, not thickened but sometimes risen around the inconspicuous interstylar aperture, translucent, capped by the withered corolla. Seeds 2–4 per capsule, 1–1.4 × 1–1.4 mm, angled or slightly dorsoventrally compressed, elliptic to round, hilum region 0.3–0.5 mm in diameter, scar 0.7–0.11 mm long, seed coat alveolate/papillate. Figures 3F; 4 G–J; 5E; 7 A–D.

Etymology—From “iguana,” alluding to the aspect given by the crest of multicellular protuberances on the bracts and calyx lobes.

Note—*Cuscuta iguanella* is quite distinct morphologically because of the crest-like multicellular protuberances present on bracts, calyx and corolla lobes. It shares the sessile flowers, bract(s) at the base of the calyx, and cylindrical styles with *C. toteca*, from subclade B (Figs. 1, 2); however, *C. iguanella* differs by the carinate bracts, narrower calyx lobes with multicellular protuberances, longer styles, and smaller seeds (see description of *C. toteca*). There is little morphological similarity between *C. iguanella* and *C. insolita* other than the presence of multicellular protuberances (see identification key).

Distribution and Ecology—*Cuscuta iguanella* is endemic to Mexico in Jalisco (Trans-Mexican Volcanic Belt) and Nayarit (Sierra Madre Occidental) (see Appendix 2). The species was collected from grassy depressions of open oak forests at elevations of 1,500–2,000 m. Its hosts are unknown. Flowering takes place in Aug–Sep and flowers are fragrant. We searched repeatedly for this species at and around the type collection site (in 2007, 2008, 2009, and 2010), and also at the previous collection sites in Nayarit (Appendix 2) but we could not find it again. This indicates that the species is either very rare or extirpated.

3. *Cuscuta insolita* Costea & I. García, sp. nov.—TYPE: MEXICO. Nayarit, Mpio. Tepic: a 8.6 km al NE de (Santiago de) Pochotitan, 21°35 N, 105°43 W. Hemiparasita, flor blanca, sobre *Tephrosia*; veg. [vegetación] pastizal deprivado de encinar, con Gramineae, *Aeschynomene*, *Byrsonima*, Compositae, *Asclepias*, etc.; 20 Jun 1987, *Tellez & Miller 10525* (holotype: MEXU!; isotypes: MO!, XAL!).

Cuscuta insolita resembles morphologically *C. purpusii* but is distinguished by the multicellular protuberances on the calyx lobes and the papillae on the corolla lobes.

Stems medium, orange. Inflorescences lax, corymbiform, not confluent; pedicels 1–3 mm long; bracts 1 at the base of clusters, usually absent at the base of flowers, 1.2–2 × 1–1.15 mm, ovate to lanceolate, acute, carinate and sometimes with multicellular protuberances, margins entire. Flowers 5-merous, 4.8–5.8 mm long, membranous, white when fresh, creamy-yellow (brown) when dried; papillae present on corolla lobes; laticifers visible in the calyx and corolla lobes, elongated, arranged in rows. Multicellular protuberances present on both calyx and corolla; on the calyx they are conical, distributed along the midveins of lobes, 0.1–0.2 mm long, on the corolla they are subterminal, conical, 0.1–0.3 mm long; calyx 2.7–3.3 mm long, yellow, membranous, more or less reticulate, ± glossy, campanulate, shorter than corolla tube, divided 1/5–1/4 the length, tube 0.4–0.7 mm long, lobes 2.2–2.6 mm long, overlapping at base, ovate, not carinate, with multicellular protuberances present on the midveins, margins entire, apex acute; corolla 4.5–5 mm long, tube 2.5–3 mm long, cylindrical, lobes 1.5–2 mm long, initially erect, later reflexed, shorter than the tube, ovate-triangular, overlapping, margin entire, apex acute, straight; stamens exerted, shorter than corolla lobes, anthers 0.6–0.8 mm long, ovate to oblong, filaments 0.6–0.7 mm long; pollen tricolpate, 17–19 μm long, subprolate to prolate, tectum imperforate or with a few small, scattered puncta, 0.2–0.3 μm in diameter; infrastaminal scales 2.8–3.1 mm long, equalling to longer than corolla tube, bridged at 1–1.5 mm, oblong to slightly obovate, uniformly dense-fringed, fimbriae 0.1–0.2 mm long, cylindrical; styles 1.4–2 mm long, 0.2–0.25 mm thick, longer than the ovary, cylindrical, with multicellular protuberances; stigmas not lobed. Capsules circumscissile, 3–3.6 × 2.2–2.5 mm, ovoid, not thickened and/or risen around the inconspicuous interstylar aperture, translucent, capped by the withered corolla. Mature seeds 1 (–2) per capsule, 1.3–1.5 × 1.3–1.5 mm, angled, subround; hilum region 0.4–0.6 mm in diameter, scar 0.1–0.15 mm long; seed coat cells alveolate/papillate or wrinkled. Figures 3E; 4 A–F; 5D; 6 C–D, I; 7 E–I.

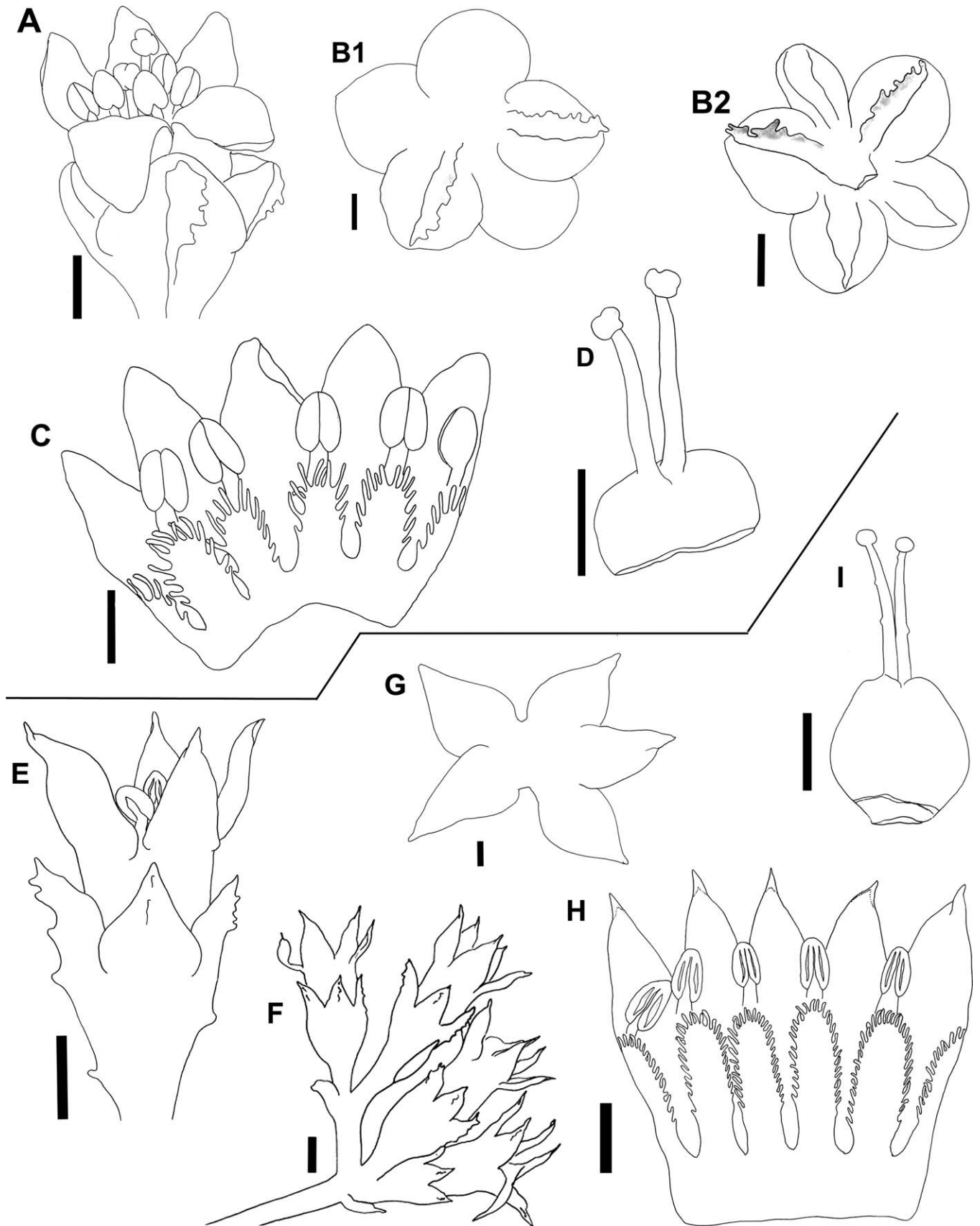


FIG. 7. *Cuscuta iguanella* Costea & I. García (Pringle 4529). A. Flower. B1–B2. Dissected calyx variation, dorsal side. C. Dissected corolla (opened, ventral side). D. Capsule. *Cuscuta insolita* Costea & I. García (Tellez & Miller 10525). E. Flower. F. Inflorescence. G. Dissected calyx, dorsal side. H. Dissected corolla (opened, ventral side). I. Capsule. Scale bars = 1 mm.

Etymology—From the Latin adjective “*insolitus*” meaning unusual, strange, uncommon.

Note—*Cuscuta insolita* is closest related to *C. iguanella*, however, with the exception of the multicellular protuberances on the calyx, these species have little in common morphologically (see identification key and descriptions). *Cuscuta insolita* resembles superficially *C. purpusii* from subclade A (e.g. corymbiform inflorescences, acute calyx lobes), but the presence of multicellular protuberances and papillatae corolla lobes easily distinguishes the former species. Although *C. insolita* is known only from the three type specimens, we are fully confident of its validity because the specimens have both mature flowers and capsules, which allowed both a thorough morphological investigation and the inclusion in the molecular analysis. As a matter of fact, we have extracted and compared DNA from two of the three specimens.

Distribution and Ecology—*Cuscuta insolita* is known only from Nayarit in Sierra Madre Occidental; the only known host is *Tephrosia* and flowering takes place in late June. Our search at and around the type collection site in 2007, 2008, and 2009 failed to recover the species, which indicates that *C. insolita* is probably either very rare or it has been extirpated, similarly to other dodder species (e.g. *C. jepsonii*; Costea and Stefanović 2009a).

4. ***Cuscuta jalapensis*** Schltld., *Linnaea* 8: 515–516. 1833.—TYPE: MEXICO. Veracruz, prope Jalapam, [May 1829], *Schiede* 152 (lectotype: HAL, MO!, NY!; Yuncker 1932). The herbarium of D. F. L. v. Schlechtendal is at HAL where one of the Schiede collections, “prope Jalapam” dated May 1829 is found, but with no collector number. The specimens from MO and NY do not have indicated the collection date.

Stems medium to coarse, orange. Inflorescences dense, corymbiform, usually confluent; pedicels 1–3 mm long; bracts 1 at the base of inflorescences, absent at the base of pedicels/flowers, 1.5–3.2 × 1.2–2.5 mm, ovate to lanceolate, acute to obtuse. Flowers 5-merous, 4–7 mm long, fleshy, white-creamy when fresh, grey-brownish upon drying; papillae absent; laticifers visible more in the corolla and less in the calyx, isolated, ovoid to elongate; calyx 1.6–3 mm long, brownish, not reticulate and shiny, cupulate, ca. 1/2 of the corolla tube, divided ca. 2/3 to the base, tube 0.6–1.2 mm long, lobes 1–2.6 mm long, ovate, not overlapping or only slightly so at the base, not carinate but fleshy in the median part, margins membranous, entire, apex rounded (Fig. 3B); corolla 3.6–6.8 mm long, tube 2–4.2 mm long, cylindrical but becoming suburceolate at fructification, lobes 1.5–2.8 mm long, initially erect, later spreading to patent, shorter than the tube, ovate, not carinate or with multicellular protuberances, slightly overlapping, margins entire, apex rounded to obtuse, straight; stamens exerted, shorter than the lobes, anthers 0.8–1.1 mm long, broadly-elliptic to oblong, filaments 0.8–2 mm long; pollen tricolpate, 27–30 μm long, subprolate to prolate, tectum microreticulate, lumina 0.6–1.8 μm in diameter; infrastaminal scales 2–4.3 mm long, equalling corolla tube, oblong to ovate, bridged at 0.8–1.5 mm, densely fringed, fimbriae 0.2–0.5 mm, cylindrical; styles 0.5–1.5 mm long, 0.4–1 mm thick, shorter to equalling the ovary, conical but becoming subulate in fruit; stigmas

lobed. Capsules circumscissile, 4–6 × 4–6 mm, ovoid to globose, not translucent, surrounded by the withered corolla. Seeds 1–3 per capsule 1.6–2.7 × 1.7–2.8 mm, angled or slightly dorsoventrally compressed, subround to wider than long, seed coat cells alveolate/papillate or wrinkled, hilum region 0.5–0.67 mm in diameter, scar 0.12–0.6 mm long.

Distribution and Ecology—*Cuscuta jalapensis* is the most common dodder species in central and southern Mexico (Chiapas, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Veracruz), Guatemala, and Honduras (see Appendix 2). It occurs in all the major mountain ranges of these geographical areas, and it grows in mesic, montane cloud forests at elevations between 900 and 3,000 m. It parasitizes numerous hosts, which are both herbaceous and woody: *Alnus*, *Calliandra*, *Cassia*, *Eupatorium*, *Lopezia*, *Phaseolus*, *Phytolacca*, *Piper*, *Ricinus*, *Rubus*, *Salvia*, *Sambucus*, *Solanum*, and *Senecio*. Some herbarium collections indicated in their labels that flowers are scented and plants have local medicinal uses. Flowering was most commonly noted between Oct–Feb but flowering specimens were also collected in Jun–Aug.

5. ***Cuscuta lindsayi*** Wiggins, *Contr. Dudley Herb.* 5: 133 (–135; Fig. 1). 1959.—TYPE: MEXICO, Sinaloa, 55.7 miles E of Villa Union, Sinaloa, on talus slope; growing on several shrubs, including *Lippia pringlei* Briq., *Buddleia wrightii* Robins., and *Viguiera seemannii* Sch.-Bip., alt. 6,210 ft, 18 Mar 1955, *Wiggins* 13185 (holotype: DS!; isotypes: F!, MO!).

Stems medium to coarse, orange. Inflorescence dense, corymbiform to subglomerulate, confluent or not; pedicels 1–5 mm long; bracts 1 at the base of inflorescences, absent at the base of pedicels/flowers, 2–3 × 0.8–1.5 mm, ovate, acute to obtuse. Flowers 5-merous, 6–7 mm long, fleshy, white-creamy when fresh, reddish upon drying; papillae absent; laticifers inconspicuous; calyx 2.5–3 mm long, brown-reddish, not reticulate and shiny, cupulate, ca. 1/2 of the corolla tube, divided ca. 1/2 to the base, tube 1–1.5 mm long, lobes 1.4–1.7 mm long, broadly-ovate triangular, not overlapping or only slightly so, not carinate but fleshy in the median part, margins membranous entire, apex rounded to subacute (Fig. 3I); corolla 5.8–6.4 mm long, tube 4–4.5 mm long, cylindrical-campanulate but becoming urceolate at fructification, lobes 1.8–2 mm long, initially erect, later spreading to patent, shorter than the tube, ovate, finely carinate but multicellular protuberances absent, slightly overlapping, margins entire, apex rounded to obtuse, straight; stamens exerted, shorter than the lobes, anthers 0.9–1.1 mm long, elliptic, filaments 0.3–0.4 mm long, prolonged and prominent on the corolla tube for another 1–1.5 mm; pollen tricolpate, 23–27 μm long, sphaerical to subprolate, tectum perforate, puncta 0.2–0.6 μm in diameter; infrastaminal scales 3–3.5 mm long, shorter than corolla tube, obovate to spatulate, bridged at 0.5–0.6 mm, dentate-fringed, fimbriae 0.15–0.3 mm, with no visible laticifers; styles 0.8–1.6 mm long, 0.3–0.4 mm thick, ca. as long as the ovary, cylindrical; stigmas not lobed. Capsules circumscissile, 3.5–4 × 3.2–4 mm, globose to slightly depressed, not thickened or risen around the small interstylar aperture,

not translucent, surrounded by the withered corolla. Seeds not seen.

Distribution and Ecology—Originally known only from the type collection in Sinaloa, Sierra Madre Occidental (Wiggins 1959), we have also discovered this species in Jalisco, in the Trans-Mexican Volcanic Belt. Based on the very few herbarium collections available, it is probably a rare species. It grows in mesic pine forests at 1,800–2,300 m elevation, and the hosts are mostly shrubs: *Baccharis*, *Buddleia*, *Lippia*, and *Viguiera*. Flowering takes place between Feb–Mar.

6. *Cuscuta mitriformis* Engelm. ex Hemsl., *Diagn. Pl. Nov. Mexic.* 2: 54. 1879 (as *C. 'mitraeformis'*).—TYPE: MEXICO. En route from San Luis Potosí to Tampico, Dec 1878–Feb 1879, *Palmer s.n.* (holotype: MO!; isotypes: GH!, NY!).

Stems medium to coarse, orange. Inflorescences dense, corymbiform-glomerulate; pedicels 0.5–2 mm long; bracts 1 at the base of clusters, usually absent at the base of pedicels, 2–3.5 × 1.3–2.2 mm, ovate-triangular, margins entire, apex acute to obtuse. Flowers 5-merous, 3.2–5.5 mm long, fleshy; papillae absent; laticifers not visible; calyx 2–3.5 mm long, brownish, ± reticulate and shiny, shallowly cupulate, nearly as long as the corolla tube, divided ca. 1/3 the length, tube 0.6–1 mm long, lobes 1.5–3 mm long, basally overlapping, broadly ovate, external lobes carinate and sometimes with a dorsal multicellular appendage, margins entire, apex obtuse (Fig. 3C); corolla 3–5 mm long, white when fresh, brown-creamy when dried, the tube 1.5–2.2 mm long, campanulate, lobes 1.5–2.3 mm long, initially erect, later spreading to reflexed, ca. as long as the tube, broadly-ovate, margins entire, apex obtuse, straight; stamens slightly exerted, shorter than the lobes, anthers 0.5–0.8 mm long, ovate to broadly elliptic, filaments 0.5–0.9 mm long; pollen tricolpate, 23–33 μm long, sphaerical to prolate, tectum perforate, puncta 0.2–0.6 μm in diameter (Fig. 6 E–F); infrastaminal scales 1.5–3.5 mm long, equalling corolla tube, ovate to oblong, bridged at 0.4–0.7 mm, truncate to rounded, sparsely fimbriate (sometimes only distally), fimbriae 0.1–0.4 mm long, cylindrical; styles 0.9–2 mm long, 0.4–1 mm thick, conical but becoming subulate in fruit, shorter than the ovary; stigmas lobed. Capsules circumscissile, globose, 4–7 × 4–6 mm, thickened and risen around the large interstylar aperture, not translucent, surrounded by the withered corolla at the base. Seeds 4 per capsule, 1.8–2.3 × 1.7–2.3 mm, angled, subround to broadly elliptic or ovate, hilum region 0.5–0.75 mm in diameter, scar 0.2 mm long; seed coat wrinkled radially when dry.

Distribution and Ecology—*Cuscuta mitriformis* is distributed in the U. S. A. (Cochise Co., SE Arizona) and Mexico: Chihuahua, Coahuila, Durango, Estado de México, Guanajuato, Hidalgo, Michoacán, Nayarit, Nuevo León, Querétaro, Puebla, San Luis Potosí, Veracruz, and Zacatecas. The species is rare in the U. S. A. but relatively common and sometimes weedy in Mexico (see Appendix 2). It grows in forests of *Quercus* and *Pinus*, often in clearings and meadows at elevations of 1,500–2,600 m. Hosts are most commonly herbaceous: *Ageratina*, *Ambrosia*, *Bouvardia*, *Cestrum*, *Commelina*, *Desmodium*, *Drymaria*, *Encelia*, *Eupatorium*, *Lonicera*, *Lupinus*, *Phaseolus*, *Porophyllum*, *Salvia*, *Solanum*, *Stevia*, *Thalictrum*, *Verbena*, *Vinca*. It flowers in Aug–Dec and Jul–Sep.

7. *Cuscuta montana* Costea & Stefanović, sp. nov.—TYPE: MEXICO. Durango, Mpio. San Dimas: Mesa Pinalosa, ca. 0.5 km al S, al W del Puerto de Buenos Aires, 23°41'13" N, 105°44'40" W, 2,100 m. Bosque mesófilo de montaña (*Carpinus*, *Ostrya*, *Pinus*, *Quercus*, *Nectandra*, *Cornus*, *Tilia*, escasa *Magnolia*) cañada. Enredadera, común, sobre arbustos (*Salvia* y compuesta), 4 Sep 2002, *González, Reznicek & Ruiz 6697* (holotype: CIIDIR!, isotypes: IEB!, MEXU!, MICH!, WLU!).

Cuscuta montana resembles *C. volcanica* but differs in the presence of one bract at the base of the flowers and smaller flowers with calyx lobes that are broader than long. From *C. rugosiceps* it differs in the capsules with small interstylar aperture capped by the withered corolla, and the larger seeds that lack a radial wrinkling pattern when dry.

Stems coarse, orange. Inflorescences dense, glomerulate, confluent or not; pedicels absent; bracts 1–2 at the base of clusters, 1 at the base of each flower, 3–5 × 3–6 mm, ovate, orbicular or sometimes broader than long, rounded, not carinate, margins entire. Flowers 5-merous, 5.5–6.5 mm long, fleshy, white when fresh, creamy-yellow when dried; papillae absent; laticifers barely visible in the calyx and corolla lobes, isolated, ovoid to elongated; multicellular protuberances absent; calyx 3.5–4 mm long, brown, more or less reticulate, not glossy, campanulate-globose, ca. equalling corolla tube, divided 1/2–2/3 to the base, tube 1.2–2 mm long, lobes 1.8–2.4 mm long, broadly overlapping, round to 2.25 times broader than long, outer two lobes often carinate, margins membranous, entire, auriculate, apex rounded; corolla 5–6 mm long, tube 2.5–3.5 mm long, campanulate-globose but becoming globose at fructification, lobes 2.5–3 mm long, initially erect, later reflexed, equalling the tube, ovate, broadly overlapping, auriculate, margin entire, apex rounded, straight; stamens exerted, shorter than corolla lobes; anthers 0.6–0.8 mm long, elliptic to oblong, filaments 0.6–0.8 mm long; pollen tricolpate, 20–24 μm long, sphaerical to oblate, tectum perforate, puncta 0.3–0.6 μm in diameter; infrastaminal scales 2.5–3.5 mm long, equalling corolla tube, bridged at 1–1.6 mm, oblong, sparsely fimbriate, fimbriae 0.2–0.5 mm long, cylindrical; styles 1.2–2 mm long, 0.4–0.9 mm thick, equalling to longer than the ovary, cylindrical to ± enlarged at the base, conical; stigma lobed. Capsules circumscissile, 4–5.5 × 3–3.5 mm, globose, narrowed and slightly risen around the small interstylar aperture, not translucent, capped by the withered corolla. Seeds 1–4 per capsule, 2–2.8 × 1.9–2.4 mm, angled or dorsoventrally compressed, subround to broader than long, hilum area 0.5–0.6 mm in diameter, scar 0.1–0.12 mm long, seed coat cells alveolate/papillate. Figures 3 O1–O2; 4L; 5 K1–K2; 8 E–H.

Etymology—From “montanus,” “of the mountains,” alluding to the habitat of the species.

Note—All the herbarium specimens of *C. montana* were previously identified as *C. rugosiceps* because of the similar calyx and corolla morphology. These two species belong to different subclades (Figs. 1–2) and differ in the morphology of the capsules and seeds (see key).

Distribution and Ecology—*Cuscuta montana* is currently known only from Durango in Sierra Madre Occidental at elevations over 2,000 m. Habitats include mesic forests

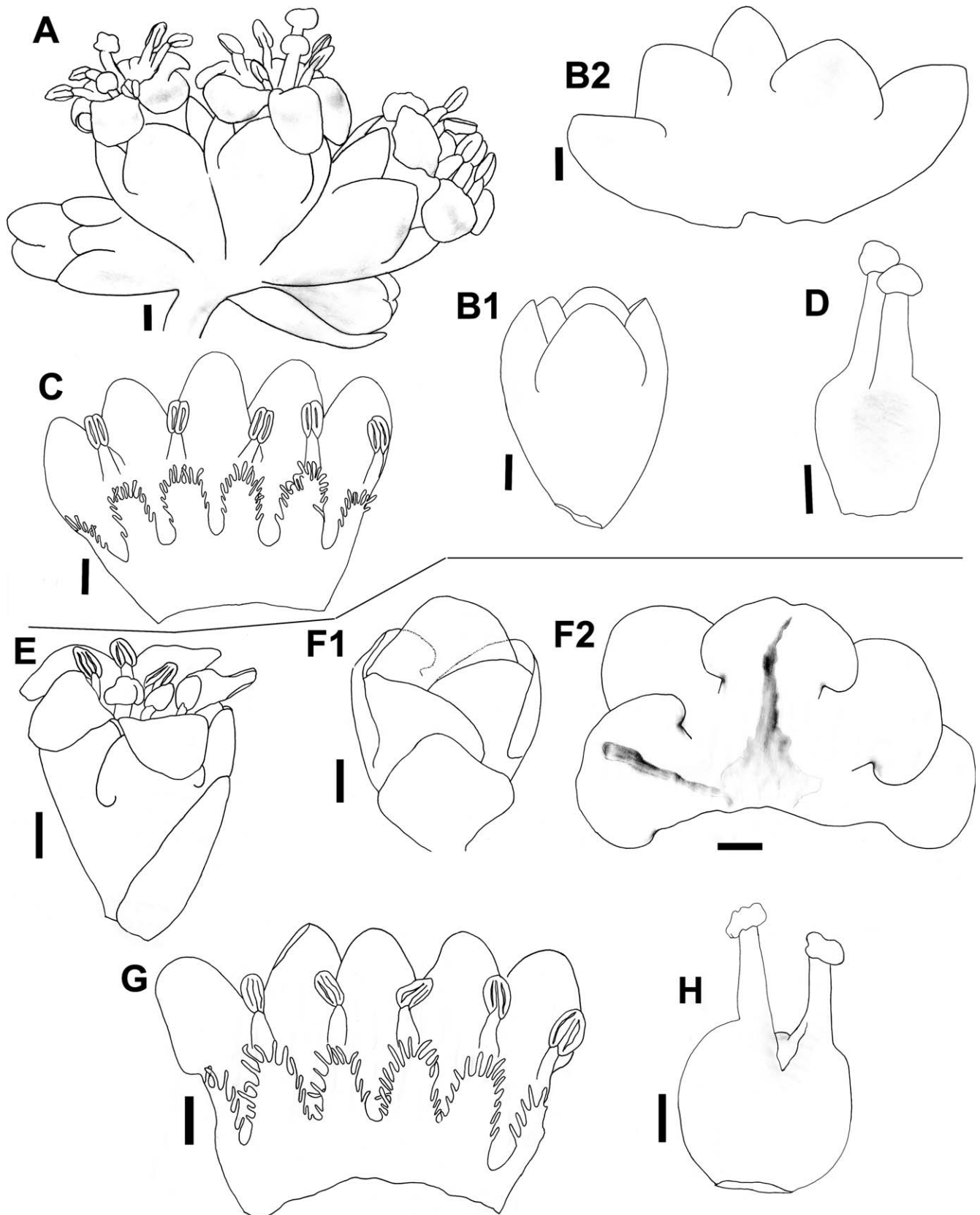


FIG. 8. *Cuscuta volcanica* Costea & I. García (García Ruiz & Costea 8416). A. Inflorescence. B1. Calyx. B2. Dissected calyx, dorsal side. C. Dissected corolla (opened, ventral side). D. Gynoeceium. *Cuscuta montana* Costea & Stefanović (González, Reznicek & Ruiz 6697). E. Flower. F1. Undissected calyx. F2. Dissected calyx, dorsal side. G. Dissected corolla (opened, ventral side). H. Capsule. Scale bars = 1 mm.

of oak and pine, sometimes with a degree of human disturbance. Hosts are both herbaceous and woody plants; the only information about the host range is available from the type. Flowering takes place from Sep–Dec.

8. *Cuscuta purpusii* Yunck., Illinois Biol. Monogr. 6 (2–3): 37 (–38, Fig. 23). 1921.—TYPE: MEXICO. San Luis Potosí, Minas de San Rafael, on *Helietta*, Jul 1911, *Purpus* 5444 (holotype: UC!; isotypes: F, GH!, MO!, NY!, US!).

Stems medium, orange. Inflorescences dense, corymbiform; pedicels 1–5 mm long; bracts 1 at the base of clusters, usually absent at the base of flowers, 0.8–2.4 × 0.9–1.2 mm, ovate to lanceolate, margins entire, apex acute. Flowers 5-merous, 5–7 mm long, membranous; papillae absent; laticifers visible in all the flower parts, arranged in rows, elongated; calyx 3.5–4 mm long, brownish, not reticulate or shiny, campanulate, ca. as long as the corolla tube or somewhat shorter, divided ca. 1/4 the length, tube 0.8–1 mm long, lobes 2.5–3 mm long, overlapping at the base, ovate-lanceolate to ovate-triangular, not carinate, margins entire, apex acute to obtuse (Fig. 3 R1–R2); corolla 4.5–6.5 mm long, white when fresh, brown-reddish when dried, the tube 3–4 mm long, cylindrical, lobes 2–2.5 mm long, spreading to reflexed, shorter than the tube, ovate-lanceolate to ovate-triangular, margins entire, apex obtuse to subacute, straight; stamens exerted, shorter than the lobes, anthers 0.8–1.1 mm long, broadly elliptic to oblong, filaments 0.2–0.4 mm long; pollen tricolpate, 23–33 μm long, obovate, sphaerical to prolate, tectum perforate or microreticulate, puncta or lumina 0.2–1.6 μm in diameter; infrastaminal scales 2–3.5 mm long, equalling corolla tube, oblong to ovate, bridged at 0.5–0.9 mm, rounded, densely fimbriate, fimbriae 0.25–0.35 mm long; styles 1.6–2.3 mm long, 0.15–0.22 mm thick, longer than the ovary, cylindrical (Fig. 5G1); stigmas not lobed. Capsules circumscissile, globose (Fig. 5G2) to slightly depressed, 3–3.5 × 2–2.5 mm, not risen at the base of the styles, interstylar aperture inconspicuous, translucent, capped by the withered corolla at the base. Seeds 1(–2) per capsule, 1.4–1.9 × 1.4–1.6 mm, subround to oblong; hilum region 0.3–0.5 mm in diameter, scar 0.7–0.12 mm long; seed coat alveolate/papillate.

Distribution and Ecology—*Cuscuta purpusii* is endemic to Mexico; it is encountered in Nuevo León, Querétaro, San Luis Potosí, and Tamaulipas (Meseta Central and Sierra Madre Occidental). *Cuscuta purpusii* grows in chaparral and open rocky places at elevations between 1,000 and 2,000 m; hosts are both woody and herbaceous from genera *Acacia*, *Croton*, *Haploppapus*, *Helietta*, *Karwinskia*, *Rhus*, and *Salvia*. It flowers from May–Oct.

9. *Cuscuta rugosiceps* Yunck., Illinois Biol. Monogr. 6(2–3): 27(–28, Fig. 1). 1921.—TYPE: MEXICO, Oaxaca, Sierra de San Felipe. Alt. 7,500 ft, 6 Oct 1894, *Pringle* 4967 (holotype: US!; isotype: NY!).

Stems coarse, orange. Inflorescences dense, glomerulate; pedicels absent to 0.5 mm long; bracts 1–2 at the base of clusters, 1 at the base of each flower, 2.5–5.5 × 3–4 mm, ovate to broader than long, margins entire, apex rounded. Flowers 5-merous, 5–7 mm long, fleshy; papillae absent; laticifers visible only in the anthers and fimbriae of infrastaminal scales; calyx 3–4 mm long, brownish, ± reticulate and shiny, campanulate-globose and becoming

cupulate in fruit, shorter than the corolla tube, divided ca. 2/3 the length, tube 1.8–2.5 mm long, lobes 1–1.4 mm long, broadly overlapping, round to 2–4 times wider than long, external lobes carinate, margins entire, apex obtuse (Fig. 3A); corolla 4–6.5 mm long, white when fresh, brown-creamy when dried, the tube 2.3–4 mm long, campanulate-globose, lobes 2–2.5 mm long, spreading to reflexed, somewhat shorter than the tube, broadly-ovate, margins entire, apex obtuse, straight; stamens barely exerted, shorter than the lobes, anthers 0.6–0.8 mm long, broadly elliptic, filaments subulate, 0.4–0.7 mm long; pollen tricolpate, 27–32 μm long, subsphaerical to subprolate, tectum perforate to microreticulate, puncta/lumina 0.2–1.6 μm in diameter; infrastaminal scales 2.3–2.4 mm long, equalling corolla tube, oblong, bridged at 1.2–1.4 mm, rounded, sparsely fimbriate (sometimes only distally), fimbriae 0.3–0.5 mm long, club-shaped; styles 0.5–2 mm long, 0.4–1 mm thick, conical but becoming subulate in fruit (Fig. 5 A₁–A₂), shorter than the ovary; stigmas lobed. Capsules circumscissile, globose or globose-depressed, 3.5–5 × 1.5–3 mm, thickened and risen around the large interstylar aperture, usually not translucent, surrounded by the withered corolla at the base. Seeds 2–4 per capsule, 1.5–2.1 × 1.5–2.4 mm, angled, subround to broader than long; hilum region 0.4–0.6 mm in diameter, scar 0.15–0.2 mm long; seed coat wrinkled radially when dry (Fig. 6 J–K).

Distribution and Ecology—*Cuscuta rugosiceps* is distributed in Central and SW Mexico (Estado de México, Querétaro and Oaxaca) and Guatemala. It grows in pine and oak mesic forests at elevations of 1,200–2,500 m. Hosts were not specified in any herbarium collection. Flowering takes place between Jul–Mar. *Cuscuta rugosiceps* was confused in the past with *C. volcanica* and *C. montana*, and therefore it is more rare than previously thought (see Appendix 2). The species is little known from biological and ecological points of view.

10. *Cuscuta tasmanica* Engelm., Trans. Acad. Sci. St. Louis 1: 512. 1859.—TYPE: AUSTRALIA, Tasmania, Hobartstown, *Gunn* 1991 (holotype: K).

Stems slender, pale-yellow to orange. Inflorescence fasciculate to umbellate, pauciflore; pedicels 4–12 mm long; bracts 1 at the base of inflorescences, absent at the base of flowers, 1.2–2 × 0.9–1.3 mm, ovate, subacute, margins entire. Flowers (4–)5-merous, 2.5–5 mm long, membranous, creamy-white when fresh, creamy-brown when dried; papillae absent; laticifers isolated or in rows, elongated; calyx 1.4–2.3 mm long, yellow-cream to brown, not reticulate or glossy, shallow campanulate to cupulate, equalling corolla tube or somewhat longer, divided 1/3–1/4 the length, tube 0.4–0.7 mm long, lobes 1–1.3 mm long, not overlapping, oblong to ovate, not carinate or with multicellular protuberances on the midveins, margins entire, apex rounded (Fig. 3H); corolla 2.4–4.5 mm long, tube 1.2–2.2 mm long, campanulate, lobes 1.2–2.2 mm long, initially erect, later reflexed, equalling or shorter than the tube, oblong-ovate, not overlapping, margins entire, apex rounded, straight; stamens exerted, shorter than corolla lobes, anthers 0.5–0.7 mm long, oblong, filaments 0.7–0.9 mm long; pollen tricolpate, 22–25 μm long, commonly prolate but sometimes sphaerical, tectum imperforate or with a few small, scattered puncta, 0.2–0.35 μm in

diameter; infrastaminal scales 1.2–2.5 mm long, equalling corolla tube or longer, oblong, bridged at 0.4–0.6 mm, uniformly dense-fringed, fimbriae 0.2–0.35 mm long, cylindrical; styles 0.8–1.6 mm long, 0.25–0.4 mm, shorter to equalling the ovary, cylindrical to conic; stigma lobed. Capsules indehiscent, 3.8–5 × 3–5 mm, globose to ovate, slightly risen around the small interstyler aperture, translucent, surrounded by the withered corolla. Seeds 3–4 per capsule, 1.8–2.4 × 1.4–1.8 mm, angled, broadly-elliptic to round, hilum area 0.4–0.5 mm in diameter, scar 0.1–0.2 mm long, seed coat cells alveolate/papillate.

Distribution and Ecology—*Cuscuta tasmanica* is endemic to Australia (South Australia, Victoria, New South Wales, and Tasmania; for detailed distribution see Australia's Virtual Herbarium 2013). The species grows in saline areas and brackish marshes at low elevations (20–650 m); its hosts are: *Chenopodium*, *Lythrum*, *Ranunculus*, *Selliera*, *Wilsonia* (Curtis 1967). Flowering takes place between Nov–May.

11. ***Cuscuta timida*** Costea & Stefanović, sp. nov.—TYPE: MEXICO. Hidalgo [Mpio. Jacala?], along Mexico Hwy 85 between Tamazunchale (“Tamanzinchale”) and Zimapàn, 90 km S of border with San Luis Potosí, 40 km N of Zimapàn, oak forest; stems and inflorescences orange; 10 Oct 1985, *Spellenberg, Zucker, and Zimmerman 8359* (holotype: NMC!; isotype: MEXU!).

Cuscuta timida is morphologically similar to *C. tolteca* from which it differs in the calyx 1/2–3/4 as long as corolla tube, longer styles, and capsules that are narrowed and risen around the interstyler aperture.

Stems medium, orange. Inflorescences dense, glomerulate, confluent or not; pedicels absent; bracts 1–2 at the base of clusters, 1 at the base of each flower, 2–3 × 2–4.5 mm, membranous, broadly-ovate to orbicular or broader than long, rounded, not carinate, margins entire. Flowers 5-merous, 6–7.5 mm long, membranous, white when fresh, reddish-brown when dried; papillae absent; laticifers ± visible in the calyx and corolla lobes, isolated, ovoid to elongated. Multicellular protuberances absent; calyx 3–4.4 mm long, brown, more or less reticulate, not glossy, campanulate, 1/2–3/4 as long as corolla tube, divided 1/2–2/3 to the base, tube 1.2–2 mm long, lobes 1.8–2.4 mm long, broadly overlapping, round to 2.5 times broader than long, not carinate, margins membranous, entire, auriculate, apex rounded; corolla 5.5–6 mm long, tube 3–3.7 mm long, campanulate but becoming urceolate at fructification, lobes 1.8–2.2 mm long, initially erect, later reflexed, shorter than the tube, ovate, broadly overlapping, auriculate, margin entire, apex rounded, straight; stamens exerted, shorter than corolla lobes, anthers 0.6–0.8 mm long, elliptic to oblong, filaments 0.6–0.8 mm long; pollen tricolpate, 20–25 µm long, oblate to spherical, tectum perforate to microreticulate, puncta/lumina 0.4–1 µm in diameter; infrastaminal scales 3–3.8 mm long, equalling corolla tube, ovate to oblong, bridged at 1.2–2.5 mm, sparsely fimbriate, fimbriae 0.2–0.5 mm long, club-shaped; styles 1.5–3.3 mm long, 0.3–0.4 mm thick, longer than the ovary, cylindrical; stigma lobed. Capsules circumscissile, 3–4 × 2.6–3.3 mm, globose-ovoid, narrowed and risen around the inconspicuous interstyler aperture, not translucent, capped by the withered corolla. Seeds 2–3 per capsule, 1.8–2.2 × 1.5–2.2 mm, angled, subround to round, hilum area 0.4–0.6 mm in diam-

eter, scar 0.1–0.15 mm long, seed coat alveolate/papillate. Figures 3N; 5H; 6B; 9 E–H.

Etymology—from the Lat adjective “timidus;” timid, shy, passing unnoticed.

Note—As indicated in the “Discussion” section, in the past, *C. timida* was erroneously considered to be *C. floribunda* (treated as a variety of *C. tinctoria* in this study). The morphological and evolutionary affinities of *C. timida* are with *C. tolteca*, from which it differs in the calyx shorter than corolla tube, longer styles, and a different capsule morphology (see key and descriptions).

Distribution and Ecology—*Cuscuta timida* is distributed in Central and SE Mexico: Hidalgo, Querétaro, San Luis Potosí, and Veracruz (part of the Trans-Mexican Volcanic Belt, Meseta Central, and Sierra Madre Occidental), at elevations between 1,950 and 2,800 m. Habitats include oak forests, mountain slopes or matorral, with rocky substrates. Hosts are both herbaceous and woody, but their identity has not been indicated in any of the herbarium specimens. Flowering takes place between Jul–Oct.

12. ***Cuscuta tinctoria*** Mart. ex Engelm., Trans. Acad. St. Louis 1: 480 (1859).—TYPE: MEXICO, Oaxaca, 1827, *Karwinsky s.n.* (lectotype MO!; isolectotype NY!).

Stems medium to rarely coarse, yellow to orange. Inflorescences dense, corymbiform to subglomerulate usually confluent; pedicels 0.5–2.6 mm long; bracts 1 at the base of clusters, absent at the base of flowers, 1.2–3 × 0.6–1.2 mm ovate, oblong to oblong lanceolate, acute to obtuse, margins entire. Flowers 5-merous, 2.8–5.2 mm long, fleshy, white when fresh, reddish-brownish or creamy-white when dried; papillae absent; laticifers numerous, visible in the calyx, corolla, isolated or in rows, ovoid to elongated; calyx 1.5–3 mm long, reddish-brown, more or less reticulate, ± glossy, campanulate, equalling corolla tube or 1/2 as long as it, divided 1/3–1/4 the length, tube 0.5–1 mm long, lobes 1–2.2 mm long, broadly overlapping, round to 1.5 times broader than long, not carinate or with multicellular protuberances, margins entire, apex rounded (Fig. 3 J–L); corolla 2.8–5 mm long, tube 1.4–3 mm long, campanulate, lobes 1.4–2.5 mm long, initially erect, later reflexed, equalling or shorter than the tube, oblong-ovate, overlapping, margin entire, apex rounded, straight; stamens exerted, shorter than corolla lobes, anthers 0.5–1.1 mm long, oblong-elliptic, filaments 0.3–1.2 mm long; infrastaminal scales 1.5–3.2 mm long, equalling corolla tube, oblong to ovate, bridged at 0.5–1.3 mm, uniformly dense-fringed, fimbriae 0.1–0.5 mm long, cylindrical; styles 0.5–2.1 (–3) mm long, 0.2–0.3 mm thick, equalling to longer than the ovary, cylindrical; stigmas not lobed (Fig. 5F). Capsules circumscissile, 2.2–3 × 1.8–2.5 mm, globose to depressed-globose, not thickened and/or risen around the small interstyler aperture, translucent, capped by the withered corolla. Seeds (2–)4 per capsule, 1.5–2 × 1.2–1.9 mm, angled or slightly dorsoventrally compressed, elliptic-oblong to subround, seed coat cells alveolate/papillate, hilum area 0.3–0.4 mm in diameter, scar 0.1–0.15 mm long.

Note—*Cuscuta tinctoria* was used by the Aztecs to produce a yellow dye called “Zacatlaxcalli” (Sahagún 1950–1982). Given their morphological similarity, it is most likely that other species in this group were used as well.

12a. *Cuscuta tinctoria* var. *tinctoria*

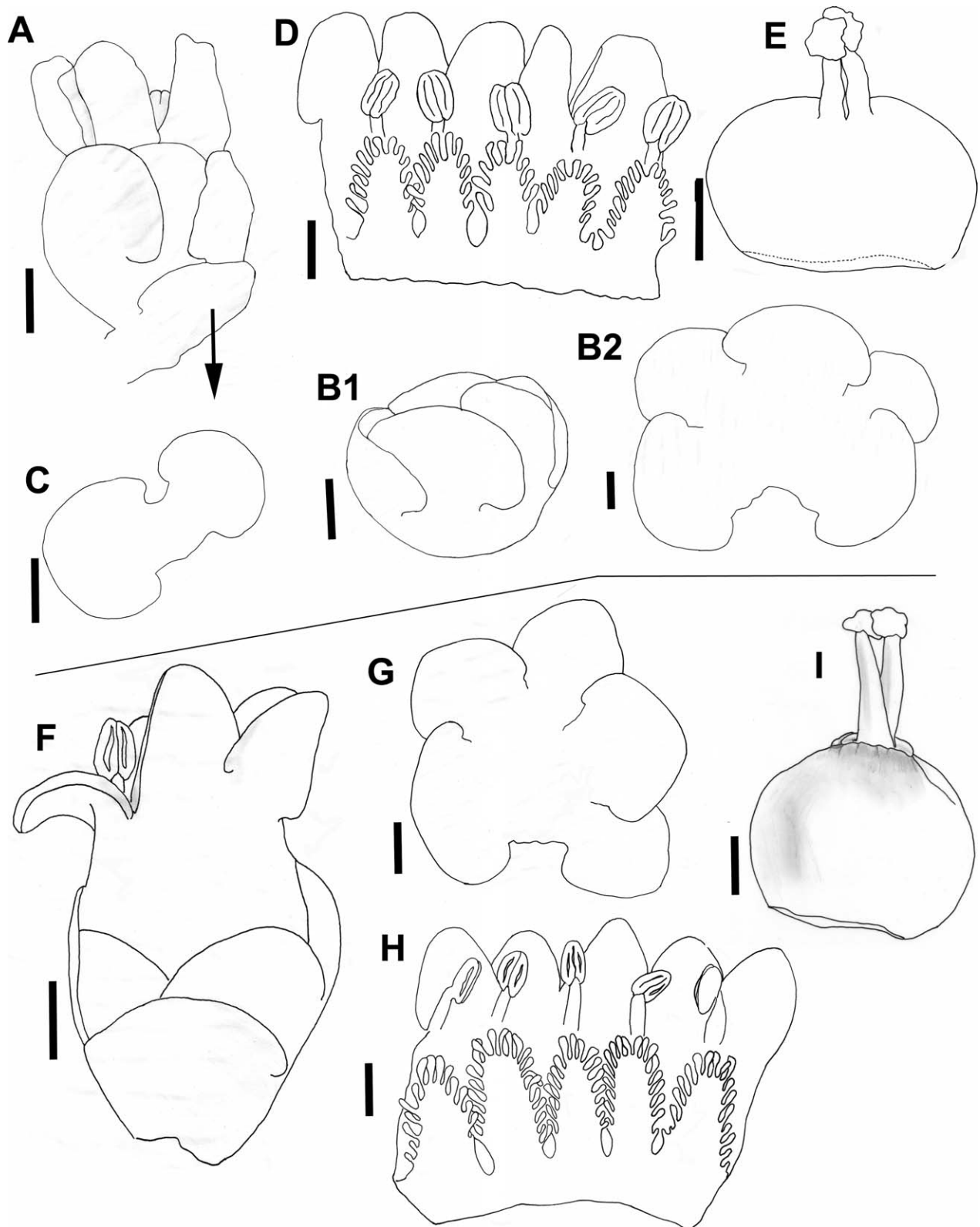


FIG. 9. *Cuscuta tolteca* Costea & Stefanović (Spellenberg 8334). A. Flower. B1. Calyx. B2. Dissected calyx, dorsal side. C. Bracts at the base of calyx. D. Dissected corolla (opened, ventral side). E. Capsule. *Cuscuta timida* Costea & Stefanović (Spellenberg et al. 8359). F. Flower. G. Dissected calyx, dorsal side. H. Dissected corolla (opened, ventral side). I. Capsule. Scale bars = 1 mm.

Flowers 4–5.2 mm long; calyx 2–3 mm long, equalling corolla tube; corolla 3.5–5 mm long, tube 2.3–3 mm long, lobes 1.5–2.5 mm long; pollen tricolpate, 22–26 μ m long, prolate to subprolate, tectum perforate to micro-

reticulate, puncta/lumina 0.4–1.2 μ m in diameter; infrastaminal scales 2.5–3 mm long, bridged at 0.8–1.2 mm, fimbriae 0.2–0.5 mm long; styles 1.2–2.1 (–3) mm long; capsules 2–3 \times 1.8–2.5 mm; seeds 1.5–2 \times 1.2–1.9 mm.

Distribution and Ecology—Variety *tinctoria* is the second most common taxon in Mexico after *C. jalapensis* occurring in Guanajuato, Estado de México, Jalisco, Guerrero, Hidalgo, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí, and Tamaulipas, at elevations between 1,000 and 2,600 m. There is also a herbarium record from Sonora where it was likely introduced with cultivated *Schinus terebinthifolia* (Costea et al. 2012). Hosts are more commonly woody: *Schinus*, *Pithecellobium*, *Acacia*, arborescent *Euphorbia*, *Quercus*, and *Salvia*. It flowers in Jul–Nov, and between Jan–Jun.

12b. ***Cuscuta tinctoria* var. *floribunda*** (Kunth) Costea, comb. nov. *Cuscuta floribunda* Kunth, Nov. Gen. Sp. [H.B.K.] 3: 123. 1818 [ed. quarto]; 96 [ed. folio]. 1819.—TYPE: MEXICO, Morelos, Puente de Ixtla, 3,024 ft, [April 1803] *Bonpland s.n.* (holotype: MO!).

Flowers 4–5.2 mm long; calyx 1.5–2 mm long (Fig. 3K), 1/2–2/3 of the corolla tube length; corolla 3.8–5 mm long, tube 2.6–3 mm long, lobes 1–1.5 mm long; pollen tricolpate, 21–24 μm long, prolate to subprolate, tectum perforate, puncta 0.4–0.7 μm in diameter; infrastaminal scales 3.2–3.8 mm long, bridged at 1–1.3 mm, fimbriae 0.3–0.4 mm long; styles 2–3 mm long; capsules 2.5–3.2 \times 2.2–2.5 mm; seeds 1.4–1.6 \times 1.4–1.6 mm.

Note—The calyx shorter than the corolla tube and narrower flowers allow usually an easy identification of this variety.

Distribution and Ecology—*Cuscuta floribunda* has not been included in any Mexican floristic or taxonomic study (see “Discussion”). The new combination at varietal rank reinstates this dodder and elucidates, at least in part, its geographical distribution and ecology. The taxon occurs in: Chihuahua, Coahuila, Colima, Estado de México, Guerrero, Michoacán, Morelos (Meseta Central, Trans-Mexican Volcanic Belt, and Sierra Madre del Sur). Most notably, var. *floribunda* expands the northern distribution range of *C. tinctoria* to Chihuahua and Coahuila. Hosts are rarely identified in herbarium specimens (e.g. *Ricinus communis*; *Solanum*). Habitats include dry-semideciduous tropical forest, bosque de encino at elevations of 900–2,250 m. Flowering takes place in Jun–Jan.

12c. ***Cuscuta tinctoria* var. *aurea*** (Liebm.) Costea, comb. nov. *Cuscuta aurea* Liebm., Förh. Skand. Naturf. Möte 1847: 193. —TYPE: MEXICO, [Puebla,] *Plantae mexicanae* Liebm. 1841–43, Chapulco 12/1841, *Liebm. 12354* (lectotype: C!; isolectotypes: NY!, US!). There syntype collections are available at C (*Liebm. 12354*, *12356*, *12369*) but *12354* is in the best condition and it is selected here as a lectotype.

Flowers 2.8–3.8 mm long; calyx 1.5–2 mm long (Fig. 3L), equalling corolla tube; corolla 1.8–3.8 mm long, tube 1.4–1.9 mm long, lobes 1.4–1.9 mm long; pollen tricolpate, 17–20 μm long, prolate to subprolate, tectum imperforate to perforate, puncta, 0.2–0.6 μm in diameter; infrastaminal scales 1.5–1.8 mm long, bridged at 0.5–0.7 mm long, fimbriae 0.1–0.2 mm long; styles 0.5–2 mm long; mature capsules and seeds not seen.

Distribution and Ecology—As in the case of var. *floribunda*, these are the first floristic and ecologic data for *C. tinctoria* var. *aurea*. It is distributed in: Estado de

México, Guerrero, Puebla, and Querétaro (Sierra Madre Oriental and Sur) at elevations of 750–2,350 m. Hosts are: *Acacia*, *Aphelandra*, *Helicteres*, *Schinus*, and *Quercus*. Flowering takes place in Jan–Mar and Jul–Oct.

13. ***Cuscuta tolteca*** Costea & Stefanović, sp. nov.—TYPE. MEXICO. Hidalgo, Mpio. Zimapán: 3.5 km NW of Zimapán on road to Purisma, hard limestone hills, ca. 1,800 m elev., 20°46'N, 99°25'W; stems deep orange; flowers cream; 9 Oct 1985, *Spellenberg 8334* (holotype: NMC!; isotypes: MEXU!, UC!).

Cuscuta tinctoria var. *kellermaniana* Yunck., Illinois Biol. Monogr. 6(2–3): 32, f. 16. 1921. —TYPE. GUATEMALA. Dept. Sacatepéquez, Volcano Agua, Alt. 9,000 ft, 4 Feb 1908, *Kellerman 7567* (holotype: NY!).

Cuscuta tolteca is similar to *C. tinctoria* but has sessile and larger flowers subtended by 1–2 bracts. From *C. timida* it differs in having smaller flowers with the calyx equalling the corolla tube, shorter styles, and capsules that are not narrowed apically.

Stems medium. Inflorescences dense, glomerulate, not confluent; pedicels absent; bracts 1–2 at the base of clusters, 1 at the base of each flower, 2–5 \times 2.5–6 mm, ovate, orbicular to broadly-deltoid or broader than long, rounded, not carinate, margins entire. Flowers 5-merous, 4–6 mm long, fleshy, white when fresh, creamy-yellow when dried; papillae absent; laticifers \pm visible in the calyx and corolla lobes, isolated or in rows, ovoid to elongated; multicellular protuberances absent; calyx 2.5–4.4 mm long, yellow, more or less reticulate, \pm glossy, globose, ca. equalling corolla tube, divided 1/2–2/3 to the base, tube 1.2–2 mm long, lobes 1–2.4 mm long, broadly overlapping, round to 2 times broader than long, not carinate, margins membranous, entire, auriculate, apex rounded; corolla 4–6 mm long, tube 2–3 mm long, campanulate-globose but becoming globose or urceolate at fructification, lobes 1.5–2.5 mm long, initially erect, later reflexed, equalling or somewhat shorter than the tube, subround or ovate, broadly overlapping, auriculate, margin entire, apex rounded, straight; stamens exerted, shorter than corolla lobes, anthers 0.6–0.8 mm long, elliptic to oblong, filaments 0.6–0.8 mm long; pollen tricolpate, 19–24 μm long, subsphaerical to spherical, tectum perforate to microreticulate, puncta/lumina 0.2–1.1 μm in diameter; infrastaminal scales 2–3 mm long, equalling corolla tube, oblong to ovate, bridged at 0.5–0.8 mm, densely fringed, fimbriae 0.2–0.5 mm long, club-like; styles 0.5–1 mm long, 0.3–0.4 mm thick, shorter to equalling the ovary, cylindrical; stigma lobed. Capsules circumscissile, 2.5–3 \times 1.6–2 mm, depressed-globose, globose or ovoid, not thickened or risen around the inconspicuous interstylar aperture, translucent, capped by the withered corolla. Seeds 2–4 per capsule, 1.6–2.1 \times 1.5–2.2 mm, angled or dorsoventrally compressed, subround to broader than long, hilum area 0.5–0.6 mm in diameter, scar 0.1–0.12 mm long, seed coat cells alveolate/papillate. Figures 3M; 4K; 5I; 9 A–E.

Etymology—from “Toltec,” old Mezoamerican culture centered in the current State of Hidalgo, Mexico.

Note—*Cuscuta tolteca* has been included in the past in *C. tinctoria*, however, the two species have a different evolutionary history (Figs. 1, 2) and morphology. Namely,

the former species has sessile and larger flowers subtended by 1–2 bracts (also see “Discussion”, identification key and descriptions). From *C. timida* it differs in having smaller flowers, shorter corolla tube and styles, and capsules that are not narrowed apically.

Distribution and Ecology—*Cuscuta tolteca* is distributed in Mexico (Hidalgo, Guanajuato, and Querétaro) and Guatemala. It grows in mesic *Quercus* and *Pinus* forests at elevations of 1,800–2,300 m. Hosts are both woody and herbaceous: *Dyscritothamnus*, *Juniperus*, *Salvia*, and *Stevia*. Flowering takes place in Jul–Jan.

14. *Cuscuta victoriana* Yunck., Mem. Torrey Bot. Club 18(2): 129 (–130, Fig. 4). 1932.—TYPE: AUSTRALIA. South Australia on *Tribulus*, 1900, *Winnecke s.n.* (holotype: NSW, not seen).

Stems slender, orange. Inflorescences dense, subglomerulate, usually confluent; pedicels 0.5–2.5 mm long; bracts 1 at the base of clusters, absent at the base of flowers, 1–1.5 × 0.6–1.2 mm, ovate to lanceolate, acute to obtuse, margins entire. Flowers 4–5-merous, 1.5–2.5 mm long, membranous, white when fresh, reddish-brownish when dried; papillae absent; laticifers visible in the calyx, corolla, isolated or in rows, ovoid to elongated; calyx 1.2–1.5 mm long, yellow-brown, more or less reticulate, ± glossy, campanulate, longer than corolla tube, divided ca. 1/2 the length, tube 0.3–0.6 mm long, lobes 0.6–1.2 mm long, not overlapping, ovate-triangular, not carinate or with multicellular protuberances on the midveins, margins entire, apex rounded (Fig. 3G); corolla 1.4–2.3 mm long, tube 0.3–0.5 mm long, campanulate, lobes 1–1.8 mm long, initially erect, later spreading, longer than the tube, oblong-ovate, not overlapping, margin entire, apex obtuse to subacute, sometimes ± inflexed; stamens not exerted or barely so, shorter than corolla lobes, anthers 0.3–0.4 mm long, round, filaments 0.4–0.5 mm long; pollen tricolpate, 21–28 μm long, prolate to subprolate, tectum imperforate or with a few isolated puncta, 0.2–0.3 μm in diameter; infrastaminal scales 0.4–0.8 mm long, longer than corolla tube, oblong to bifid, bridged at 0.2–0.3 mm, fimbriae few, 0.1–0.2 mm long; styles 0.1–0.3 mm long, 0.1–0.3 mm thick, much shorter than the ovary, cylindrical (Fig. 5C). Capsules indehiscent, 3–4 × 1.5–2.2 mm, depressed-globose, not thickened and/or risen around the relatively large interstylar aperture, translucent, surrounded by the withered corolla. Seeds 3–4 per capsule, 1.3–7 × 1.3–1.7 mm, angled, broadly-elliptic to subround, seed coat cells alveolate/papillate, hilum area 0.2–0.3 mm in diameter, scar 0.05–0.15 mm long.

Distribution and Ecology—*Cuscuta victoriana* is endemic to Australia (for detailed distribution see Australia’s Virtual Herbarium 2013). It parasitizes various herbs from genera such as: *Boerhavia*, *Calotis*, *Sida*, and *Tribulus*. Flowering takes place between Sep and Jun (most commonly from Mar to May).

15. *Cuscuta volcanica* Costea & I. García, sp. nov.—TYPE: MEXICO. Michoacán, Mpio. Patamban: Sirio, salida a Guarachanillo-Patamban. A orilla de la carretera ca. zanja o arroyo de temporal. Parásita de tallos largos sobre *Buddleja* sp. y *Solanum* sp. Altitud aprox. 2,000 msnm, 31 Mar 2009, García Ruiz 8072 (holotype: CIMI!; isotypes: IEB!, MEXU!, NY!, US!, WLU!).

Similar to *C. montana* but distinguished by its larger and fleshier flowers with calyx lobes that are oblong to broadly elliptic or round (not broader than long), and at least the outer lobes carinate. From *C. woodsonii* it differs in having larger and fleshier flowers with carinate calyx lobes, and capsules surrounded and capped by the withered corolla.

Stems medium to coarse, orange. Inflorescences dense, glomerulate, confluent or not; pedicels 0.2–1.3 mm long; bracts very thick and fleshy, 1–2 at the base of clusters, absent at the base of flowers, 3.5–5 × 2.5–3.5 mm, ovate to oblong, margins entire, rounded to subacute. Flowers 5-merous, 7–9 mm long, fleshy, white-creamy when fresh, brown upon drying; papillae absent; laticifers barely visible in the calyx and corolla, isolated, ovoid to elongated; calyx 4.5–5.5 mm long, brown, not reticulate and shiny, campanulate, equalling the corolla tube, divided ca. 2/3 to the base, tube 1.5–2.2 mm long, lobes 2.5–3 mm long, oblong to broadly elliptic or round, very fleshy, overlapping, at least outer lobes carinate, margins membranous entire, apex rounded; corolla 6.5–8 mm long, tube 3.5–5 mm long, cylindrical-campanulate but becoming globose at fructification, lobes 2.5–3 mm long, initially erect, later spreading to patent, shorter than the tube, ovate, not carinate or with multicellular protuberances, basally overlapping, margins entire, apex rounded, straight; stamens exerted, shorter than the lobes, anthers 0.9–1.2 mm long, oblong, filaments 0.5–0.9 mm long; pollen tricolpate, 19–25 μm long, spherical to oblate, tectum perforate, puncta/lumina 0.1–1 μm in diameter; infrastaminal scales 3.5–4.5 mm long, equalling corolla tube, bridged at 1–1.7 mm, oblong, sparsely fringed, fimbriae 0.2–0.3 mm long, cylindrical; styles 1.5–2.2 mm long, 0.4–1 mm thick, ca. as long as the ovary, cylindrical or conical; stigmas lobed. Capsules circumscissile, 5–6 × 3–4 mm, globose to slightly depressed, not thickened or risen around the relatively small interstylar aperture, not translucent, surrounded and capped by the withered corolla. Seeds 1–2 per capsule, 2.3–3 × 2.6–3.3 mm, subround to broader than long, seed coat cells alveolate/papillate; hilum area 0.7–0.9 mm in diameter, scar 0.15–0.20 mm long. Figures 3P; 5 J1–J2; 6 G–H; 8 A–D.

Etymology—from “volcano,” in reference to its geographical distribution and ecology.

Distribution and Ecology—*Cuscuta volcanica* is endemic to Mexico in the Trans-Mexican Volcanic Belt of Guerrero, Jalisco, and Michoacán, where it is quite common. It grows in mesic forests of *Abies religiosa*, *Quercus*, *Pinus*, and *Clethra* at elevations of 2,000–3,200 m. Hosts are more commonly woody plants but herbaceous are also possible: *Alnus*, *Buddleja*, *Cestrum*, *Cuphea*, *Eupatorium*, *Lupinus*, *Phytolacca*, *Podachaenium*, *Ricinus*, *Rumfordia*, *Salvia*, *Senecio*, *Senna*, *Solanum*, and *Stevia*. Flowering takes place from Aug–Mar. In a comparative study of the breeding systems in 145 dodder species, *C. volcanica* had the highest pollen count (ca. 17,000 pollen grains/flower; Wright et al. 2012).

16. *Cuscuta woodsonii* Yunck., Ann. Missouri Bot. Gard. 26(4): 305 (Fig. 3). 1939.—TYPE: PANAMA: Chiriquí: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1,500–2,000 m, June 28–July 2, 1938, on a species of *Eupatorium*, *Woodson*, *Allen*, and *Seibert* 950 (holotype: MO!; isotypes: GH!, NY!).

Stems coarse, orange. Inflorescence dense corymbiform, confluent or not; pedicels 0.5–2.5 mm long; bracts 1–2 at the base of clusters, absent at the base of pedicels/flowers, ovate to subround, 2.2 × 2.2 mm, ovate, acute, margin entire. Flowers 5-merous, 6–7 mm long, fleshy, white-creamy when fresh, brown upon drying; papillae absent; laticifers visible in corolla and anthers, isolated, ovoid to elongated; calyx 3–3.8 mm long, brown-reddish, not reticulate and shiny, campanulate, shorter to almost equalling the corolla tube, divided ca. 1/3 to the base, tube 0.6–1.2 mm long, lobes 1.5–2 mm long, broadly ovate to round, about as long as wide, broadly overlapping and forming rounded sinuses at the base, at least outer lobes fleshier in the median part but not distinctly carinate, margins membranous entire or irregular, apex rounded (Fig. 3Q); corolla 5–6 mm long, tube 2.5–3.2 mm long, campanulate but becoming subglobose at fructification, lobes 2.3–2.8 mm long, initially erect, later spreading to patent, ca. as long as the tube, broadly-ovate to subround, not carinate or with multicellular protuberances, basally overlapping, margins entire, apex rounded, straight; stamens exerted, shorter than the lobes, anthers 0.5–0.7 mm long, broadly-ovate, filaments 0.5–0.7 mm long; pollen tricolpate, 21–25 µm long, subprolate, spherical to oblate, tectum perforate, puncta 0.2–0.6 µm in diameter; infrastaminal scales 2.7–3.4 mm long, equal or somewhat longer than corolla tube, bridged at 0.9–1.2 mm, oblong, sparsely fringed, fimbriae 0.4–0.6 mm long, cylindrical; styles 1.5–2 mm long, 0.5–0.8 mm thick, ca. as long as the ovary, thick, conical (Fig. 5 L1–L2). Capsules circumscissile, 5.5–7 × 4–5 mm, ovate to globose, not thickened or risen around the relatively small interstylar aperture, not translucent, surrounded in the lower 1/2 by the withered corolla. Seeds 2–4 per capsule, 2.4–2.8 × 2–2.5 mm, angled, broadly-elliptic to subround, seed coat cells alveolate/papillate; hilum area 0.6–0.7 mm in diameter, scar 0.25 mm long.

Distribution and Ecology—Originally known only from Panama (Wiggins 1959), we also found *C. woodsonii* in southern Mexico (Chiapas) and Guatemala at elevations of 1,500–2,700 m. A previous report of this species from the territory of Flora del Bajío (Carranza 2008) is based on a specimen of *C. jalapensis* (Rzedowski 54246, IEB and WLU; see Appendix 2). Similarly, we could not find any specimens of *C. woodsonii* from Hidalgo, Jalisco, Puebla, Michoacan and Veracruz (Carranza 2008). *Cuscuta woodsonii* is known only from relatively few herbarium specimens (Appendix 2) and data on its ecology are scarce. Recorded hosts are *Eupatorium* and *Salvia*; flowering takes place from June to Apr.

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APPENDIX 1. Taxa, DNA extraction numbers, sources of plant material from which DNA was extracted, and GenBank accession numbers for sequences used in this study. DNA extraction numbers are indicated on the phylogenetic trees 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 cotijana: 1140, García Ruiz et al. 7412 (WLU), **KC485354, KC485378; 1225**, García et al. 8338 (WLU), **KC485355, KC485379**. *Cuscuta iguanella*: 765, McVaugh 18719 (MICH), **KC485356, KC485380; 1303**, Stevens 1465 (ENCB), **KC485357, KC485381/ KC485382**. *Cuscuta insolita*: 802/802b, Tellez & Müller 10525 (XAL, MO), **KC485358, KC485383**. *Cuscuta jalapensis*: 518, Nee & Hansen 18685 (F), EF194379, **KC485384; 606**, Lorence & Irigos 4076 (NY), EF194378, EF194608; **607**, Ton & Lopez 9826 (MICH), EF194377, EF194609; **617**, Breedlove & Thorne 31083 (NY), EF194380, **KC485385**. *Cuscuta lindsayi*: 927, Wiggins 13185 (F), EF194406, EF194625; **1302**, García Ruiz et al. 7569 (WLU), **KC485359, KC485386**. *Cuscuta mitriformis* 556, Eastoe & Clothier s.n. (ARIZ), EF194381, **KC485387; 584**, Carrillo 356 (MEXU), EF194382, EF194611; **815**, Wardlee 146728 (CHR), **KC485360/ KC485361**, EF194610. *Cuscuta montana*: 581, García 4456 (NY), **KC485362, KC485388; 1299**, Sanders et al. 21268 (UCR), **KC485363, *****. *Cuscuta purpusii*: 898, Henrickson 6608 (RSA), EF194399, EF194622; **928**, Purpus 5444 (F), EF194402, EF194623; **1013**, Hinton et al. 23503 (TEX), EF194400, **KC485389/ KC485390; 1025**, Correll & Johnson 19796 (ASU), EF194401, *******. *Cuscuta rugosiceps*: 517, Cosminsky 71 (F), EF194374, **KC485391; 745**, Brenckle 47-269 (NY), EF194376, EF194607; **915**, Williams et al. 41476 (F), EF194375, EF194606. *Cuscuta tasmanica*: 680, Craven s.n. (CANB), EF194387, **KC485392; 681**, Lepesch 908 (CANB), EF194388, EF194612; **682**, Tawes 729 (CANB), EF194389, EF194613. *Cuscuta timida*: 978/978b, Spellenberg et al. 8359 (NMC, MEXU), EF194403, **KC485393**. *Cuscuta tinctoria* var. *tinctoria*: 573, Ortega s.n. (NY), EF194393, EF194617/ **KC485394/ KC485395/ KC485396; 574**, Ortega 149 (GH), EF194394, EF194618; **766**, Moore & Wood 3879 (MICH), EF194395, **KC485397; 798**, Zerón 22 (XAL), **KC485364, ***; 1226**, García Ruiz et al. 8341 (WLU), **KC485365, KC485398**. *Cuscuta tinctoria* var. *floribunda*: 489, Grimaldo 492 (F), EF194396, *****; 1009**, Prather & Soule 1221 (TEX), EF194397, **KC485399; 1010**, King & Soderstrom 5053 (TEX), EF194398, EF194619. *Cuscuta tinctoria* var. *aurea*: 506, Chiang et al. 2161 (MICH), EF194391, EF194620; **562**, Moreno 13 (ASU), **KC485366, KC485400; 799**, Rzedowski 27017 (XAL), **KC485367, ***; 800**, Hernández & Arias 21117 (XAL), EF194392, EF194621; **1023**, King 2281 (TEX), EF194390, **KC485401**. *Cuscuta tolteca*: 852, Gilly & Camp 2 & 4 (NY), **KC485368, KC485402; 1297**, Spellenberg 8334 (MEXU), **KC485369, KC485403/ KC485404/ KC485405/ KC485406/ KC485407/ KC485408; 1298**, Prather &

Soule 920 (CAS), ***, **KC485409/ KC485410/ KC485411/ KC485412/ KC485413/ KC485414**. *Cuscuta victoriana* Yunck.: **678**, *Cowie* 9624 (CANB), EF194383, EF194616; **683**, *Mitchell* 6089 (CANB), EF194384, **KC485415; 684**, *Latz* 14050 (CANB), EF194385, EF194614; **685**, *Smyth* 261 (CANB), EF194386, EF194615. *Cuscuta volcanica*: **560**, *Rzedowski & McVaugh* 592 (ARIZ), **KC485370, ***, 595**, *Pichardo* 93 (MICH), **KC485371, KC485416; 1007**, *McVaugh* 10023 (TEX), **KC485372, KC485417; 1044**, *McVaugh* 10023 (US), **KC485373, ***, 1152**, *García Ruiz et al.* 7567 (WLU), **KC485374, KC485418; 1153**, *García & Alvarez s.n.* (IEB), **KC485375, KC485419; 1154**, *García Ruiz* 5108 (CIMI), **KC485376, KC485420; 1208**, *García Ruiz* 7772 (WLU), **KC485377, KC485421**. *Cuscuta woodsonii*: **729**, *Davidson* 967 (GH), EF194404, **KC485422; 916**, *Standley* 81878 (F), EF194405, EF194624.

Outgroups—*C. americana* L.: **698**, *Garneau et al.* 1470 (TRT), EF194363, ***, **699**, *Buswell* 6231 (NY), ***, EF194597. *C. applanata* Engelm.: **535**, *Johnston* 8826 (F), EF194372, EF194605. *C. haughtii* Yunck.: **601**, *Svenson* 11281 (QFA), EF194350, EF194590.

APPENDIX 2. List of herbarium specimens examined for morphology. Country, locality details, date, collectors, and herbaria in which the specimens are deposited are provided for all specimens. Underlined collector information indicates the specimens that were also used in the molecular study.

1. *CUSCUTA COTIJANA* (FOR ADDITIONAL SPECIMENS SEE COSTEA ET AL. 2008b)—MÉXICO. Colima: Mpio. Quisería, exit from Rd. Quisería to San Antonio, close to Montitlán, 1,420 m, 14 Mar 2010, *García et al.* 8337 (CIMI, WLU); N side of exit to El Carrizal from Rd. Quisería-San Antonio, 1,300 m, 14 Mar 2010, *García et al.* 8338 (CIMI, WLU). Jalisco: Mpio. Quitupan, Rd from Valle de Juárez to Sta. Maria del Oro, N of El Montoso, 1,950 m, 9 Sep 2008, *García Ruiz et al.* 8089 (CIMI, WLU); 19°42'42.1"N, 102°55'42.2"W, 2,019 m, 10 Aug 2009, *García Ruiz et al.* 8263 (CIMI, WLU). Michoacán: Mpio. Cotija, approx. km. 10.5 carr. Cotija-Los Gallineros (entre Las Peñas y Los Amoles), 19°43'57.26"N, 102°41'28.76"W, 2,014 m, 21 Feb 2013, *García & Costea* 8638 (CIMI, WLU).

2. *CUSCUTA IGUANELLA*—MÉXICO. Jalisco: (Mpio. Zapopan?), wooded hills near Guadalajara, 2 Sep 1893, *Pringle* 4529 (F, GH, K, MEXU, NY, MO, S, US); near Guadalajara, 30 Sep 1903, *Rose & Painter* 7473 (NY, US); Río Blanco, 17 Sep 1886, *Palmer* 579 (NY); Nayarit: (Mpio. Xalisco?), along Hwy 15 ca. 18 mi SE of Tepic, 26 Aug 1971, *Stevens* 1465 (MO, NY, XAL); near km 866 ca 24–25 mi SE of Tepic, 1,300 m, 4 Sep 1960, *McVaugh* 18719 (MICH).

3. *CUSCUTA INSOLITA*—See the *type*.

4. *CUSCUTA JALAPENSIS*—MÉXICO. Chiapas: Mpio. Amatenango del Valle, near the center of Amatenango, 1,798 m, 23 Aug 1965, *Breedlove* 12181 (DS). Mpio. Chanal, 2 mi SE of Chalapa, 7 Aug 1957, *Alava* 1233 (DS); Mpio. Mendoza, 45–50 km NE of Huixtla on Rd to Motozintla, 1,900 m, 28 Dec 1972, *Breedlove & Thorne* 31083 (CAS, MEXU, NY); Mpio. San Cristóbal de Las Casas, Santa Cruz in San Felipe, 15 Nov 1986, *Ton & Lopez* 9826 (CAS, GH, MICH, NY); Cerro Huitepec, 2,700 m, *Breedlove* 23027 (DS, MEXU); Mpio. Tenejapa, Paraje Shohleh, 2,560 m, 12 Jan 1966, *Ton* 603 (DS, F, GH, NY); W of Tenejapa along trail on Paraiso, 2,077 m, 4 Aug 1964, *Breedlove* 6815 (DS, F, MEXU); above Tenejapa Center, 2,077 m, 12 Jul 1965, *Breedlove* 10838 (DS, F, MEXU); Mpio. Unión Juárez, Hills above Unión Juárez, lower slopes of Volcán Tacaná, 15°06'N, 92°05'W, 1,900–2,010 m, 5 May 1987, *Miller et al.* 2720 (MEXU, MO); 3 May 1987, *Miller et al.* 2638 (MEXU, MO); Mpio. Zinacantán, near Zinacantán Center, 2,072 m, 30 Sep 1966, *Laughlin* 2245 (DS); Guanajuato: Mpio. Xichú, Puerto de Tabla, 2,100 m, 21 Sep 1996, *Sánchez* 23 (IEB). Guerrero: Mpio. Chichigualo, near Puerto Hondo, 3 Dec 1963, *Dieterle* 3232 (MICH); Mpio. Leonardo Bravo, ca. 15 km S of Puerto Gral. Nicolás Bravo (Filo de Caballos), 17°34'N, 99°55'W, ca. 3,000 m, 21 May 1987, *Miller & Campos* 2838 (MEXU, MO); Mpio. Malinaltepec, Malinaltepec, 2,000 m, 8 Feb 1991, *Wagenbreth* 535 (MEXU); Hidalgo: Mpio. Chapulhuacán, Chapulhuacán, July 1937, *Lundell & Lundell* 7169 (NY, S); Mpio. Eloxochitlan, 1 km N of San Agustín Eloxochitlan, 11 Oct 1981, *Martínez* 188 (MEXU); Mpio. Jacala de Ledezma, 8 mi NE of Jacala, 1 Aug 1972, *Dunn & Dunn* 19045 (MO); 29.1 km NE of Jacala, 1,650 m, 20 Dec 1991, *Prather & Soule* 925 (CAS, LL, MEXU, TEX); Mpio. Mineral del Chico, vicinity of Peña del Cuervo, 5 km SE of El Chico, 2,800 m, 20 Jul 1986, *Medina* 3102 (F, MICH); El Conejo, 3 km SW of El Chico, 2,550 m, 29 Aug 1987, *Medina* 3538 (F, MEXU); El Ocote, ca. 3 km SE of El Chico, 2,700 m, 1 Sep 1989, *Zamora & Barquín* 865 (IEB); Mpio. Metztlán, Paraje 'El Cerro', 3 Mar 1992, *García & Ramos* 33 (MEXU); Mpio. Molango, Xochicoatlán, 13 Sep 1964, *Quintero* 1581 (IEB); Mpio. San Bartolo

Tutotepec, 1,650 m, 6 May 1972, *Gimate* 620 (F, IEB, MEXU, XAL); Ranchería Río Chiquito, 1,400 m, 24 Feb 1973, *Gimate* 886 (MEXU, XAL); Mpio. Tenango de Doria, km 41.5 on the Rd Tulancingo – Tenango de Doria, 8 Feb 1981, *Muñoz* 16 (F, MEXU); Mpio. Tepehuacan, San Juan Ahuehuco, ca. 1,600 m, 25 Dec 1992, *Rangel* 160 (MEXU); Mpio. Tianguistengo, 5 km E of Tianguistengo, 2,000 m, 21 Dec 1981, *Hernández* 6908 (MEXU, XAL); Mpio. Tlanchinol, 2.5 km E of Tlanchinol, 1,550 m, 21 May 1976, *Flores* 258 (IEB, MEXU, XAL); Mpio. Zacualtipán, SE of Zacualtipán, 2,020 m, 20 Jul 1992, *García* 413 (CHAP, IEB, MEXU); Mpio. Zimapán, 41.5 mi from Zimapán on Hwy 85, 30 Dec 1970, *Dunn et al.* 17404 (MEXU); Jalisco: Mpio. Talpa de Allende, El Paso Hondo, 1,640 m, 10 Mar 2001, *Lomelo* 3474 (MEXU, GUADA); Michoacán: Mpio. Indaparapeo, cerca de Peña Blanca, ca. 4 km W of Las Peras, 2,600 m, 30 Sep 2006, *Rzedowski* 54246 (IEB, WLU); Mpio. Morelia, Loma la Lagunita, close to San Miguel del Monte, 2,300 m, 15 Feb 1986, *Martínez* 1177 (IEB, WLU); Mpio. Queréndaro, ca. 6 km of San José Lagunillas, 2,600 m, 27 May 2006, *Carranza & Silva* 7184 (IEB, WLU); ca. 2 km E of San José Cumbre, 2,660 m, Dec 1993, *Carranza* 4735 (IEB, WLU); vicinity of Puerto de los Morillos, 2,750 m, 7 Dec 1991, *Rzedowski* 51367 (IEB, WLU); Mpio. Tingambato, Rd Tingambato-Uruapan approx. km 32.5, 2,150m, 26 Nov 2011, *García Ruiz et al.* 8438 (CIMI, WLU); Mpio. Tzintzuntzan, N part of Cerro Tariaqueri, close to Tarerío, 2,300 m, 23 Jan 1993, *Días & Zamudio* 7381 (IEB, WLU); Morelos: Mpio. Huitzilac, km 61 on Hwy México-Cuernavaca, 2,100 m, [no date], *Gold* 257 (MEXU); Oaxaca: Mpio. Comaltepec, Hwy 175, 17°35'35"N, 96°28'35"W, 2,300m, 11 Oct 1991, *Boyle & Boyle* 507 (MEXU); Mpio. Espíritu Santo Tamazulapan, Espíritu Santo Tamazulapan, 2,080 m, 26 Jun 1991, *Palacios* 9337 (MEXU); Mpio. Ixtlán, close to Cerro Pelón, 19 May 1975, 2,950 m, *Rzedowski* 32999 (IEB, MEXU); Sierra de Juárez, 2,650 m, 18 Apr 1982, *Lorence & Irigos* 076 (MEXU, NY). Mpio. San Pablo Macuilianguis, San Pablo Macuilianguis, 2,300 m, *Nolasco* 791 (CHAP, IEB); Mpio. San Juan Mixtepec, Cerro de Tejocotes, 2,700 m, 16 Nov 1988, *Reyes* 1281 (MEXU); Mpio. San Martín Peras, 2 km from bifurcation to Escobedo, 17°17'N, 97°19'W, 16 Feb 1995, *Calzada* 19723 (NY); Mpio. Santiago Xiacui, along trail from San Pedro Nolasco to Llano Verde, 17°18'N, 96°15'W, 2,000–2,200 m, 26 Jul 1973, *McPherson* 841 (MEXU, MICH); Puebla: Mpio. Chignautla, at the base of Cerro Chignautla, 2,100 m, Sep 1981, *Chazaro* 1713 (XAL); Mpio. Cuetzalan, Cuetzalan, 940 m, 4 May 1976, *Ortega* 169 (F, IEB, MEXU, XAL); Mpio. Honey, Arroyo Grande, 7 km SE of Chila, 1,750 m, 23 Feb 1987, *Tenorio et al.* 12510 (MEXU); Mpio. Huauchinango, near Huauchinango, 1,525 m, 27 Mar 1945, *Sharp* 45380 (MEXU, NY); Mpio. Teziutlán, El Carrizal, 3 km NE Teziutlán, 1,800 m, 26 Dec 1968, *Pineda* 660 (IEB); Mpio. Zacapoaxtla, Cañada del Río Apulco, 22 Jun 1977, *Lozoya et al. s.n.* (MEXU); Apulco, 1,400 m, 5 Feb 1974, *Rzedowski* 31758 (MEXU, XAL); Querétaro: Mpio. Jalpan, ca. 3 km E of San Juan de los Durán, 1,700 m, 17 Feb 2005, *Zamudio & Piedra* 12905 (IEB, WLU); Mpio. Landa, Puerto de Arrastradero, ca. 5 km W of Yesca, 1,940 m, 12 Dec 1988, *González* 240 (IEB, WLU); N part of Llano Chiquito, 21°24'11"N, 99°06'11"W, 2,250–2,400 m, 15 Jun 2000, *Zamudio et al.* 11468 (IEB, WLU); S (SW) of Pemoche, 1,200 m, 16 Mar 1999, *Carranza* 5716 (IEB, WLU); 7 km SE of Agua Zarca, 1,150 m, 16 Mar 1987, *Rzedowski* 42811 (IEB, WLU); Mpio. Pinal de Amoles, 5 km NE of Pinal de Amoles, 2,450 m, 14 Apr 1980, *Zamudio* 3721 (IEB, WLU); Puerto de Agua Fría, ca. 10 km S of Pinal de Amoles, 2,800 m, 5 Sep 1985, *Alamilla* 3068 (IEB); San Gaspar, 2,850 m, 13 Sep 1989, *Zamudio et al.* 7495 (IEB, WLU); Mpio. San Joaquín, Ruinas "Las Ranas", 2,330 m, 30 Sep 1996, *Pérez & Zamudio* 3469 (IEB, WLU); San Luis Potosí: Mpio. Xilitla, Xilitla, 1,000 m, 5 May 1959, *Rzedowski* 10535 (MEXU); Mpio. Zaragoza, Zaragoza, 1,950 m, *Rzedowski* 3519 (MEXU); Tamaulipas: Mpio. Jaumave, 7 km S of Caranbanchel, 2,000 m, 22 Sep 1971, *Medrano & Martínez* 3697 (F, MEXU). Veracruz: Mpio. Acatlán: 1 km SW of Acatlán, 19°41'N, 96°51'W, 1,800 m, 25 Sep 1985, *Martínez* 773 (XAL). Mpio. Atzalán: Atzalán, 1,500 m, 17 Nov 1991, *García & Barrientos s.n.* (MEXU); vicinity of Puente de Rieles, 1,750 m, 28 Jun 1980, *Nee & Hansen* 18685 (F, MEXU, XAL); Mpio. Calchualco, Cañada río Ayohuxtla, 19°9'30"N, 97°9'50"W, 2,170 m, 10 Oct 2001, *Rincón & Durán* 2695 (XAL); Mpio. Chiconquiaco, El Barrial, 1,200 m, 12 Sep 1980, *Ortega & Pedraza* 1527 (F, IEB, XAL); Mpio. Coatepec, ca. 19°28'N, 96°57'W, 2 Dec 1981, *Flügel* 6014 (B); Mpio. Dos Ríos, Estanzuela, 1,000 m, 9 Jan 1974, *Ventura* 9466 (CAS, IEB, MEXU, XAL); Mpio. Huayococotla, Rd to Cruz del Milagro, 2,110 m, 12 Feb 1972, *Hernández* 1511 (F, MEXU, XAL); SW entrance to Huayococotla, 2,150 m, 21 Jul 1982, *Diggs & Nee* 2959 (F, XAL); Mpio. Ixhuacán de los Reyes, El Chorro, 1,590 m, 28 Oct 1979, *Barrera et al.* 87 (MEXU); Mpio. Las Minas, Las Minas, 19°42'N, 97°9'W, 2,250 m, 26 Sep 1986, *Castillo-Campos* 4604 (XAL);

Mpio. Teocelo, Cascadas de Texolo, 5 km of Teocelo, 22 Oct 1975, *Calzada* 2073 (XAL); Mpio. Xalapa, El Salto del Gato, 1,300 m, 18 Apr 1974, *Ventura* 9892 (MEXU, XAL). Mpio. Xico, 6 km W of Xico, 19°25'N, 97°00'W, 1,600 m, 20 Jan 1988, *García* 184 (XAL); Mpio. Yacuatla, Espizo del Diabolo, 19°48'N, 96°47'W, 1,500 m, 16 Dec 1987, *Gutiérrez* 2978 (XAL); GUATEMALA. Dept. Chimaltenango: ca. 8 km NW of Tecpán, 2,300 m, 7 Sep 1973, *Sousa* 4230 (MEXU, RSA); Dept. El Quiché: Nebaj, ca. 8 km S of Sacapulos Rd, 2,133 m, 12 Jun 1964, *Contreras* 4958 (CAS, MO); vicinity of Nebaj, 1,981–2,286 m, 25 Jun–17 Aug 1964, *Proctor* 25063, 25375 (F, MO); Dept. Huehuetenango: Todos Santos, La Maceta, 2,926 m, 5 Jun 1995, *Vélix* 3720 (BIGUA, MO); Cruz de Limón between San Mateo Ixatán and Nucá, 2,600–2,300 m, 31 Jul 1942, *Steyermark* 49837 (US); Sierra Cuchumatanes to San Juan Ixcuy, 3,500 m, Jan 12–23 1966, *Molina* et al. 16584 (US); Dept. Jalapa: vicinity of Soledad, Montaña Miramundo, 2,000–2,500 m, 4 Dec 1939, *Steyermark* 32618 (F, NY); Dept. Quezaltenango: Chiquihuite, 1,410 m, 8 Mar 1939, *Standley* 68106 (F, NY); Finca Chicabal, 1,380 m, 6 Mar 1939, *Standley* 68069 (F, GH). Dept. San Marcos: Sierra Madre Mts., ca. 6 km N of San Marcos, 2,700 m, 13 Dec 1963, *Williams* et al. 25913 (F, NY); near San Andrés, 2,900 m, 2 Jan 1965, *Williams* et al. 27026 (F, GH, NY); near La Vega ridge along Río Vega and NE slopes of Volcán Tacaná, in vicinity of San Rafael, 2,500–3,000 m, 20 Feb 1940, *Steyermark* 36203 (F); Dept. Totonicapán: above Totonicapán on Rd to Desconsuelo, 2,500–2,800 m, 23 Jan 1948, *Standley* 84397 (F, NY). HONDURAS. Dept. Intibucá: vicinity of La Esperanza, along Intibucá River, 1,600 m, 12 Mar 1970, *Molina & Molina* 25525 (F, MO, US).

5. *CUSCUTA LINDSAYI*—MÉXICO. Jalisco: Mpio. Mazamitla, Vicinity of Las Dos Aguas, S of Mazamitla, 19°51'33.6"N, 102°59'38.3"W, 2,240 m, 17 Feb 2007, *García Ruiz et al.* 7569, 7571 (CIMI, WLU); Mpio. Quitupán, Plan de Cervantes, Rd from Valle de Juárez to Sta. María del Oro, 2,170 m, 12 Apr 2008, *García Ruiz et al.* 8076 (CIMI, WLU); km 26.2, Rd to Santa María del Oro, 2,240m, 15 Mar 2011, *García Ruiz* 8419 (CIMI, WLU); Sinaloa: Mpio. Concordia, 55.7 mi E of Villa Unión, 1,893 m, 18 Mar 1955, *Wiggins* 13185 (DS, F, MO).

6. *Cuscuta mitriformis*—U.S.A. Arizona: Cochise County, Cave Creek Canyon, Chiricahua Mts, 22 Sep 1929, *Harrison* 6176 (ARIZ); MÉXICO. Chihuahua: Mpio. Bocoyna, Cañón Basihuare, 1,980 m, 15 Sep 1988, *Mateos* 121 (MEXU); [Mpio. Chihuahua] near Chihuahua, 26 Oct 1886, *Pringle* 291 (G, K, MO, RSA, UPS, US); Sierra Madre, 2 Oct 1887, *Pringle* 1342 (MEXU, MO); W of San Antonio, 10 Oct 1935, *LeSueur* 261 (BRIT, CAS, GH). Sierra Madre, near Colonia García, 31 Aug 1899, *Townsend & Barber* 294 (MO); Mpio. Guachochic, Cusarare, 15 Sep 1973, *Bye* 50488 (UCR); Mpio. Ocampo, National Park Cascada Basaseachi, 28°11'N, 108°12'30"W, 1,570 m, 4 Oct 1966, *Spellenberg* 8827 (MEXU, NMC); Guaynopa Canyon, Sierra Madre Mts., 2,133 m, 14 Sep 1903, *Jones* s.n. (RSA); Coahuila: Mpio. Saltillo, Sierra Zapalinamé, 14 km SE Saltillo, 2,200 m, 17 Mar 1983, *Villarreal et al.* 1991 (ARIZ, BRIT, MEXU, SD); ca. 22 mi WNW of Cuatro Ciénegas, 1,525–1,830 m, 28 Sep 1973, *Henrickson* 13638 (RSA); ca. 54 mi NW of Músquiz, 1,700–1,960 m, 17 Sep 1999, *Henrickson* et al. 22532 (US); Durango: Mpio. Durango, 23°36'53"N, 105°09'24"W, 2,500 m, 9 Nov 2001, *Carrillo* 356 (MEXU); Mpio. El Salto, 52.1 mi SW of Durango, 2,347 m, 1 Sep 1967, *Oliver et al.* 689 (MO); Estado de México: Mpio. Naucalpan de Juárez, 2 km SE of San Francisco Chimalpa, 2,600 m, 3 Sep 1967, *Rzedowski* 24306 (MEXU); Mpio. Texcoco, Cerro Tetzcutzingo, 8 km E of Texcoco, 2,270–2,600 m, 15 Sep 1979, *Pulido* 217 (MEXU); Guanajuato: Mpio. Atarjea, El Coporito, 2,000 m, 4 Jun 1991, *Ventura & López* 9215 (IEB); Mpio. Guanajuato, Mesa de los Hernández, 21°09'06"N, 101°10'58"W, 2,460 m, 19 Oct 1997, *Martínez-Cruz* 712 (MEXU); Mpio. San Diego de la Unión, 21°27'35"N, 101°00'25"W, 2,300 m, 23 Aug 1996, *Carranza & Zepeda* 5046 (IEB); Mpio. Victoria, ca. 2 km NE of Joya Fria, 2,300 m, 29 Sep 1998, *Carranza* 5658 (IEB); 53 km al E de San Luis de la Paz, sobre la carretera a Xichú, 2,450 m, 29 Oct 1986, *Rzedowski* 41379 (IEB, MEXU); Hidalgo: Mpio. Metztitlán, Paraje "El Cerro", 3 Mar 1992, *López García* s.n. (CHAP, IEB); Mpio. Tepeapulco, Cerro del Jihuingo, 2,700 m, 20 Jul 1976, *Ventura* 1847 (CIMI, IEB, MEXU); Mpio. Tula de Allende, Tula, 2,300 m, 27 Aug 1950, *Matuda* 19371 (MEXU, MO); Mpio. Zempoala, Cerro del Tecajete, 2,700 m, 11 Sep 1975, *Ventura* 257 (IEB, MO); Mpio. Zimapan, near Rancho Encarnación, 6 Aug 1948, *Moore & Wood* 4329 (MICH); Michoacán: Mpio. Pátzcuaro, ca. 18 mi S of Pátzcuaro, 2,713–2,745 m, 20–25 Nov 1961, *King & Soderstrom* 5214 (MICH, NY); Mpio. Salvador Escalante, vicinity of Lagunita de San Gregorio, 2,700 m, 8 Oct 1995, *Rzedowski* 52794 (IEB, WLU); (Mpio?) Mountains near Lake Chapala, 18 Nov 1893, *Pringle* 4330 (G, GH, MEXU, MICH, MO, NY, S, US); Nayarit: Mpio. Tepic, Las Tierritas: 2 km NE of Izote, Cerro San Juan, 21°31'N, 104°59'W, 1,200 m, 23 Mar 1989, *Tenorio et al.* 15618 (MEXU); Nuevo

León: Mpio. Galeana, Galeana, Hacienda Pablillo, 1 Aug 1936, *Taylor* 38 (DS, GH, K, MEXU, RSA, S); in canyon between Linares and Galeana, 1,220 m, 10 Jul 1945, *Sharp* 45651 (NY); Mpio. General Zaragoza, Puerto El Pino, 2,610 m, 29 Sep 1979, *Hinton* 17631 (IEB, MEXU); Mpio. Santiago, closest to Cola de Caballo, 25°23'N, 100°10'W, 800 m, 10 Aug 1984, *Villareal et al.* 2945 (XAL); Mpio. Zaragoza, 15 mi W of Dulces Nombres, 2,400 m, 19 Aug 1948, *Meyer & Rogers* 3034 (G, NY, MO); 13 km E of San Antonio Pena Nevada, 2,000–2,200 m, 24 May 1992, *Hernández et al.* 2715 (LL, MEXU, TEX); Querétaro: Mpio. Tolimán, El Derramadero, ca. 21 km NW of Tolimán, 2,600 m, 15 Jul 1989, *Zamudio & Pérez* 7721 (IEB); Puebla: Mpio. Puebla, Cerro Chiquihuite, 2,205 m, 1907–1908, *Arsène* 2217 (K, MEXU); San Luis Potosí: Mpio. San Luis Potosí, Alvarez, 5 Sep 1902, *Palmer* 137 (MEXU, MO, US); 2,200–2,400 m, 30–31 Jul 1934, *Pennell* 17887 (US); San Luis Potosí, 1,880 m, 8 Feb 1968, *Takaki* s.n. (MEXU); 1,600 m, 2 Nov 1954, *Rzedowski* 5388 (MEXU); 11–13 Dec 1924, *Orcutt* 1610 (DS); Tamaulipas: Mpio. Güemes, 3 km SW of Los San Pedro, 1,900 m, 15 Oct 1989, *González* 17296 (MEXU); Veracruz: Mpio. Las Vigas de Ramírez, S of Joya Chica, 19°40'N, 97°05'W, 2,075 m, 22 Dec 1991, *Prather & Soule* 949 (LL, EXU, TEX); Zacatecas: Mpio. Concepción del Oro, 16 mi E of Concepción del Oro, 2,073 m, 22 Sep 1973, *Henrickson* 13382 (MEXU, RSA).

7. *CUSCUTA MONTANA*—MÉXICO. Durango: Mpio. El Salto, Sierra Madre Occidental: SE of Mesa Redonda, along Hwy 40 (Mazatlán-Durango), ca. 4 km E of Los Ángeles, km post 179, 23°38.6'N, 105°49'W; 2,360 m, 2 Sep 1997, *Sanders et al.* 21268 (UCR); Along Hwy 40, 10.6 mi El Palmito, 2,286 m, 30 Dec 1962, *Breedlove* 4261 (MICH); along Mexico Hwy 40, 0.6 mi W of Los Angeles and 3.6 mi E of Revolcadero, 27 Sep 1973, *Reveal & Atwood* 3616 (NY); El Salto, ca. 92 km on Rd to Mazatlan, 23°37'N, 105°50'W, 2,050 m, *González & García* 4333 (CIIDIR); Mpio. Pueblo Nuevo, La Cueva del Muerto, 23°40'53"N, 105°44'39" W, 2,200 m, 20 Sep 2001, *García* 4456 (CIIDIR); Mpio. San Dimas, Mesa Pinalosa, ca. 0.5 km al S, al W del Puerto de Buenos Aires, 23°41'13"N, 105°44'40"W, 2,100 m, 4 Sep 2002, *González et al.* 6697 (CIIDIR, IEB, MEXU, MICH, WLU).

8. *CUSCUTA PURPUSI*—MÉXICO. Nuevo León: Mpio. Aramberri, 27.5 mi NE of Dr. Arroyo on Hwy 29, 9 Sep 1971, 1,830 m, *Henrickson* 6608 (MEXU, RSA); Mpio. Galeana, Mpio. General Zaragoza, Cerro el Viejo, Zaragoza, 1,930 m, 23 Sep 1993, *Hinton et al.* 23503 (ARIZ, IEB); Mpio. Iturbide, 5.4 mi W of Iturbide, 1,676 m, 1 Aug 1959, *Bell & Duke* 16544 (MEXU); 4.2 mi E of Iturbide, 23 Sep 1973, *Reveal & Atwood* 3388 (MEXU); Mpio. Linares, 22–25 mi W of Linares on Rd to Galeana, 19 Jul 1958, *Correll & Johnson* 19796 (ASU, MEXU); Mpio. Pesquería, Sierra Madre Oriental, Dulce Nombres, 2,000 m, 8 Aug 1948, *Meyer & Rogers* 2878 (G, GH, K, MO, NY, UPS); 1,646 m, 2 Aug 1939, *Chase* 7736 (ARIZ, MO, NY); Querétaro: Mpio. Cadereyta, ca. 1 km NE of La Tinaja, 1,760 m, 16 Sep 2001, *Carranza & Silva* 6242 (IEB); Parador El Tepozán, 20°54'27"N, 99°58'57"W, 2,350 m, 18 Sep 2006, *Zamudio & Alcalá* s.n. (IEB); San Luis Potosí: Mpio. Guadalcázar, Cerro El Calvario, 22°36'N, 100°23'W, 1,068 m, 31 Jul 2000, *Torres Colín* 15864 (MEXU); 6.8 mi E of Rd Mex 57 on Rd to Guadalcázar, 2 Jul 1966, *Mears* 159e (MEXU); Minas de San Rafael, Nov 1910, *Purpus* 4972 (MO); Tamaulipas: Mpio. Altamira, 22 km SE of Miquihuana, 2,500 m, 12 Aug 1941, *Stanford et al.* 876 (NY); Mpio. Miquihuana, camino al Cañon del Soldado, 1,900 m, 16 May 1986, *Martínez* 1033 (MEXU); Mpio. Palmillas, 16 km S of Palmillas, 1,600 m, 15 Oct 1984, *McDonald* 1076 (IEB).

9. *CUSCUTA RUGOSICEPS*—MÉXICO. Hidalgo: Mpio. Zapotlán. NW of Santiago Tlazala, 2,700 m, 2 Dec 1979, *Equihua* 602 (IEB); Estado de México: Mpio. Huehuetoca, W side of Cerro Sincoque, 2,500 m, 17 Oct 1976, *Rzedowski* 34441 (IEB); Oaxaca: Mpio. Comaltepec, S Comaltepec, ca. 2,000 m, 17°33'N, 96°31'W, 28 Dec 1989, *López* 396 (MEXU); Mpio. San Andrés Huayapam, Rd from Oaxaca to Ixtlan, 2,500–2,590 m, 24 Jul 1964, *Mickel* 1406 (NY); Between Oaxaca and Valle Nacional, 19.5 km of Hwy 175, 2,560 m, 22 Oct 1985, *Bartholomew et al.* 3272 (CAS, GH, NY); Mpio. Yolox, along Rd between Yolox and Comaltepec, 1,700 m, 12 Mar 1981, *Martin* 413 (MO); (Mpio. ?) Sierra de San Felipe, Oct 1894, 2,286 m, *Smith* 903 (MEXU); Querétaro: Mpio. Jalpan, 2–3 km S of Soyapilca, 1,200–1,250 m, 18 Nov 1999, *Carranza & Silva* 5997 (IEB); GUATEMALA. (Dept?): High Mts, 22 Feb 1947, *Brenckle* 47-269 (NY, S).

10. *CUSCUTA TASMANICA*—AUSTRALIA. Australian Capital Territory: Jervis Bay, Jervis Bay National Park, Blacks Waterhole, 26 Nov 1996, *Taws* 729 (CANB); New South Wales: Southern Tablelands, Lake Bathurst, W basin, 20 Jan 1996, *Crawford* 3645 (CANB); Goulburn Mulwaree Bal, W shore of Lake Bathurst, ca. 2 km NE of Tarago, 35°03'S, 49°30'E, 630 m, 23 Dec 1992, *Lepschi* 908 (CANB, MEL, NSW); Tasmania: Flinders, The Lagoons, Flinders Island, 3 Jan 1970, *Whinray* 1967

(CANB); Victoria: Moyno-North-West, between Lake Corangamite & Lake Martin, W of Berrybank-Cundare Road, 38°06'S, 142°33'E, 29 Jan 1991, *Walsh 3045* (MEL); Pyrenees-South, Southern shore of Lake Goldsmith; fronting crown allotment 4, section 12, grid J33, 37°33'S, 143°23'E, 350 m, 29 Apr 1986, *Watts 1/86* (MEL); Hobsons Bay-Altona, Truganina Swamp, Altona. Enter through Grant Avenue, on E extremity of swamp, 1 Feb 1994, *Stajsic 964* (MEL).

11. *CUSCUTA TIMIDA*—MÉXICO. Hidalgo: (Mpio. Jacala?), Along Hwy 85 between Tamazunchale and Zimapan, 90 km S of border with San Luis Potosí, 40 km N of Zimapan, 10 Oct 1985, *Spellenberg et al. 8359* (NMC, MEXU); Puebla: Tehuacán, [no date], *Rose s.n.* (NY); Querétaro: Mpio. Colón, SE of Cerro Zamorano, 3 km N of Los Trigos, 2,750 m, 30 Sep 2002, *Rzedowski 54044* (IEB, WLU); 2,800 m, 2 Sep 1987, *Rzedowski 44501, 44526* (IEB, WLU); San Luis Potosí: Mpio. San Luis Potosí, Los Hoyos, km 51 carretera San Luis Potosí-Río Verde, 1,950 m, 19 Oct 1958, *Rzedowski 9360* (MEXU); Veracruz: Mpio. Maltrata, Maltrata, Jan 1883, *Kerber 248* (UPS); El Puerto above Orizaba, 2,316 m, 5 Sep 1944, *Sharp 44637* (GH).

12A. *CUSCUTA TINCTORIA* VAR. *TINCTORIA*—MÉXICO. Estado de México: Mpio. Ecatepec de Morelos, 6 km W of San Cristóbal Ecatepec, the high elevation part of Sierra de Guadalupe, 2,600 m, 18 Aug 1974, *Rzedowski 32162* (IEB, MEXU); Mpio. San Andrés Chiauhtla, Tepetitlán, 2,200 m, 25 Aug 1984, *Ventura 4248* (IEB, MEXU, NY, US); Mpio. Temascalcingo, 6–8 km S of Temascalcingo, 2,580 m, 3 Apr 2010, *García Ruiz et al. 8341* (CIMI, WLU); Mpio. Temascaltepec, 1 km Rd Temascaltepec-Real Arriba and Río Verde, 1,750 m, 29 Dec 2009, *García et al. 8325* (CIMI, WLU); Mpio. Zumpango, San Juan Citlaltepec, 2,250 m, *Cervantes 149* (GH, IEB, MEXU, MO, NY); shore of Lake Zumpango, 2,250 m, 28 Nov 1976, *Rzedowski 34758* (IEB, MEXU); 1 km N of San Juan Citlaltepec, 2,240 m, 26 Oct 1980, *Zerón 22* (IEB, MEXU, XAL); Guanajuato: Mpio. San Miguel de Allende, 31 km NNW of Juventino Rosas on Rd to Celaya, 2,350 m, 22 Nov 1987, *Zamudio 5749* (IEB, WLU); Guerrero: Mpio. Apaxtla, Petlacala, 1,880 m, 18 Dec 1937, *Mexia 8995* (MEXU, K, MO, NY, S, US); Mpio. Chilpancingo, Rd Cerro Alquitrán Mazatlán, 1,500 m, 5 Jul 1966, *Chávez 31* (IEB); Mpio. Taxco, trail from Taxco to Casahuates, 1,768–1,920 m, 6 Nov 1949, *Moore 5531* (MEXU, NY); Hidalgo: Mpio. Jacala, Minas Viejas, 1,800 m, 10 Jul 1948, *Moore & Wood 3879* (MICH); Mpio. Tolcayuca, 4 km SE of Tolcayuca, 21 Nov 1978, *Ortega s.n.* (IEB, MEXU, MO, NY); Mpio. Zempoala, 2,500 m, 11 Jul 1981, *Benítez 917* (MEXU); Michoacán: Mpio. Briseñas, Rd from Briseñas to Vista Hermosa, 20°15'41.1"N, 102°33'3.9"W, 1,538 m, 14 Aug 2009, *García Ruiz & Costea 8279* (CIMI, WLU); Mpio. Charo, close to Pontezuela, 25 km E of Morelia, on Rd to Mil Cumbres, 2,200 m, *Rzedowski 42430* (IEB); Mpio. Erongaricuaru, 0.5 km from Erongaricuaru on Rd to Napizaro, 2,100 m, 1 May 1996, *Barriga 7517* (IEB); Mpio. Morelia, 1 km SE of Jesús del Monte, 2,100 m, 30 Oct 1988, *Medina 1434* (IEB); Mpio. Jiquiplan, Side W-NW of city 19°59'41.68"N, 102°43'30.14"W, 1,575 m, 15 Dec 2012, *García Ruiz & García 8584, 8585* (CIMI, WLU); Mpio. Quiroga, Cerro Tzirate, 30 Aug 1986, *Campos 1103* (IEB); Mpio. Sahuayo, N of Las Brisas, 20°03'39.6"N, 102°42'46.8"W, 1,535 m, 15 Dec 2012, *García Ruiz & García 8583* (CIMI, WLU); Mpio. Venustiano Carranza, San Pedro, 20°06'44.4"N, 102°39'32.7"W, 1,532 m, 20 Feb 2007, *García Ruiz et al. 7575* (CIMI, WLU); Morelos: Mpio. Jiutepec, Pedregal, SW Fuentes, Jiutepec, 9 Jul 1968, *Laguerrenne s.n.* (IEB); Oaxaca: Mpio. Ejutla, Rd. Ejutla-Miahuatlán, 5–6 km to Costa and Pochutla, 1,530 m, 7 Apr 2010, *García Ruiz et al. 8344* (CIMI, WLU); Puebla: Mpio. Tehuacan, Tehuacan, Sep 1911, *Purpus 5708* (F); vicinity of San Luis Tultitlanapa, Jul 1908, *Purpus 3553* (NY); Mpio. Tepanco de López, 2 km W of Cacaloapan, 2,000 m, 15 Sep 1965, *Vásquez s.n.* (IEB); Mpio. Tepeaca, 1 km SE of San Hipólito Xochiltanango, 11 Sep 1961, *Sousa s.n.* (MEXU, NY); Querétaro: Mpio. Cadereyta de Montes, 6 km from Rancho Nuevo, Mesa de León, 16 Sep 1989, *Gómez 554* (IEB); Mpio. El Marqués, ca. 2 km of Pocitos, 2,227 m, 28 Dec 1999, *Ocampo 856* (IEB); Mpio. Landa, 3 km W Maconí on Rd to Vizarrón, 2,950 m, 5 Jul 1992, *Rzedowski 51511* (IEB, WLU); Mpio. San Juan del Río, Cañada San Vicente, 2,150 m, 8 Jun 1995, *Hernández et al. 3541* (MEXU); San Luis Potosí: San Luis Potosí, 1879, *Schaffner 377* (CAS, NY, US); 12 Sep 1916, *Palmer 87* (NY, MO, S, US); Sonora: Mpio. Magdalena de Kino, Toll station on MEX 15 bypass at Magdalena, ca. 30°37'N, 110°57'30"W, 800 m, 29 Dec 1994, *Van Devender 94-1008* (ARIZ, MEXU, USON, WLU); Tamaulipas: Mpio. Victoria, 7.6 mi S of Victoria on Hwy 101, 1,380 m, 15 Jun 1987, *Nesom et al. 5949* (F, MEXU, MO).

12B. *CUSCUTA TINCTORIA* VAR. *FLORIBUNDA*—MÉXICO. Chihuahua: Mpio. Chihuahua, Hills and plains near Chihuahua, 2 Sep 1886, *Pringle 784*

(MEXU); Coahuila: Mpio. Muzquiz, Hacienda Mariposa, ravine near Puerto Santa Ana, 22 Jun 1936, *Wynd & Mueller 221* (MEXU, MO, NY, S); Estado de México: Mpio. Temascaltepec, E de La Peña, on Rd to Temascaltepec, ca. 13.5 km of SE Valle de Bravo, 19°05'09.93"N, 100°04'38.54"W, 2,223 m, 27 Dec 2012, *García Ruiz et al. 8588* (CIMI); Guerrero: Mpio. Chilpancingo, E slopes of Cerro Alquitrán, 17°23'10"N, 99°31'W, 2,040 m, 7 Nov 1968, *Kruse 2226* (MEXU); Mpios. Iguala & Buenavista. Cañon de La Mano, entre Los Amates and Naranjo, 900–1,000 m, 12 Oct 1986, *Catalán 303* (CHAPA, MEXU, MO); Mpio. Taxco de Alarcón, 5 km N of Taxco, 17 Jan 1941, *Frye & Frye 3137* (DS, F); Michoacán: Mpio. Acuitzio del Canje, Las Joyas, 2,000 m, 22 Oct 1985, *Barriga 1549* (IEB); Mpio. Arteaga, 37.8 km N of La Mira on Hwy 37 to Uruapan, 18°10'N, 102°20'W, 900 m, 12 Jan 1992, *Prather & Soule 1221* (CAS, LL, TEX, MEXU); Mpio. Charo, between Río del Salto and La Polvilla, 2,195–2,438 m, 9–18 Nov 1961, *King & Soderstrom 5053* (BRIT, MEXU, MICH, NY, US); Mpio. Uruapan, 12 km E of Uruapan on Rd to Pátzcuaro, 1,750 m, 23 Jan 1977, *Rzedowski 34596* (IEB); Mpio. Zacapu, El Reventón, 2,000 m, 5 Jan 1989, *Grimaldo 492* (F, IEB, MEXU, XAL).

12C. *CUSCUTA TINCTORIA* VAR. *AUREA*—MÉXICO. Estado de México: Mpio. San Juan Teotihuacán, Maquizco, 2,250 m, 1 Aug 1971, *Rzedowski 28335* (ARIZ, IEB, MEXU, XAL); Mpio. Sultepec, 5 km N of Sultepec, 2,350 m, 3 Mar 1973, *Moreno 13* (ASU, MEXU); Guerrero: Mpio. Chilpancingo, 6 km W of Mazatlán, 1,550 m, 11 Feb 1970, *Rzedowski 27017* (IEB, MEXU, XAL); Rincón Viejo, 17°17'40", N 99°30'W, 740 m, 14 Jan 1964, *Kruse 863* (MEXU); Puebla: Mpio. Cuapiaxtla, close to Tepeaca, 2,000 m, 6 Aug 1965, *Rzedowski 20380* (IEB, XAL); Mpio. Tehuacán, km 25 on Tehuacán-Puebla, 20 Jul 1986, *Hernández & Arias 21117* (CAS, MEXU, MO, XAL); Mpio. Zacapala, 4 km N of Zacapala, 7 Jul 1981, *Chiáng et al. 2161* (MEXU, MICH); Querétaro: Mpio. Jalpan, between Pinalito and El Tepozan, 1,100 m, 18 Aug 1996, *Zamudio & Pérez 9957* (IEB, WLU).

13. *CUSCUTA TOLTECA*—MÉXICO. Guanajuato: Mpio. Xichú, 6–7 km of Puerto Ocotero on Rd to Xichú, 2,080 m, 25 Jul 1997, *Carranza & García 5331* (IEB, WLU); Hidalgo: Mpio. Cardonal, 19 km E of Ixmiquilpan, 2,000 m, 9 Jul 1980, *Hernández 4615* (CAS, MEXU); Mpio. San Salvador, km 134.5 between Actopan and Ixmiquilpan on Mex-Laredo Hwy, 8 Oct 1943, *Gilly & Camp 2 & 4* (NY); km 134.5 of hwy, near Yolotepec 8 Jul 1943, *Lundell 12528* (MICH, NY). Mpio. Zimapan, about 40 km NE of Zimapan on Hwy 85 to Jacala, 1,850 m, 20°50'N, 99°15'W, 19 Dec 1991, *Prather & Soule 920* (CAS, LL, MEXU, TEX); 3.5 km NW of Zimapan on road to Purísima, 20°46'N, 99°25'W, 1,800 m, 9 Oct 1985, *Spellenberg 8334* (MEXU, NMC, UC); 9 km NW of Zimapan, on Rd to Adjuntas, 1,850 m, 3 Mar 1968, *Rzedowski 25459* (IEB, MEXU); Barranca de Toliman, on Rd from Zimapan to Mina Loma del Toro, 1,737 m, 30 Oct 1949, *Moore 5430* (NY); Querétaro: Mpio. Cadereyta, 3 km W of Maconí on Rd to Vizarrón, 950 m, 5 Jul 1992, *Rzedowski 51511* (IEB, WLU); vicinity of Maconí, 1,800 m, 10 Nov 1988, *Rzedowski 47653* (IEB, WLU); Cerro Prieto, N part of Presa Zimapan, 20°40'16", N 99°31'32"W, 1,820 m, 29 Sep 2007, *Zamudio & Guevara s.n.* (IEB, WLU); 5 km NE of San Javier de las Tuzas on Rd to Sombrerete, 2,350 m, 24 Sep 1996, *Rzedowski 55302* (IEB, WLU); Mpio. Colón, 5 km of El Coyote on Rd to Los Trigos, 2,500 m, 23 Sep 2001, *Ocampo et al. 1162* (IEB, WLU); Mpio. El Marqués, ca. 2 km of Pocitos, 2,227 m, 28 Dec 1999, *Ocampo 856* (IEB, WLU); Veracruz: Mpio. Acultzingo, 18°43'10"N, 97°17'49"W, 2,250 m, 5 Nov 1985, *Martínez & Acosta 946* (XAL); Cumbres de Acultzingo, vereda que va a Bellavista, 2,000 m, 30 Oct 1987, *Chazaro & Chazaro 4176* (XAL); GUATEMALA. Dept. Sacatepéquez: Antigua, 18 Feb 1905, *Kellerman 4812* (US).

14. *CUSCUTA VICTORIANA*—AUSTRALIA. [Western Australia?]: East Island, Ashmore Islands, 17 Jun 2002, *Cowie 9624* (CANB); Northern Territory: Petermann-Simpson, Uluru (Ayers Rock-Mt Olga) National Park, Kata Tjuta (the Olgas), on the Western ring road, 48.3 km WNW of Ranger Station, 15 Aug 1988, *Lazarides & Palmer 471* (CANB); Sandover, Allambi Station, 13 Apr 1977, *Henshall 1410* (MEL); Queensland: Paroo, Gilruth Plains, 1 Apr 1947, *Allan 321* (CANB); South Australia: Unincorp, Far North, Marree-Oodnadatta Rd, 42 km by Rd NW of William Creek, 7 Mar 1984, *Donner 9888* (MEL); Western Australia: Broome, West Lacepede Island, about 20 km W of Beagle Bay, 4 Mar 2000, *Mitchell 6089* (CANB).

15. *CUSCUTA VOLCANICA*—MÉXICO. Guerrero: Mpio. Leonardo Bravo, Chihualco, Cruz de Ocote, 43 km W of Chilpancingo, 2,000 m, 31 Jan 1965, *Rzedowski & McVaugh 288* (CAS, MEXU, MICH); Jalisco: Mpio. Ciudad Guzmán, ca. 3,000 m, Mar 1995, *García & Alvarez s.n.* (IBUG, IEB); 2,200–2,250 m, 23 Jan 1991, *Huerta et al. 41* (IBUG, IEB); a few mi S of Ciudad Guzmán, 2,630 m, 2 Jul 1956, *Gregory & Eiten*

293 (MEXU, MICH, NY, SMU); 12 km. W of Ciudad Guzmán, 2,700 m, 22 May 1988, *Pichardo 93* (MICH); El Izote, 19°37'45"N, 103°38'32"W, 2,350 m, 9 Dec 1984, *Narave & Pattison 1899* (XAL); Mpio. Mazamitla, Rd to Santa María del Oro, 19°51'34.5"N, 102°33.9"W, 2,241 m, 17 Feb 2007, *García Ruiz et al.7567* (CIMI, WLU); 19°51'27.3"N, 102°58'59.4"W, 2,194 m, *García Ruiz et al.7568* (CIMI, WLU); 1–2 km, S of Mazamitla, 2,100 m, 1 Dec 2010, *García Ruiz & Costea 8416*; *García Ruiz 8420, 8570* (CIMI, WLU); cañada of river El Jaral, 2,200 m, 16 Jan 1999, *Cházaro & Cházaro 7913* (IBUG); Mpio. Quitupan, Palo Herrado on Rd from Valle de Juárez a Sta. María del Oro, 19°52.778'N, 102°57.328'W, 2,300 m, 10 Aug 2009, *García Ruiz et al. 8262* (CIMI, WLU); Mpio. San Gabriel, close to Puerto Los Mazos, Rd to Ciudad Guzmán - El Jazmín, 27 Jan 1996, *Machuca & Cházaro 7790* (IEB, IBUG); Mpio. Sayula, 5 km E of Veladero, 2,200 m, 8 Dec 1989, *Villa et al. 389* (MICH); Mpio. Tonila, Volcán Nevado de Colima, 3,100 m, 9 Aug 1986, *Zamudio 4274* (IEB, MEXU, MICH); Rd of Atenquique to Nevado de Colima, 2,900 m, 10 Jan 1965, *Rzedowski 19384* (IEB, MEXU); W side of Nevado de Colima, 3,200 m, 2 May 1966, *Rzedowski 22273* (IEB, MEXU); N slope below La Joya, 3,200 m, 20 Nov 1968, *Boutin & Brandt 2327* (DS, MEXU, MICH); NW slopes above Jazmín, 2,600 m, 25 Mar 1949, *McVaugh 10023* (TEX, MICH, NY, US, MEXU); NE slopes, below Canoa de Leoncito, 2,800 m, 10 Oct 1952, *McVaugh 13419* (MICH); Mpio. Valle de Juárez, 1.8 km north to El Tigre, road to Valle de Juárez, 2,550 m, 16 Aug 2012, *García Ruiz 8471* (CIMI, WLU); 2.7 km W to El Tigre, 2,480m, 15 Nov 2012, *García Ruiz 8569* (CIMI, WLU); ca. 1.5 km al W de Valle de Juárez, cerca de la carretera hacia Mazamitla, 19°56'30.80"N, 102°58'41.7"W, 1,988 m, 19 Feb 2013, *García & Costea 8629* (CIMI, WLU); Mpio. Venustiano Carranza, 25 km S of Ciudad Guzmán, 2,310 m, 3 Oct 1988, *Fuentes 809* (IEB); El Floripondio, Zapotlán El Grande, 19°39'12"N, 103°37'06"W, 2,250 m, 20 Nov 1998, *Castellanos et al. s.n.* (IBUG); Mpio. Zapotitlán, between Puerto el Floripondio and the hill of the Radio Station Viboras, 2,430 m, *Cházaro & Reyna 4419* (IBUG, IEB); 10 km on the exit

to Nevado de Colima from Fresnito, 2,510 m, *Mendoza et al. 3817* (MEXU); Michoacán: Mpio. Los Reyes, ca. 2.5 km E of Juan Díaz, 2,750 m, *Torres 570* (IEB); Mpio. Nahuatzen, Cerro El Pilón, 2,900 m, 6 Feb 1991, *García & Pérez 3667* (IEB); Mpio. Patamban, Sirio, salida a Guarachanillo-Patamban, 2,000 m, 31 Mar 2009, *García Ruiz 8072* (CIMI, WLU); Mpio. Pueblo Nuevo Parangaricutiro, South face of Volcán Tancitaro, 2,700 m, 20 Mar 1977, *Puga et al. s.n.* (MEXU); Mpio. Tancitaro, W slopes of Volcán Tancitaro, ca. 3 km NE of El Jazmín, 2,900 m, 29 Sep 1989, *García Ruiz 2918* (CIMI, MEXU); Volcán Tancitaro, 27 km W of Uruapan, 3 km E of Paso la Nieve, 19°28'32"N, 102°20'36"W, 2,650 m, 26 Feb 1997, *García Ruiz 4542* (CIMI, IEB, UCR); 19°22'10"N, 102°21'05"W, 2,350 m, 12 Mar 1998, *García Ruiz 5108* (CIMI, IEB); Rd Tancitaro-Uruapan, 19°21'50.1"N, 102°15'26.8"W, 23 Aug 2007, *García Ruiz 7772* (CIMI, WLU); Mpio. Tangancicuaro, NW part of Cerro Patamban, 2,600–2,750 m, 18 Nov 1971, *Rzedowski & McVaugh 592* (ARIZ, ASU, IEB, MEXU, MICH); 3.5 km S of Patamban, at the base of the volcano, 2,550 m, *Torres 577* (IEB).

16. *CUSCUTA WOODSONII*—MÉXICO. Chiapas: Mpio. Motozintla, Along the Rd from Route 190 to El Porvenir, 15°27'N, 92°20'W, 2,400 m, 5 Jan 1992, *Prather & Soule 1082* (LL, MO, TEX); GUATEMALA. Dept. Chimaltenango: Reg. Santa Elena, Cerro Tecpám, 2,400–2,700 m, 26 Dec 1938, *Standley 61106* (US); Dept. Huehuetenango: Santa Eulalia, 2,800 m, 19 Nov 1999, *Véliz et al. 99.7506* (BIGUA, MO); Dept. Totonicapán: Sierra Madre Mts, 10–15 km S of Totonicapán, 2,800 m, 20 Dec 1972, *Williams et al. 41476* (F); PANAMA. Prov. Chiriquí: Volcán Chiriquí, 2,590 m, 15 Jul 1938, *Davidson 967* (F, GH, US); E slope of Volcán Chiriquí, 1,900–2,000 m, 19 Nov 1975, *Davidse & D'Arcy 10167* (MO); ca. 1,500 m, 21 Apr 1975, *Mori & Kallunki 5705* (MO); Potrero Muleto, 3,500–4,000 m, 13–15 Jul 1940, *Woodson & Schery 454* (GH); Llanos E of Volcán El Hato, 2,010–2,133 m, 5 Apr 1979, *Hammel et al. 6743, 6785* (MO); SW side of El Barú, 2,000–2,100 m, 11 Apr 1979, *D'Arcy et al. 13227* (MO); La Nivera, below Summit of El Barú, 3,100–3,200 m, 14 Mar 1979, *D'Arcy & Hammel 12484* (MO).