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Draining the Swamp Dodders: Systematics of *Cuscuta gronovii* s.l. (Subgenus *Grammica*, Sect. *Oxycarpae*)

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Abstract*—*Cuscuta gronovii* species complex (sensu lato, s.l.) is a North American group of species that belong to *C.* sect. *Oxycarpae* of subgenus *Grammica*. Members of *C. gronovii* s.l. are often associated with riparian or wet habitats, and their delimitation has been problematic historically. DNA sequences from multiple plastid and nuclear ribosomal non-coding regions were used to reconstruct evolutionary relationships among taxa. Molecular phylogeny supported the resurrection of *C. saururi*, a taxon that has been treated either as *C. gronovii* var. *latiflora* or a nomenclatural synonym of *C. gronovii* var. *gronovii*. *Cuscuta saururi* was inferred to be sister to *C. cephalanthi*, but the relationships among the rest of taxa, although forming a clade with moderate support, remained largely unresolved. Thus, the species limits of *C. gronovii* s.l. aggregate were also comprehensively investigated through a morphometric study. Plants with 4-merous flowers from New Brunswick and Nova Scotia, Canada, which were previously thought to be *C. cephalanthi*, were described as a new species, ***C. acadiana*. *Cuscuta acadiana, although fertile and producing abundant seeds, is unusual in that the majority of its pollen grains intergrade from zonocolpate, syncolpate, or pantocolpate, with variously shaped or twisted ectoapertures. *Cuscuta gronovii* var. *calyptrata*, a widely accepted but virtually unknown taxon, was typified and included in all the analyses. *Cuscuta umbrosa* was treated as a variety of *C. gronovii* (var. *curta*), and *C. rostrata* was maintained as a species. An identification key, detailed descriptions, illustrations, and a summary of geographical distribution, ecology, and conservation status were provided for all the members of *C. gronovii* s.l. The only taxon of this species complex found to be weedy, especially in cranberries, was *C. gronovii* var. *gronovii*.

Keywords—Atypical pollen grains, morphometry, new species, parasitic plants, molecular phylogeny, swamp dodder, weed.

Cuscuta gronovii Willd. sensu lato (s.l., swamp dodder, scaldweed, common dodder) is an intricate complex of taxa that is part *C.* sect. *Oxycarpae* (Engelm. ex Yunck.) Costea & Stefanović within *C.* subgenus *Grammica* (Lour.) Peter (Stefanović et al. 2007; García et al. 2014; Costea et al. 2015b). The group includes some of the most common and widespread native dodders in North America (Engelmann 1859; Yuncker 1932; Ho and Costea 2018). Although it has been reported as weedy in cranberry and carrots (e.g. Costea and Tardif 2006; Konieczka et al. 2009; Sandler 2010), *C. gronovii* s.l. is most frequently found in natural riparian habitats (Engelmann 1859; Yuncker 1932; Costea et al. 2006), where similarly to other native dodders it acts as a keystone species and an ecosystem engineer (Callaway and Pennings 1998; Press and Phoenix 2005). Despite its widespread distribution, and ecological and economical significance, *C. gronovii* s.l. is, paradoxically, little known from a systematics point of view. This has potentially negative repercussions both for weed control and the management of natural areas; for example, currently, it is not clear which of the members of *C. gronovii* s.l. is (are) weedy and which is (are) confined to natural habitats.

Cuscuta gronovii s.l. has had a complicated taxonomic and nomenclatural past, and a brief introduction of its members is necessary to understand the objectives of this study. Engelmann (1842) was not aware that *C. gronovii* had been described by Willdenow (Schultes 1820), and to account for the North American forms of what is currently considered to be "*C. gronovii* s.l.," he described two new species: *C. vulgivaga* Engelm. and *C. saururi* Engelm. Subsequently, Engelmann (1859) treated these two species as varieties of *C. gronovii: C. gronovii* var. *vulgivaga* Engelm., which he considered "Willdenow's original *C. gronovii*" (thus the autonym, var. *gronovii*), and *C. gronovii* var. *latiflora* Engelm., which he described to replace *C. saururi*. Engelmann (1859) also included in *C. gronovii* two additional varieties: *C. gronovii* var. *curta* Engelm., corresponding to *C. umbrosa* Hook., as well as a new variety, *C. gronovii* var. *calyptrata* Engelm. These four taxa: *C. gronovii* var. *gronovii* (= *C. gronovii* var. *vulgivaga*), *C. gronovii* var. *latiflora* (≡ *C. saururi*), *C. gronovii* var. *curta* (≡ *C. umbrosa*), and *C. gronovii* var. *calyptrata* represent the historical members of *C. gronovii* s.l. More recently, Yuncker preserved three of the Engelmann's varieties and deemed *C. gronovii* var. *curta* as a "good" species, using different names for it throughout time: *C. curta* Rydb. (Yuncker 1921, 1932) and *C. umbrosa* (Yuncker 1965).

Even though no revisionary study was attempted after Yuncker (1932, 1965), a great number of taxonomic schemes have been adopted, which range from accepting a broad *C. gronovii* with no varieties to essentially accepting Yuncker's taxonomy (Supplemental Table S1; Costea et al. 2023). Most often, when an infraspecific variation for *C. gronovii* was recognized, only *C. gronovii* var. *calyptrata* was accepted, while *C. gronovii* var. *latiflora* (≡ *C. saururi*) was discarded in synonymy with *C. gronovii* var. *gronovii* (Table S1). Two broad molecular phylogenetic studies, one of *Cuscuta* subgenus *Grammica* (Lour.) Peter (Stefanović et al. 2007) and one encompassing the entire genus *Cuscuta* L. (García et al. 2014), revealed some additional details. First, *C. gronovii* s.l. also includes *C. cephalanthi* Engelm. (button bush dodder), formerly placed by Yuncker (1932) in its own monospecific *C.* subsection *Cephalanthae* (Costea et al. 2015b). Second, *C. rostrata* Shuttlew. ex Engelm. & A.Gray (beaked dodder), was nested within a lineage that also included *C. gronovii* var. *gronovii* and *C. umbrosa* specimens (Stefanović et al. 2007; García et al. 2014). Therefore, in addition to the four historical taxa mentioned above, *C. gronovii* s.l., also includes *C. cephalanthi* and *C. rostrata*. These two phylogenetic studies (Stefanović et al. 2007; García et al. 2014) examined only a few specimens from within this species complex, and a more detailed sampling is necessary to cover the broad extent of biological

diversity and geographical distribution of the taxa involved. Four other species with numerous bracteoles at the base of the flowers or on the pedicels, *C. cuspidata* Engelm., *C. squamata* Engelm., *C. compacta* Juss. Ex Choisy, and *C. glomerata* Choisy, also belong to *C.* sect. *Oxycarpae* (Costea et al. 2015b), but their delimitation is not problematic.

Eighteen years ago, we began a revision of *C. gronovii* s.l. for the Flora of North America Project and initially solved the nomenclature of the four historical taxa, preserving the taxonomy of Yuncker (Costea et al. 2006; Table S1). The large volume of plant material from across North America that had to be examined, together with the substantial morphological variation encountered have considerably slowed down a resolution of this difficult group. Also, while recently re-examining herbarium specimens from New Brunswick and Nova Scotia (Canada), specimens that had been identified as *C. cephalanthi* or "intermediate between *C. cephalanthi* and *C. gronovii*," appeared to be a previously undescribed species within this complex.

Previous studies conducted in other species complexes or clades of *Cuscuta* subg. *Grammica* have proven the usefulness of a combined molecular and morphometric approach (e.g. Costea et al. 2009, 2015a, 2020; García et al. 2018). Here we follow this strategy for *C. gronovii* species complex, and the objectives of this study are to: 1) examine the evolutionary relationships among taxa based on multilocus sequences from plastid and nuclear genomes; and 2) study the morphological variation patterns of taxa by means of a morphometric study. Based on the results from these two goals, we also discuss and update the taxonomy of the *C. gronovii* species complex, including the resurrection of an old species (*C. saururi*) and the description of a new one (*C. acadiana*).

Materials and Methods

Taxon Sampling—Over 6000 herbarium specimens from approximately 100 herbaria, were identified, annotated, and examined for basic morphology, as well as host and geographical range for species in the *Cuscuta gronovii* s.l. species complex. Moreover, targeted field trips to areas of particular interest for this section in Canada and the USA were conducted between 2006–2020 to collect more herbarium material. Efforts were made to ensure sampling from localities across most of the known geographical range of each species (Yuncker 1932; Costea and Tardif 2006; Costea et al. 2006). The remaining, well-defined species of *C.* sect. *Oxycarpae*, *C. cuspidata*, *C. squamata*, *C. compacta*, and *C. glomerata*, have been studied as well and were incorporated in the molecular analyses to provide a general phylogenetic background, but only the members of the taxonomically difficult *C. gronovii* s.l. (see below) were included in the morphometric study and taxonomic treatment. A total of 200 herbarium specimens were selected for the morphometric study: 66 for *C. gronovii* var. *gronovii*; 21 for *C. saururi* (≡ *C. gronovii* var. *latiflora*); 10 for *C. gronovii* var. *calyptrata*; 36 for *C. cephalanthi*; 30 for *C. rostrata*; 14 for *Cuscuta gronovii* var. *curta* (≡ *C. umbrosa*); and 23 for *C. acadiana* (Appendix 1). Morphometric data generated in the study were deposited in Dryad (Costea et al. 2023).

A subset of up to 164 specimens was used for the molecular phylogenetic analyses, following a comprehensive "bottom-up" sampling approach. Compared to our broad-range studies including members of all sections of *C.* subg. *Grammica* (Stefanović et al. 2007; García et al. 2014), we substantially improved our population-level sampling across all taxa of *C. gronovii* s.l. and *C.* sect. *Oxycarpae* more broadly, representing the extent of their morphological diversity and geographical range. In addition to 26 DNA samples used previously, total genomic DNA was isolated from 138 newly obtained localities, obtained from additional herbarium material and field collections (Appendix 1). A more inclusive phylogenetic analysis indicated, with strong support, that the first split within *C.* sect. *Oxycarpae* occurs between *C. compacta* on one side, and the remainder of this section on the other (García et al. 2014; their Fig. 2). This agrees with our preliminary analyses including two outgroup species (*C. denticulata* Engelm. and *C. nevadensis* I.M.Johnst.) from *Cuscuta* sect. *Denticulatae* (trees not shown). Taking all of this into account, in our subsequent analyses we used individuals belonging to *C. compacta* as a functional outgroup, allowing for the full usage of all available plastid and nuclear sequence data.

Molecular Techniques—Total genomic DNA was isolated from newly obtained specimens by the modified CTAB method (Doyle and Doyle 1987) and purified using Wizard® minicolumns (Promega, Madison, Wisconsin). Double-stranded DNA fragments for the regions of interest were obtained via PCR from total genomic DNA. The plastid genome (ptDNA) region containing the *trnL* intron, 3′ *trnL* exon, and intergenic spacer between this exon and *trnF* (i.e. the *trnLF* region) was amplified using primers designed by Taberlet et al. (1991) while the *rbcL* gene was amplified using primers published by Olmstead et al. (1992). The internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) containing ITS1, 5.8S, and ITS2 (here called ITS) was obtained using primers described by Baldwin (1992). PCR reagents and conditions as well as amplicon purification followed the protocols detailed in Costea and Stefanović (2009). All cleaned PCR products were sequenced at the McGill University and Génome Québec Innovation Centre (Canada). Sequences newly generated for this study were deposited in GenBank (accession numbers OQ630551-OQ630766 and OQ645550-OQ645679; see Appendix 1).

Sequence Alignment and Phylogenetic Analyses—Sequencher 4.2 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble and edit chromatograms of complementary strands. Albeit sequences of all accessions were readily alignable in both the plastid and nuclear matrices, a number of gaps had to be introduced in the alignments. Preliminary phylogenetic analyses were conducted to explore the distribution of phylogenetic signal in the individual matrices with and without coded gaps. Neither resolution nor support was affected in a substantial way by inclusion of gaps (results not shown), and therefore gaps in the alignments were treated as missing data in subsequent analyses. Phylogenetic analyses were conducted under maximum parsimony (MP) and maximum likelihood (ML) criteria.

Parsimony searches, along with clade support estimates, were conducted for each individual matrix separately as well as for the cpDNA and combined datasets. Nucleotide characters were treated as unordered and all changes were equally weighted. In these analyses, searches for most parsimonious trees were performed with PAUP* v. 4.0b10 (Swofford 2002), using either a full heuristic approach or a two-stage strategy (Table 1). The former was conducted involving 1000 replicates with stepwise random taxon addition, tree bisection-reconnection (TBR) branch swapping, and MULTREES option on. For the two-stage approach, the analyses first involved 10,000 replicates with stepwise random taxon addition, TBR branch swapping saving no more than ten 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. Support for clades were inferred by nonparametric bootstrapping (Felsenstein 1985), using 500 heuristic bootstrap replicates, each with 20 random addition cycles, TBR branch swapping, and MULTREES option off. Conflict between datasets was evaluated by visual inspection, looking for strongly supported yet conflicting tree topologies resulting from individual data matrices

Maximum likelihood analyses were performed using RAxML-HPC2 v. 8.2.10 (Stamatakis 2014) and run on the XSEDE computing cluster using the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). MrModeltest v. 2.3 (Nylander 2004) was used to determine models of sequence evolution that fit best the individual as well as combined data (Table 1). We used the same model of sequence evolution, and 1000 rapid bootstrap replicates to assess branch support.

Morphology and Morphometric Analyses—Seven operational taxonomic units (OTUs) corresponding to *C. gronovii* var. *gronovii*, *C. gronovii* var. *calyptrata*, *C. gronovii* var. *curta* (≡ *C. umbrosa*), *C. saururi* (≡ *C. gronovii* var. *latiflora*), *C. cephalanthi*, *C. rostrata*, and *C. acadiana* were included in the morphometric analyses (Appendix 1). Previous morphometric studies within other sections of *C.* subgenus *Grammica* (Costea et al. 2009, 2015a; Costea and Stefanović 2010; García et al. 2018) provided a preliminary list of useful characters. In total, 47 characters (35 quantitative and 12 binary; Appendix 2) were formulated. New useful characters in this species complex include the flower merosity, morphology of the ovary/capsule apex, and the patterns of corolla persistence on the capsule (Appendix 2; see also Discussions).

Flowers removed from herbarium specimens were steeped in gradually warmed 50% ethanol, which was then allowed to boil for a few seconds to rehydrate tissues. An ethanol solution is more appropriate for

TABLE 1. Summary descriptions for sequences included in and trees derived from individual and combined datasets of *Cuscuta* sect. *Oxycarpae*. CI = consistency index (excluding parsimony uninformative characters); G = rate variation among nucleotides following a discrete gamma distribution; GTR = general time reversible model of DNA evolution; I = proportion of invariable sites; OTU = operational taxonomic unit; RI = retention index; RSA = random sequence addition; SYM = symmetrical model of DNA evolution; TBR = tree bisection and reconnection.

	trnLF	*rbcL*	ptDNA	nrITS	Combined
Number of OTUs included	164	92	164	148	164
Sequence characteristics:					
Aligned length	496	1461	1957	628	2585
Analyzed length	483	1280	1763	628	2391
Variable sites	23	53	76	51	127
Parsimony informative sites	20	44	64	38	102
Mean AT content (%)	63	57	59	50	57
MP search and tree characteristics:					
Algorithm	Full heuristic	Full heuristic	Two-stage heuristic	Two-stage heuristic	Two-stage heuristic
RSA/branch swapping/MULTREES	1000/TBR/on	1000/TBR/on	100,000/TBR/off; Memory/TBR/on	100,000/TBR/off; Memory/TBR/on	100,000/TBR/off; Memory/TBR/on
Number of trees	60	140	> 1,000,000	> 1,000,000	> 1,000,000
Length	31	58	90	58	157
CI/RI	0.84/0.99	0.93/0.99	0.89/0.99	0.90/0.99	0.84/0.98
ML search and tree characteristics:					
Model of DNA evolution	GTR+G+I	GTR+G	GTR+G+I	SYM+G	partitioned
-ln*L*	865.924	2165.171	3069.382	1266.599	4576.058

rehydration than water because it hardens the tissues, which are very delicate in *Cuscuta* flowers. For basic morphology, flowers were dissected under a Nikon SMZ1500 stereomicroscope and imaged with PaxCam Arc digital camera (MIS Inc., Villa Park, Illinois) equipped with a Pax-it 8.2 imaging software. Numerous photographs illustrating details of the floral and fruit morphology for all taxa, including their type collections, are made available on the Digital Atlas of *Cuscuta* website (Costea 2007). To examine the morphology of the pollen, unopened, dry anthers were squashed directly on the aluminum stubs and sputter-coated with 30 nm of gold using Emitech K550 sputter coater. Examination, imaging, and measurements were made using a Hitachi SU1510 scanning electron microscope (SEM) at 5–10 kV.

To determine the extent of morphological variation, the data were visualized with both ordination and clustering methods using PAST (version 4.4; Hammer et al. 2009). As the matrix had a mixture of discrete and continuous characters (Appendix 2) and some gaps for the capsules and seed traits, principal coordinates analysis (PCoA or metric multidimensional scaling) and unweighted pair-group average (UPGMA) were conducted using the Gower's coefficient of similarity.

Supplemental figures and tables were deposited in the Dryad Digital Repository (Costea et al. 2023).

RESULTS

Molecular Phylogenies—The characteristics of the sequenced regions as well as the statistics of the trees derived from the separate and combined analyses are described in Table 1. Several preliminary phylogenetic analyses were conducted to explore the distribution of phylogenetic signal in the different individual matrices. Clades recovered from these analyses were congruent with each other, although the resolution and levels of support differed among them. Being present on the same organellar genome, *trnLF* and *rbcL* are on the same linkage group and thus were also treated as one locus (ptDNA; Fig. S1). Given the repeated instances of reticulation within and among clades of *Cuscuta* subg. *Grammica* (Stefanović and Costea 2008; García et al. 2014) and rampant cases of this phenomenon in some of its sections (e.g. *C.* sections *Umbellatae*, *Cleistogrammica*, *Denticulatae*; Costea and Stefanović 2010; Costea et al. 2015b; García et al. 2018) we initially treated nuclear ITS as a separate marker (Fig. S2). However, phylogenies resulting from these separate analyses showed no topological incongruence, and hence we concatenated all available data into one combined dataset.

The trees produced by the combined data had better resolution and overall support relative to those derived from analyses of the individual genes/genomes. The relationships derived under the MP criterion are topologically congruent with those inferred through the ML approach and have received similar levels of support (Fig. 1). We present here only the maximum likelihood tree for the combined data (Fig. 1) and base our discussion on this phylogeny. Within *Cuscuta* sect. *Oxycarpae*, four species morphologically characterized by numerous bracteoles subtending base of their flowers or pedicels (*C. compacta*, *C. squamata*, *C. cuspidata*, and *C. glomerata*) can be delimited based on a combination of their strong individual support (≥ 85% BS) and molecular distinctiveness, as evidenced by the long branches subtending them (Fig. 1). However, their relationship to each other, and indeed the backbone relationships across the section remain poorly resolved and supported. The remainder of this section, referred to as *C. gronovii* s.l. species complex, is found to be monophyletic but with moderate support only (70% BS; Fig. 1). Within this species aggregate, *C. cephalanthi* and *C. saururi* were found to be sister species to each other and were recovered as reciprocally monophyletic, with relatively strong support (Fig. 1). The rest of taxa from this species complex are grouped together in a clade with moderate support (72% BS). However, the relationships among the species and individuals within this clade remain largely unresolved and poorly supported. Furthermore, neither *C. acadiana* (the new species described here) nor *C. rostrata* (a previously described species) were found to be monophyletic on the optimal trees in any of the individual or combined datasets (Fig. 1; Figs. S1, S2). This comes as one of the more surprising results of our study, given that both of these species are morphologically quite distinct and relatively restricted in their distribution compared to the other members of this species complex (see below). We hypothesize that this lack of resolution observed in molecular data is likely due to incomplete lineage sorting and/or introgression (Coyne and Orr 2004) in two groups that are in process of speciation from *C. gronovii*, a species that has a very large population size, is broadly distributed across continent, and sympatric with both incipient species.

Morphometric Analyses—Principal coordinates analysis (PCoA) resulted in four distinct groups of specimens (Fig. 2): one group that corresponded to *C. saururi* (≡ *C. gronovii* var. *latiflora*), one for *C. cephalanthi*, one for *C. acadiana*, and one for

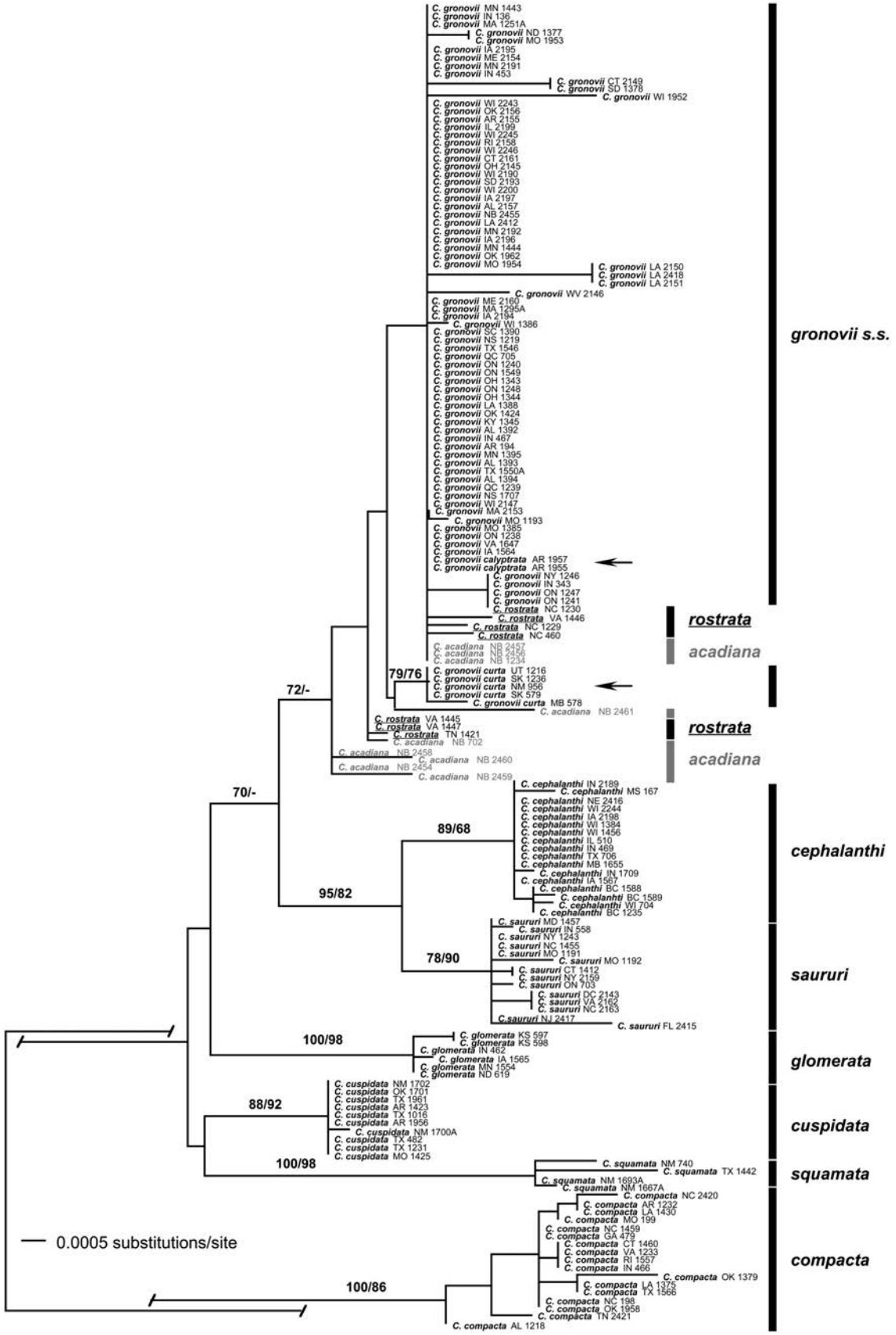

FIG. 1. Phylogram resulting from the partitioned maximum likelihood analysis of the combined plastid (*trnLF*, *rbcL*) and nuclear (nrITS) sequence data showing relationships among species of *Cuscuta* sect. *Oxycarpae*. The tree is rooted using individuals of *C. compacta* as functional outgroup. The MP search resulted in a strict consensus tree with a compatible topology. Bootstrap values (MP and ML, respectively) are indicated for nodes supported at ≥ 70%. Species names are followed by abbreviations of states/provinces in which they were collected, and their DNA accession numbers (Appendix 1). Individuals belonging to *C. acadiana* (grey), *C. rostrata* (underlined), and *C. gronovii* var. *calyptrata* (arrow) are highlighted; please see the text for further discussion.

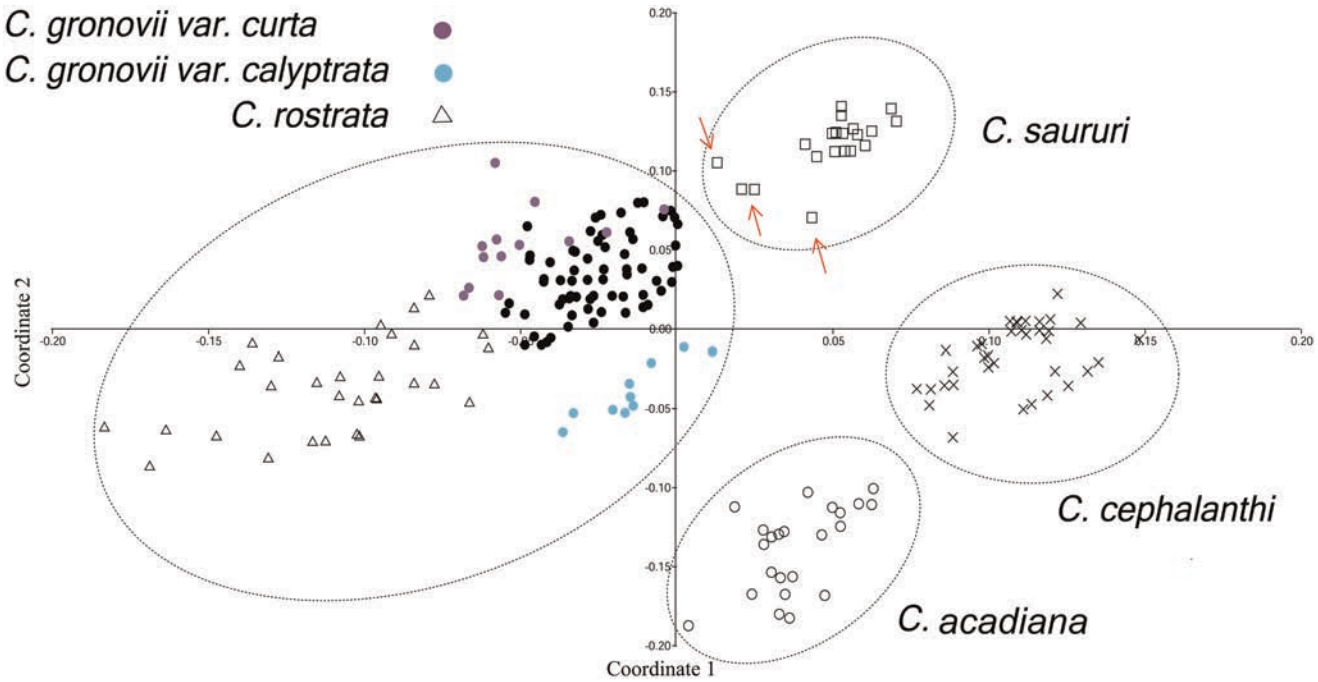

FIG. 2. Principal Coordinates Analysis (PCoA). First coordinate (33.758% of the variance) separated *Cuscuta gronovii* (including *C. gronovii* var. *gronovii*, *C. gronovii* var. *calyptrata*, *C. gronovii* var. *curta*, and *C. rostrata*) and *C. saururi*. Second coordinate (15.195% of the variation) parted *C. cephalanthi* from *C. acadiana*. Red arrows indicate specimens of *C. saururi* that superficially resemble and could be mistaken with *C. gronovii var. gronovii.*

C. gronovii var. *gronovii* together with *C.* var. *calyptrata*, *C. rostrata,* and *C. umbrosa*. Within this latter group, especially the specimens of *C. gronovii* var. *calyptrata*, and to a lesser extent those of *C. rostrata*, were separated from the amalgamated specimens of *C. gronovii* var. *gronovii* and *C. umbrosa*. The first coordinate axis accounted for 33.758% of the variance and separated *C. gronovii* (including *C.* var. *gronovii*, *C.* var. *calyptrata*, *C. umbrosa*, and *C. rostrata*) and *C. saururi* (Fig. 2). The second coordinate accounted for 15.195% of the variation and parted *C. cephalanthi* from *C. acadiana* (Fig. 2).

The UPGMA results paralleled the PCoA, but *C. rostrata* formed its own cluster (Fig. S3; cophenetic correlation = 0.8016). Also, in this visualisation, *C. gronovii* var. *calyptrata* and *C. umbrosa* formed distinct sub-clusters within the larger cluster of *C. gronovii* var. *gronovii*. Most similar to this large "gronovii" cluster was *C. saururi* followed at an increasing distance by *C. rostrata* (Fig. S3). *Cuscuta cephalanthi* and *C. acadiana* formed an even more dissimilar cluster, but were clearly separated from one another (Fig. S3).

Pollen morphology results were included in the species description.

DISCUSSION

Patterns of Corolla Persistence on the Capsule—After fertilisation, the ovary increases in size as it becomes the capsule. At the same time, the corolla dries out. Depending on the tridimensional shapes of the fresh corolla and the developing capsule, different patterns of dry corolla persistence on the capsule emerge. When the corolla tube is short, cupulate, and the capsule is spherical to depressed, as in *C. saururi*, the dry corolla persists at the base of the capsule. When the corolla is campanulate and the capsule ovoid, the dry corolla will surround the capsule and it will eventually be shed (*C. gronovii* var. *gronovii*, *C. umbrosa*, and *C. rostrata*). Finally, when the corolla is cylindrical to campanulate and the capsule spherical to globose-depressed, the dry corolla will cap the capsule, as in *C. cephalanthi*, *C. gronovii* var. *calyptrata,* and *C. acadiana*. In these latter taxa, even more subtle capping patterns can be observed. The fresh corolla of *C. cephalanthi* is narrow-campanulate to cylindrical and the capsule globose-depressed. In this species, the dry corolla resembles a tube crossed by the (persistent) styles at the top of the capsule. The fresh corolla of *C. gronovii* var. *calyptrata* and *C. acadiana* is broader, campanulate, while the capsule is ovoid to globose. In this case, the dry corolla "capping" will be less "tight" and positioned in the upper 1/2 of the capsule. A range of dry infructescences belonging to the same specimen must be examined to establish the pattern of corolla "capping." The survey of this character is best done on dry material because rehydration often causes the corolla to detach from the capsule.

Reproductive Biology of C. gronovii Species Complex—Most species of *Cuscuta* subgenus *Grammica* exhibit floral merism variation on the same plant and even within the same inflorescence (Wright et al. 2012; Costea et al. 2015b). However, each species displays a prevalence towards either 3–4-merous or 5-merous flowers. The great majority of species within *C.* subg. *Grammica* (and the genus *Cuscuta* more broadly) have mostly 5-merous flowers (Costea et al. 2015b). Species with preponderantly 3–4-merous flowers evolved multiple times in multiple clades of *C.* subgenus *Grammica* (Wright et al. 2012). Within *C. gronovii* s.l. and *C.* sect. *Oxycarpae* more broadly, 3–4-merous flowers evolved independently two times: in *C. acadiana*, within the lineage of *C. gronovii*, and in C. *cephalanthi* within the sub-clade that also includes *C. saururi.* The functional significance of merism reduction has not been studied, but it is likely associated with a decrease of pollen production, which in the context of a constant number of four ovules per ovary, may balance the

breeding systems towards selfing, thereby increasing reproductive assurance. Wright et al. (2012) reported that *C. cephalanthi* had the lowest pollen/ovule ratio (261.5) within this species complex, while *C. rostrata* and *C. gronovii* var. *gronovii* had the highest values (1290 and 1132, respectively). *Cuscuta rostrata* flowers are fragrant (Musselman 1986), exhibit numerous nectaries at the base of the ovary (Wright et al. 2012), and were unable to produce selfed seeds when artificially pollinated (McNeal et al. 2007). Very few of the examined herbarium specimens of *C. rostrata* possessed mature capsules and seeds, while in contrast, most of the *C. cephalanthi* specimens had them (see the gaps in the original dataset, Dryad; Costea et al. 2023). Similarly, most of *C. acadiana* herbarium specimens possess mature capsules and seeds. Indehiscent capsules can float for more than a month, and the seeds for more than a week (Ho and Costea 2018). Endozoochory by waterfowl is also a strong possibility of long-distance dispersal in this complex of species (Costea et al. 2016; Olszewski et al. 2020).

Taxonomic Treatment

The taxonomic changes proposed by this study supersede the upcoming taxonomic treatment of *Cuscuta* in volume 14 of *Flora of North America* (FNA; Costea and Nesom in press) whose publication has been delayed for multiple years. The first *Cuscuta* FNA draft was submitted in 2006; the last updates were made in 2017, and galleys were sent in April 2020 when these results were not available. For complete synonymy of all taxa see Yuncker (1932, 1965) and Costea et al. (2006).

What is Cuscuta acadiana?—A surprise of this study was the discovery that the plants previously thought to be *C. cephalanthi* in the Canadian Maritime Provinces, New Brunswick and Nova Scotia (Roland and Smith 1969; Hinds 2000; Munro et al. 2014; Costea and Nesom in press) were in fact an unknown member of the *C. gronovii* species complex. The confusion with *C. cephalanthi* was possible because its flowers are also (3–)4-merous and the corolla is capping the capsule. Although molecularly indistinguishable from *C. gronovii* (together with *C. umbrosa* and *C. rostrata*), *C. acadiana* was resolved as a species-distinct group/cluster by the morphometric analyses. A peculiarity of this species is the prevalence of pollen grains with irregular apertures (see the species description), which in other angiosperms were associated with hybridization and polyploidy (e.g. Ockendon 1971; Karlsdóttir et al. 2008; Reeder et al. 2016). Such "irregular" pollen grains were reported with a low frequency throughout the genus (Welsh et al. 2010), but none of the hybrid, allopolyploid species of *Cuscuta* (e.g. *C. veatchii*, *C. psorothamensis*; García et al. 2018) exhibited the prevalent pollen aperture irregularities observed in this new species. Although we did not study the pollen fertility, based on the herbarium specimens examined, C. *acadiana* produces abundant seeds. The embryology and cytogenetics of *C. acadiana* need to be studied in the future to determine the origin of these pollen forms.

Resurrection of Cuscuta saururi—Engelmann described *C. saururi* (1842) but later, without providing an explanation, changed its taxonomic status as a variety of *C. gronovii* (*C. gronovii* var. *latiflora*) (Engelmann 1859). Subsequently, Yuncker (1921, 1932, 1965) and Costea et al. (2006) preserved the varietal status of this taxon indicating the occurrence of intermediates to *C. gronovii* var. *gronovii*. Given the morphological closeness of *C. saururi* to *C. gronovii* var. *gronovii*, some specimens may appear as intermediate if examined superficially (e.g. without rehydration, floral dissection and measurements). This is especially true for specimens of *C. saururi* with larger flowers and longer corolla tube, which resemble indeed *C. gronovii* var. *gronovii* (e.g. *Musselman & Knepper s.n.*, ODU; *Weatherby & Driggs* s.n. CONN; *Moldenke 21598* SMU). However, when complete samples (flowers and fruits) were rehydrated, dissected, and closely analyzed/measured, all the specimens of *C. saururi* and *C. gronovii* var. *gronovii* separated into species-distinct groups/clusters. This reinforces the necessity to rehydrate, dissect and closely examine *Cuscuta* flowers/fruits in difficult species complexes in order to ensure high confidence for the identity of the material examined.

The acceptance of *C. saururi* in practice will be met with more resistance than that of more "popular" dodders in this species complex (e.g. *C. rostrata*, *C. gronovii* var. *calyptrata*), and its reintegration in practice will be more difficult in the North American regional floras that have discarded *C. gronovii* var. *latiflora* in synonymy with *C. gronovii* var. *gronovii* (Table S1). However, the recognition of *C. saururi* is necessary to reflect its evolutionary history and morphological dissimilarity. The morphological characters provided in the identification key, in the description, and illustrations, should allow its unequivocal morphological identification if flowers and capsules are present. The difficulties in the identification of *C. saururi* are much reduced compared to the near-cryptic dodders recently discovered in other clades of *C.* subg. *Grammica* (e.g. *C. psorothamnensis* in *C.* sect. *Denticulatae*, García et al. 2018; *C. difficilis* in *C.* sect. *Californicae*, Costea et al. 2020).

Typification and Taxonomic Status of C. gronovii var. calyptrata—It is interesting to contrast the widespread abandonment of *C. saururi*, for which numerous annotated herbarium specimens (both historical and modern) are available in many herbaria, with the prevalent recognition of *C. gronovii* var. *calyptrata*, which is a virtually unknown taxon for which no (correctly) annotated specimens could be found.

Engelmann (1859) did not cite particular herbarium specimens in the protologue; just mentioned their general locality and collector: "Western Louisiana, Gregg" and "Texas, Lindheimer." Yuncker also repeated the protologue information without indicating any specimens [1921: "Louisiana Gregg, in the Engelmann Herb"; 1932: "Western Louisiana, Gregg (in the Herbarium of the Missouri Botanical Garden)]". Wolf (1988), in a synopsis of Engelmann's types at MO, reiterated the same information. Therefore, this taxon needs lectotypification. There are three possible *Gregg s.n.* syntypes (art. 9.6; Turland et al. 2018) at MO. Although their labels are slightly different, they are most likely part of the same plant gathering (Turland et al. 2018) that was made by (Dr.) Josiah Gregg from Red River bottoms, Shreveport on 28 September 1847. The American explorer and naturalist sporadically lived in or visited Shreveport in western Louisiana, where his brother, John Gregg, resided (Ruffin 1973). The exploration of the Red River, which passes through Shreveport, was detailed by Gregg in a letter he sent to Engelmann on 24 Nov 1847 from New Orleans (Lee 1931). Gregg sent a part of the collected plant material to Engelmann in Saint Louis, and a part to Charles W. Short in Louisville, Kentucky. Of the plant material sent to St. Louis, two herbarium sheets were mounted, and Engelmann identified one as *C. tenuiflora* (MO, 2758365), a synonym of *C. cephalanthi*, and the other one as "*Cuscuta gronovii*? *Cuscuta tenuiflora*?" (MO, 2757269). Charles W. Short eventually sent his material to Engelmann, which remained identified in the herbarium of the latter author as "*Cuscuta*?" . Although none of

these specimens were labeled or annotated as *C. gronovii* var. *calyptrata*, we think this is the "Western Louisiana, Gregg" plant that Engelmann had in mind. The author wrote on the label of MO 2757269: "pentandrous: questionable whether the corolla is not calypt. […] on top of capsules. Flowers pentandrous. An intermediate form" [between C. *gronovii* and *C. cephalanthi*]. The second specimen (MO 7758365) also indicates "flowers 5-parted". Engelmann must have subsequently reconsidered these *C. gronovii*-looking specimens with calyptrate corolla on the capsule (like *C. cephalanthi*), as a different taxon, *C. gronovii* var. *calyptrata*, but did not update the specimen labels (or if new labels were added, they were lost). We included these three specimens in the morphometric analyses, and they were very similar indeed. As there are no other possible Gregg specimens in Engelmann's herbarium, we selected MO 2757269 as a lectotype for *C. gronovii* var. *calyptrata*. The other two sheets, MO 7758365 and MO 2758486, although bearing slightly different labels, can be considered isolectotypes because as indicated above, they are most likely parts of the same gathering divided by Gregg and sent to Engelmann and Short. Alternatively, the selection of a *Lindheimer* specimen as a lectotype is also possible, but in this case at least six specimens collected in 1841,1842, and 1844 from Texas are available. Among these, only one was annotated by Engelmann as "*Cuscuta* var. *calyptrata*": "Texas, Coll. F. Lindheimer 1844" (MO 2758814!), but this specimen consists only of two dissected flowers glued on a small piece of paper. We included five of these specimens in the morphometric analysis (Appendix 1) and they grouped together with the *Gregg s.n.* specimens, indicating they are also *C. gronovii* var. *calyptrata*.

Cuscuta gronovii var. *calyptrata* has received widespread and uninterrupted taxonomic acceptance (Table S1), and it was even treated as a species, *C. calyptrata* (Small, 1903; in Flora of the Southeastern United States). This suggests a mature taxon with established geographical distribution, biology, and ecology. This is far from the reality! *Cuscuta gronovii* var. *calyptrata* remains the most mysterious member of *C. gronovii* species complex. Despite its inclusion in numerous floras (Table S1), there are no annotated specimens in the Engelmann and Yuncker collections or in other herbaria. The only herbarium specimen we previously considered to be *C. gronovii* var. *calyptrata* and included in molecular phylogenetic studies (Stefanović et al. 2007; García et al. 2014), *Cory 52529* (TEX/LL), proved to be at a closer examination *C. cephalanthi*. The current study rectifies this error and shows that *C. gronovii* var. *calyptrata* is closely allied to *C. gronovii*.

Taxonomic Status of C. rostrata and C. umbrosa—*Cuscuta rostrata* is one of the most recognizable North American dodders because of its large flowers and the beaked ovary/capsule (Engelmann and Gray 1845; Yuncker 1921, 1932). The species grows in the Allegheny Mountains from Virginia to Tennessee, and its species status has not been questioned. Both the morphometric and the molecular results strongly suggest that this taxon is closely allied to *C. gronovii* s.s. and would be perhaps best recognized as one of its varieties. However, considering its continuous and unchallenged recognition, we have retained the specific status for *C. rostrata*. *Cuscuta umbrosa* formed a moderately supported lineage within the *C. gronovii* s.s. clade (Fig. 1), but it was more similar morphologically to this taxon compared to *C. rostrata* (Fig. 2). *Cuscuta umbrosa* has been treated in the past as a variety of *C. gronovii*, and this is likely the most appropriate status for this taxon.

Key to species of *Cuscuta gronovii* species complex

For identification keys and descriptions of the other members of *Cuscuta* sect. *Oxycarpae* (*C. cuspidata*, *C. squamata*, *C. compacta*, and *C. glomerata*) see Yuncker (1932, 1965); Costea and Nesom (in press).

1. Numerous bracteoles similar to the calyx lobes present at the base of flowers or on the pedicels. . . . *C. cuspidata, C. squamata, C. compacta, C. glomerata*
1. Bracteoles at the base of flowers or on pedicels absent or 1–2. . . . 2
   2. Ovary and capsule with a beak (rostrum) at the base of styles, 1–1.5 mm long. . . . *C. rostrata*
   2. Ovary and capsule raised and thickened around the interstylar aperture, but without a beak (rostrum). . . . 3
      3. Flowers mostly 3–4-merous. . . . 4
         4. Flowers (3.8–)4–4.6 mm long; at least 2 calyx lobes are acute; corolla (3.3–)3.8–4.3 mm long, tube (2.2–)2.5–2.8 mm long, broadly campanulate; capsules ovoid to globose; seeds 1.7–2.3 × 1.7–2.2 mm. . . . *C. acadiana*
         4. Flowers 2.2–3 mm long; all calyx lobes are rounded or obtuse; corolla 2–2.9 mm long, tube 1.2–2 mm long, cylindric-campanulate to cylindric; capsules depressed-globose to globose; seeds 1.2–1.7 × 1.2–1.8 mm. . . . *C. cephalanthi*
      3. Flowers mostly 5-merous. . . . 5
         5. Flowers 2.3–3.1 mm long; calyx ca. as long as the corolla tube or slightly shorter, lobes oblong-ovate, not overlapping basally; corolla 2.2–2.7(–3) mm long, tube 0.8–1.5(–2) mm long, broadly campanulate to cupulate; infrastaminal scales longer than the corolla tube; capsules surrounded by the withered corolla in the lower 1/2. . . . *C. saururi*
         5. Flowers 3–4.5 mm long; calyx ca. reaching the middle of the corolla tube, lobes ovate to suborbicular, basally overlapping; corolla 3–4.4 mm long, tube (1.7–)2–2.5(–2.8) mm long, campanulate, infrastaminal scales shorter than the corolla tube to nearly reaching filament bases; capsules 3/4 surrounded by the withered corolla or capped in the distal 1/2 by it. . . . *C. gronovii s.s.*

1. ***Cuscuta acadiana*** Costea and Stefanović, sp. nov. Type: Canada. New Brunswick. Kouchibouguac National Park (46°42′09″–46°57′43″N; 64°47′25″– 65°02′53″W). Kent Co.: Carleton St., Charles St., St. Louis Parish, 2.6 mi into Park on Cap St. Louis R. E., 275 yds along shore past gate, growing on *Convolvulus sepium* and *Aster* sp., *Convolvulus* was being killed, a large patch present, "UTM 541811," 09 Sep 1977, *Munro & Cody 1786* (holotype: UNB!; isotypes: ACAD!, DAO!, GH).

Cuscuta acadiana resembles *C. gronovii* var. *calyptrata* in the morphology of the corolla and capsule (including corolla capping the capsule), but differs in the presence of numerous 3–4-merous flowers with atypical pollen grains. It is also similar to *C. cephalanthi*, but flowers are larger, (3.8–)4–4.6 mm long. From both *C. gronovii* (all varieties) and *C. cephalanthi* it contrasts in the presence of at least two calyx lobes that are acute to subacute, ovate triangular to lanceolate.

Stems medium, yellow to orange. **Inflorescence** paniculiform to glomerulate; **pedicels** (0.5–)1–2.1 mm long; **bracts** 1 at the base of cymes, ovate-triangular, membranous, margins entire or serrulate, apex acute to obtuse; bracteoles 1, often at the base of flowers, similar to calyx lobes. **Flowers** 3–4-merous (a few 5-merous flowers may be present), (3.8–)4–4.6 mm long, white-creamy when fresh, light brown when dried. **Laticifers** ± visible, translucent in the calyx, corolla, and ovary, isolated, round to ovoid. **Calyx** 1.7–2.4 mm long, fleshy, not reticulate, not glossy, cupulate, ca. 3/4 as long as the corolla tube, divided 3/4 to nearly to the base, tube 0.2–0.5 mm long, lobes 1.5–2.1 mm, ovate-triangular to lanceolate, at least 2 lobes acute to subacute, the rest acute to obtuse, not or only slightly overlapping basally, margins serrulate; **corolla** (3.3–)3.8–4.3 mm long, tube (2.2–)2.5–2.8 mm long, broadly campanulate, lobes (1.2–)1.4–1.7 mm long, shorter than the tube corolla tube, initially erect, later spreading to reflexed; ovate-triangular, margin entire to serrulate, apex rounded, slightly cucullate; **stamens** exserted, shorter than corolla lobes; anthers 0.5–0.7 mm long, elliptic to oblong, filaments 0.4–0.8 mm long. **Pollen** 30–41 μm long, polymorphic within the same anther, > 90 of pollen grains deviate sharply from the typical 3(–4) zonocolpate of other species in the different number of apertures (2–9), as well as their arrangement, position, orientation, and shape. A huge number of "types" could be described as transitions or variations from zonocolpate, syncolpate or pantocolpate, with variously shaped or twisted ectoapertures (Fig. 4F–U); typical 3-zonocolpate are rare or absent; when present, their apertures are S-twisted; tectum usually perforate with puncta 0.2–1.2 μm in diameter, rarely imperforate with a few puncta or approaching micro-reticulate); sexine scabrate usually with isolated granule. **Infrastaminal scales** 2–2.6 mm long, equalling the corolla tube, ovate to oblong, rounded, bridged at 0.4–0.8 mm, fimbriae 0.4–0.9 mm long; **styles** cylindrical, 1.8–2.6 mm long; stigmas capitate, globose. **Capsules** 3–3.6 × 3–4.2 mm, indehiscent or irregularly dehiscent, ovoid to globose, thickened and raised at the top, interstylar opening relatively small, capped by the withered capsule. **Seeds** 2–3 per capsule, 1.7–2.3 × 1.7–2.2 mm, dorsoventrally compressed to obscurely angled, broadly-ovate to round; hilum subterminal, subrotund, 0.5–0.7 mm in diameter, vascular scar of funiculum linear, 0.20–0.40 mm long, vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate when hydrated. **2*n*** =? Figs. 3, 4F–U.

Etymology—From "Acadia" (French "Acadie"), historical region in northeastern North America including the Maritime Provinces of Canada, referring to the approximative distribution of the species. Acadia may be derived from "Arcadia" (or "Arkadia"), a real region or mythical realm in Greece, used to convey the idea of an idyllic, pristine place. It may also be derived from the Mi'kmaq language, in which "Cadie" means "fertile land" (Landry and Lang 2001).

Distribution and Ecology—Canada—New Brunswick and Nova Scotia where it is sympatric with *C. gronovii* var. *gronovii*. A more detailed search in the field and local herbaria may also reveal its presence in neighboring Atlantic United States such as Maine and Massachusetts. The species grows in moist meadows and alder swales above hightide, barrier beaches, salt and brackish marshes, often on a gravelly substrate. The most common hosts are *Symphyotrichum novi-belgii* (L.) Nesom and *Calystegia sepium* (L.) R.Br., followed by *Lycopus uniflorus* Michx., *Viburnum cassinoides* Willd., *Solidago sempervirens* L., *Betula populifolia* Marshall, *Pteridium aquilinum* (L.) Kuhn., and *Vaccinium* sp.

Conservation Status—Based on the conservation status of *C. cephalanthi* reviewed by NatureServe (2023) for New Brunswick and Nova Scotia, *C. acadiana* is Imperilled (S2). The collectors of the available herbarium specimens often noted a reduced abundance of the species at the collection sites.

2. CUSCUTA CEPHALANTHI Engelm., Amer. J. Sci. Arts 43: 336, plate 6, Figs. 1–6. 1842. LECTOTYPE (Yuncker 1921): "n.sp. [U.S.A.] Missouri, St. Louis, Sep 1841, *Engelmann s.n.*" (MO, the left specimen!).

Note: Yuncker (1921) did not indicate "n. sp" or "Sep" in the type information, but this is the only possible specimen that the author could have referred to. There are multiple other Engelmann specimens at MO that can be considered syntypes: one collected by Engelmann in 1838 and three collected in Sep 1841; all of them have more elaborate labels that also include the host and sometimes habitat information (Fig. 5P–X).

= *Cuscuta tenuiflora* Engelm. in Gray Manual of Botany: 350. 1848.

Note: One year after the description of *C. cephalanthi*, Engelmann (1843) expressed regret for his choice of the specific epithet which implied that the species was confined to *Cephanthus* as a host, and indicated the intention to change the name to *C. tenuiflora*. The name change took place in Gray (1848) without an indication of specimens, but since the author clearly stated that *C. tenuiflora* is a name replacement, a lectotype is not necessary. Also in 1859, while maintaining *C. tenuiflora* as a synonym of *C. cephalanthi*, Engelmann enumerated multiple herbarium specimens among which he noted "Missouri and Illinois, Engelmann!", therefore including type material of *C. cephalanthi*.

Stems yellow-orange, medium. **Inflorescences** dense to loose, glomerulate to paniculiform, sometimes confluent; bracts at base of clusters 1–2, bracteoles at base of pedicels and/or flowers 0–1, ovate, membranous, margins entire or serrulate, apex obtuse to acute. **Pedicels** 0.4–1.1 mm long. **Flowers** 3–4-merous (but a few 5-merous flowers can be present), 2.2–3 mm long, white-cream when fresh, brown when dried. **Laticifers** ± visible, translucent in the calyx, corolla, and ovary, isolated, round to ovoid. **Calyx** 1.1–1.5(–1.8) mm long, fleshy, not reticulate, not glossy, cupulate, ca. 1/2 length of corolla tube, divided ca. 4/5 its length, tube 0.1–0.4 mm long, lobes 0.9–1.5 mm long, oblong-ovate, rounded to obtuse, slightly overlapping at base, margins serrulate; **corolla** 2–2.9 mm long, tube 1.2–2 mm long, cylindric-campanulate to cylindric, lobes 0.7–1.1 mm long, shorter than the tube corolla tube, initially erect, later remaining mostly erect or just spreading; ovate, margin entire to serrulate, apex rounded, bent inwards, cucullate; **stamens** exserted, shorter than corolla lobes; anthers 0.25–0.5 mm long, elliptic to oblong, filaments 0.2–0.5 mm long; **pollen** 3-zonocolpate, 26–32 μm long, subprolate to prolate; tectum perforate with puncta 0.2–0.5 μm in diameter; sexine scabrate with isolated granules; **infrastaminal scales** 1.3–2 mm long, equaling the corolla tube, ovate to oblong, rounded, bridged at 0.2–0.4 mm, fimbriae 0.1–0.4 mm long; **styles**, 0.5–2 mm long; stigmas capitate, globose. **Capsules** 2–2.8 × 2.2–4 mm, indehiscent or irregularly dehiscent, depressed-globose to globose, thickened and raised at

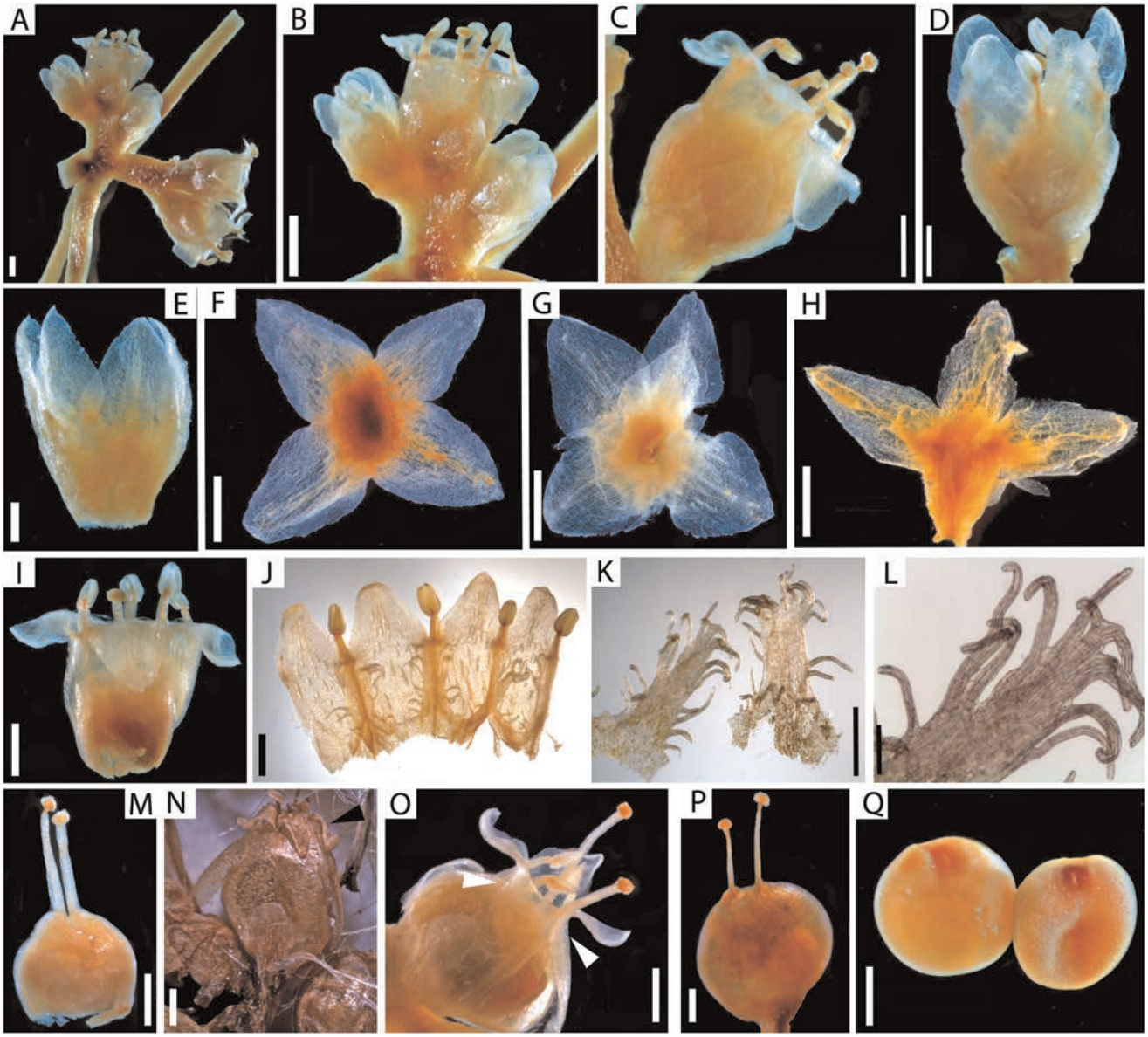

FIG. 3. Morphology of *Cuscuta acadiana*. A. Inflorescence fragment. B. Monochasial cyme. C–D. Flowers. E. Calyx 3D. F–H. Dissected calyx, variation (note that at least some calyx lobes are acute or subacute). I. Corolla 3D. J. Dissected corolla. K–L. Details of infrastaminal scale. M. Gynoecium. N. Capsule (not hydrated) capped by persistent corolla. O. Hydrated corolla capped by persistent corolla (indicated with arrow). P. Capsule after removal of corolla. Q. Seeds present within a capsule. Scale bars = 1 mm, except K = 0.5 mm; L = 0.3 mm.

the top, interstylar opening relatively small, capped by the withered capsule. **Seeds** 1–2 per capsule, 1.2–1.7 × 1.2–1.8 mm, dorsoventrally compressed to obscurely angled, broadly-ovate to round; hilum subterminal, subrotund, 0.4–0.6 mm, vascular scar of funiculus linear, 0.15–0.25 mm long, vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate when hydrated. ***2n*** = 60 (García et al. 2019; Ibiapino et al. 2022).

Distribution and Ecology—Canada—Alberta, British Columbia, Manitoba, Ontario, Quebec. **USA:** Arizona, Arkansas, California, Connecticut., District of Columbia, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Massachusetts, Michigan, Minnesota, Nebraska, Nevada, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Utah, Virginia, Washington, Wisconsin. As previously indicated, plants considered to be *C. cephalanthi* in New Brunswick and Nova Scotia (Roland and Smith 1969; Hinds 2000; Munro et al. 2014; Costea and Nesom in press) belong to *C. acadiana*. *Cuscuta cephalanthi* grows on margins of streams, lake shores, marshes, and floodplain forests at elevations up to 1500 m; it flowers from June to October. The most common hosts are species of *Achillea* L., *Boehmeria* Jacq., *Campsis* Lour., *Cephalanthus* L., *Cirsium* Mill., *Decodon* J.F.Gmel., *Eurybia* (Cass.) Cass., *Hypericum* L., *Ilex* L., *Iva* L., *Justicia* L., *Lycopus* L., *Lysimachia* L., *Lythrum* L., *Mentha* L., *Persicaria* (L.) Mill., *Physostegia* Benth., *Potentilla* L., *Pycnanthemum* Michx., *Salix* L., *Saururus* L., *Scutellaria* L., *Solanum* L., *Solidago* L., *Spiraea* L., *Symphyotrichum* Nees, *Teucrium* L., *Toxicodendron* Mill., *Tradescantia* L., *Vernonia* Schreb., and *Vicia* L.

Conservation Status—The species is Secure globally but was assessed as Imperiled (S2) in Ontario, Pennsylvania, and Kansas, and Critically Imperiled (S1) in Manitoba, New Jersey, New York, Vermont, Virginia, as well as North and

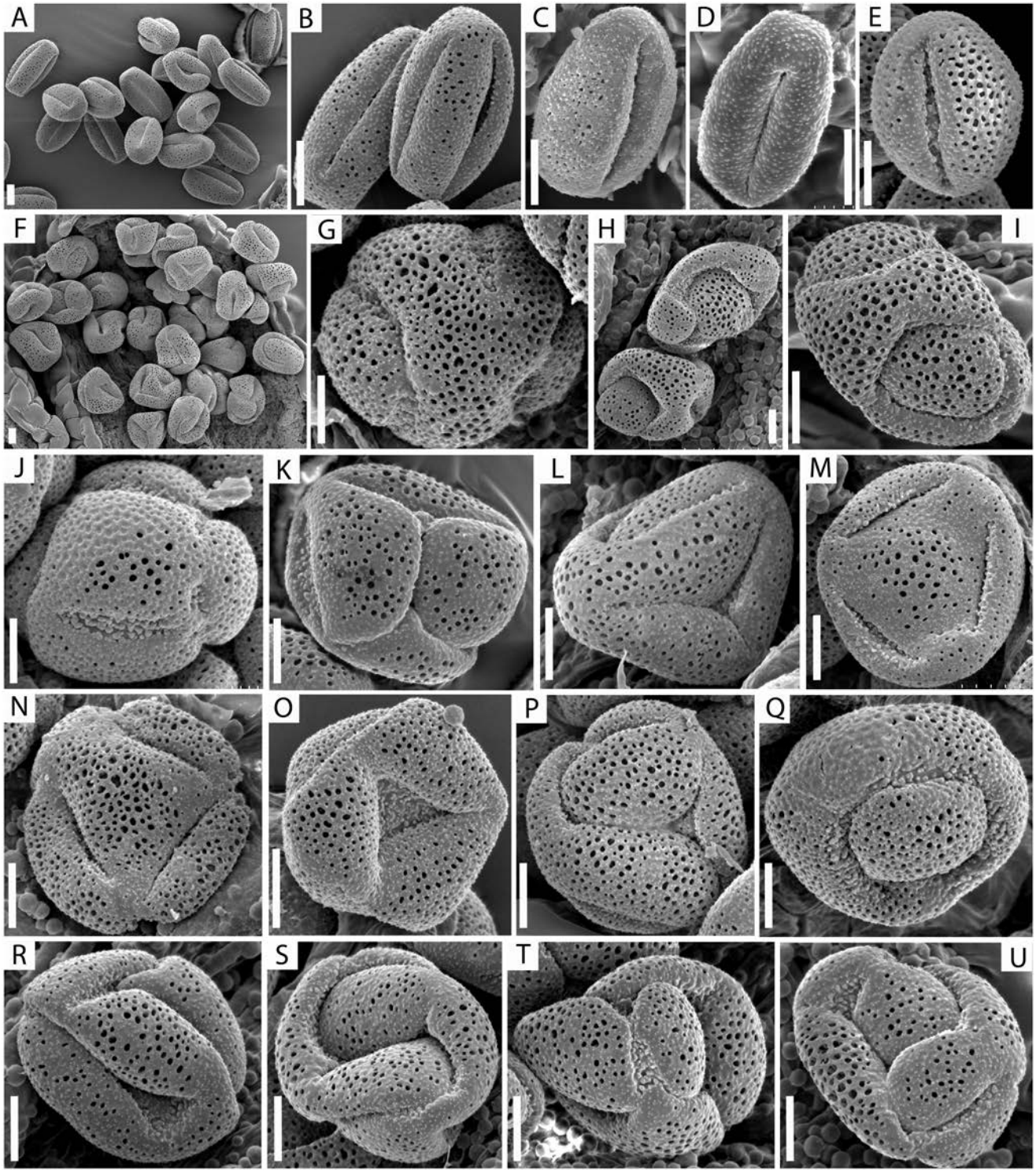

FIG. 4. Morphology of pollen. A. *C. gronovii* var. *gronovii*. B. *C. gronovii* var. *curta*. C. *C. gronovii* var. *calyptrata*. D. *C. saururi*. E. *C. rostrata*. F–U. *C. acadiana*. Majority of pollen grains are "irregular" and vary from zonocolpate, syncolpate, or pantocolpate, with variously shaped or twisted ectoapertures.

South Carolina (reviewed by NatureServe 2023). It has also been recently reported from Quebec where it is known only from one herbarium specimen (Burt et al. 2021).

3. CUSCUTA GRONOVII Willd. ex Roem. & Schult., Syst. Veg. 6: 205. 1820. TYPE (Yuncker 1943): North America, unspecified locality, *Willdenow 3160–10* (B!).

Stems medium, yellow to orange. **Inflorescence** loose or dense, paniculate, sometimes confluent; **pedicels** 0.75–2.2 mm long; **bracts** 1 at the base of cymes, rarely with 1(–2) bracteoles on the pedicels (bracteoles at the base of flowers are always absent), ovate to triangular, membranous, margins entire or serrulate, apex acute to obtuse. **Flowers** 5-merous

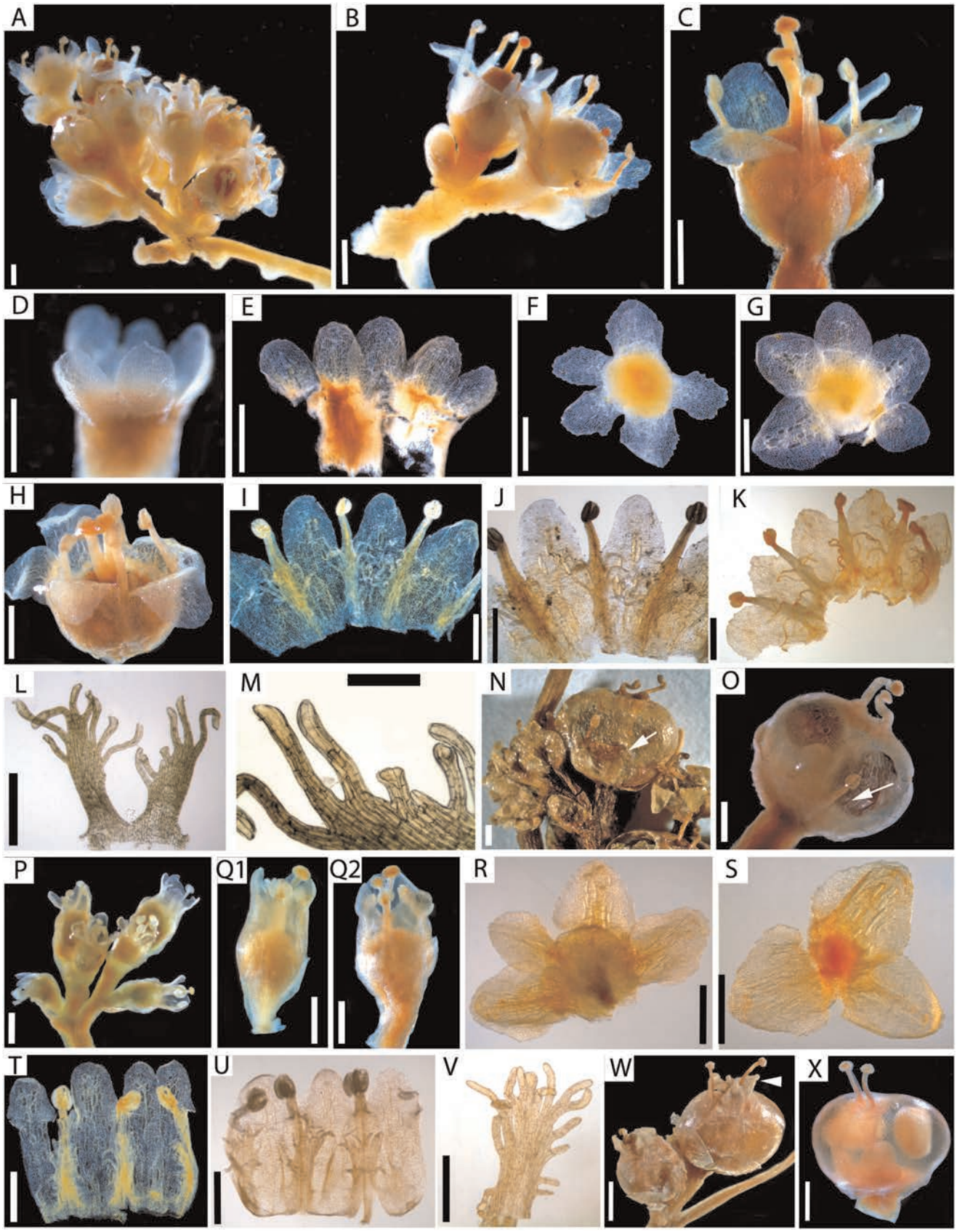

FIG. 5. Morphology of *Cuscuta saururi* and *C. cephalanthi*. A–O. *Cuscuta saururi*. A. Inflorescence. B. Flowers. C. Flower. D. Calyx 3D. E–G. Dissected calyx; variation. H. Corolla, 3D. I–K. Corolla, dissected; variation. L–M. Infrastaminal scales, details. N. Capsule, not hydrated. O. Capsule, hydrated. Note the persistent corolla at the bottom of capsule (indicated by arrows). P–X. *Cuscuta cephalanthi*. P. Inflorescence. Q1–Q2. Flowers. R–S. Dissected calyx, variation. T–U. Dissected corolla. V. Infrastaminal scale, detail. W. Capsule, not hydrated (note the persistent corolla topping the capsule). X. Capsule, rehydrated and corolla removed. Scale bars = 1 mm, except L, V = 0.5 mm; M = 0.3 mm.

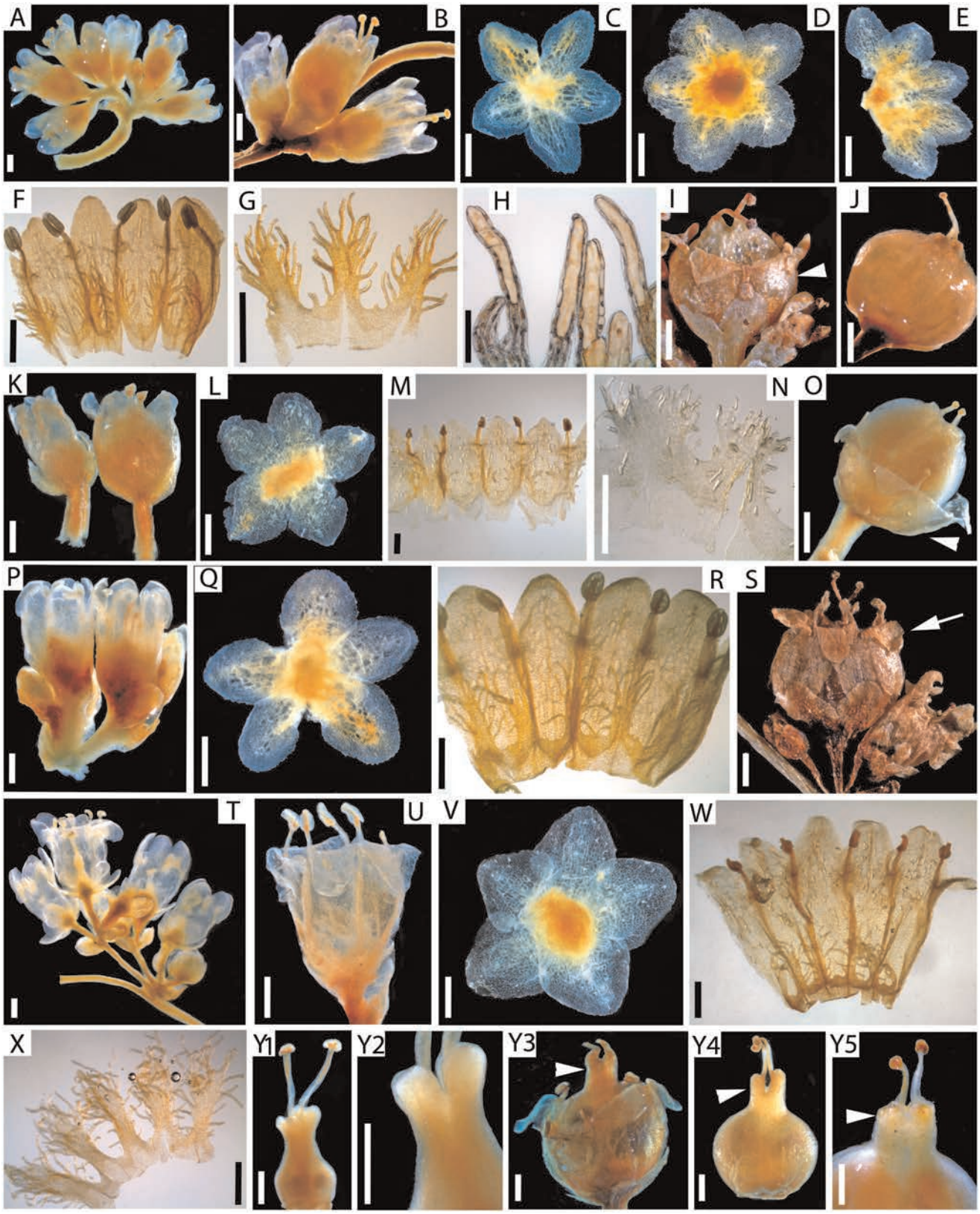

FIG. 6. Morphology of *Cuscuta gronovii* and *C. rostrata*. A–S. *C. gronovii*. A–J. *C. gronovii* var. *gronovii*. A. Inflorescence. B. Flowers. C–E. Dissected calyx, variation. F. Corolla, dissected. G. Infrastaminal scales removed from the corolla. H. Detail of infrastaminal scale fimbriae with laticifers. I. Capsule (not hydrated) surrounded by corolla (indicated with arrow). J. Capsule, hydrated and without corolla). K–O. *C. gronovii* var. *curta*. K. Flowers. L. Dissected calyx. M. Dissected corolla. N. Infrastaminal scales. O. Capsule (hydrated), surrounded by corolla (indicated with arrow). P–S. *C. gronovii* var. *calyptrata*. P. Flowers. Q. Dissected calyx. R. Dissected corolla. S. Capsule (not hydrated), capped by corolla (indicated by arrow). T–Y5. *C. rostrata*. T. Inflorescence. U. Flower. V. Dissected calyx. W. Dissected corolla. X. Infrastaminal scales removed from corolla. Y1, Y2. Ovary. Y3–Y5. Capsule (arrows indicate beak). Y3. Surrounded by corolla. Y4. Corolla removed. Y5. Detail of beak and styles. Scale bars = 1 mm, except G, N, X = 0.5 mm; H = 0.2 mm.

(but a few 4-merous flowers are possible within the same cyme), 3–4.5 mm long, white-cream when fresh, light brown when dried. **Laticifers** ± visible, translucent in the calyx, corolla, and ovary, isolated, round to ovoid. **Calyx** 1.4–2.5 mm long, fleshy, not reticulate, not glossy, campanulate, reaching to ca. the middle of the corolla tube, divided ca. 3/5–4/5 to the base, tube 0.3–0.7 mm long, lobes (0.8–)1–1.7 mm, ovate to suborbicular, apex rounded or obtuse, basally overlapping, margins entire to serrulate; **corolla** 2.9–4.4 mm long, tube (1.7–)2–2.5(–2.8) mm long, campanulate, lobes 1–1.6 mm long, shorter than the tube corolla tube, initially erect, later spreading to reflexed; ovate, margin entire to serrulate, apex rounded, straight; **stamens** exserted, shorter than corolla lobes; anthers 0.4–0.8 mm long, elliptic to oblong, filaments 0.5–1 mm long; **Pollen** 3(–4)-zonocolpate, 18–36 μm long, from spheroidal to perprolate (subprolate and prolate being the most frequent); tectum imperforate with a few puncta, rarely tectum perforate with puncta 0.3–0.6 μm in diameter; sexine scabrate usually with isolated granules; **infrastaminal scales** (0.5–)1.8–2.6 mm long shorter than the corolla tube to nearly reaching filament bases, oblong or broadly-oblong, rounded or truncate and bifid, bridged at 0.5–1 mm, fimbriae 0.4–0.9 mm long; **styles** distinct, cylindrical, 0.1–1.5(–1.8) mm long; stigmas capitate, globose. **Capsules** 3–4.5(–5.2) × 2.7–4 mm, indehiscent or irregularly dehiscent, globose, ovoid to globose-conic or subobpyriform, thickened and raised at the top, interstylar opening relatively small, sometimes with a short and broad but discernible neck, surrounded or capped by the withered corolla. **Seeds** 2–4 per capsule, 1.2–1.7(–2.4) × 1.2–1.6(–2), dorsoventrally compressed to obscurely angled, subrotund to broadly-ovate; hilum subterminal, subrotund, 0.4–0.5 mm, vascular scar of funiculum linear, 0.18–0.25 mm long, vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate when hydrated. Figures 4A–C, 6A–S.

KEY TO VARIETIES OF *C. GRONOVII*

1. Infrastaminal scales 1/2–1/3 as long as the corolla tube, apex truncate to bilobed; styles 0.1–0.7 mm long. . . . . b. *C. gronovii* var. *curta*
1. Infrastaminal scales ca. reaching filament bases (rarely shorter), apex rounded; styles (0.6–) 1.1–2.5 mm long 2
   2. Corolla tube 1.4–2.5 mm long, withered corolla loosely surrounding the capsule before falling. . . . . a. *C. gronovii* var. *gronovii*
   2. Corolla tube 2.2–2.8 mm long, withered corolla capping the capsule. . . . . c. *C. gronovii* var. *calyptrata*

a. CUSCUTA GRONOVII VAR. GRONOVII (for synonyms see Yuncker 1932; Costea et al. 2006).

Flowers 3–3.8(–4) mm long; calyx 1.4–1.7(–2) mm long; **corolla** 2.9–3.5(–3.8) mm long; tube 1.4–2.5 mm long, **anthers** 0.4–0.6 mm; **pollen** 3(–4)-colpate, 18–36 μm long, from spheroidal to perprolate, tectum imperforate or perforate with puncta 2–7 μm long; **infrastaminal scales** (1.6–)1.8–2.3 mm long nearly reaching filament bases, oblong or broadly-oblong, apex rounded; **styles** 0.7–1.7 mm long; **capsules** 3–4.3 × 2.7–4.3 mm, globose, ovoid to globose-conic or subobpyriform; **seeds** 2–4 per capsule, 1.2–1.7 × 1.2–1.6 mm. ***2n*** = 60. (Fogelberg 1938; García et al. 2019; Ibiapino et al. 2022). Figures 4A, 6A–J.

Distribution and Ecology—This is the most frequent variety of *C. gronovii* in North America. Based on both herbarium specimens and field work, this is the only member of the *C. gronovii* species complex that we have found to parasitize cultivated plants, especially cranberry (Costea and Tardif 2006). **Canada:** Alberta, British Columbia, Manitoba (only a few collections), Ontario, New Brunswick, Nova Scotia, Prince Edward Island, Québec, Saskatchewan (only a few collections). **USA:** Alabama, Arkansas, Arizona, Colorado, Connecticut, District of Columbia, Florida, Georgia, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin, Wyoming.

The variety was also introduced in West Indies (Yuncker 1932, 1965). In North America it grows in a wide variety of habitats but apparently preferring shaded and/or wet environments. It flowers from June to October. Hosts are numerous species from hundreds of genera of herbaceous and wood plants in various families, including Acanthaceae, Anacardiaceae, Apiaceae, Asteraceae, Bignoniaceae, Brassicaceae, Caprifoliaceae, Commelinaceae, Convolvulaceae, Cornaceae, Balsaminaceae, Betulaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Polygonaceae, Primulaceae, Rosaceae, Rubiaceae, Solanaceae, Urticaceae, Verbenaceae, Vitaceae, and others (see also Gaertner 1950).

Conservation Status—Secure.

b. CUSCUTA GRONOVII Willd. ex Roem. & Schult. VAR. CURTA Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859. ≡ *Cuscuta curta* (Engelm.) Rydb., Bull. Torrey Bot. Club 40:466. 1913. LECTOTYPE (Yuncker 1921): "Northwest America (Fremont's 3rd Exped. 79), the type, in the Engelmann Herbarium (MO!)".

= *Cuscuta umbrosa* Beyr. ex Hook., Fl. Bor. Amer. 2:78. 1840. ≡ *Cuscuta megalocarpa* Rydb., Bull. Torrey Bot. Club 28:501. 1901. For types, see Costea et al. (2006).

Flowers 3.3–4.1 mm long; **calyx** 1.4–2.2 mm long; **corolla** 3.2–4 mm long; tube 1.7–2.5 (–2.9) mm long, anthers 0.4–0.5 mm; **pollen** 3 (–4)-colpate, 24–26 μm long, from spheroidal to perprolate, tectum imperforate or perforate with puncta 2–6 μm long; **infrastaminal scales** (0.5–)1.4–2.1 mm long, 1/2–1/3 as long as the corolla tube, apex truncate to bilobed; **styles** 0.1–0.7 mm long; **capsules** 4–5.2 × 3–5 mm, globose to ovoid; **seeds** 2–4 per capsule, 1.7–2.4 × 1.6–2 mm. ***2n*** =? (the material used by García et al. 2019 belongs to *C.* var. *gronovii*). Figures 4B, 6K–O.

Distribution and Ecology—Canada—Alberta, Manitoba, NW Ontario (only one collection), and Saskatchewan. **USA:** Colorado, Kansas, Minnesota, Montana, Nebraska, New Mexico, New York (as reported by Mitchell and Tucker 1997; possibly a waif), North Dakota, Oklahoma, South Dakota, Utah, and Wyoming. It flowers from July to October. It grows in shaded and/or wet environments and the most common hosts are species of *Ampelopsis* Michx., *Convolvulus* L., *Clematis* L., *Epilobium* L., *Linum* L., *Salix*, *Scutellaria*, *Symphoricarpos* Duhamel, and other genera.

Note—*Cuscuta gronovii var. curta* is similar in some aspects of flower, fruit, and seed morphology to *C. rostrata*. Both have infrastaminal scales shorter than the corolla tube and large

capsules and seeds, but *C. rostrata* is recognizable by the narrower infrastaminal scales and especially by the prominently beaked ovary and capsule.

Conservation Status—Secure globally, but Critically Imperilled in Alberta, Utah, and Wyoming (NatureServe 2023 under the more recent heterotypic synonym "*C. megalocarpa*").

c. CUSCUTA GRONOVII VAR. CALYPTRATA Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859. ≡ *Cuscuta calyptrata* (Engelm.) Small, Fl. S.E. U.S. 969. 1903. LECTOTYPE here designated (see Discussions): "Cuscuta gronovii? Cuscuta tenuiflora pentandrous: questionable whether the corolla is not calypt. […] on top of capsules. Flowers pentandrous. An intermediate form" MO 2757269!; isolectotypes: MO 7758365! and MO 2758486!

Flowers 3.8–4.5 mm long; **calyx** 1.7–2.5 mm long; **corolla** 3.5–4.4 mm long; tube 2.2–2.8 mm long, **anthers** 0.6–0.8 mm; **pollen** 27–33 μm, subspherical to subprolate, tectum perforate with puncta up to 1 μm. A small number of pollen grains (< 5%) possess atypical apertures like those illustrated in *C. acadiana*; **infrastaminal scales** 1.9–2.6 mm long, ca. equalling the corolla tube, apex rounded; **styles** 0.9–1.6 mm long; **capsules** 3.4–4.3 × 2.9–4 mm, globose to ovoid; **seeds** 2–3 per capsule, 1.4–1.7 × 1.4–1.6 mm. ***2n*** =? Figs. 4C, 6P–S.

Distribution and Ecology—USA—Arkansas, Louisiana, and Texas. It flowers from August to October. Hosts are both woody and herbaceous plants, but no specific information is available at the moment. Further research is necessary to establish the evolutionary relationships of this variety, as well as to elucidate its geographical distribution, ecology, and biology. It is possible that some *C. gronovii* (var. *gronovii*) and *C. cephalanthi* specimens from Eastern North America are in fact *C.* var. *calyptrata*. European populations of *C. gronovii* have been reported to belong to *C.* var. *calyptrata* [W and Central Europe (Feinbrun 1970); Belgium (Verloove 2023); France, Luxemburg (Lambinon et al. 2004); Germany (Duvigneaud 1978; Yuncker 1932); and the Netherlands (Van der Meijden 2005)]. As we did not study *C. gronovii* material from Europe, the identity of this taxon requires confirmation.

Conservation Status—Needs evaluation.

4. CUSCUTA ROSTRATA Shuttlew. ex Engelm. & A. Gray, Boston. J. Nat. Hist. 5: 225. 1845. LECTOTYPE (Yuncker 1932): USA. North Carolina. In regione media montium Little Craggy Ms., Carolina Sept., Aug 1841, *Rugel* s.n. (BM, GOET, K, MO!, ODU!, P).

Stems medium to coarse, yellow to orange. **Inflorescence** dense, paniculiform to glomerulate; **pedicels** 0.8–2.2 mm long; **bracts** 1 at the base of cymes, ovate to laceolate-triangular, membranous, margins entire or serrulate, apex acute to obtuse; bracteoles absent. **Flowers** 5-merous (but a few 4-merous flowers are possible), (4.2–)5–6.4 mm long, white-creamy when fresh, light brown when dried. **Laticifers** ± visible, translucent in the calyx, corolla, and ovary, isolated, round to ovoid. **Calyx** 1.7–2.5 mm long, fleshy, not reticulate, not glossy, campanulate, reaching 1/3–1/2 of corolla tube length, divided 3/5–2/3, tube 0.3–0.6 mm long, lobes, 1.2–2 mm long, broadly ovate, apex rounded, basally overlapping, margins entire to serrulate; **corolla** (4–)5–6.2 mm long, tube 2.7–4.5 mm long, broadly campanulate, lobes 1.2–2.3 mm long, shorter than the tube corolla tube, initially erect, later spreading to reflexed; broadly ovate, margin entire, apex rounded, straight; **stamens** exserted, shorter than corolla lobes; anthers 0.6–0.9 mm long, elliptic to oblong, filaments 0.5–1.2 mm long; **pollen** 3-zonocolpate, 29–34 μm long, prolate-spheroidal to subprolate or prolate; tectum perforatum with puncta 0.5–1.3 μm in diameter (approaching microreticulate in some grains), sexine scabrate with isolated granules; **infrastaminal scales** 2–3 mm long shorter than the corolla tube, oblong, rounded or truncate and bifid, bridged at 0.5–1.2 mm, fimbriae 0.5–1.3 mm long; **styles** cylindrical, 0.8–2.6 mm long; stigmas capitate, globose. **Capsules** 3.5–7 × 3–4 mm, indehiscent or irregularly dehiscent, ovoid, thickened and raised at the top, with a beak (rostrum) at the base of persistent styles, 1–1.5 mm long, interstylar opening small, surrounded by the withered corolla. **Seeds** 2–3 per capsule, 1.6–2.4 × 1.6–2.2 mm, dorsoventrally compressed to obscurely angled, subrotund to broadly-ovate; hilum subterminal, subrotund, 0.6–0.8 mm, vascular scar of funiculum linear, 0.2–0.4 mm long, vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate when hydrated. ***2n*** =? Figs. 4E, 6T–Y5.

Distribution and Ecology—USA—Georgia, Kentucky, Maryland, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia. It is morphologically distinguished by its large, fragrant flowers, beaked ovaries/capsules, and its Appalachian range. *Cuscuta rostrata* is the most xenogamous taxon of the *C. gronovii* species complex. The most common hosts are species of *Collinsonia* L., *Diervilla* Mill., *Eupatorium* L., *Eurybia*, *Hydrangea* Gronov., *Impatiens* L., *Laportea* Gaudich, *Rubus* L., *Rudbeckia* L., *Salix*, *Solidago*, *Symphoricarpos*, *Symphyotrichum*, and *Urtica* L. It grows in forests, especially along streams, at 800–2000 m elevation, and it flowers between July and September.

Conservation Status—Apparently Secure globally but Critically Imperiled in Maryland, Virginia, and North Carolina (NatureServe 2023).

5. CUSCUTA SAURURI Engelm., Amer. J. Sci. Arts 43: 339. 1842. LECTOTYPE (Yuncker 1932): U.S.A. MISSOURI. Margin of lakes and swamps, in the "American Bottom" opposite Saint Louis, on *Saururus*, Sep 1841, *Geyer s.n.* (MO!, US!). *Cuscuta gronovii* var. *latiflora* Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859. LECTOTYPE (Yuncker 1921): U.S.A. MISSOURI. Margin of lakes and swamps, in the "American Bottom" opposite Saint Louis, on *Saururus*, Sep 1841, *Geyer s.n.* (MO, US). Engelmann (1859) cited "*C. saururi*, Engelm.!" in synonymy of *Cuscuta gronovii* var. *latiflora*. *Cuscuta gronovii* Willd. ex Roem. & Schult. var. *saururi* (Engelm.) MacMill., Metasp. Minnesota Valley 430. 1892.

Stems medium, yellow to orange. **Inflorescence** dense, paniculiform; **pedicels** 0.7–1.6 mm long; **bracts** 1 at the base of cymes, ovate to lanceolate-triangular, membranous, margins entire or serrulate, apex acute to obtuse; bracteoles absent. **Flowers** 5-merous (but a few 4-merous flowers are possible), 2.3–3.1 mm long, white-cream when fresh, light brown when dried. **Laticifers** ± visible, translucent in the calyx, corolla, and ovary, isolated, round to ovoid. **Calyx** 1.3–1.6(–1.8) mm long, fleshy, not reticulate, not glossy, cupulate, ca. as long as the corolla tube or slightly shorter, divided 3/4–4/5 to the base, tube 0.3–0.5 mm long, lobes 1.1–1.4 mm, oblong-ovate, apex rounded or obtuse, not overlapping basally, margins usually serrulate; **corolla** 2.2–2.7(–3) mm

long, tube 0.8–1.5(–2) mm long, broadly campanulate to cupulate, lobes 1.2–1.5 mm long, equalling to somewhat longer than the tube corolla tube, initially erect, later reflexed; oblong, margin entire to serrulate, apex rounded, straight; **stamens** exserted, shorter than corolla lobes; anthers 0.3–0.5 mm long, elliptic to oblong, filaments 0.6–1 mm long; **pollen** 3-zonocolpate, 18–24 μm long, subprolate, prolate or perprolate; tectum imperforate or with a few puncta, 0.2–0.4 μm in diameter; sexine scabrate with isolated granules; **infrastaminal scales** 1.4–2(–2.3) mm long, longer than the corolla tube, oblong to obovate, rounded, bridged at 0.25–0.4 mm, fimbriae 0.4–0.8 mm long; **styles** cylindrical, 0.5–1(–1.6) mm long; stigmas capitate, globose. **Capsules** 2.4–3 (–4) × 2–3.3 (–4.22) mm, indehiscent or irregularly dehiscent, globose to globose-depressed, thickened and raised at the top, interstylar opening relatively small, surrounded by the withered corolla in the lower 1/2. **Seeds** 2–4 per capsule, 1–1.3(–2) × 1.2–1.7(–2.4), dorsoventrally compressed to obscurely angled, broadly-ovate to round; hilum subterminal, subrotund, 0.3–0.5 mm, vascular scar of funiculus linear, 0.16–0.24 mm long, vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate when hydrated. **2*n*** =? Figs. 4D, 5A–O.

Distribution and Ecology*—*Canada—Ontario and Quebec. **USA:** Arkansas, Connecticut, District of Columbia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, Rhode Island, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin. Habitats include stream banks, mudflats, margins of wetlands, wet meadows and alluvial forests at elevations between 20 and 200 m. The most common hosts are species of *Acalypha* L., *Bidens* L., *Boehmeria*, *Decodon*, *Cephalanthus*, *Impatiens*, *Penthorum* L., *Persicaria*, *Salix*, *Saururus*, *Sium* L., *Solidago*, and others. Flowering takes place from July to October.

***Conservation Status*—**Not reviewed by NatureServe (2023) because the species was considered synonymous with *C. gronovii* var. *gronovii*. Although it seems Secure globally, it may require conservation in certain areas.

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Author Contributions

MC did field work, examined and annotated all the herbarium material used in the study, conducted the morphometric analyses, wrote the bulk of manuscript, and prepared the morphology figures. MARW did molecular work, including DNA extractions and generating sequences included in this study. MG dissected and imaged most of the flowers used in the morphometric study, and imaged some of the pollen. WG did the pollen study. SS did field work, conducted the phylogenetic analyses, wrote the corresponding sections, as well as edited the rest of the manuscript.

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APPENDIX 1. Herbarium specimens used for the morphometric analysis of *Cuscuta gronovii* species complex and for the molecular analyses of the entire *C.* sect. *Oxycarpae*. Country, state/province, locality information, data, collector information, and herbarium in which the specimens are deposited are listed. For material used in molecular phylogenetic analyses, DNA extraction and GenBank accession numbers (plastid *trnL-F* and *rbcL*, nuclear ITS rDNA) are given in square brackets. Newly generated sequences are indicated in bold; 'n/a' indicates sequences that are not available. Abbreviations of herbaria follow Index Herbariorum (Thiers 2023).

Cuscuta acadiana. Canada.—

NEW BRUNSWICK: Charlotte Co.: Ferry landing area for Dear Island, 28 Aug 1982, *Hinds 5639* (UNB). Gloucester Co.: Mouth of Tetagouche River, in salt marsh, 15 Aug 1982, *Hinds 4656* (UNB); Frequent in salt meadow at mouth of Middle River just below bridge, 28 Aug 1988, *Hinds 9052* (UNB) [**2459; OQ630713**, n/a, **OQ645627**]; Janeville, 17 km SE of Bathurst, 47.00002°N, 65.45133°W, 7 Aug 2013, *Mills et al. 13-107.1* (NBM); 200 m ESE of Rte 134 bridge, 47.74597°N, 65.710426°W, 13 Aug 2013, *Mazerolle 4334* (UNB) [**2461; OQ630714**, n/a, n/a]. Kent Co.: Kouchibouguac National Park, Carleton St., Charles St., St. Louis Parish, 2.6 mi into Park on Cap St. Louis, UTM 541-811, 9 Sep 1977, *Munro & Cody 1786* (the type; ACAD, DAO, UNB) [**2454; OQ630715**, n/a, **OQ645628**]; Kouchibouguac National Park, 4.2 mi E of St. Louis de Kent, 11 Aug 1978, *Munro 2111* (UNB); Richibucto Harbour and vicinity, 15 Sep 1979, *Hinds & Breen 1489* (UNB). Kings Co.: Meenans Cove Rd, 24 Aug 1987, *Johnston s.n.* (NBM); Garden of Eden Cove, Long Island, Kennebecasis Bay, 25 Aug 2000, *Bagnell & Bishop 3481* (UNB) [**1234; OQ630716**, **OQ630592**, **OQ645629**]. Northumberland Co.: Neguac Provincial Park picnic site at edge of beach, 14 Aug 1982, *Hinds 4630* (UNB) [**2460; OQ630717**, n/a, **OQ6456230**]. Restigouche Co.: Mouth of Eel River, W of N end of bridge, 6 Aug 1995, *Hinds 11582* (UNB) [**702;** EF194427, **OQ630593**, EF194641]. Saint John Co.: Partridge Island, 25 Aug 1882, *Hay s.n.* (NBM); Partridge Island, 25 Aug 1882, *Hay 10601* (NBM) [**2456; OQ630718**, n/a, **OQ645631**]. Victoria Co.: 1 mi above Aroostook, 25 Aug 1959, *Hinds s.n.* (UNB); 1 mi above Aroostook, 46°49′N, 67°43.5′W, 25 Aug 1959, *Cunningham s.n.* (UNB) Westmorland Co.: 14 km NW of Port Elgin, 12 Aug 1989, *Harries & Fairbanks 890812-07* (NBM); Edge of marsh at Cap Pelé, Sandy Beach, 18 Aug 1991, *Hinds 10335* (UNB) [**2457; OQ630719**, n/a, **OQ645632**]. *Hinds et al. 4582* (UNB) [**2458; OQ630720**, n/a, **OQ645633**]. —NOVA SCOTIA: Annapolis Co.: Allains River, head of tide, N of Dugway Rd, 12 Aug 2012, *Proulx s.n.* (ACAD). Pictou Co.: Abercrombie, 1 Sep 1951, *Sampson 107* (ACAD). Yarmouth Co.: Tusket, edge of river, 28 Aug 1951, *Erskine 51.1429* (ACAD). Tusket Falls, Hewitts Bridge, about 3 mi from Tusket Falls Rd., 10 Aug 2012, *Proulx s.n.* (ACAD). Tusket Falls, E shore between railroad and Hwy 3 bridges, 43°51′60″N, 65°58′54″W, 29 Aug 2005, *Blaney & Boates 5780* (ACAD, NSPM). Tusker River bank, Pleasant Lake, 12 Aug 1954, *Smith et al. 12081* (ACAD).

Cuscuta cephalanthi. Canada. —

BRITISH COLUMBIA: Metro Vancouver, Surrey, Crescent Beach, 23 Aug 1988, *Lomer 88-133* (UBC) [**1235; OQ630629**, **OQ630551**, **OQ645550**]. Vancouver Island, Little Qualicum River estuary, 49°21′58″N, 124°2954″W, 31 Jul 2001, *Lomer 6100* (UBC) [**1588; OQ630630**, **OQ630552**, **OQ645551**]; *Lomer 4472* (UBC) [**1589; OQ630631**, **OQ630553**, **OQ645552**]. South of Okanagan Falls, E side of Vaseux Lake, 3 Oct 2013, *McIntosh et al. 2013-91* (UBC). —MANITOBA: Lake Manitoba, near Delta Waterflow and Wetlands Research Station, Delta Beach, 19 Jul 1985, *Ryan s.n.* (UVIC) [**1655; OQ630632**, n/a, **OQ645553**]. **USA.** —ILLINOIS: Marshall Co.: SE side of Illinois River (lake), vicinity of mouth of Brown Run, Lacon, NW 1/4 sect. 18, 16 Sep 1997, *Hill 29748* (NY) [**510;** EF194414, **OQ630554**, EF194633]. Peoria Co.: Peoria, Illinois river bottom, Aug 1894, *McDonald s.n.* (NMC). Saint Clair Co.: Scoot Air Force Base, 38°32′34.8″N, 89°50′12.6″ W, 19 Sep 2001, *Hill 34308* (BRIT). Woodford Co.: 5 Sep 1879, *Seymour s.n.* (DUKE). —INDIANA: Carroll Co.: Wildcat Creek where it is crossed by Delph and Frankfort Rd, 3 Sep 1914, *Deam 15304* (IND); Floyd Co.: Voucher grown at UTM greenhouse from seeds [**1709; OQ630633**, **OQ630555**, **OQ645554**]; Gibson Co.: 2.5 mi SW of Fetters, 24 Sep 1921, *Deam 25113* (IND); Jefferson Co.: Madison, 10 Sep 1934, *Banta s.n.* (IND, NY); Porter Co.: Dune Acres Rd., Indiana Dunes, 41°38′35″N, 87°05′12″W, 20 Jul 2018, *Stefanović SS-18-01* (TRTE, WLU) [**2189; OQ630634**, n/a, **OQ645555**]; Sullivan Co.: 6 mi SW of Carlisle, 4 Oct 1931, *Deam 51439* (IND) [**469;** EF194413, KJ436619, EF194632]. —IOWA: Dickinson Co.: Okoboji Station, Aug 1901, *Shimek s.n.* (WIS); Voucher grown at UTM greenhouse from seeds collected in Iowa, *Tallent s.n.* (UTM-1567; TRTE, WLU) [**1567; OQ630635**, **OQ630556**, **OQ645556**]; Scott Co., Credit Island, island access road, 41°30′16″N, 90°36′30″W, 29 Jul 2018, *Stefanović SS-18-09* (TRTE, WLU) [**2198; OQ630636**, n/a, n/a]. —MASSACHUSETTS: Nantucket Co.: Nantucket Island, Gibbs Pond, 17 Aug 1959, *MacKeever 365* (DAO, NY). —MINNESOTA: Houston Co.: Houston, Rt. 26, 2.7 mi N of Iowa border at New Albin, Milestone Landing Wildlife Refuge, 26 Aug 1979, *Ownbey & Wheeler 5349* (SMU). St. Louis Co.: Shore of Iron River, just below Crooked Lake, 22 Aug 1952, *Lakela 15575* (DAO, NY). —MISSISSIPPI: Jefferson Co.: Along Big River near mouth of Mammoth Creek, 10.5 km W of DeSoto, 38°7′30″N, 90°40′30″W, 24 Jul 1986, *Raven 27211* (WTU) [**167;** EF194412, KJ436618, EF194631]. —MISSOURI: St Louis County: St Louis, on *Rhus toxicodendron*, Aug 1845, *Engelmann s.n.* (GH). —OHIO: Stark Co.: Sugar Creek Twp, 15 Sep 1935, *Camp 931* (NY). —NEBRASKA: Kearney Co.: Minden, 14 Aug 1930, *Hapeman s.n.* (OKLA) [**2416; OQ630637**, n/a, **OQ645557**]. —NEW MEXICO: Otero Co.: Round Mt, 20 Aug 1899, *Wooton s.n.* (NMC); Tulerosa Creek (Round Mts), 20 Aug 1899, *Wooton s.n.* (NMC). —TEXAS: Rockwall Co.: *Cory 52529* (TEX/LL) [**706;** EF194416, KJ436655, EF194635]. —UTAH: Salt Lake City Co.: Salt Lake City, 22 Aug 1880, *Jones 1918* (CAS, NY). —WASHINGTON: Snohomish Co.: Marysville, 1 Jul 1928, *Grant s.n.* (RSA). —WISCONSIN: Brown and Outagamie Co.: Howard, 21 Aug 1890, *Umbach 38606* (WIS). Columbia Co.: ca. 0.5 mi W of Hwy 22, 1.5 mi N of junction with Hwy 33, 2.5 mi N of Pardeeville, T13N; R10; E; Sec. 21, 31 Aug 1984, *Bewick 108* (WIS) [**704;** EF194415, KJ436656, EF194634]. Crawford Co.: Gays Mills, 6 Sep 1937, *Roberts s.n.* (WIS). Dane Co.: N of Pheasant Branch, E of Low Rd (T8N; R8E; Sect. 36), 21 Aug 1958, *Peters s.n.* (WIS). Green Lake Co.: Lake Puckaway, 1 mi WNW of Marquette, small linear island, 43.753283°N, 89.166422°W, 30 Sep 1976, *Hansen et al. 4793* (WIS) [**1456; OQ630638**, **OQ630557**, **OQ645558**]. Iowa Co.: Tower Hill State Park, 21 Aug 1971, *Cochrane 3081* (WIS) [**1384; OQ630639**, **OQ630558**, **OQ645559**]; Tower Hill SP, camp site #3, 43°08′53″N, 90°02′54″W, 31 Jul 2018, *Stefanović SS-18-14* (TRTE, WLU) [**2244; OQ630640**, n/a, **OQ645560**]; Jefferson Co.: Milford Twp., T8N; R14E, S19, 3 Sep 1977, *Partch s.n.* (WIS). Richland Co.: Vicinity of Knapp Creek in Wisconsin floodplain, T8N; R2W; Sec. 7, W1/2 NW1/4, 21 Aug 1977, *Nee 15848* (WIS). Sauk Co.: Baraboo, 8 Aug 1932, *Davis s.n.* (WIS). Sheboygan Co.: beach of Lake Michigan about 200-400 yds. from present shore, T.13 N; R.23E; Sect. 30, 2 mi E of Cedar Grove, 10 Sep 1956, *Iltis & Koeppen 8248* (WIS). Walworth Co.: Walworth, T4N R17E, Sect. SW1/4, SW1/4, 14 Aug 1975, *Hansen & Tans 1414* (WIS); Wet marsh edge along road 1.5 mi N of Troy Center, 17 Aug 1975, *Hansen & Tans 3595* (WIS).

Cuscuta compacta. USA. —

ALABAMA: 2009, grown from seed, *Goertzen s.n.* (TRTE) [**1218**; **OQ630754**, n/a, **OQ645667**]. —ARKANSAS: Columbia Co.: wet baygall woods besides Co. Rd. #8, at Hwy 98 at Atlanta, SE of Magnolia, 33.121425°N, 93.056446°W, 15 Oct 2001, *Thomas 172211* (NY) [**1232**; **OQ630755**, **OQ630621**, **OQ645668**]. —CONNECTICUT: New London Co.: Pachaug State Forest, Voluntown, on Pachaug river bank, 41.574809°N, 71.873474°W, 13 Aug 1981, *Hemingson s.*n. (CONN) [**1460**; **OQ630756**, **OQ630622**, **OQ645669**]. —GEORGIA: Berrien Co.: Nyssa pond, 24 Sep 1976, *Kerby 7* (ASU) [**479**; EF194426, **OQ630623**, **OQ645670**]. —INDIANA: Crawford Co.: 2 Sep 1937, *Deam 58335* (IND) [**466**; EF194425, **OQ630624**, n/a]. —LOUISIANA: Grant Pa.: Catahoula district, Kisatchie National Forest, Breezy Hill vicinity, 14 Set 2000, *Hyatt 9667* (LSU) [**1375**; **OQ630757**, **OQ630625**, **OQ645671**]; St. Tammay Pa., La Comba, Hwy 190, 1 mi E of Lacombe, bridge over Bayou Lacombe, 0.5 mi E of intersection w/434, 30.313086°N, 89.936468°W, 2 Aug 2013, *Stefanović SS-13-49* (TRTE, WLU) [**1430**; **OQ630758, OQ630626,** n/a]. —MISSOURI: 11 Aug 1891, *Eggert s.n.* (WTU) [**199**; EF194424, KJ436627, EF194640]. —NORTH CAROLINA: Harnett Co.: 2.8 miles S of Lee County line on NC 87 (~1.6 mi SE of Olivia), 4 Oct 1956, *Laing 411* (WTU) [**198**; EF194423, KJ436626, n/a]; Pasquotank Co.: Great Dismal Swamp, Hwy 158, near Gates Co. line, 12 Sep 1984, *Musselman 6381* (ODU) [**1459**; **OQ630759, OQ630627, OQ645672**]; Scotland Co.: Lake Kinney Cameron, ca. 3.2 mi S of Hoffman on Monroe Rd., 6 Sep 2003, *Wilbur 76527* (DUKE) [**2420**; **OQ630760,** n/a, **OQ645673**]. —OKLAHOMA: McCurtain Co.: 3 mi N of Broken Bow, along creek in woods, 13 Oct 1957, *Waterfall 14770* (WIS)

[**1379**; **OQ630761,** n/a, **OQ645674**]; Beavers Bend State Park, S of Broken Bow Hydroelectric Plant, 34°08′16″N, 94°41′13″W, 25 Sep 2017, *Stefanović SS-17-119* (TRTE, WLU) [**1958**; **OQ630762,** n/a, **OQ645675**]. —Rhode Island: Washington Co.: South Kingston, Worden Pond, roadside, S side, 41.428317°N, 71.574147°W, 6 Sep 1931, *Collins s.n.* (CONN) [**1557**; **OQ630763,** n/a, **OQ645676**]. —Texas: Grown from seed, *UTM-1566* (TRTE) [**1566**; **OQ630764,** n/a, **OQ645677**]. —Tennessee: Coffee Co.: banks of Duck River, ca. 2 mi inside Manchester, E of I-24, 11 Oct 1980, *Flexner 142* (AUA) [**2421**; **OQ630765,** n/a, **OQ645678**]. —Virginia: Halifax Co.: floodplain hardwoods along Difficult Creek, just above state rd. #719 bridge, ca. 7.5 km S of Clover, 36.767371°N, 78.719302°W, *Wiebodlt et al. 8779* (QUE) [**1233**; **OQ630766, OQ630628, OQ645679**].

Cuscuta cuspidata. USA. —

Arkansas: Scott Co., Hwy 71, ca. 7 mi S of Waldron, 34°49′32″N, 94°02′16″W, 25 Sep 2017, *Stefanović SS-17-117* (TRTE, WLU) [**1956**; **OQ630742,** n/a, **OQ645656**]. Washington Co.: 3 mi SE of Fayetteville on White River, above dams, 17 Sep 1930, *Moore s.n.* (WIS) [**1423**; **OQ630743, OQ630612, OQ645657**]. —Missouri: Barton Co.: near Verdella, 27 Aug 1952, *Palmer 54991* (WIS) [**1425**; **OQ630744**, **OQ630613,** n/a]. —New Mexico: Union Co.: Kiowa National Grassland, Hwy 402, ca. 10 mi S of Clayton (intersection 402/562), 36°16′29″N, 103°11′06″W, 18 Aug 2016, *Stefanović SS-16-83* (TRTE, WLU) [**1700A**; **OQ630745, OQ630614, OQ645658**]. Seneca, Hwy 406, ca.7 mi N of Hwy 412, 36°38′28″N, 103°07′02″W, 18 Aug 2016, *Stefanović SS-16-85* (TRTE, WLU) [**1702**; **OQ630746, OQ630615, OQ645659**]. —Oklahoma: Cimmaron Co.: 7 mi W of Boise City on Hwy 325 (E0190 Rd.), 36°44′00″N, 102°39′56″W, 18 Aug 2016, *Stefanović SS-16-84* (TRTE, WLU) [**1701**; **OQ630747, OQ630616, OQ645660**]. —Texas: Hansford Co.: Palo Duro creek, 14 Aug 1978, *Higgins 16322* (ASU) [**482**; **OQ630748, OQ630617, OQ645661**]; Randall Co., Palo Duro Canyon, ca. 2 mi NE of canyon, off I-27, 2 Sep 1977, *Higgins 11405* (NY) [**1231**; **OQ630749, OQ630618, OQ645662**]; Rains Co., Hwy 19, bridge over Sabina river, NE corner, 32°46′52″N, 95°47′48″W, 26 Sep 2017, *Stefanović SS-17-122* (TRTE, WLU) [**1961**; **OQ630750,** n/a, **OQ645663**]; Walker Co.: [Huntsville], San Jacinto, 30°34′37″N, 95°41′32″W, 19 Oct 1993, *Carr 13221* (TEX) [**1016**; EF194429, KJ436637, EF194643].

Cuscuta glomerata. USA. —

Indiana: Vermillion Co.: 1978, *McClain 2448* (IND) [**462**; EF194430, KJ436651, **OQ645651**]. —Iowa: Grown from seed, *UTM-1565* (TRTE) [**1565; OQ630740, OQ630608, OQ645652**]. —Kansas: 1979, *Freeman 293* (NY) [**597**; EF194432, KJ436652, **OQ645653**]; 1984. *Freeman 2235* (NY) [**598**; EF194433, **OQ630609**, EF194644]. —Minnesota: Goodhue Co.: Zumbrota, 1892, *Ballard s.n.* (WIS) [**1554; OQ630741, OQ630610, OQ645654**]. —North Dakota: 1961, *Stevens 2546* (DAO) [**619**; EF194431, **OQ630611, OQ645655**].

Cuscuta gronovii var. gronovii. Canada. —

New Brunswick: Saint John Co.: City of Saint John, along Kennebecasis River, 45.3298°, 66.0659°W, 22 Aug 2019, *Gray s.n.* (NBM, WLU) [**2455**; **OQ630641**, n/a, **OQ645561**]. —Nova Scotia: *Stefanović SS-07-100* (TRTE, WLU) [**1219**; **OQ630642**, **OQ630559**, **OQ645562**]. Antigonish Co.: South River, 2012. *Sharpe s.n.* (TRTE, WLU) [**1707**; **OQ630643**, **OQ630560**, **OQ645563**]. —Ontario: 3 Sep 1990, *Catling 5111* (DAO) [**1238**; **OQ630644**, **OQ630561**, **OQ645564**]. Hamilton-Wentworth Co.: Flamborough Twp., 1 km NW of Dundas, Spencer Gorge Conservation Area, 24 Aug 1990, *Macdonald 21756* (HAM) [**1240**; **OQ630645**, **OQ630562**, **OQ645565**]. Kent Co.: Rondeau Provincial Park, 18 Aug 1985, *Bakowsky s.n.* (TRTE) [**1248**; **OQ630646**, **OQ630563**, **OQ645566**]. Niagara Regional Municipality: Fort Erie, Pt. Albino, 22 Aug 1988, *MacDonald 19918* (TRTE) [**1247**; **OQ630647**, **OQ630564**, n/a]; Oxford Co: Zorra, 8 Sep 1990, *Oldham 11825* (TRTE) [**1241**; **OQ630648**, **OQ630565**, n/a]. Peel Regional Municipality: Caledon, Terra Cotta, Credit River, 43°42′58″N, 79°56′05″W, 26 Jul 2015, *Stefanović SS-15-25* (TRTE) [**1549**; **OQ630649**, **OQ630566**, **OQ645567**]. Perth Co.: 2 mi E of Stratford, N. Easthope Twp, 25 Aug 1972, *Wellwood s.n.* two specimens on different hosts (WLU); Stratford 43°22′26″N, 80°58′38″W, 11 Aug 2019, *Glofcheskie 21* (WLU). —Québec: Comté d'Argenteuil: Le long de la piste est-ouest de la presqu'île Robillard, 10 Aug 1986, *Guertin 1334* (AUA, QFA). Comté de Laprairie: Près de Laprairie, 7 Sep 1925, *Marie-Victorin 21801* (WIS). Comté de Lotbinière: Sainte-Croix-de-Lotbinière, 2 km au SE de la Pointe-Platon, 46°39′10″N, 71°49′30″W, 1989, *Garneau & Roy 89-626-M* (DAO) [**705**; EF194422, **OQ630567**, EF194639]. Saint Nicolas Les Chutes-de-la-Chaudière Ouest, 200 m E du Pont de Québec, 46°44′30″N, 71°17′05″W, 3 Oct 1990, *Garneau & Roy 90-297-M* (QFA) [**1239**; **OQ630650**, **OQ630568**, **OQ645568**]. **USA.** —Alabama: Choctaw Co.: 25 Aug 1994, *Crouch 1162* (AUA) [**1394**; **OQ630651**, **OQ630569**, **OQ645569**]. Dallas Co.: 10 Oct 1982, *Gunn 1319* (AUA) [**2157**; **OQ630652**, n/a, **OQ645570**]. Pike Co.: Bear Sink Creek Rd at the W side of Beeman Creek, 5 Oct 1999, *Diamond 8864* (AUA) [**1392**; **OQ630653**, **OQ630570**, **OQ645571**]. Wilcox Co.: 2 Oct 1982, *Gunn 1356* (AUA) [**1393**; **OQ630654**, **OQ630571**, **OQ645572**]. —Arkansas: Ashley Co.: Hamburg, 28 Sep 1941, *Demaree 22592* (OKLA) [**2155**; **OQ630655**, n/a, **OQ645573**]. Jefferson Co.: Bluffs of Arkansas River, Pine Bluff. 22 Oct 1938, *Demaree 18594* (WTU) [**194**; EF194419, **OQ630572**, **OQ645574**]. —Connecticut: Litchfield Co., Litchfield, 8 Sep 1970, *Parker & Parker 70.125* (CONN) [**2161**; **OQ630656**, n/a, **OQ645575**]. New Haven Co.: Branford, outer island, 41°14′31″N, 72°24′53″W, 21 Aug 1982, *Mehrhoff 6889* (CONN) [**2149**; **OQ630657**, n/a, n/a]. —Florida: Alachua Co.: At edge of Bivens Arm at US 441, S side of Gainesville city limit, 1 Oct 1966, *D'Arcy 1400* (RSA). Nassau Co.: White Oak Plantation bordering on the St. Mary's River about 10 mi NW of Yulee, about 1/10 mi from the E Gate Guard House on Wingate Landing Rd starting just beyond gate, 24 Oct 1997, *Wilbur 69645* (DUKE). —Illinois: Jo Davis Co.: Apple River Canyon SP, Sunshine trail, 42°27′02″N, 90°03′23″W, 2018, *Stefanović SS-18-11* (TRTE) [**2199**; **OQ630703**, n/a, **OQ645618**]. Stark Co.: Near Wady Petra, 24 Aug 1898, *Chase 169* (NMC). —Indiana: Jackson Co.: About 1/4 mi N of Houston, 31 Aug 1939, *Deam 59416* (DUKE). Lawrence Co.: Flood plain of Spider Creek, 1 mi SW of Bedford, 4 Oct 1934, *Kriebel 2802* (DUKE). Martin Co.: Martin State Forest, Hardwood Lake, Sep 2004, *Stefanović SS-04-161* (TRTE, WLU) [**467**; EF194421, KJ436654, **OQ645576**]. Monroe Co.: *Palmer 931* (IND) [**136**; **OQ630658**, n/a, **OQ645577**]; Griffy Lake, near Bloomington, Sep 2002, *Stefanović SS-02-03* (TRTE, WLU) [**343**; EF194418, EU883479, EF194637]; Griffy Lake, near Bloomington, 25 Jul 2004, *Stefanović SS-04-143A* (TRTE, WLU) [**453**; EF194420, n/a, EF194638]. Putnam Co.: In pasture on E side of Route 43, N of Greencastle, 7 Oct 1947, *Welch 9129* (RB). —Iowa: Cerro Gordo Co., 13 Sep 2013, *Watson s.n.*, Grown from seed, *UTM-1564* (TRTE) [**1564**; **OQ630659**, **OQ630573**, **OQ645578**]. Benton Co.: ca. 3 mi S of Urbana, Wildcat Bluff Rec. Area, 42°11′34″N, 91°53′10″W, 29 Jul 2018, *Stefanović SS-18-07* (TRTE, WLU) [**2195**; **OQ630660**, n/a, **OQ645579**]; Clay Co.: 3 mi E of Spencer along Hwy 18 on the floodplain of the Little Sioux River, 17 Aug 1935, *Hayden 3013* (NMC). Linn Co.: Palisades-Kepler SP, trail, 41°54′11″N, 91°30′14″W, 29 Jul 2018, *Stefanović SS-18-08A* (TRTE, WLU) [**2196**; **OQ630661**, n/a, **OQ645580**]; just passed Ennic Co. Park, Cedar River Rd, 41°53′31″N, 91°28′34″W, 2018, *Stefanović SS-18-08B* (UTM) [**2197**; **OQ630662**, n/a, **OQ645581**]; Webster Co.: Dolliver Memorial SP, service trail, 42°23′53″N, 94°04′31″W, 28 Jul 2018, *Stefanović SS-18-06* (TRTE, WLU) [**2194**; **OQ630663**, n/a, **OQ645582**]. —Kentucky: Lincoln Co.: 3/4 mi NE of Hall's Gap, 13 Sep 1939, *Gleason & Griffiths 565* (NCSC). McCreary Co.: Daniel Boon Nat'l Forest, Yamacraw loop trail, 13 Jul 2012, *Stefanović SS-12-06* (TRTE) [**1345**; **OQ630664**, **OQ630574**, **OQ645583**]. —Louisiana: Ascension Parish: On edge of ponds between New River and La. 429, 0.9 Rd mi E. junction with La. 431, St. Amant, 12 Oct 1974, *Bulat 39* (LSU) [**2151**; **OQ630665**, n/a, **OQ645584**]; St. Amant, abundant at pond between New River and LA431, 12 Oct 1974, *Palazzo 75* (LSU) [**2418**; **OQ630666**, n/a, **OQ645585**]. Chicot Co.: Woods N of Ark. 52 on W side of Boeuf River SW of Eudora, Oct 1999, *Thomas 163598* (DUKE). East Baton Rouge Parish: Baton Rouge, 300 yd NNE of the E end of Seyburn Dr., Bottomland hardwoods, 30 Oct 1971, *Self s.n.* (LSU) [**2150**; **OQ630667**, n/a, **OQ645586**]; Scotland, 5 Oct 1935, *Brown 6147* (LSU) [**2412**; **OQ630668**, n/a, **OQ645587**]. Franklin Parish: On fence row 0.4 mi S of La 4, 4 mi W of Fort Necessity, Sec. 32, T13N, R6E, 17 Sep 1981, *Thomas & Joye 78515 & 1970* (DUKE). Madison Parish: Old road along Judd Brake in Tensas River National Wildlife Refuge S of Quebec, T16N, R11E, Sec. 7 & 17, 27 Sep 1983, *Thomas 85968* (AAU). Natchitoches Parish: Low woods, 28 Sep 1915, *Palmer 8710* (CAS). St. Helena Parish: Along the Tickfaw River about 2 mi E of Greensburg in T2S R6E, Sec 53, 29 Aug 1971, *Allen 1444* (LSU); Abandoned field known locally as Strickland Field, about 3 mi E of Greensburg, 11 Nov 1970, *Allen 347* (LSU). St. Landry Parish, forest 3 mi E of Plaucheville, 1 mi S of the parish line, 22 Sep 1984, *Allen 13013* (LSU) [**1388**; **OQ630669**, **OQ630575**, **OQ645588**]. Tensas Parish: Tensas, on W side of La. 604 just S of Lake Bruin State Park, N of St. Joseph, T11N, R12, Sec. 2, 1 Oct 1987, *Thomas 102241* (DUKE). West Feliciana Parish: Along La 15, 6.8 mi N of its junction with La 1; or

0.1 mi N of the West Feliciana-Point Coupee parish line, 6 Nov 1988, *Lievens 3349* (LSU); On Thompson Creek where it crosses US 61, 27 Oct 1981, *Givens 2366* (LSU). —Maine: Aroostook Co.: Allagash, river tank of St. John River, near Walker Brook, 47°06′37″N, 69°08′06″W, 6 Aug 1981, *Mehrhoff 4712* (CONN) [**2154**; **OQ630670** n/a, **OQ645589**]. Knox Co.: between Back Cove and Wildrake Beach, Wooden Ball Island, Matinicus Isle, 43.852583°N, 68.821188°W, 19 Aug 1988, *Rossbach 10617* (CONN) [**2160**; **OQ630671**, n/a, **OQ645590**]. —Massachusetts: Franklin Co.: N end of Pine Hill, Deerfield, 12 Sep 1966, *Ahles 64633* (SMU) Hampden Co.: Springfield, 30 Aug 1926, *Seymour G453* (DUKE). Hampshire Co.: Northampton, Connecticut River, 18 Aug 1978, *Ahles 86319 (*OKLA) [**2153**; **OQ630672**, n/a, n/a]. Plymouth Co.: University of Massachusetts Cranberry Experimental Station, Maple Spring, 2009, two populations grown from seed [**1251A**; **OQ630673**, n/a, **OQ645591**]; [**1295A**; **OQ630674**, n/a, **OQ645592**]. —Michigan: Washtenaw Co.: Low bank of Huron River, 20 Aug 1936, *Hermann 8385* (CAS). —Minnesota: Big Stone Co.: At edge of woods, Toqua Lakes State Scenic Wayside Park, 1/2 mi S of Graceville, 12 Sep 1946, *Moore & Huff 19268* (OKLA) [**1444**; **OQ630675**, n/a, **OQ645593**]. Dakota Co.: at bridge across Vermillion River, Rte no. 54 (91), Hastings, N of river, W of bridge, 44.733851°N, 92.837910°W, 10 Sep 1976, *Ownbey 5520* (WIS) [**1443**; **OQ630676**, n/a, **OQ645594**]. Houston Co.: just N of Reno, Rt-26, 43.603054°N, 91.272452°W, 27 Aug 1976, *Ownbey & Wheeler 5366* (NDSU) [**1395**; **OQ630677**, **OQ630576**, **OQ645595**]. Renville Co.: Skalbekken Country Park, picnic area E, 44°43′49″N, 95°24′24″W, 2018, *Stefanović SS-18-04* (TRTE) [**2192**; **OQ630678**, n/a, **OQ645596**]. Steel Co.: Rice Lake SP, service trail, 44°05′08″N, 93°03′53″W, 2018, *Stefanović SS-18-03* (TRTE) [**2191**; **OQ630679**, n/a, **OQ645597**]. —Missouri: Bollinger Co.: 37.1666600°N, 90.0833300°W, 19 Sep 2001, *Brant & O'Donnell 4807* (MO) [**1193**; **OQ630680**, **OQ630577**, **OQ645598**]. Douglas Co.: Brush Creek, Hwy 14, 36°51′09″N, 92°20′30″W, 2017, *Stefanović SS-17-112* (TRTE) [**1954**; **OQ630681**, n/a, **OQ645599**]. Jefferson Co.: 6 mi W of DeSoto Twp, ca. 0.3 mi SE of Harness Bluff, Big River, 38°07′30″N, 90°40′31″W, 29 Aug 1991, *Raven & Raven 27930* (NDSU) [**1385**; **OQ630682**, **OQ630578**, **OQ645600**]. Shannon Co.: Round Spring, along Current River, 37°16′57″N, 91°24′20″W, 2017, *Stefanović SS-17-111* (TRTE) [**1953**; **OQ630683**, n/a, n/a]. —North Carolina: Durham Co.: Along Western Railway tracks E of Old Oxford Hwy (County Rd 1004) ca. 2.6 mi N or Durham City boundary, approx. 36°05′N, 78°52′W, 7 Oct 1983, *Smith 874* (DUKE); Bottomland woods along the jogging trails between US 15-501 Bypass and the Duke Golf Course at the W edge of Duke University Campus, 29 Sep 1991, *Wilbur 59557* (DUKE); Bald cypress swamp on Erwin Road (County Rd 1306), ca. 3 mi from the West Campus of Duke University, 15 Sep 1998, *Wilbur 71959* (DUKE). Gates Co.: Along SR 1318, ca. 1.4 mi SW of junction with SR 1305, 9 Sep 1984, *Musselman 6383* (ODU). Macon Co.: Highlands, 15 Sep 1910, *Anderson 1858* (BRIT). Orange Co.: Gate 12 of the Duke Forest, near the W end of NC 751 ca. 4 mi from Duke University's West Campus, 21 Sep 1988, *Wilbur 50784* (DUKE). Wake Co.: Crabtree Lake Park along the W shore, ca. 3.5 mi NE of Morrisville on Aviation Parkway, 18 Oct 2003, *Wilbur 76816* (DUKE). —New York: Suffolk Co.: Fisher Island, Hawks Nest Pt., 41.270467°N, 72.009456°W, 19 Sep 1990, *Tucker & Horning 5859* (TRTE) [**1246**; **OQ630684**, **OQ630579**, n/a]. —North Dakota: Cass Co., Fargo, 9 Sep 1990, *Stevens 8228* (WIS) [**1377**; **OQ630685**, n/a, **OQ645601**]. —Ohio: Adams Co.: ca. 2 mi NW of West Union, Adams Lake SP, along the lake shore, 38.814050°N, 83.526112°W, 12 Jul 2012, *Stefanović SS-12-05* (TRTE, WLU) [**1344**; **OQ630686**, **OQ630580**, n/a]. Coshocton Co.: North Appalachian Experimental Watershed, near Coshocton, 12 Sep 1942, *Moldenke 13948* (NCSC). Lorain Co.: Henrietta Twp, 9 Sep 1915, *Grover s.n.* (OKLA) [**2145**; **OQ630687**, n/a, **OQ645602**]. Morrow Co.: Mt. Gilead, Mt. Gilead SP, 8 Jul 2012, *Stefanović SS-12-01* (TRTE, WLU) [**1343**; **OQ630688**, **OQ630581**, **OQ645603**]. Ottawa Co.: Turtle Creek, Ottawa National Wildlife Refuge, N side Oh 2, junction Oh 590, 22 Aug 1996, *Hill 28542* (BRIT). —Oklahoma: Delaware Co.: along N side of Lake Eucha, Upper Spavinaw, 2 mi E from the bridge on state Hwy 10, s.d., *Taylor 2352* (WIS) [**1424**; **OQ630689**, **OQ630582**, **OQ645604**]. Mayes Co.: Locust Grove; SH 82, 2.8 mi NE of Locust Grove, 25 Sep 1957, *Wallis 5774* (OKLA); Spavinaw picnic area, 2 mi S of intersection of Hwys 5/82 on Hwy 82, 19 Sep 1974, *Kichler 25* (OKLA) [**2156**; **OQ630690**, n/a, **OQ645605**]. Bryan Co.: Johnson Creek Recreation Area, 33°59′56″N, 96°34′21″W, 2017, *Stefanović SS-17-123* (TRTE) [**1962**; **OQ630691**, n/a, **OQ645606**]. —Pennsylvania: West Chester Co.: [no date], *Jeffries 1836-79* (CAS). —Rhode Island: Providence Co.: West Greenwich, Smithfield, Wenscott Reservoir, 10 Aug 1921, J. *Franklin Collins s.n.* (OKLA) [**2158**; **OQ630692**, n/a, **OQ645607**]. —South Carolina: Berkeley Co.: roadside ditch, ca. 1.1. mi S of Moncks Corner at US-52, 23 Sep 1966, *Bradley & Sears 3536* (NDSU) [**1390**; **OQ630693**, **OQ630583**, **OQ645608**]. —South Dakota: Roberts Co.: Sica Hollow SP, Spirits trail, 45°44′45″N, 97°13′06″W, 2018, *Stefanović SS-18-05* (TRTE) [**2193**; **OQ630694**, n/a, **OQ645609**]; Lake Traverse, 20 Sep 1974, *Williams 2489* (NDSU) [**1378**; **OQ630695**, n/a, **OQ645610**]. —Texas: Titus Co.: ca. 7 mi SW of Mt. Pleasant ca. 1.5 mi N of Monticello, 12 Oct 1977, *Ajilvsgi 7203* (BRIT). Trinity Co.: ca. 3 mi NNE of the center of Groveton, E side of Hwy 94 and S of FM 3317, NW side bounded by an old RR tramway, Davy Crockett NF, 24 Oct 1996, *Nesom K2Ah-8* (SHSU) [**1546**; **OQ630696**, **OQ630584**, **OQ645611**]. Walker Co.: along Hwy 75, 10 mi N of Huntsville, Nelson Creek crossing, 30.812169°N, 95.716790°W, 1 Sep 2015, *Stefanović SS-15-27* (TRTE) [**1550A**; **OQ630697**, **OQ630585**, **OQ645612**]. —Virginia: Scott Co.: Scott, near moist pasture along Holston River, near Kingsport TN, along SR 707, 1.5 mi E of US 23, 13 Aug 1984, *Musselman 6334* (ODU). Southampton Co.: Hwy 460, ca. 1 mi NW of Zuni, 36°52′20″N, 76°50′30″W, grown from seed collected 27 Apr 2016, *Stefanović SS-16-47* (TRTE) [**1647**; **OQ630699**, **OQ630586**, **OQ645614**]. —West Virginia: Cabell Co.: 1.5 mi W of C & O Depot, near Milton, 3 Oct 1936, *Williams 542* (WIS). Pocahontas Co.: In swamp flooded by beaver 2 or 3 years ago, above Big Glade of Cranberry Glades, near Cranberry River, 11 Sep 1966, *Rossbach 7303* (OKLA) [**2146**; **OQ630698**, n/a, **OQ645613**]. —Wisconsin: Dane Co.: Governors Island, 31 Aug 1933, *Frank s.n.* (WIS); Pheasant Branch Conservancy, 43.11164°N, 89.483308°W, 26 Aug 2017, *Schneider 1045* (TRTE) [**1952**; **OQ630700**, n/a, **OQ645615**]. Iowa Co. Governor Dodge SP, Cox Hollow Lake, 43°00′50″N, 90°06′58″W, 2018, *Stefanović SS-18-13* (TRTE) [**2243**; **OQ630701**, n/a, **OQ645616**]; Tower Hill SP, camp site #3, 43°08′53″N, 90°02′54″W, 31 Jul 2018, *Stefanović SS-18-14* (TRTE, WLU) [**2245**; **OQ630702**, n/a, **OQ645617**]. Jefferson Co.: Bean Lake, T7N-13E-Sect. 22, 17 Aug 1966, *Tans s.n.* (WIS). Lafayette Co.: Yellowstone Lake SP, 42°45′46″N, 89°58′00″W, 2018, *Stefanović SS-18-12* (TRTE) [**2200**; **OQ630704**, n/a, **OQ645619**]. Monroe Co.: Fort McCoy, 6 Sep 2001, *Williams 1151* (WIS) [**1386**; **OQ630705**, **OQ630587**, **OQ645620**]. Richland Co.: Richland County Farm Land on NE side of Pine River, 8 Sep 1968, *Nee 1381* (WIS). Rock Co.: Avon Twp., Nelson Rd., Sugar River bottom, 6 Sep 1957, *Fell 57-1217* (WIS) [**2147**; **OQ630706**, n/a, n/a]. Taylor Co.: Along a beaver pond on McKenzie Creek, 21 Sep 1995, *Fields 2841* (WIS). Walworth Co.: Lake Geneva, 1888, *Snyder s.n.* (SD). Washington Co.: Formerly city of Hartford dump early 1900 s. T10 N; R18 E; SE1/4 NE1/4 Sect. 20, 31 Aug 1993, *Spuhler 93-295* (WIS). Walworth Co.: Natureland Park, along trail and lake, 42°44′46″N, 88°42′48″W, 2018, *Stefanović SS-18-02* (TRTE) [**2190**; **OQ630707**, n/a, **OQ645621**. Waupaca Co.: Hartman Creek SP, Hartman Lake, 44°19′33″N, 89°12′07″W, 2018, *Stefanović SS-18-17* (TRTE) [**2246**; **OQ630708**, n/a, **OQ645622**].

Cuscuta gronovii var. calyptrata. USA. —

Arkansas: Johnson Co.: Hwy 123, 35°30′50″N, 93°20′25″W, 2017, *Stefanović SS-17-114* (TRTE) [**1955; OQ630709#**, n/a, **OQ645623**]. Yell Co.: Hwy 28, W side of Fourche La Fave River, 34°54′39″N, 93°34′56″W, 2017, *Stefanović SS-17-118* (TRTE) [**1957; OQ630710**, n/a, **OQ645624**]. —Louisiana: Shreveport, Red River bottom, 28 Sep 1847, *Gregg s.n.*, MO 2757269, MO 2758365, MO 2758486 (MO). —Texas: 1844, *Lindheimer 235* (MO 2758813), *Lindheimer s.n.* (MO2758814); Houston, 1841 *Lindheimer s.n.* (MO); Houston, wet thickets, June 1842, *Lindheimer s.n.* (MO). Near Houston, banks of Bagon River, Oct 1841, *Lindheimer s.n.* (MO).

Cuscuta gronovii var. curta (≡ C. umbrosa). Canada. —

Manitoba: Sans Souci, 29 Jul 1956, *Bernard 56/5473* (QFA). Winnipeg Metropolitan Region: Winnipeg, Mulvey Av, Sep 1975, *Fields s.n.* (WIN) [**578;** EF194435, KJ436728, EF194646]. Delta, S13-T14-R7, 20 Aug 1953, *Löve & Löve 6199* (DAO). Red River, Saint-Boniface, 12 Aug 1960, *Boivin 13852* (SASK). —Saskatchewan: Nipawin, 30 Jul 1951, *Breitung 1433* (DAO, SASK). Little Manitou Lake, 20 Aug 1992, *Hudson 5082* (SASK) [**579;** EF194436, **OQ630588**, EF194647]; SE Saskatchewan, Antler River Valley, ca. 10 mi S and 0.5 mi E of Gainsborough, NE1/4 sec9 T1 R30W1, 49.062555°, 101.399346°W, 28 Jul 1988, *Harms 39594* (DAO) [**1236; OQ630711**, **OQ630589**, **OQ645625**]. **USA.** —Colorado: Dome Rock, Platte Canyon, 8 Aug 1878, *Jones 571* (MO, RSA); Wilbanis Canyon, near Manitou, 19 Aug 1924, *Bacigalupi 870* (CAS). —Iowa: No location, 1878. *Leiberg s.n.* (OSU). —New Mexico: Lincoln Co.: White Mountains, 25 Aug 1907, *Wooton & Standley 3488* (BRIT, NMC); S Fork

of Eagle Creek, 5 km W of Alto, in the White Mts., 7480 ft, Jul 1969, *Hutchinson 2262* (RSA) [**956;** EF194437, **OQ630590**, EF194648]. —North Dakota: Rolette Co.: Foothills of the Turtle Mts near Dunseith, 18 Aug 1907, *Leeds s.n.* (CAS, IND). —Montana: Park County Co.: Livingston, 6 Sep 1884, *Seymour s.n.* (DUKE). —Utah: City Creek Canyon, 20 Aug 1880, *Jones 1914* (CAS, K); Utah Co.: Wasatch Mt. SP, Sundance, trail leading from BYU Alumni lodge, 31 Jul 2009, *Stefanović SS-09-42* (TRTE, WLU) [**1216; OQ630712**, **OQ630591**, **OQ645626**].

Cuscuta rostrata. USA. —

Georgia: White Co.: Annie Ruby Falls, 14 Aug 1967, *Jones & Jones 15058* (LSU). —North Carolina: Ashe Co.: Bluff Mt., 17 Sep 1966, *Boseman et al. 45268* (WIS) [**460;** EF194428, KJ436709, EF194642]; Bluff Mt, 3 Oct 1961, *Radford 44426* (BRIT); Bluff Mt, just W of Jefferson, 13 Sep 1970, *Clark et al. 3929* (DUKE). Buncombe Co.: Near Balsam Gap, 08 Aug 1935, *Correll & Oosting 3823* (DUKE); Blue Ridge Pkwy at Pinnacle Gap, 9 Aug 1953, *Sargent 6515* (NCSC). Haywood Co.: On Blue Ridge Parkway between Balsam Gap and Beech Gap, 14 Sep 1963, *Hardin 2438* (NCSC); Pisgah Ridge and Mt. Pisgah, northern red oak forest, 1 Sep 1972, *Thomas 281* (NY) [**1230; OQ630721**, **OQ630594**, n/a]. Macon Co.: between Yellow Mt Gap and Cole Mt Gap, N of Highlands, 16 Aug 1951, *Godfrey & O'Connell 51883* (DUKE). Mitchell Co.: Creekbottom, 0.6 mi W SW of Huges Gap on Rd to Buladean, 25 Sep 1958, *Ahles & Duke 49884* (NY). Randoph Co.: On W slopes of the main Alleghany Ridge, just E of Horton, 17 Sep 1904, *Moore 2317* (CAS). Swain Co.: First Gap NW of Indian Gap, SE of Clingman's Dome, 13 Sep 1959, *Fosberg 40303* (RSA). Watauga Co.: Roadside N of Grandfather Mt, 30 Sep 1961, *Hardin 2454* (NSCS); Grandfather Mt, old logging road paralleling N Fork Boone Rd, 9 Oct 1966, *Daggy 3451* (DUKE). Yancey Co.: near Stepps Gap, 10 Sep 1966, *Bozeman et al. 45198* (ODU); Mt Mitchell, 22 Jul 1970, *Downs 11298* (NCSC). TYPE: Little Craggy Mts, Aug 1841, *Rugel* s.n. (MO, ODU); woodland cove, 3.8 mi N of Swiss, 9 Oct 1958, *Ahles & Duke 50722* (DAO) [**1229; OQ630722**, **OQ630595**, **OQ645634**]. —Tennessee: Carter Co.: Carvers Gap, Roan Mt, 04 Aug 1934, *Brown 120* (DUKE). Sevier Co.: Jake's Gap, 20 Aug 1936, *Jennison 2824* (NY); Great Smoky Mts National Park, Newfound Gap, 14 Aug 1942, *Lundell & Lundell 11480* (WIS) [**1421; OQ630723**, **OQ630596**, **OQ645635**]. Unicoi Co.: Along Rd to top of Samson Mt, 11 Aug 1993, *Churchill 93217* (CAS). —Virginia: Grayson Co.: Whitetop Mt, 15 Aug 1984, *Musselman 6338* (NCSC) [**1447; OQ630724**, **OQ630597**, **OQ645636**]; Whitetop Mt, along SR-600, 0.5 mi NE of US-58, 36.620045°N, 81.584440°W, 15 Aug 1984, *Musselman 6339* (NCSC) [**1446; OQ630725**, **OQ630598**, **OQ645637**]; Along SR 600, 0.5 mi NE of US 58, Whitetop Mt, 15 Aug 1984, *Musselman 6335* (ODU). Smyth Co.: Elk Garden near trail to Mt Rogers, 15 Aug 1984, *Musselman 6337* (ODU) [**1445; OQ630726**, **OQ630599**, **OQ645638**]. —West Virginia: Pendleton Co.: N of Shiver Mt, 16 Aug 1936, *Allard 2092* (NY). Tucker Co.: At head of Fisher Spring Run and National Forest Rd, Allegheny Front, 24 Sep 1960, *Rossbach 2340* (AAU); 6.6 km (4.1 mi) from the intersection of Jordan Rd and U.S. Forest Service Rd 75 (Rd to Dolly Sods) on 75, 12 Aug 1979, *Boufford et al. 21328* (AAU). Yancey Co.: Mount Mitchell, 19 Aug 1925, *Kraus s.n.* (WIS).

Cuscuta saururi. Canada.—

Ontario: Wilson Island, E end, 4 km W of Glen Ross, 44°15′30″N° 77°38′00″W, 1989, *Catling s.n.* (DAO) [**703;** EF194417, **OQ630600**, EF194636]. —Quebec: Le Haut-Richelieu Co.: Saint-Georges-de-Clarenceville, 45.0843°N, 73.2156°W, 9 Sep 2009, *Garon-Lebreque and Léveillé 200909-05* (MT, WLU). **USA.** —Connecticut: Fairfield Co.: Fairfield, 13 Oct 1892, *Eames 2997* (CONN). Hartford Co.: Burnside Mill, 29 Aug 1905, *Weatherby & Driggs s.n.* (CONN); Southington, 41°35′47″N, 72°56′52″W, 27 Aug 1979, *Mehrhoff 2826* (CONN); 27 Jul 1988, *Zebryk 5260* (CONN). Middlesex Co.: Wadsworth Falls State Park, Rockfall, 14 Aug 1986, *Hill 17037* (NY) [**1412; OQ630727**, **OQ630601**, **OQ645639**]; East Hampton, Cobalt Kettle hole N of route. 66, 2 mi W of town line, 25 Aug 1992, *Mehroff 16105* (CONN). New Haven Co.: Guilford, West Lake, 41°20′18″N, 72°43′53″W, 24 Aug 1981, *Mehrhoff 5094* (CONN). New London Co.: N Stonington near mouth of Shunock Brook into Pawcatuck River, 9 Sep 1988, *Tucker 4100* (CONN). —District of Columbia: Kenilworth, 21 Sep 1916, *Tiderstrom 7969* (WIS) [**2143; OQ630728**, n/a, **OQ645640**]. —Florida: Pasco Co.: Big Cypress Swamp, 28.275896°N, 82.407306°W, Aug 1924, *O'Neill 1549* (WIS) [**2415; OQ630729**, n/a, **OQ645641**]. —Indiana: Pike Co.: 2 mi E of Oakland City, 24 Aug 1984, *Yatskievych et al. 84-162* (ARIZ) [**558; OQ630730**, **OQ630602**, **OQ645642**]. —Maryland: Worcester Co.: 1.85 mi S of town of Girdletree, 38.069275°N, 75.401315°W, 9 Aug 1999, *Musselman & Bray 99191* (ODU) [**1457; OQ630731**, **OQ630603**, **OQ645643**]. —Massachusetts: E Sandwich, 26 Aug 1928, *Fernald et al. 480* (MO, WIS). —Minnesota: Houston Co.: Island 7, Mississippi River mile #687, 9 T103N R4W Sec 36, 20 Aug 1975, *Ziegler & Leykoon 2327* (DAO). —Missouri: Butler Co.: W edge of Poplar Bluff, ca. 5 mi NE of junction with County Hwy M of County Rd 450, 28 Aug 1994, *Yatskievych 94-208* (MO); 6 Sep 1993, *Summers 6367* (MO) [**1191; OQ630732**, **OQ630604**, **OQ645644**]. Crawford Co.: Campbell Bridge Public Fishing Access, 38°04′57″N, 91°09′00″W, 28 Sep 2003, *Davidse 39104* (MO); Margin of lakes and swamps, in the "American Bottom" opposite Saint Louis, Sep 1841, *Geyer s.n.* (MO, the type); Margin of lakes, American bottom, opposite St Louis, Aug 1845, *Engelmann s.n.* (MO); Howell Co.: 24 Aug 2004, *Smith 4006* (MO) [**1192; OQ630733**, **OQ630605**, **OQ645645**]. —New Jersey: Mercer Co.: Hightstown, Aug 1915, *MacKenzie 6647* (DUKE). Morris Co.: Morristown, 14 Sep 1974, *Moldenke & Moldenke 28944* (MO). Union Co.: Watchaug ridge, 1 Aug 1977, *Barringer 582* (CONN); Aug 1977, *Barringer 586* (CONN) [**2417; OQ630734**, n/a, **OQ645646**]. —New York: Dutchess Co.: Hyde Park, Vanderbilt Mansion NHS, 41.796535°N, 73.944977°W, 3 Oct 1995, *Glenn 2044* (CONN) [**2159; OQ630735**, n/a, **OQ645647**]; Putnam Co.: Patterson, Croton river, 16 Sep 1989, *Tucker & Zika 5090* (TRTE) [**1243; OQ630736**, **OQ630606**, **OQ645648**]. —North Carolina: Chowan Co.: Along edge of Dillard's mill pond, 7 Sep 1990, *Musselman & Knepper s.n.* (2 specimens ODU) [**1455; OQ630737**, **OQ630607**, **OQ645649**]; Currituck Co., on the Northwest River, 1 mi S of Coleman's Boy's Camp, 8 Oct 1978, *Minkin 57* (ODU) [**2163; OQ630738**, n/a, n/a]. —Rhode Island: Washington Co: Tuckertown, 13 Aug 1987, *Hill 18611* (GH, MO). —Texas: Wood Co.: Lake Ellis, 2 Sep 1942, *Lundell 11721* (BRIT, NY). —Virginia: Virginia Beach City, North Landing River, ca. 0.2 mi N (upstream) of North Landing, 36.719723°N, 76.097442°W, *Clampitt 1149* (ODU) [**2162; OQ630739**, n/a, **OQ645650**].

Cuscuta squamata. USA. —

New Mexico: Chaves Co.: on One Horse Rd., 1–2 mi E of Hwy 285, 33.584328°N, 104.487619°W, 17 Aug 2016, *Stefanović SS-16-76* (TRTE, WLU) [**1693A**; **OQ630751, OQ630619, OQ645664**]; Doña Ana Co.: White Sands Missile Range, 3 mi E of Main Post, E Dry Lake Playa near Range Rd. 3 between LC 33 and C Station, *Anderson & Brice 8057* (NMC) [**740**; EF194434, KJ436716, EF194645]; Valencia Co.: Hwy 314, 1 mi N of Belen, 34° 40′41″N, 106° 46′19″W, 9 Aug 2016, *Stefanović SS-16-50* (TRTE, WLU) [**1667A**; **OQ630752, OQ630620, OQ645665**]. —Texas: Garza Co.: 4.1 mi NW of Post, 5 Jul 1965, *Hutchins 643* (WIS) [**1442**; **OQ630753,** n/a, **OQ645666**].

Outgroups. Cuscuta subsect. *Denticulatae* Yunck. *Cuscuta denticulata* Engelm. USA. —

Nevada: Humboldt Co.: Calico Mountains, foothill area W of main Gerlach-Soldier Meadow Road, 1.6 mi due W of Wagner Spring, 41.138602°N, 119.169972°W, 6 Jul 2000, *Tiehm 13319* (ASU) [**485**; EF194410, KJ436639, EF194627]. ***Cuscuta nevadensis* I.M. Johnst. USA.** —California: *Morefield 2119a* (NY) [**585**; EF194408, KJ436689, EF194630].

Appendix 2. Characters scored for the morphometric study (for details see Costea et al. 2023).

Continuous traits: 1. Flower pedicel length (mm). 2. Flower length — measured from tips of petals to base of receptable (mm). 3. Calyx length (mm). 4. Calyx lobe length (mm). 5. Calyx lobe width (mm). 6. Calyx lobe length to width ratio (mm). 7. Size of overlapping portion between calyx lobes (mm). 8. Calyx tube length (mm). 9. Circumference calyx tube (mm). 10. Corolla length (mm). 11. Corolla lobe length (mm). 12. Corolla lobe width (mm). 13. Corolla lobe length to width ratio (mm). 14. Corolla tube length (mm). 15. Circumference of corolla tube at the base of staminal filaments (mm). 16. Length of infrastaminal scales (mm). 17. Length of free portion of infrastaminal scales (fimbriae not included) (mm). 18. Width at base of infrastaminal scales (mm). 19. Width at middle infrastaminal scales (mm). 20. Width at top infrastaminal scales (mm). 21. Length of bridge infrastaminal scales (mm). 22. Length of longest fimbriae (mm). 23. Number of fimbriae per infrastaminal scale. 24. Stamen filament length (mm). 25. Anther length (mm). 26. Anther width (mm). 27. Length of longest style (mm). 28. Length of shortest style (mm). 29. Length of thickened apical

part/beak (mm). 30. Capsule length (mm). 31. Capsule width (mm). 32. Seed length (mm). 33. Seed width (mm). 34. Hilum scar diameter (mm). 35. Hilum opening length (mm).

Binary traits: 36. Flowers mostly 5-merous: present (1), absent (0). 37. Flowers 4- or 3-merous: present (1), absent (0). 38. At least some calyx lobes acute or subacute: present (1), absent (0). 39. Calyx lobes serrated/irregular: present (1), absent (0). 40. Infrastaminal scales truncate or bifid present (1), absent (0). 41. Additional fimbriae present on the bridge of infrastaminal scales: present (1), absent (0). 42. Tips of fimbriae exerted from corolla tube: present (1), absent (0). 43. Beak present on ovary: present (1), absent (0). 44. Strangulated corolla capping capsule: present (1), absent (0). 45. Corolla somewhat capping capsule but not strangulated: present (1), absent (0). 46. Corolla surrounding most of capsule: present (1), absent (0). 47. Corolla surrounding base of capsule: present (1), absent (0).