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To Lump or to Split? Revision of *Cuscuta* section *Indecorae* Using a Combined Morphometric, Phylogenetic, and Host Range Approach

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Abstract—*Cuscuta* section *Indecorae* is an infrageneric clade of *Cuscuta* subgenus *Grammica* that originated in North America which includes three species: *C. indecora*, *C. coryli*, and *C. warneri*. Some forms of *C. indecora* are agricultural weeds, while *C. warneri* and *C. coryli* face conservation problems regionally or globally. *Cuscuta indecora* is a morphologically diverse species with three recognized varieties: *C. indecora* var. *indecora*, *C. indecora* var. *longisepala*, and *C. indecora* var. *attenuata*. Two recent broad-scale molecular phylogenetic studies raised questions about the circumscription of *C. indecora* and the validity of its infraspecific taxa. Therefore, we conducted an extensive morphometric study, and used DNA sequences from plastid and nuclear ribosomal non-coding regions to reconstruct evolutionary relationships among taxa. In addition, we studied the host range of all taxa using herbarium specimens, bipartite networks, and Venn diagrams. Results from all types of evidence confirmed the circumscription of the three species, but differed on the infraspecific structure of *C. indecora*. The molecular phylogeny inferred *C. indecora* as paraphyletic, consisting of two distinct clades, with *C. coryli* nested within one of them. The morphometric and host range studies uncovered extensive overlaps both among the traditional varieties of *C. indecora* as well as between the two molecular lineages of *C. indecora*. Previously, *Iva annua* had been considered the sole host of *C. indecora* var. *attenuata* (*C. attenuata*) and this presumed host specificity was the main criterion for accepting this taxon. We found that the type of *C. indecora* var. *longisepala* was also growing on *Iva annua*, which together with the morphological and genetical similarity, indicates that *C. indecora* var. *attenuata* is identical to *C. indecora* var. *longisepala*. Overall, considering the lack of morphological, host range, and geographical patterns distinguishing either the current three varieties of *C. indecora* or the two cryptic lineages, the most appropriate solution is to tentatively recognize *C. indecora* as variable species without recognizing any infraspecific taxa.

Keywords—Cryptic speciation, dodder, host specificity, parasitic plants.

Cuscuta section *Indecorae* is part of *C.* subgenus *Grammica* (Yuncker 1921, 1932, 1960; Stefanović et al. 2007; García et al. 2014; Costea et al. 2015b) and is composed of only three North American species (Stefanović et al. 2007; Costea et al. 2015b): *C. warneri* (Warner's Dodder), *C. coryli* (Hazel Dodder), and *C. indecora* (Pretty Dodder, Bigseed Alfalfa Dodder). Two species previously included in *C.* sect. *Indecorae* (Yuncker 1921, 1932, 1965), *C. stenolepis* Engelm. and *C. jepsonii* Yunck., were reassigned to *C.* sect. *Cleistogrammica* and *C.* sect. *Californicae*, respectively (Costea et al. 2015b) based on phylogenetic results (Stefanović et al. 2007; García et al. 2014). This small clade is both economically and ecologically important. Some forms of *C. indecora* are noxious weeds (see below) while *C. warneri* and *C. coryli* are of conservation concern regionally or globally (Argus and Pryer 1990; Costea et al. 2006; IUCN 2012; NatureServe 2024).

Cuscuta warneri was described by Yuncker (1960) based only on the type collections made by Lloyd Warner in 1957 from Utah, USA, which were considered a teratological form of *C. indecora* by Beliz (1986). Subsequent morphological (Costea et al. 2006; Clayson et al. 2014) and molecular studies (Stefanović et al. 2007; García et al. 2014) showed that *C. warneri* is a distinct species. *Cuscuta warneri* is currently considered Critically Imperiled in New Mexico and possibly Extirpated in Arizona and Utah (reviewed by NatureServe 2024).

Cuscuta coryli was described by Engelmann (1842), and although it was regarded by Beliz (1986) as a variety of *C. indecora* (without effective publication), it has not been deemed taxonomically problematic (Yuncker 1921, 1932, 1965; Costea et al. 2006; Costea and Nesom 2023). *Cuscuta coryli* does not attack crops and is currently considered Critically Imperiled in several Canadian Provinces and American States (Burt et al. 2021; reviewed by NatureServe 2024).

In contrast to the previous two species, *C. indecora* has had a complicated taxonomic history due to extensive morphological variation across a broad geographical distribution (Engelmann 1842, 1843, 1859; Yuncker 1921, 1932, 1965; Costea et al. 2006). Multiple species and varieties were gradually merged within *C. indecora* and then synonymized within the infraspecific autonym, *C. indecora* var. *indecora* (Yuncker 1921, 1932, 1965; Costea et al. 2006). Yuncker (1921) described *C. indecora* var. *longisepala*, with lanceolate calyx lobes. *Cuscuta attenuata* (Tapertip dodder), a relatively recent species (Waterfall 1971), was subsequently shown to be morphologically similar to *C. indecora*, but was maintained either as a distinct species (Prather et al. 1995) or as a variety of *C. indecora* (Costea et al. 2006) because of its alleged host specificity to *Iva annua* L. and putative reproductive barriers separating it from *C. indecora* (Prather 1990). In its most recent taxonomic interpretation, *C. indecora* was circumscribed to include three varieties: *C. indecora* var. *indecora*, *C. indecora* var. *longisepala*, and *C. indecora* var. *attenuata* (Costea et al. 2006; Costea and Nesom 2023).

Cuscuta indecora var. *indecora* is the most common form, distributed from southern Canada to South America (Yuncker 1921, 1932, 1965; Hunziker 1950; Costea et al. 2006), where it parasitizes numerous hosts, and it is sometimes an agricultural pest, especially in fields of *Medicago sativa* L. (Alfalfa) (Parodi 1936; Hunziker 1950; Orloff et al. 1989; Cudney et al. 1992). *Cuscuta indecora* var. *longisepala* is found from southern USA to South America, and on the latter continent was also reported as a pest of alfalfa (Parodi 1936; Hunziker 1950). Finally, *Cuscuta indecora* var. *attenuata* is known only from Kansas, Texas, and Oklahoma, USA, where it is considered nationally Imperiled (reviewed by NatureServe 2024).

Two broad-scale phylogenetic studies of *Cuscuta* subgenus *Grammica* and the entire genus *Cuscuta* using multiple DNA sequences (*trnLF*, nrITS, *rbcL*, and nrLSU) confirmed that *C.* sect. *Indecorae* (excluding *C. stenolepis* and *C. jepsonii*), is monophyletic with very strong support in both studies (Stefanović et al. 2007; García et al. 2014). In contrast, the relationships within *C.* sect. *Indecorae* varied between studies, and received substantially weaker support. In the phylogeny of *C.* subgenus *Grammica* (Stefanović et al. 2007), *C. warneri* was sister to *C. indecora*, and *C. coryli* was nested within the latter (Stefanović et al. 2007). In the whole genus phylogeny (García et al. 2014), both *C. warneri* and *C. coryli* were nested within *C. indecora*, with *C. indecora* var. *indecora* rendered polyphyletic. Although these results were based on a very limited sampling, especially of *C. indecora*, they strongly suggested that the current delimitation of *C. indecora* and its varieties should be reevaluated.

The main goal of this study is to resolve relationships within *C.* section *Indecorae*, especially of *C. indecora*, and to revise taxonomy by redefining, if necessary, the boundaries of taxa. To achieve this goal, the following objectives were pursued: 1) conducting an extensive morphometric study to assess morphological variation patterns; 2) generate an updated molecular phylogeny based on additional sampling to infer evolutionary relationships; and 3) carry out a host range study to compare host preferences with the morphological variation and phylogenetic relationships.

Materials and Methods

Taxon Sampling—1402 herbarium specimens from 108 herbaria were examined and annotated for basic morphology, host range, geographical distribution, and habitat occurrence. Moreover, we conducted a series of targeted field surveys between 2016–2023 for species of *C.* sect. *Indecorae* in the U.S.A, and between 2021–2022 for *C. coryli* in Ontario, Canada.

For the morphometric analyses, 188 herbarium specimens were used: one *Cuscuta warneri*, 14 *C. coryli*, 14 *C. indecora* var. *attenuata*, 100 *C. indecora* var. *indecora*, 25 *C. indecora* var. *longisepala*, and 34 specimens that after examination appeared to be morphologically intermediate between *C. indecora* var. *indecora* and *C. indecora* var. *longisepala* (Appendix 1; see Results). For the molecular studies, 114 specimens were sampled (Table 1). Compared to our previous broad-scale studies (Stefanović et al. 2007; García et al. 2014), population-level sampling across all taxa within *C.* sect. *Indecorae* was greatly improved to accurately capture the morphological diversity and geographical range distribution. In addition to 15 DNA samples used previously (Stefanović et al. 2007), total genomic DNA was isolated from 99 newly obtained specimens, focusing especially on representatives of different putative *C. indecora* varieties (Appendix 1). A previous more inclusive phylogenetic analysis indicated that the first split within *C.* sect. *Indecorae* occurs between *C. warneri* on one side, and the remainder of this section on the other (Stefanović et al. 2007; their Fig. 4). Hence, in our analyses we used individuals belonging to *C. warneri* as a functional outgroup, allowing for the full usage of all available plastid and nuclear sequence data within *C.* sect. *Indecorae*.

Morphology and Morphometric Analyses—A total of 47 morphological characters (Appendix 2) were selected based on previous work in *C.* sect. *Indecorae* (Costea et al. 2006) and six genus-wide character evolution studies of *Cuscuta* flowers, infrastaminal scales, gynoecium, fruits, and seeds (Wright et al. 2011, 2012; Riviere et al. 2013; Ho and Costea 2018; Olszewski et al. 2020). In addition, the characters used in morphometric studies conducted in other sections of *C.* subg. *Grammica* were considered (Costea et al. 2009, 2015a, 2020, 2023; Costea and Stefanović 2010; García et al. 2018; Appendix 2).

Flowers and fruits were rehydrated by gradually warming herbarium plant material in a solution of 50% ethanol and 50% de-ionized water until it was brought to the boiling point. Ethanol was used in the rehydration process to harden plant tissues and to protect the fragile corollas and infrastaminal scales during dissections. Calyces and corollas were dissected, flattened, and together with the gynoecia and capsule/seeds were examined with a Nikon SMZ1500 stereomicroscope and imaged/measured with a PaxCam Arc digital camera equipped with Pax-it! 2 version 1.5.1.0 imaging software (MIS Inc, Villa Park, IL). Pollen of all the specimens was also examined using the scanning electron microscopy methodology from Welsh et al. (2010). However, the pollen data (not shown) were uniform among taxa and therefore not included in the morphometric analysis. 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).

The extent of morphological variation was visualized with both principal coordinates analysis (PCoA or multidimensional scaling) and unweighted pair-group average (UPGMA), using the Gower's coefficient of similarity (Gower 1971). PCoA and Gower's coefficient were used because the primary dataset contained a combination of binary, multistate qualitative and quantitative characters, as well as missing data resulted especially from the absence of capsules and seeds in many of the herbarium specimens (e.g. Marhold 2011; Costea et al. 2023). A second dataset was obtained after the removal of the specimens with missing data. Analyses were conducted on both datasets using PAST software (version 4.09; Hammer et al. 2009). Morphometric data generated in the study were deposited in Dryad (Burt et al. 2024, File 1).

Molecular Phylogenetic Analyses—To infer the phylogenetic relationships among the members of *C.* sect. *Indecorae*, sequences from two plant genomes were used. We targeted a non-coding *trnLF* region from the plastid genome (ptDNA) as well as sequences from the internal

Table 1. Summary descriptions for sequences included in and trees derived from data sets of *Cuscuta* sect. *Indecorae*. CI = consistency index (excluding parsimony uninformative characters); G = rate variation among nucleotides following a discrete gamma distribution; F81 = Felsenstein 1981 model of DNA evolution; I = proportion of invariable sites; OTU = operational taxonomic unit; RI = retention index; RSA = random sequence addition; HKY85 = Hasegawa-Kishino-Yano 1985 model of DNA evolution; TBR = tree bisection and reconnection.

Description	*trnLF*	nrITS
Number of OTUs included	114	44
Sequence characteristics:		
Analyzed length[a]	453	574
Number of coded gaps[b]	11	5
Variable sites[b]	24	81
Parsimony informative sites[b]	21	76
Mean AT content (%)	63	53
MP search and tree characteristics:		
Algorithm	Full heuristic	Two-stage heuristic
RSA/branch swapping/MULTREES	1000/TBR/on	100,000/TBR/off; Memory/TBR/on
Number of trees	164	>1,000,000
Length	28	86
CI/RI	0.929/0.992	0.977/0.997
ML search and tree characteristics:		
Model of DNA evolution (gaps)	F81 + G+I (Mkv)	HKY85 (Mkv)
-ln*L*	732.405	1245.433

[a] Excluding portions of the alignment spanning primer regions and ambiguously aligned regions

[b] Including coded gaps

transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA). Total genomic DNA was isolated from newly obtained specimens (Appendix 1). DNA extractions, polymerase chain reaction (PCR) reagents and conditions, amplicon purifications, cloning, and sequencing procedures follow Stefanović et al. (2007). The sequences generated in this study have been submitted to GenBank accession numbers PQ232221–PQ232319 (*trnLF*) and PQ205355–PQ205385 (ITS)]. Newly obtained sequences were incorporated into previously aligned matrices (Stefanović et al. 2007). Gaps in the alignments were treated as missing data; however, we manually coded gaps as binary characters and appended them to the sequence matrix. Phylogenetic analyses were conducted under maximum parsimony (MP) and maximum likelihood (ML) criteria.

For parsimony searches, characters (both nucleotide and coded gaps) 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 100,000 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). The Markov k-state (Mkv) model, a generalized JC69 model, allowing any changes to be equally probable (Lewis 2001), was used for the indel partition for both plastid and nuclear datasets. We used the same model of evolution, and 1000 rapid bootstrap replicates to assess branch support.

Host Range Assessment—Out of the 1402 specimens examined in the study, 964 included host plants that could be identified at species, genus or family level (Burt et al. 2024, File 2). "False" hosts, used by dodders only for support, were eliminated based on the lack of haustorial penetration, as observed under a Nikon SMZ1500 stereomicroscope. Host data were used to generate a host frequency indicator (HFI) at each taxonomic level (family, genus, species; García et al. 2018; Costea et al. 2020). The HFI shows the frequency (percentage) of a *Cuscuta* taxon to be encountered on a particular host (at family, genus, and species level), in relation to the total number of host occurrences. Thus, HFI can also be considered an indirect measure of the host preference; the host taxa with higher HFI values are also those that are more preferred. In some cases, host identification was possible only at genus level, but their HFI values were kept in the species level dataset (as Genus "sp.") to avoid the distortion of HFI values. HFI data were mapped into a directed bipartite network using Cytoscape (Shannon et al. 2003) to visualize host range and frequency of occurrence across taxa of *C.* sect. *Indecorae*. In *C. indecora*, only the hosts of specimens that could be unambiguously assigned to a variety were included. To visualize the numbers of shared versus unique hosts, Venn diagrams were also generated for the entire dataset using InteractiVenn (Heberle et al. 2015). Host data generated in the study were deposited in Dryad (Burt et al. 2024, File 2).

Finally, based on the same specimens used for the host range, we verified geographical distributions and general habitat information.

RESULTS

Morphology and Morphometric Analyses—Overall, PCoA analyses showed a distinct separation of three groups of specimens that corresponded to *C. warneri*, *C. coryli*, and *C. indecora* s.l., but overlap was evident among the infraspecific taxa of *C. indecora* (Fig. 1A–B). In the PCoA of the entire dataset, coordinate 1 accounted for 41.21% of the variation and separated *C. indecora* sensu lato (s.l.) from *C. coryli* and *C. warneri*. Coordinate 2 accounted for 32.27% of the variation and separated *C. coryli* from *C. warneri*. A continuous gradient of calyx lobe morphology was observed across the variation spectrum of the three infraspecific taxa of *C. indecora*, which ranged from short, triangular-ovate to long, attenuate calyx lobes (Fig. 2). Thirty-four specimens of *C. indecora* possessed an intermediate calyx morphology, and therefore confident identification to variety level was not possible (Fig. 2). Such specimens were labeled as *C. indecora* "intermediate" (marked with an asterisk in Appendix 1). There was no separation between *C. indecora* var. *attenuata* and *C. indecora* var. *longisepala*. While there was a divergence trend between *C. indecora* var. *indecora* and the other two varieties, overlap was also present, and in addition, all the "intermediate" specimens fell in between the three varieties making their separation impossible (Fig. 1A). It is relevant to note that some of the *C. indecora* "intermediate" specimens had received conflicting infraspecific identifications on their duplicates found in different herbaria, which confirms their ambiguous morphological nature.

In the analysis of the second dataset (with major gaps removed; Fig. 1B), coordinate 1 accounted for 21.98% of the variation and separated *C. indecora* s.l. from *C. coryli* and *C. warneri*. Coordinate 2 accounted for 8.90% of the variation. All infraspecific ranks of *C. indecora*, as well as the *C. indecora* "intermediates" were inseparable from one another (Fig. 1B). The two putative cryptic lineages observed in *C. indecora* s.l. by the molecular study (clades 1 and 2; see below) were also not apparent in the morphological variation.

UPGMA results mirrored to those of the PCoA. *Cuscuta warneri* was the most dissimilar. *Cuscuta coryli* formed as a distinct subcluster adjacent to the large cluster of *C. indecora* (Figs. S1, S2). The dendrogram based on the entire dataset (Fig. S1; cophenetic correlation = 0.7949) displayed extensive overlaps between the infraspecific taxa of *C. indecora*, and did not produce any subclusters that would correspond either to the three varieties or to the cryptic lineages revealed by the molecular study. Similar results were obtained in the dendrogram that excluded the specimens with major gaps in their data (Fig. S2; cophenetic correlation = 0.83).

Molecular Phylogeny—Summary descriptions for sequences obtained from *trnLF* and nrITS regions are presented in Table 1. The *trnLF* region was readily amplifiable and sequenceable across the sampling, yielding results for 114 individuals. Amplicons could not be obtained from a few older herbarium specimens, including efforts to amplify the fragments in two parts, presumably due to the poor quality of the DNA extracted from those samples. The success of amplification for the nrITS was comparable to that of *trnLF*. However, because of multiple poly(A/T) tracts found in this nuclear region, and 'slippage' during sequencing reaction when DNA polymerase reaches simple sequence repeats (> 15 bp), usable ITS sequences were obtained only from 44 individuals. This represents approximately 40% of the specimens sequenced for *trnLF*, but they are randomly distributed throughout the sampling, and hence unlikely to bias the phylogenetic results. Surprisingly, the *trnLF* sequences showed quite low variability, with only 13 sequence sites being polymorphic (2.87%). Inclusion of 11 coded gaps somewhat increased variability, to 5.3%. This contrasts with the nrITS sequences that showed much higher variability, with 13.25% and 14.11% of variable characters, without and with five indels included, respectively.

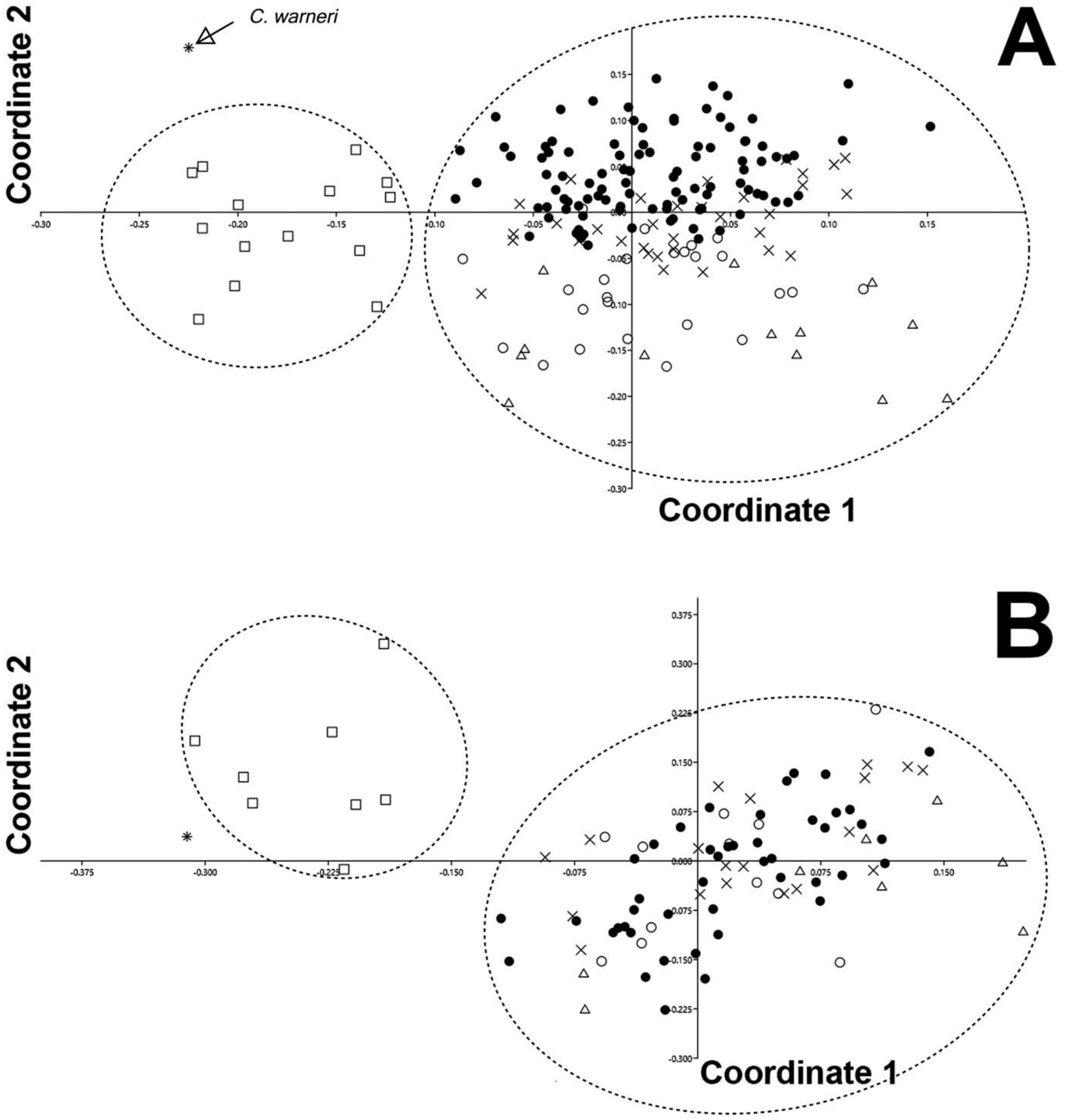

FIG. 1. Principal coordinates analysis (PCoA) of taxa in *Cuscuta* sect. *Indecorae*. A. The complete dataset of specimens. Coordinate 1 accounted for 41.21% of the variation and coordinate 2 accounted for 32.27% of the variation. B. Dataset where specimens with significant gaps in measurements were removed. Coordinate 1 accounted for 21.98% of the variation and coordinate 2 accounted for 8.90% of the variation. Star = *C. warneri*; squares = *C. coryli*; black circles = *C. indecora* var. *indecora*; hollow circles = *C. indecora* var. *longisepala*; triangles = *C. indecora* var. *attenuata*; × = *C. indecora* specimens with intermediate morphology that could not be assigned to one of the varieties.

Several preliminary phylogenetic analyses were conducted using parsimony to explore the distribution of phylogenetic signal in the different individual matrices, with and without coded gaps (results not shown). Summary descriptions trees derived from individual datasets are presented in Table 1. For all analyses, the strict consensuses of equally parsimonious trees (not shown) resulted in relationships that were topologically identical or nearly identical to the respective results derived under the ML criterion (Figs. 3, S3). Given the distribution of phylogenetic signal, it is not surprising that in this study the bulk of results on evolutionary relationships among species and individuals of *C.* sect. *Indecorae* comes from the nrITS sequences (Fig. 3).

Four well-defined lineages are delimited on the nrITS tree, based on a combination of their strong individual support (93–100% BS) and molecular distinctiveness, as evidenced by

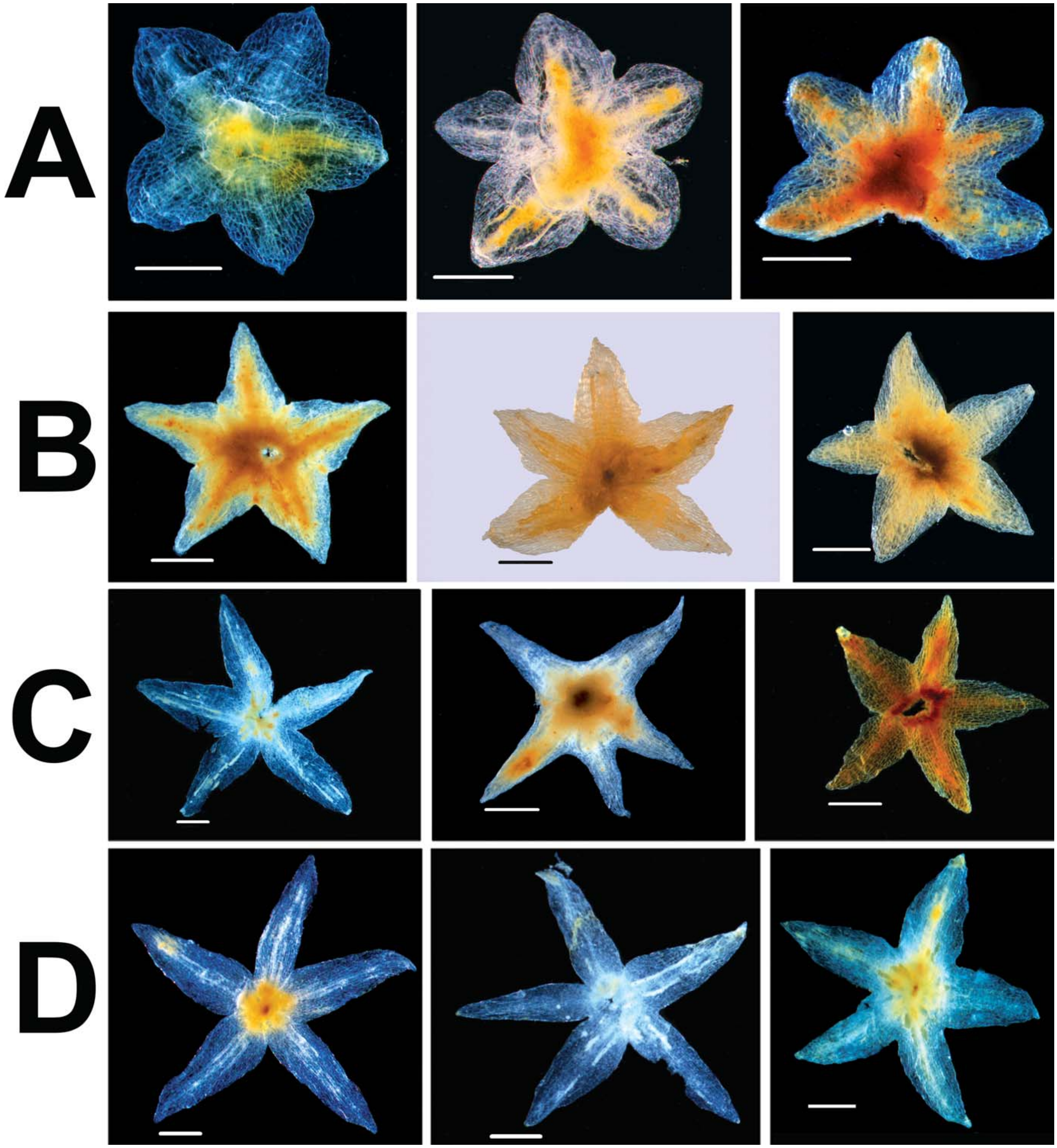

FIG. 2. Variation of calyx morphology among the infraspecific taxa of *Cuscuta indecora*, including those with intermediate morphology. Row A = *C. indecora* var. *indecora*; Row B = specimens with intermediate morphology; Row C = *C. indecora* var. *longisepala*; Row D = *C. indecora* var. *attenuata*. Scale bars = 1 mm.

the substantial length of branches subtending them. Two of those lineages correspond to two morphologically accepted species, *C. warneri* and *C. coryli*, both of which have achieved reciprocal monophyly. The other two lineages (labeled as clades 1 and 2 in Fig. 3) both contain individuals attributed to *C. indecora* s.l. Using *C. warneri* as functional outgroup, *C. coryli* is found nested within one of these two lineages, specifically as sister of *C. indecora* clade 1 with 100% BS, thereby rendering *C. indecora* paraphyletic. It should be noted that any alternative rootings of this phylogenetic network resulted in *C. indecora* paraphyly. These two clades of *C. indecora* do not correspond to any of the infraspecific taxonomic or geographic subdivisions previously proposed for this species. At the species level, these molecular results further corroborate our findings based on morphology (e.g. compare with Figs. 1, S1, and S2), and are also consistent with both morphological

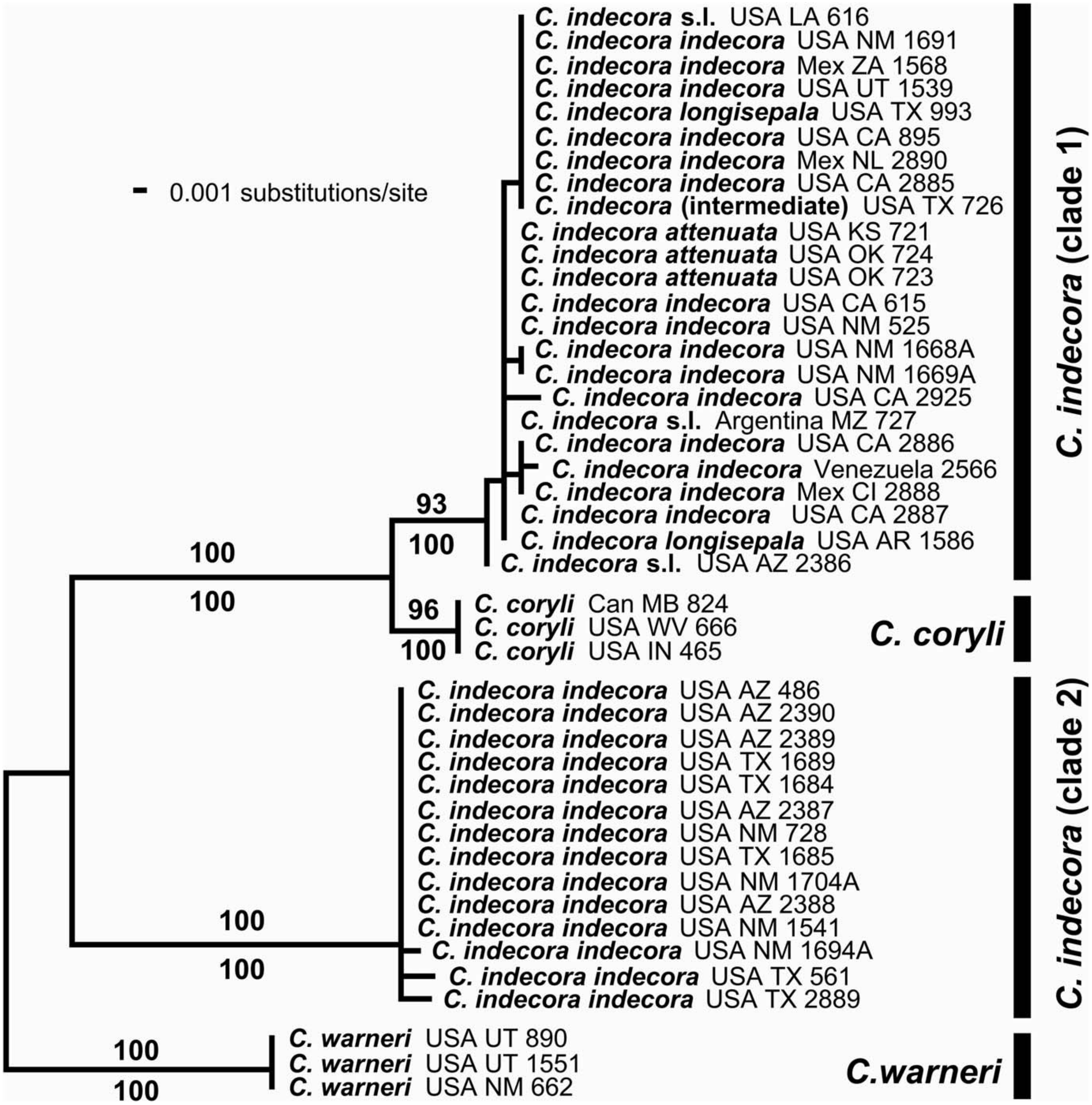

FIG. 3. Phylogram resulting from the partitioned maximum likelihood analysis of nuclear ribosomal ITS sequence data showing relationships among species and individuals of *Cuscuta* sect. *Indecorae*. The tree is rooted using *C. warneri* as functional outgroup. Bootstrap values (MP above and ML below branches) are indicated for nodes supported at ≥ 70%. Species names are followed by abbreviations of countries and states/provinces in which they were collected, and their DNA accession numbers (Appendix 1).

as well as phylogenetic species concepts, which allows for paraphyletic species (see Coyne and Orr 2004 and references therein).

In contrast, the backbone relationships on the *trnLF* tree (Fig. S3) were essentially unresolved and unsupported. Only two lineages received moderate to strong support, *C. coryli* and *C. warneri*. Albeit unsupported, this tree also shows *C. indecora* as paraphyletic, with *C. coryli* nested among its individuals. Despite the lack of phylogenetic signal from the *trnLF* data, this phylogeny is fully compatible with the relationships inferred from the nrITS sequences, on which our all our further discussions are based.

Host Range—The host range of all taxa within *C.* sect. *Indecorae* included 66 families, 223 genera, and 362 species. A summary of the most frequent (top five) hosts for each taxon within the section is provided in Table 2. *Cuscuta indecora* var. *indecora* had the largest host range, parasitizing 56 families, 185 genera, and 280 species (Figs. 4, 5, S4, S5). *Cuscuta warneri* had the smallest host range, parasitizing only two families, two genera, and three species (Figs. 4, 5, S4, S5). *Cuscuta warneri* was previously

TABLE 2. Top five host plants of taxa in section *Indecorae* based on the Host Frequency Index (HFI) at family, genus, and species-level. HFI is the % of the number of instances a *Cuscuta* taxon was found on each of the hosts (at family, genus, species levels) from the total number of host occurrences recorded for that particular *Cuscuta* taxon. Identification of the hosts to species was not possible sometimes, but these specimens were included in the species level analyses as Genus "sp.", to avoid a distortion of the HFIs.

Parasite	Host Family	HFI	Host Genus	HFI	Host Species	HFI
C. indecora var. *indecora*	Asteraceae	41.59	*Medicago* L.	10.70	*Medicago sativa* L.	10.70
	Fabaceae	29.71	*Ambrosia* L.	7.67	*Ambrosia sp.*	3.83
	Amaranthaceae	3.33	*Iva* L.	3.35	*Iva frutescens* L.	2.40
	Convolvulaceae	2.46	*Symphyotrichum* Nees	3.35	*Symphyotrichum* sp.	2.24
	Polygonaceae	2.03	*Solidago* L.	3.04	*Xanthium* sp.	2.08
C. indecora var. *attenuata*	Asteraceae	100.00	*Iva* L.	90.91	*Iva annua* L.	86.36
			Symphyotrichum Nees	4.55	*Iva* sp.	4.55
			Verbesina L.	4.55	*Symphyotrichum* sp.	4.55
					Verbesina sp.	4.55
C. indecora var. *longisepala*	Asteraceae	38.46	*Medicago* L.	32.61	*Medicago sativa* L.	32.61
	Fabaceae	34.62	*Baccharis* L.	8.70	*Iva annua* L.	8.70
	Bignoniaceae	3.85	*Iva* L.	8.70	*Baccharis* sp.	6.52
	Primulaceae	3.85	*Ambrosia* L.	4.35	*Ambrosia* sp.	4.35
	Solanaceae	3.85	*Primula* L.	4.35	*Primula* sp.	4.35
C. coryli	Asteraceae	53.06	*Solidago* L.	19.05	*Solidago* sp.	7.94
	Fabaceae	8.16	*Symphyotrichum* Ness	11.64	*Helianthus* sp.	6.88
	Lamiaceae	6.12	*Helianthus* L.	11.11	*Symphyotrichum* sp.	6.35
	Betulaceae	5.61	*Corylus* L.	5.82	*Desmodium* sp.	4.23
	Rhamnaceae	3.57	*Desmodium* Desv.	5.29	*Helianthus divaricatus* Michx.	3.70
C. warneri	Verbenaceae	80.00	*Phyla* Lour.	80.00	*Phyla cuneifolia* (Torr.) Greene	60.00
	Fabaceae	20.00	*Medicago* L.	20.00	*Phyla nodiflora* (L.) Greene	20.00
					Medicago sativa L.	20.00

reported to only parasitize the genus *Phyla*; however, a hitherto overlooked Fabaceae host in one of the isotype specimens was identified in this study as *Medicago sativa*.

No single family, genus, or species was shared by all the taxa of *C.* sect. *Indecorae* (Figs. 4, 5, S4); however, there are several notable instances of overlap at different taxonomic levels. At the family-level, Asteraceae was an important component of the HFI for all taxa excluding *C. warneri*, as was Fabaceae for all taxa except *C. indecora* var. *attenuata* (Table 2; Figs. S4, S5). At the genus-level, *Medicago* comprised a large portion of the HFI for all taxa apart from *C. indecora* var. *attenuata* (Table 2; Figs. 4, S4). At the species-level, *Medicago sativa* represented a high percentage of the HFI of all taxa except for *C. indecora* var. *attenuata* (Table 2; Figs. 5, S5).

Comparing strictly the infraspecific taxa of *C. indecora*, at the family-level, Asteraceae are the most common hosts for all three varieties (Table 2; Fig. S6). Fabaceae are shared by *C. indecora* var. *indecora* and *C. indecora* var. *longisepala*, but not by *C. indecora* var. *attenuata* (Table 1; Fig. S6). At the genus-level, *Iva* is a common host of all three varieties (Table 2; Figs. 4, S6). *Symphyotrichum* is parasitized by *C. indecora* var. *indecora* and *C. indecora* var. *attenuata*, but it is absent from the host range of *C. indecora* var. *longisepala* (Table 2; Fig. 4). No single species was shared among the host ranges of the three intraspecific taxa of *C. indecora* (Table 2; Fig. 5). *Iva annua* was the dominant host of *C. indecora* var. *attenuata* and was a major component of *C. indecora* var. *longisepala* HFI, but it was absent from the host range of *C. indecora* var. *indecora* (although *Iva frutescens*, closely related to *I. annua*, made up 2.4% of *C. indecora* var. *indecora* HFI; Table 2; Fig. 5). *Cuscuta indecora* var. *attenuata* was also encountered on an unidentified species of *Verbesina*.

The type specimen of *C. indecora* var. *longisepala* was found in this study to be growing on *Iva annua*, a host that was unknown for this variety. This is important because the host specificity to *Iva annua* had remained the sole (extrinsic) trait used to separate *C. indecora* var. *attenuata* from *C. indecora* var. *longisepala* (Costea et al. 2006) or *C. attenuata* from *C. indecora* (Prather 199; Prather and Tyrl 1993; Prather et al. 1995).

DISCUSSION AND TAXONOMIC TREATMENT

The taxonomic changes proposed by this study supersede the recent taxonomic treatment of *Cuscuta* in volume 14 of Flora of North America (FNA; Costea and Nesom 2023) whose publication was delayed since 2017 when these results were not available.

Cuscuta warneri—Our results confirmed that *C. warneri* is a distinct species (Yuncker 1960; Costea et al. 2006; Stefanović et al. 2007; García et al. 2014). Morphologically, this is one of the most striking *Cuscuta* species (in general), easily distinguishable by its pronounced horn-like projections with stomata on the calyx lobe apices and collar-like apex of the capsule; (Fig. S7). Stomatiferous projections (SPs) in this species are among the largest in *Cuscuta* (reviewed by Clayson et al. 2014). SPs on the perianth have evolved multiple times in different clades of *Cuscuta* subg. *Grammica* in species that grow in arid climates (reviewed by Clayson et al. 2014). Water loss through the SPs stimulates the hosts to absorb more water by increasing the negative pressure/tension in the xylem of the host, via the haustoria connection (Clayson et al. 2014).

Cuscuta warneri is currently known only from three collections: one in Utah (*Warner s.n.*, the type with ca. 30 isotypes) and two in New Mexico (*Spellenberg 13890*, BRIT, NMC, NY, WLU; *Peterson 98–699* NMC). Our extensive search at and near the type locality (Flowell, Millard Co., Utah) in Sep 2023 failed to rediscover this species, although the suitable alfalfa host (*Medicago*, Fabaceae) was present. Also, an earlier report from Arizona (Correll and Correll 1972) was not substantiated by herbarium vouchers, and has not been found again in the wild since the original report (Kartesz 2018). Thus, the Critically Imperiled conservation status mentioned in the introduction for this species is more than justified.

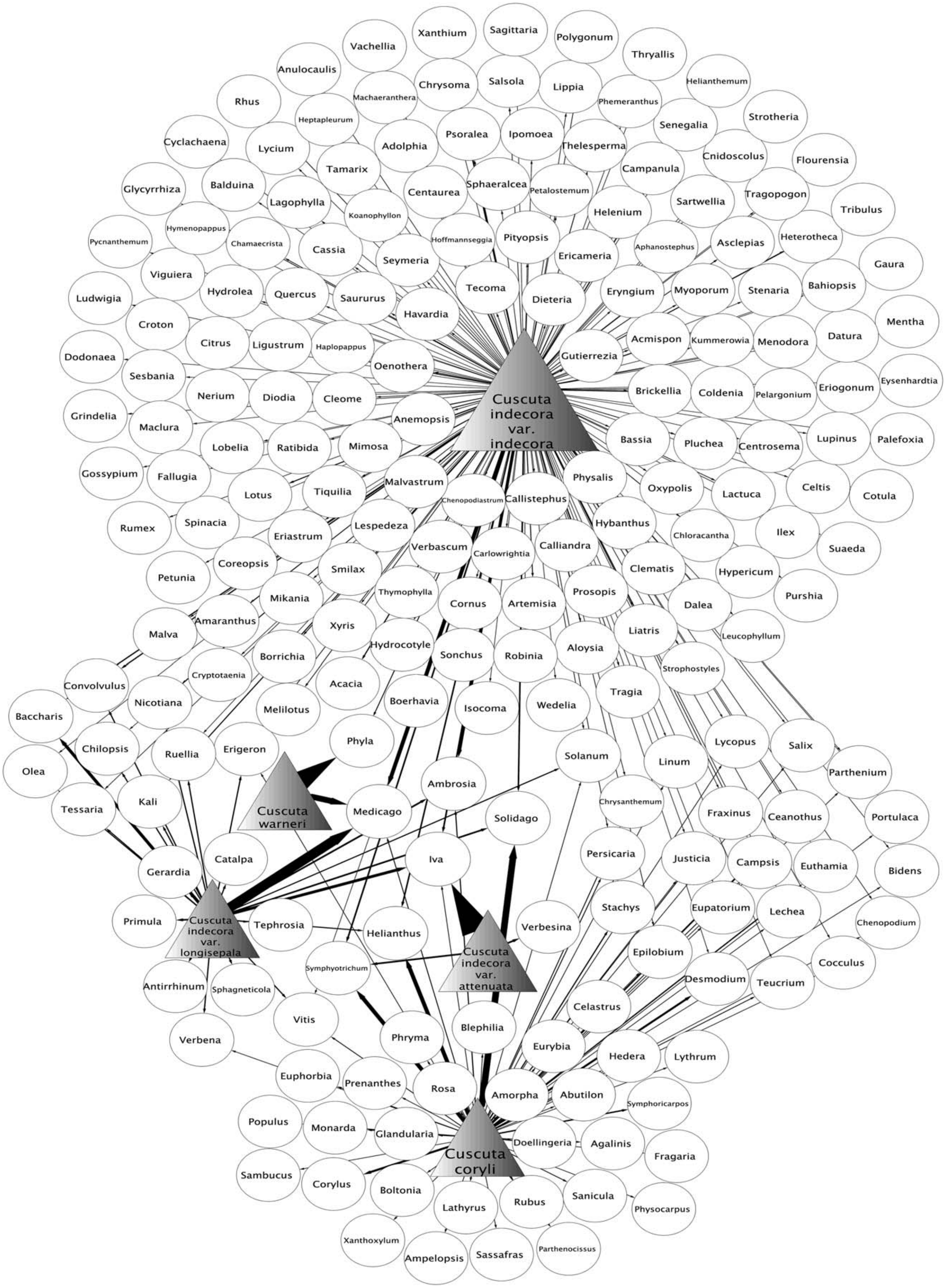

FIG. 4. Genus-level host range of taxa in *Cuscuta* sect. *Indecorae* visualized as a directed bipartite network. Taxa within *Cuscuta* section *Indecorae* (represented as triangles) are the main nodes connected to the corresponding nodes of their hosts (represented as circles). Frequency of each *Cuscuta* taxon-host genus association is indicated by the proportionally thickened edges (lines) using the host-frequency indicator (HFI). The common or distinct edges (lines) directed toward the host nodes indicate the amount of overlap or separation, respectively of corresponding *Cuscuta* taxa host range.

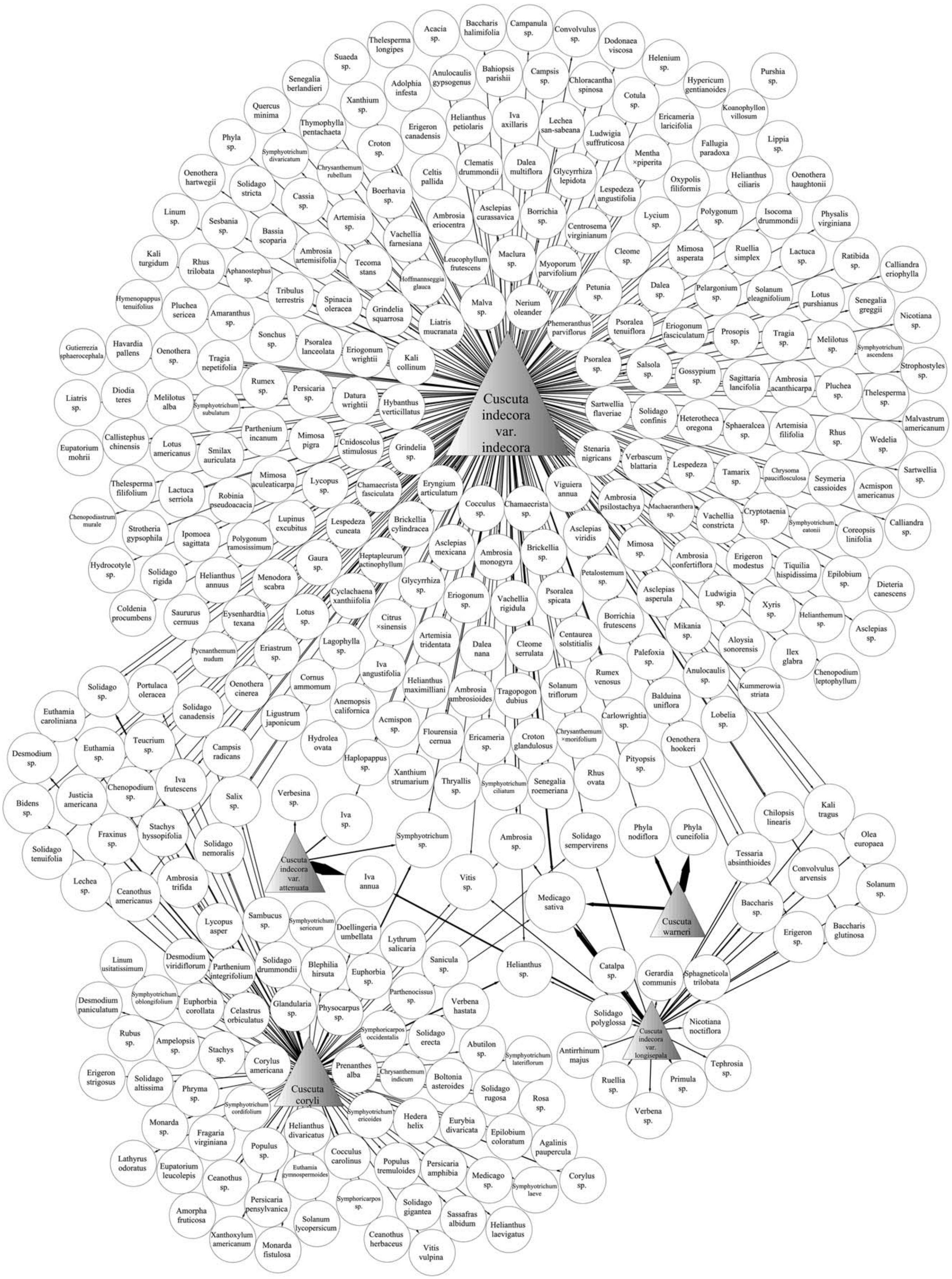

FIG. 5. Species-level host range of taxa in *Cuscuta* sect. *Indecorae* visualized as directed bipartite network. Taxa within *Cuscuta* section *Indecorae* (represented as triangles) are the main nodes connected to the corresponding nodes of their host species (represented as circles). Hosts that could not be identified to species level were kept in the dataset and indicated as Genus "sp." Frequency of each *Cuscuta*-host species association is indicated by the proportionally thickened edges (lines) using the host-frequency indicator (HFI). Shared edges (lines) between host nodes indicate overlaps between their host ranges, while single edges show unique host-parasite interactions.

Cuscuta coryli—This species is similar to *C. indecora* but morphometric results consistently differentiated the two species. Hazel dodder has smaller flowers, erect corolla lobes, and (often) bifid infrastaminal scales or with fewer fimbriae (See also Identification Key; Figs. S8, S9). Phylogenetic results showed that *C. coryli* formed a distinct clade (Fig. 1) sister to one of the two lineages of *C. indecora*, suggesting that *C. coryli* is derived from within *C. indecora*.

The divergence of C. *coryli* may be related to a shift of its breeding system in tandem with a segregation on a different host range. Based on Cruden's breeding system categories (Cruden 1977), *C. coryli* is facultatively autogamous, while in *C. indecora* s.l. is facultatively xenogamous (Wright et al. 2012). Also, despite the fact that *C. indecora* s.l. has a much broader host range, *C. coryli* has 67 species unique to its host range, especially among woody plants (Table 2; Fig. 5). The speciation of *C. coryli* may also be related to the peculiar cytogenomic makeup of *C. indecora* s.l. (see below) with which *C. coryli* shares the same number of chromosomes ($n = 15$; Fogelberg 1938; García et al. 2019; Ibiapino et al. 2020).

The evolution of *C. coryli* within *C. indecora* renders the latter paraphyletic. While the autapomorphic species concept and its proponents may refute the idea of a species that is not monophyletic (Mishler and Brandon 1987; Mishler and Budd 1990; Ebach et al. 2006; Schmidt-Lebuhn 2012), instances of paraphyletic species have been widely documented in vascular plants (e.g. Rieseberg and Brouillet 1994; Crisp and Chandler 1996; Amico et al. 2007; Amico and Nickrent 2009; Hörandl and Stuessy 2010; Stuessy 2010; Carnicero et al. 2019; Kato et al. 2019). Together with the cryptic lineages revealed within *C. indecora* s.l. (see below), *C. coryli* represents an ideal system to study speciation in *Cuscuta*. A future line of investigation would be to explore the role of different classes of repetitive DNA and associated cytogenetic changes in the cladogenesis (e.g. Ibiapino et al. 2020, 2022; Vondrak et al. 2021) together with the host range segregation and shifts in the breeding system.

The Separation of Currently Accepted Varieties of C. indecora Is Not Feasible—The extensive morphological overlap among the infraspecific taxa of *C indecora* s.l., together with the molecular results agree that their current separation is impossible to justify and maintain. *Cuscuta indecora* var. *longisepala* and *C. indecora* var. *attenuata* are morphologically similar, and together they form an intergrading morphological continuum with *C. indecora* var. *indecora* in which only the extreme calyx lobe shape variations are recognizable. Large geographic overlaps also occur between the morphotypes with different calyx lobe shapes, and in some cases, forms corresponding to all three varieties co-occur within the same state in the USA. Host range overlaps exist as well, but the most common form in North and South America (corresponding to *C. indecora* var. *indecora*) has by far the most extensive host range and therefore unique hosts (Figs. 5, S6). Both typical and narrow calyx lobe morphotypes have been introduced to new areas (e.g. South America) via contaminated *Medicago sativa* seeds (Parodi 1936; Hunziker 1950; Orloff et al. 1989; Cudney et al. 1992), and thus *C. indecora* s.l. added new plants to their host range. The geographical range of *C. indecora* has also expanded beyond the Americas. There are unpublished new records based on herbarium specimens from Belgium, Morocco, and Greece (Miguel García, personal communication). Finally, there was no correspondence between the morphological variation and the two lineages revealed by the molecular phylogeny.

As indicated in the introduction, *C. indecora* var. *attenuata* is currently considered nationally Imperiled in the USA. (reviewed by NatureServe 2024). In this study, we have shown that the alleged host specificity of *C. indecora* var. *attenuata* to *Iva annua* is artificial since *C. indecora* var. *longisepala* is also growing on this host. Also, *C. indecora* var. *attenuata* has also been found in this study growing on *Symphyotrichum* sp., *Verbesina* sp., and it was successfully grown on "*Coleus hybridus*" (Prather and Tyrl 1993).

The only argument left in favor of preserving *C. indecora* var. *attenuata* was its alleged reproductive barrier with *C. indecora* var. *indecora* and *C. indecora* var. *longisepala* (Prather et al. 1995). *Cuscuta attenuata* had been reported to be self-fertile by Prather and Tyrl (1993). In the hybridization experiments conducted (Prather et al. 1995), no control pollination crosses were made among individuals of the same taxon to corroborate their reproductive output. In a genus-wide study of the breeding systems based on pollen-ovule (P/O) ratios, Wright et al. (2012) found different P/Os for the three varieties, but all the values fell under Cruden's facultative xenogamy category (Cruden 1977). Thus, it is possible that the reported reproductive barrier (Prather et al. 1995) was a technical/experimental artifact.

In view of the findings of this study, *C. indecora* var. *attenuata* and *C. indecora* var. *longisepala* cannot be distinguished morphologically or molecularly, and together they are inseparable from *C. indecora* var. *indecora*. It is uncertain if the conservation of the populations of *C. indecora* associated with *Iva annua* from Eastern Texas, Oklahoma, and southern Kansas is valuable from the point of view of biodiversity preservation, but this remains to be decided by local regulatory agencies.

Incipient Cryptic Speciation Within C. indecora s.l.—Molecular phylogeny diverged from the morphological results in that it revealed two well-supported clades within *C. indecora* s.l. (Fig. 3). The first clade (clade 1) is sister to *C. coryli* and includes morphological forms that correspond to all three infraspecific taxa of *C. indecora*. The second clade (clade 2) comprises only individuals of *C. indecora* var. *indecora* (Fig. 3). Thus, in theory, these could be considered two cryptic speciation events.

Cuscuta indecora has the largest genome size in *C.* subgenus *Grammica* (C = 22.68, 24.46 and 32.05 pg; McNeal et al. 2007; Ibiapino et al. 2020, 2022), which has resulted through rampant accumulation of 5S and 35S ribosomal DNA site at rates that may vary even at the population level (Ibiapino et al. 2020). Together with the phylogenetic results, this suggests a recent and rapid diversification within *C. indecora* s.l. (Ibiapino et al. 2022).

Many *Cuscuta* species, in general, are notoriously difficult to distinguish morphologically, but even in the most problematic cases, species circumscription has been possible by a combination of molecular phylogeny, morphometry, cytology, host range, and geographical evidence (e.g. Costea et al. 2015a, 2020, 2023; Costea and Stefanović 2010). Two recently described *Cuscuta* species approach a "cryptic" definition: *C. psorothamnensis* in *C.* sect. *Denticulatae* (García et al. 2018) and *C. difficilis* in *C.* sect. *Californicae* (Costea et al. 2020). However, in the former case, karyologic traits, cytogenetic data, host specificity and geographical distribution separated *C. psorothamnensis* from the morphologically identical *C. veatchii*, which resulted through an earlier reticulation event between the same parental species (García et al. 2018). *Cuscuta difficilis* was initially thought to be cryptic, but a similar integrative approach to that of this study revealed both discrete morphological traits and host range differentiation that distinguished it from other members of *C. californica* species complex (Costea et al. 2020).

The examples above are not the case with *C. indecora*. We could not find a single morphological trait that could be used to separate the two clades (Fig. 3), despite examining a full range of morphological features. While it could be contended that the two lineages have not yet acquired morphological divergence, *C. indecora* s.l. is actually diverse morphologically, but as we have shown, this variation is continuous and not congruent with the molecular phylogeny. Furthermore, no host range or geographical patterns were observed to support the two cryptic lineages.

Nevertheless, the discovery of these two incipient cryptic lineages within *C. indecora* is significant and deserves further study. Reproductive biology, development, physiology, biochemistry, cytogenetics, and additional molecular tools should be employed (e.g. reviewed by Struck et al. 2018; Bateman 2022; Martynov and Korshunova 2022) to understand early diversification mechanisms in *Cuscuta* and parasitic plants more broadly. In the absence of such knowledge, these interesting molecular results cannot serve any tangible applied use. Given the lack of morphological, ecological, and geographic patterns distinguishing the two major clades mentioned above, it seems more appropriate to tentatively recognize *C. indecora* as a single, variable paraphyletic species. This solution also has a practical advantage, as the identification of this taxon will be unambiguous.

KEY TO SPECIES OF *CUSCUTA* SECTION *INDECORAE*

Complete synonymy, typification, and descriptions of all taxa (but disregarding the varieties of C. indecora) are available in Yuncker (1932, 1965), Costea et al. (2006), and Costea and Nesom (2023).

1. Calyx lobes with distinct horn-like appendages near apex, corolla lobes connivent at anthesis, capsules with distinct collar at apex....... *Cuscuta warneri*
1. Calyx lobes without horn-like appendages, corolla lobes open at anthesis, capsules with at most a thickened portion at apex.......................... 2
    2. Flowers mostly 4-merous (often with 5-merous flowers on the same plant), corollas 1.5–2.8 mm long, corolla lobes erect to slightly spreading, Infrastaminal scales often bifid (occasionally truncate) with 1–7(–13) fimbriae.. *Cuscuta coryli*
    2. Flowers always 5-merous, corollas 2.3–4.6 mm long, corolla lobes spreading, IFS subspatulate-spatulate, with 10–38 fimbriae. .....*Cuscuta indecora*

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AUTHOR CONTRIBUTIONS

CB did fieldwork, examined the herbarium material used in the study, dissected, imaged, conducted the morphometric analyses, compiled the host dataset, did the Venn diagrams, and wrote the bulk of the manuscript together with MC, who also did field work, dissected, photographed, examined, and initially annotated most of the herbarium material. CF produced the host networks. SS did field work, conducted the phylogenetic analyses, wrote the corresponding sections, as well as edited the rest of manuscript.

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Appendix 1. List of herbarium specimens examined for morphometric and molecular analyses of *Cuscuta* section *Indecorae*. Country, locality details, date, collectors, and herbaria in which the specimens are deposited are provided for all specimens. In addition, for material used in molecular phylogenetic analyses accession numbers are given in the square brackets. Asterisks (*) indicate specimens of *C. indecora* with intermediate morphology that could not be confidently assigned to a variety. Abbreviation of herbaria follow Index Herbariorum (Thiers 2017).

Cuscuta coryli *Engelm.: Canada.* —

Saskatchewan: S of Qu'Appelle Valley, [no date], *Ledingham 3160* (USAS); —Manitoba: Interlake Region: Selkirk, Riviere Rouge, entre l'Ile au Sucre et embouchure de la riviere lui de-Boule, 26 Aug 1960, *Boivin & Champagne 13869* (ALTA, QFA) [**824**]; —Ontario: Essex Co.: Windsor, Tall Grass Prairie Heritage Park, 42.26416 N, 83.06633 W, 24 Aug 2021, *Burt & Consiglio 196* (WLU); Windsor, Ojibway Prairie Provincial Nature Reserve, 42.2582916 N, 83.0629686 W, 24 Aug 2021, *Burt & Consiglio 205* (WLU); **USA. —**Arkansas: Cross Co.: Levesque, 24 Jul 1939, *Demaree 19603* (CAS); —Indiana: Perry Co.: Ohio River, just below Derby, 11 Sep 1931, *Deam 51589* (IND) [**465**]; n.d. *Thomas 145* (OSU); —Kansas: Republic Co.: Belleville, 10 Aug 1960, *Morley 747* (SMU); —Michigan: St. Clair Co.: near Port Huron, 18 Aug 1896, *Dodge 2193* (WIS); —North Carolina: Currituck Co.: 3 mi N of Woodleigh, 20 Aug 1984, *Musselman 6350* (ODU); —North Dakota: Wahpeton, 9 Aug 1926, *Purcell s.n.* (OSU); Texas. Lieut. A.W. Whipple's Exploration for a Railway Route, from the Mississippi River to the Pacific Ocean, near the 35th parallel of Latitude, in 1853-4. Fort Smith to the Rio Grande, 1853-1854, *Bigelow s.n.* (MO) [**type of *Cuscuta inflexa* Engelm**.]; —West Virginia: OHIO CO.: on bank of Ohio River just below 8th Street, Wheeling, 16 Sep 1951, *Bartholomew 0-923* (NY) [**666**]; —Wisconsin: 1981, *Cochrane et al. s.n.* (WIS); GRANT CO.: Village of Highland, ~2.5 mi (air) W of the Iowa Co. line and 5 mi (air) W of Highland, 18 Aug 2009, McFarland s.n. (WIS) [**2248**];

Cuscuta indecora *var.* attenuata *(Waterf.) Costea: USA.* —

Kansas: Cowley Co.: 5 mi W of Arkansas City, 7 Sep 1966, *Kodi 2156b* (NY); Douglas Co.: 2 mi. SE of Lawrence, 26 Aug 1946, *McGregor 10* (NY) [**722**]; Republic Co.: 2 mi W and 2 mi N of Wayne, 13 Sep 1952, *Horr 4410* (NY) [**721**]; —Oklahoma: Choctaw Co.: 3 mi W of Fort Towson, 24 Jun 1956, *Waterfall 12432* (OKLA); Comanche Co.: Wichita Mts NWR; Quanah Parker Lake, E shores of the Lake, by Hwy 49, 34°42′45″N, 98°37′58″W, 2017, *Stefanović SS-17-124* (WLU) [**1963**]; Pawnee Co.: Cleveland. South Canadian River floodplain, 5 Sep 1961, *Buck 524* (OKLA); Mccurtain Co.: along Hwy 259, near Waterfall Creek, 33°46′45″N, 94°48′08″W, 2017, *Stefanović SS-17-120* (TRTE) [**1959**]; Along Waterfall Creek, 8 mi S and 2 mi E of Idabel, near Hwy 259, 11 Sep 1979, *Taylor 28173* (LSU); R24E, T9S, Sec 10, SW1/4, SW 1/4, banks and pastures adjacent to Waterfall Creek N-side of U.S. Hwy 259 bridge ca. 8.5 mi S of Idabel, Sep 1978, *Tyrl 1648* (OKLA) [723]; along Waterfall Creek, 7 mi S and 2 E of Idabel, 16 Sep 1965, *Waterfall 17191* (OKLA) [724]; Edge of pond in Waterfall Creek, 7 mi S and 1.5 mi E of Idabel, 3 Sep 1970, *Waterfall 17496* (GH) [**604**]; —Texas: Cameron Co.: Rabb's Ranch, 1/2 mi N of the Ranch house, 10 Aug 1941, *Runyon 2873* (NY) [**725**]; RAINS CO.: Hwy 19, bridge over Sabina River, NE corner (same as SS-17-122). 32°46′52″N, 95°47′48″W, 2017, *Stefanović SS-17-121* (WLU) [**1960**]; Van Zandt Co.: Near Ocean Lake, N of Edgewood, 6 Sep 1946, *Whitehouse 16472* (BRIT).

Cuscuta indecora *var.* indecora *Choisy: Argentina.* —

De Buenos Aires: San Justo, Casanova, 19 Dec 1943, *Hunziker 3959* (SP); **Jamaica.** —St. Catherines Parish: Ewarton, 6 Mar 1916, *Killip 396* (US); **Mexico. —**Aguascalientes: Cosío, Santa María de la Paz, 22.38679 N, 102.28786 W, 7 Nov 2011, *Manuel & Contreras-Romero 24273-12P0000772* (WLU) [**2827**]*; De Rincón de Ramos, 22°16337 N, 102°29765 W, 26 May 2011, *Conteras-Romero 2011-00551* (WLU) [**2835**]; —Chihuahua: Aldama, 28.84701 N, 105.83445 W, 14 Jul 2011, *Aguilar-Pérez 2011-01004* (WLU) [**2850**]; Buenaventura, 23 Jun 2010, *Alvares-Perea 2010-01780* (WLU) [**2828**]*; Delicas, 28.05935 N, 105.53227 W, 28 Jul 2010, *Gutiérrez-Galagos 2011-01002* (WLU) [**2806**]; Km 92, 28.115 N, 105.504 W, 28 Jul 2011, *Gutiérrez-Galagos 2011-01001* (WLU) [**2805**]*; Guadalupe, Ejido Guadalupe, 31.336312 N, 106.0544 W, 8 Jul 2011, *Jiménez D. 2011-01003* (WLU) [**2803**]; Meoqui, Predio Daniel Medina, 12 Aug 2009, *Gutiérrez-Galagos s.n.* (WLU) [**2888**]; Ejido Meoqui, 28.31174 N, 105.55138 W, 22 Jul 2011, *Gutiérrez Galagos 2011-01000* (WLU) [**2807**]*; Jiménez, R. el Capricho, 22 Jul 2011, *Domînguez 2011-01261* (WLU) [**2784**]; 1 Aug 2011, *Domînguez 2011-01256* (WLU) [**2785**]*; —Hidalgo: Progreso de Obregón, el jardín, 20.35911 N, 99.21314 W, 1 Sep 2012, *Martínez-Quijada 33494*12P0049797* (WLU) [**2804**]*; —Jalisco: Ocotlán, Paso de la comunidad, 20.35914 N, 102.74182 W, 25 Jul 2012, *Pérez & Ramírez 30806*12P0022314* (WLU)*; —Nuevo León: Allende, San Antonio, 25.31480 N, 100.04552 W, 29 Sep 2012, *Cortez-Ortega 37367*13P0006312* (WLU) [**2892**]; General Terán, La Esperanza, 25.31761 N, 99.71841 W, 01 Nov 2012, *Cortez-Ortega 37367*13P0006309* (WLU) [**2834**]; San Pedro, 25.27676 N, 99.63720 W, 6 Nov 2012, *Cortez-Ortega 37367*13P0006308* (WLU) [**2833**]; 25.27676 N, 099.63720 W, 25 Sep 2012, *Cortez-Ortega 37367*13P0006315* (WLU) [**2832**]; California, 25.31602 N, 099.74378 W, 1 Nov 2012, *Cortez-Ortega* 27367*13P0006311 (WLU) [**2893**]; 25.31730 N, 099.74506 W, 1 Nov 2012, *Cortez-Ortega 37367*13P0006310* (WLU) [**2894**]; Santiago, La Nogalera, 25.34601 N, 100.16745 W, 30 Sep 2012, *Cortez Ortega 37367*13P0006314* (WLU) [**2890**]; 25.34300 N, 100.17645 W, 30 Sep 2012, *Cortez-Ortega 37367*13P0006313* (WLU) [**2891**]*; **—**Tamaulipas: Matamoros, Mexicum ad Matamoros. Sep 1830, *Berlandier 2285* (MO) [**isotype of *Cuscuta indecora* var. *indecora*]; Sonora.** 9 Aug 2010, *Estrada Diaz 2010-01573* (WLU); Bácum, 27.47867 N, 110.17674 W, Campo 60, block 315, Lo. Fl. 1,3, 9 Aug 2010, *García 2010-01574* (WLU) [**2812**]; Benito Juárez, Villa Juárez, 27.10720 N, 109.83382 W, 5 Jul 2010, *García 2010-01575* (WLU) [**2801**]*; Etchojoa, Modulo 15, lot 63251, 26.95106 N, 109.60548 W, 24 Mar 2010, *Sainz 2010-01978* (WLU) [**2810**]; canal at edge between remnant marsh and agricultural areas on the NE side of Cerro Bayajuri, NE of Buaysiacobe (27° 05′N, 109° 38′W), 7 Mar 1994, *Sanders & Helmkamp 14461* (UCR) [**2922**]; Huatabampo, Ejido la Unión, 26.82392N, 109.57216 W, 20 Jul 2011, *Corral-Vega 2011-00922* (WLU) [**2849**]; Navojoa, 26.93808 N, 109.49350 W, 21 Aug 2010, *Ley 2010-019980* (WLU) [**2809**]; San Luis Río Colerado, Emiliano Zapata, 32.23753 N, 114.97265 W, 17 Aug 2011, *Rojas Ayala 2011 -01453* (WLU); Ej. Monumentos, 32.46011 N, 114.89570 W, 17 Nov 2011, *Rojas Ayala 2011-01452* (WLU) [**2782**]*; Navojoa, 2 km W of Tierra y Libertad on northern road to Camahuiroa, 26° 33′ 50″N, 109° 12′ 50″W, 24 Nov 1993, *Van Devender et al. 93-1283* (ARIZ, CAS) [**2779**, **2923**]*; San Ignacio Río Muerto, 27.36284 N, 110.27966 W, 5 Jul 2010, *García 2010-01573* (WLU) [**2811**]*; —Querétaro: Corregidora, El Pueblito, 20.36574 N, 100.4683 W, 28 Nov 2012, *Rodríguez Mancina 35695*12P0056641* (WLU) [**2831**]; Purísima de San Rafael, 20.46936 N, 100.3907 W, 17 Sep 2012, *De Los Angeles Rodríguez Mancina 35695*12P0056639* (WLU) [**2829**]*; Pedro Escobedo, Los Álvarez, 20°5422 N, 100°14687 W, 6 Jun 2011, *Piña-Monrreal 2011-00669* (WLU) [**2825**]; San Juan del Río, Vistha, 20°45093 N, 100°00113 W, *Piña-Monrreal 2011-00670* (WLU) [**2786**]; Pedro Escobedo, 29 Sep 2010, *Piña-Monrreal 2010-01867* (WLU) [**2808**]; —Zacatecas: 14 Aug 2012, A.V. *Ibarra s.n.* (SAGARPA, WLU) [**1568**]; Ojocaliente, 22.58233 N, 102.27076 W, 20 Sep 2011, *Valdez Ibarra 23475-11P0038309* (WLU) [**2783**]; Loreto, El Tepetate, 22.36323 N, 102.08333 W, 26 Sep 2011, *Valdez Ibarra 23475-11P0038310* (WLU) [**2787**]; Luis Moya, Predio San Jorge, 22.44327 N, 102.28824 W, 14 Aug 2012, *Valdez-Ibarra 32854*12P0046463* (WLU) [**2781**]*; **USA.** [**EU330311 McNeal**]; **—**Alabama: Mobile Co.: Dauphin Island, on the sandy W end of the island, 18 Sep 1973, *Taylor & Taylor 15374* (BRIT); Collected roadside of wet

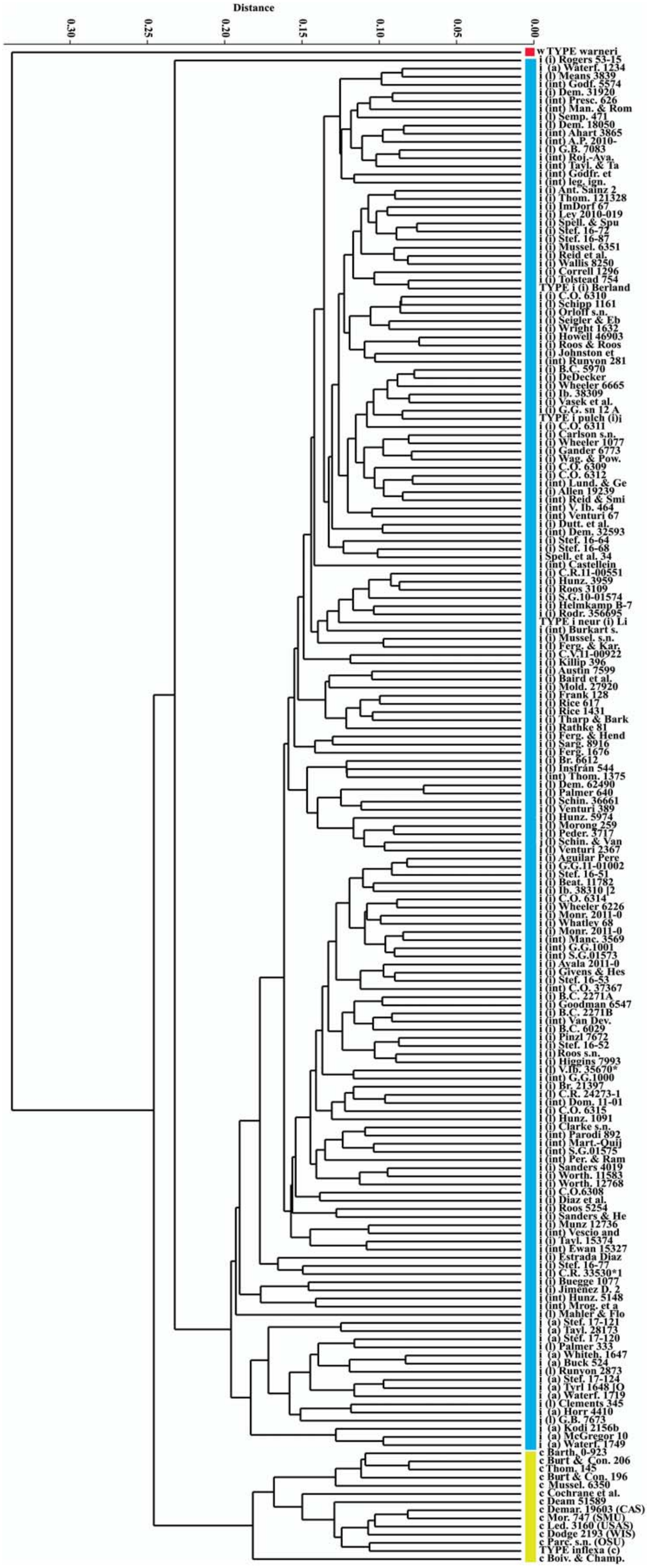

FIG. S1. Dendrogram obtained from the complete dataset of *Cuscuta* sect. *Indecorae* resulted from the unweighted pair-group average (UPGMA) analysis using the Gower's coefficient of similarity. i(int) = *C. indecora* with intermediate morphology. Red horizontal bar highlights the position of *C. warneri*, the yellow vertical bar shows the position of *C. coryli*, and the large blue vertical bar includes the *C. indecora* s.l. taxa and intermediate specimens.

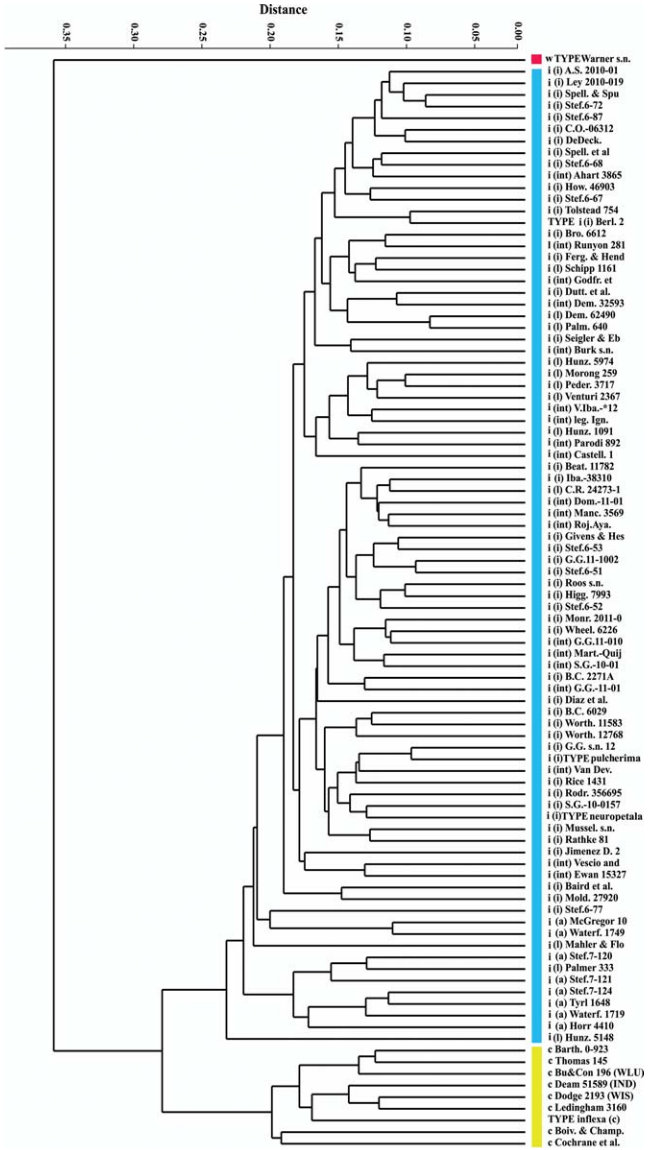

FIG. S2. Dendrogram of *Cuscuta* sect. *Indecorae* based on the partial dataset in which the specimens with significant gaps were excluded using unweighted pair-group average (UPGMA) and Gower's coefficient of similarity. i(int) = *C. indecora* with intermediate morphology. Red horizontal bar highlights the position of *C. warneri*, yellow vertical bar indicates the position of *C. coryli*, and the large blue vertical bar includes all the *C. indecora* s.l. taxa and intermediate specimens.

ditches and mowed banks. Pinewoods in the centre of the island., 05 Jul 2014, *Taylor & Taylor 16519* (BRIT)*; —ARIZONA: Gila Co.: North of Pueblo Canyon, Sierra Ancha Wilderness Area in Tonto National Forest; 27.3 mi N of Cherry Creek Rd. (FSR 203) from lower jct. with state Hwy. 288. T6N, R14E, S14, NE1/4, 7 Aug 1991, *Imdorf & Landrum 67* (UCR) [**2910**]; North of Winkelman, S of Globe, along roadside, 16 Aug 1973, *Moldenke & Moldenke 27920* (AAU); Hwy 87/260, 6 mi S of Pine, 2019, *Stefanović SS-19-44* (TRTE) [**2387**]; Hwy 60/77, 1 mi S of intersection with Hwy 73, 2019, *Stefanović SS-19-45* (TRTE) [**2388**]; Hwy 60, N entrance to Globe, 2019, *Stefanović SS-19-46* (TRTE) [**2389**]; Graham Co.: Coronado National Forest, Goat Mountain. T7S, R21E, sec 2, SW. S side of mountain, 20 Aug 1999, *Buegge 1077* (UCR) [**2911**]; Maricopa Co.: By road to Horseshoe Dam, (N of Phoenix), circa 2 mi past junction at Cave Creek, 15 Jul 1965, *Frank 128* (UBC); Superstition Wilderness Area. Horrell Creek; at the end of Forest Rd 273, on Pinto Creek turnoff past Magma Copper Mine, ca 15 mi off Hwy 60. Trail 213. 33.5022 N, 111.077 W, Tonto National Forest, 5 Sep 1992, *Rice 1431* (ASU) [**486**]; Pinal Co.: Tonto National Forest Superstition Wilderness Area, Woodbury Trailhead, N of Hwy 60 ca. 12 mi. on Queen Creek turnoff to Forest Rd 172, trail 106, 28 Jun 1991, *Rice 617* (SD); Near Peppersauce Campground on N side of Santa Catalina Mountains. Ca 15 mi SE of Oracle, 32.54 N, 110.7 W, 30 Aug 1989, *Austin & Austin 7599* (RSA); Hwy 177, ~2 mi S of Superior, 2019, *Stefanović SS-19-47* (TRTE) [**2390**]; Yavapai Co.: Sonoran Desert: along Hwy 93, NW of Hwy 97 junction (34° 27′ N, 113° 17′ W), 18 Sep 1967, *Vasek et al. HMS-253* (UCR) [**2896**]; —ARKANSAS: Ashley Co.: Along ARK 52 at Crossett Airport North & East of Crossett, Sec. 1., 12 Sep 1993, *Thomas 137502* (DUKE)*; Nevada Co.: P.O. Prescott, Junction Hwy 3 & 24, 15 Aug 1970, *Demaree 62617* (OKLA)*; —CALIFORNIA: 25 Sep 1951, *Roos 5254* (UCR) [**2913**]; Inyo Co.: W side of Owen's Lake, 3 m N of Olancha, 28 Aug 1955, *Roos & Roos 6563* (UCR); Big Pine, 18 Sep 1965, *Roos s.n.* (UCR) [**2860**]; Owas Valley, Moffat Rd, E of Hogbeach Creek, 1982, *DeDecker 5383* (RSA) [895]; Kern Co.: Kernville, 27 Jul 1970, *Howell & True 46903* (NY) [**615**]; Los Angeles Co.: 1 m N of Covina, 20 Aug 1997, *Wheeler 6226* (UCR) [**2766**]; Riverside Co.: River bottom just W of Lake Evans, Fairmont Park, 7 Sep 1970, *Clarke s.n.* (UCR); San Bernardino Co.: Newberry Springs, at the DeJong Ranch, corner of Harvard and Fairview. Mojave Desert SE of Barstow, 20 Aug 1985, *Orloff s.n.* (UCR) [**2886**]; Morango Valley, Big Morango Preserve of the Nature Conservancy, 8 Sep 1983, *Helmkamp B-7* (UCR) [**2858**]; Mojave Desert/Little San Bernardino Mountains, Big Morongo Preserve of the Nature Conservancy in Big Morongo Canyon, S of town of Morongo Valley (Morongo Valley: 34° 02.83′N, 116° 34.02 W; T1S R4E S28, SE/4; T1S R4E S33, E/2; 11S NH-3E, 6N), 12 Sep 1983, *Sanders & Fellows 4019* (UCR) [**2790**]; San Gabriel Mountains, Cajon Canyon, SE of Lost Lake, 17 Jul 1948, *Wheeler 6665* (UCR) [**2789**]; Glen Ranch, Lytle Creek (Sportsman) Park, 15 Sep 1967, *Wheeler 10774* (CTES); The Pipes, 34.17167 N, 116.54417 W, 5 Sep 1946, *Roos 3109* (UCR) [**2887**]; 2 mi W of Redlands, 20 Aug 1932, *Munz 12736* (CAS); San Diego Co.: Near Foster, Ramona Rd, 32.90838 N, 116.92614 W, 20 Sep 1938, *Gander 6773* (SD); Solano Co.: Sacramento Valley: 2 mi S of Davis, Putah Creek, Merrit, 38°31.0′N, 121°45.2′W, 21 Sep 1954, *Crampton 2271A* (UCR) [**2764**]; *Crampton 2271B* (UCR) [**2925**]; 2.5 mi SW of Davis, along S fork of Putah Creek, 38°31.1′N, 121°46.3′W, 16 Aug 1961, *Crampton 5970* (UCR) [**2924**]; 3 mi S of Davis, along S fork Putah Creek, 28° 31′N, 121° 45.2′W, 11 Sep 1961, *Crampton 6029* (UCR) [**2765**]; Sutter Co.: Sutter, ca 0.5 mi N of Meyers home along driveway, Meyers Ranch, 11 Sep 1982, *Ahart 3865* (DS)*; —FLORIDA: Putnam Co.: 2.5 mi. S of San Mateo, 26 Jul 1961, *Godfrey & Reinert 61139a* (NY)*; —LOUISIANA: Cameron Parish: Along the Gulf of Mexico, ca. 10.5 mi SE of Rockefeller Wildlife Refuge and Game Preserve headquarters via the Headquarter and Humble canals and Joseph Harbour Bayou, T16S, R4W, 16 Jun 1984, *Dutton et al. 2348.7518* (DUKE); Desoto Parish: Dickson Prairie, S9 T1SN R14W; 32° 18′ 27″ N, 93° 48′ 24″ W, 29 Sep 2006, *Reid et al. 5923* (LSU); Iberia Parish: Marsh Island Refuge, shoreline just E of Mound Point and mouth of Oyster Bayou, 29.478 N, 91.818 W, T18S R6E Sec14 NW1/4, 12 Jul 2004, *Reid & Smith 5125* (LSU)*; Jefferson Parish: Fort Polk, off LA 1 in Grand Isle, 27 Jun 2003, *Allen 19239* (BRIT); N of Mud Lake and E of Little Lake, ca. 30 km E of Cut Off., 29.49880 N, 90.02200 W, 6 Aug 2008, *Ferguson 1676* (LSU); Lafourche Parish: Fourchon Beach, at the end of LA 3090, 29.103 N, 90.187 W, 7 Aug 2004, *Ferguson & Henderson 1560* (LSU); Saint Bernard Parish: Lone Oak Island, 17 Jul 1936, *Brown 6612* (LSU); Terrebonne Parish: Around Louisiana Universities Marine Consortium Lab Buildings and along La. 56 in Cocodrie S of Houma; T21S, R18E, 12 Aug 1989, *Thomas 111592* (NY) [**616**]; Behind low dune area at E end of Timbalier Island, 26 Sep 1988, *Givens & Hester 5523* (LSU); Vermilion Parish: Red Fish Point, Vermilion Bay, 27 May 1970, *Brown 21397* (LSU); Winn Parish: Saline open area beside Saline Creek N of U.S. 84 W of Castor Creek and W of Tullos; Sec. 22, T1ON, R1E, 28 Sep 1990, *Thomas 121328* (DUKE); —MARYLAND: Calvert Co.: Long Beach Drive, St. Leonard, shoreline of the Chesapeake Bay, 22 Jul 2011, *Carlson s.n.* (DAWES); —MISSISSIPPI: Harrison Co.: Ship Island, P.O. Biloxi [Gulf Islands National Seashore], 15 Jun 1952, *Demaree 31920* (NY); Jackson Co.: Pascagoula. Petit Bois Island, 7 Aug 1952, *Demaree 32593* (DUKE)*; Pearl River Co.: 4 mi. NW of Picayune, *Sargent 8916* (OKLA); —NEBRASKA: Arthur Co.: Arapaho Prairie, at edge of E pond, 41.4887 N, 101.859 W, 27 Jul 1977, *Vescio & Kruse 174* (NY)*; —NEVADA: Mineral Co.: Schurz, NW of hospital, T13N, R28E, SW114, S26, 27 Aug 1986, *Pinzl 7672* (NY) [**602**]; Nye Co.: Rt 52 near Rt 16 jnct, Pahrump area, 26 Sep 1970, *Beatley 11782* (CAS); —NEW MEXICO: 1851–1852, *Wright 1632* (S); Chaves Co.: Bottomless Lakes SP, Bottomless Lakes Rd., 3 mi S of Hwy 380. 33° 21′31″N, 104° 20′16″W, 2016, *Stefanović SS-16-77* (TRTE) [**1694A**]; on the bluffs on the E side of the Pecos River, E of Roswell., 25 Jul 1973, *Spellenberg et al.*

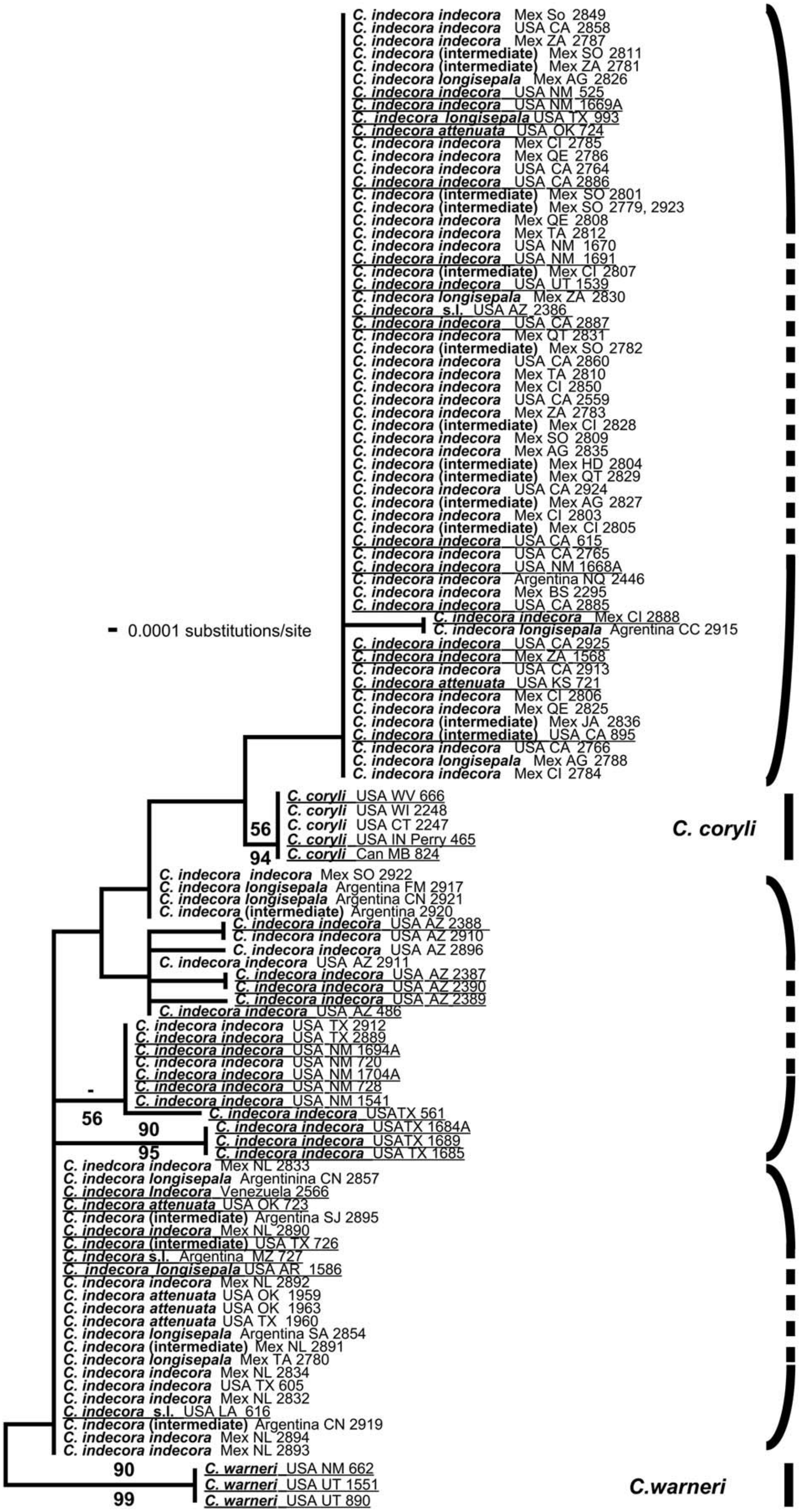

FIG. S3. Phylogram resulting from the partitioned maximum likelihood analysis of plastid (*trnLF* intron/spacer) sequence data showing relationships among species of *Cuscuta* sect. *Indecorae*. The tree is rooted using *C. warneri* as functional outgroup. Bootstrap values (MP above and ML below branches) are indicated for nodes supported at ≥ 50%. Species names are followed by abbreviations of countries and states/provinces in which they were collected, and their DNA accession numbers (Appendix 1). Individuals sequenced for nrITS and included in the nuclear phylogeny (compare with Fig. 3) are underlined.

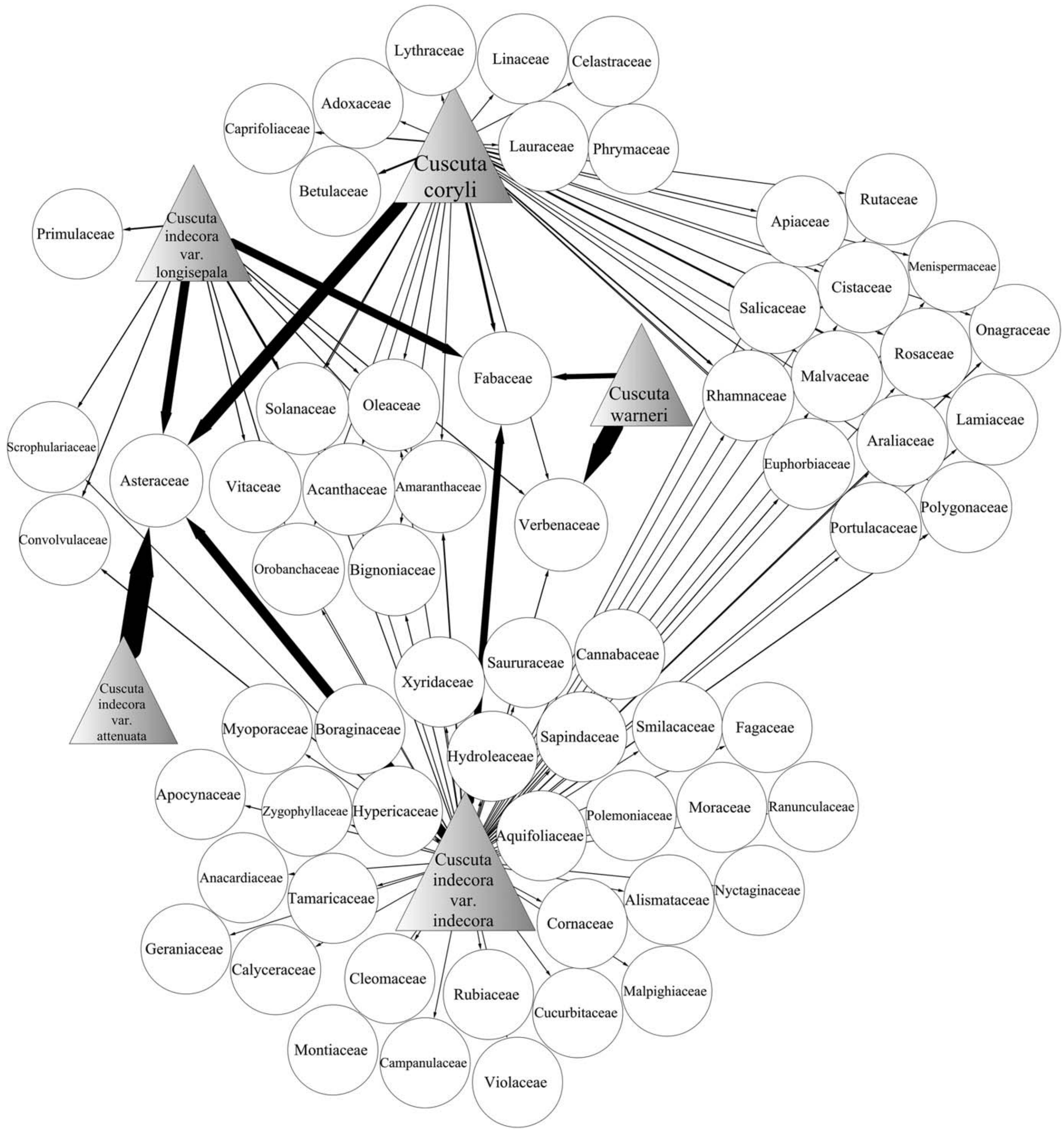

FIG. S4. Family level host range relationships of *Cuscuta* sect. *Indecorae* visualized as a directed bipartite network. Taxa within *Cuscuta* sect. *Indecorae* (represented as triangles) are the main nodes connected to the corresponding nodes of their host families (represented as circles). Frequency of each *Cuscuta*-host family association is indicated by the proportionally thickened edges (lines) using the host-frequency indicator (HFI). The number of lines directed toward host nodes indicates the amount of overlap or separation of corresponding *Cuscuta* taxa host range.

3427 (NY, NMC) [**720, 1541**]; Roswell, corner E McCune and S Main St (Hwy 285), 33° 22′15″N, 104° 31′00″W, 2016, *Stefanović SS-16-74* (TRTE) [**1691**]; Eddy Co.: A few meters N of the Texas border, ca. 1/2 air miles SE of U. S. Hwy. 62-180, 1 Sep 1985, *Spellenberg & Spurrier 8256* (NY) [728]; Guadalupe Co.: Puerto de Luna, Hwy 203, ~2 mi SW of Hwy 91. 34°47′55″N, 104°38′05″W, 2016, *Stefanović SS-16-87* (TRTE) [**1704A**]; San Juan Co.: Fruitland, N of San Juan River, 36.71989927 N, 108.4135444 W, 18 Aug 1976, *Wagner & Powell 2493* (UNM) [**525**]; Socorro Co.: Hwy 116, 1 mi N of intersection with Hwy 60 and I-25, N of La Joya. 34° 26′06″N, 106° 49′31″W, 2016, *Stefanović SS-16-51* (TRTE) [**1668A**]; Lemitar, Hwy 408. 34° 09′41″N, 106° 53′59″W, 2016, *Stefanović SS-16-52* (TRTE) [**1669A**]; on Pueblitos Rd., 1/3 mi E of Escondida Bridge Park (1/2 mi E of Hwy 408). 34° 07′18″N, 106° 52′55″W. 2016, *Stefanović SS-16-53* (TRTE) [**1670**]; Union Co.: past 360 along Hwy 18 N of Nara Visa, 3 Aug 1973, *Higgins 7993* (NMC) [**603**]; —TEXAS: 1846, *Lindheimer 475* (MO) [**holotype of *Cuscuta pulcherrima***]; Anderson Co.: Northwest of Mantalba, 9 Sep 1942, *Lundell & Geiser 11907* (OKLA)*; Brazoria Co.: Near Freeport, 22 Sep 1948, *Rogers 53-150* (DUKE); Brewster Co.: Big Bend

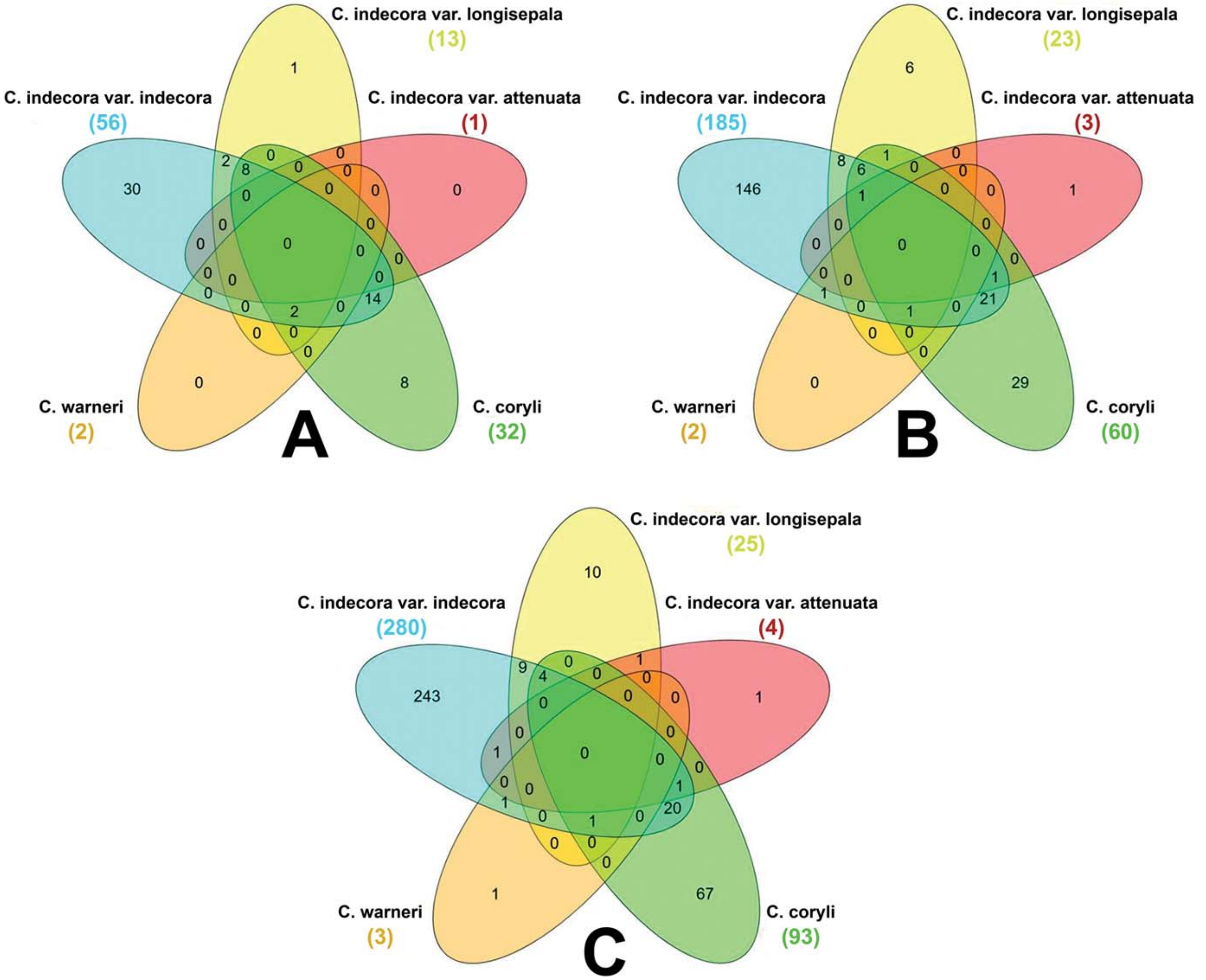

FIG. S5. Number of shared and unique hosts of *Cuscuta* sect. *Indecorae* taxa visualized as Venn diagrams at three taxonomic levels: family (A), genus (B), and species-level (C). Each taxon is represented as a differently colored ellipse. Hosts unique to a particular taxon can be found at the tips of ellipses, while the shared number of hosts are at the base, where the ellipses overlap. Total number of hosts within the host range of a taxon is indicated outside the Venn diagrams under the text of that taxon.

NP, between miles 1-2 on Chisos Mts Rd. 29°19′06″N, 103°15′29″W, 2016, *Stefanović SS-16-72* (TRTE) [**1689**]; Brown Co.: Steep slopes of Round Mt., 1 mi. W. of Brownwood, 27 Jun 1968, *Rathke 81* (OKLA); Cooke Co.: Tyler Bluff, western edge of county, 2 Jul 1946, *Correll & Correll 12964* (SMU); EL PASO CO.: Along hwy. US 62-180 4.0 E of jct. with hwy. 659, 23, Sep 1983, *Worthington 11583* (UCR) [**2912**]; Hueco Mt., first hills S of hwy. US 62-180, 5.5 rd mi. E of jct. with TX 659, 31°49′12″N, 106°07′11″W, 14 Sep 1984, *Worthington 12768* (UCR) [**2889**]; Galveston Co.: East end of Galveston, 20 Aug 1959, *Wallis 8250* (OKLA); Jamaica Beach near Tern Road, 29 Jun 1972, *Whatley 68* (AUA); Harris Co.: In wet prairies near Houston, Aug 1843, *Lindheimer 124* (MO) [**Lectotype of *Cuscuta neuropetala***]; Jackson Co.: Along river south of Vanderbilt: 28.749164 N, -96.586648 W, 2 Nov 1943, *Tharp & Barkley 13A127* (DUKE); La Salle Co.: Cotulla. NW of Mare's Pond, Chaparral Wildlife Management Area, 8 mi W of Artesia Wells, 22 May 2001, *Seigler & Ebinger 14940* (DAO) [**605**]; Presidio Co.: Hwy 170, 7-8 mi E of Presidio. 29°31′05″N, 104° 15′51″W, 2016, *Stefanović SS-16-67* (TRTE) [**1684**]; Hwy 170, 12 mi E of Presidio, 29°29′37″N, 104°13′15″ W, 2016, *Stefanović SS-16-68* (TRTE) [**1685**]; Taylor Co.: At Camp Barkeley, 1 Jul 1943, *Tolstead 7540* (NCSC); Zavala Co.: near Uvalde-Zavala County line, at Nueces River, 2 May 1954, *Johnston et al. 3616.* (DUKE); —Utah: Tooele Co.: 15 mi E of Grantsville, 22 Aug 1957, *Goodman 6547* (OKLA); Utah Co.: 1/2 m E of Genola turnoff on Hwy 50-6. T10S, R1E, Sec. 4, 8 Sep 1984, *Baird et al. 1513* (NY); Weber Co.: collected at the Howell Experimental Fruit Farm, Pleasant View North Ogden, 7 Sep 1967, *Nye s.n.* (NY) [**1539**]; —Virginia: City of Chesapeake, along Baum Rd., 0.5 mi W of Virginia Beach city limits, 20 Aug 1984, *Musselman 6351* (ODU); along branch of Elizabeth River at Indian River Road bridge, 20 Aug 1984, *Musselman s.n.* (ODU); **Venezuela.** —Bolivar: Ciudad Bolivar, Rio Orinoco, 3 km from Puente Angostura, 8°15′ N, 65°30′ W, Dec 1997, *Diaz et al. 3377* (MO) [814, **2566**].

Cuscuta indecora* var. *longisepala Yunck.: **Argentina.** n.d., *leg. ign, s.n.* (MERL 10658)*; 18 Jan 1994, *Burkart s.n.* (KEW)*; 13 Sep 1949, *Bertoni 4763* (CTES) [**2920**]*; —Buenos Aires: Pergimino Dep.: Pergamino, Estacion J.S. Pena, 3 Dec 1989, *Parodi 8929* (US)*; —Chaco: San Fernando Dep.: Alrededores Peunte General Belgrano, rfo Tragadero, 25 Nov 1981, *Schinini & Vanni 21736* (CTES) [**2915**]; —Cordoba: Dep. Punilla: A orillas del Lago San Roque, 22 May 1945, *Hunziker 5974* (SP); —Corrientes: Dep. Belle Vista: Nameless Island in the R. Paraná, ca. 2 km above Bella Vista, 28 Jan 1956, *Pedersen 3717* (US) [**2857**]; Dep. Capital: Corrientes, vivero de los cordobeses, 21 Sep 2005, *Schinini 36661* (CTES) [**2921**]; General Paz Dep.: Santa Lucía, 15 km E de Itá Ibaté, 9 Mar 1972, *Mroginski et al. 557* (CTES) [**2919**]*; —Formosa: Dep.

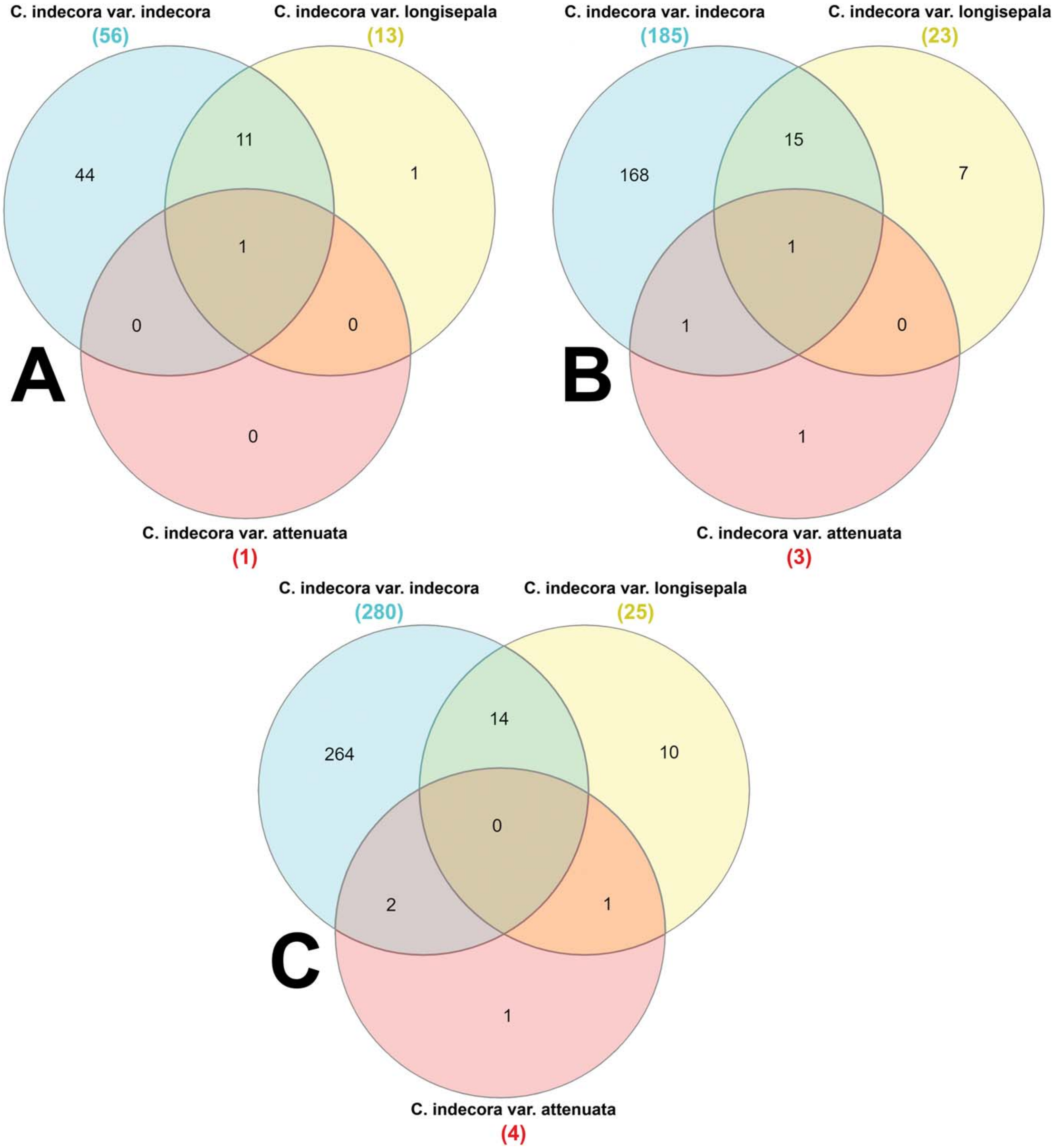

FIG. S6. Number of shared and unique hosts of *Cuscuta indecora* varieties visualized as Venn diagrams at three taxonomic levels: family (A), genus (B), and species-level (C). Each variety is indicated as a circle of different color. Hosts unique to a particular variety can be found at the periphery of the circles, while the shared number of hosts are at the base, where the circles overlap. Total number of hosts is indicated outside the Venn diagrams, under the text of each variety.

Pirane.: El Colorado, Nov 1970, *Insfrán 544* (CTES) [**2917**]; —LA RIOJA: Alrededores de la Rioja, 29 Feb 1944, *Hunziker 5148* (US)*; —MENDOZA: Departmento Capital: Santa Rosa: Las Catitas, 3-4 Mar 1942, *Leal 7964/208* (NY) [**727**]. —SALTA: Dep. La Viña: Coronel Moldes, *Hunziker 1091* (US) [**2854**]; —SAN JUAN: El Barreal, 25 Mar 1945, *Semper 471* (CTES); Dep. Calingasta: de Tamberías a Villa Corral, 26 Jan 1950, *Castellanos 15107* (US) [**2895**]*; —TUCUMÁN: Dep. Capital: Villa Leejaw(?), 5 Mar 1919, *Venturi 389* (US); Dep. Cruz Alta: 26 Sep 1923, *Venturi 2367* (US); Dep. Leales: 10 Dec 1919, *Venturi 679* (US)*; **Honduras.** Malfredi Lagoon, 1 May 1933, *Schipp 1161* (S); **Mexico.** —AGUASCALIENTES: Pabellón de Arteaga, 22.12749 N, 102.27627 W, 19 Sep 2011, *Contreras-Romero 24273-12P0000773* (WLU) [**2826**]; Tepezala, Carboneras, 22.19988 N, 102.24532 W, 19 Sep 2012, *Contreras-Romero 33530*12P0050050* (WLU) [**2788**]; —CHIAPAS: Catazajá, Orilla de Laguna de Catazaja, 17°43′57″N,

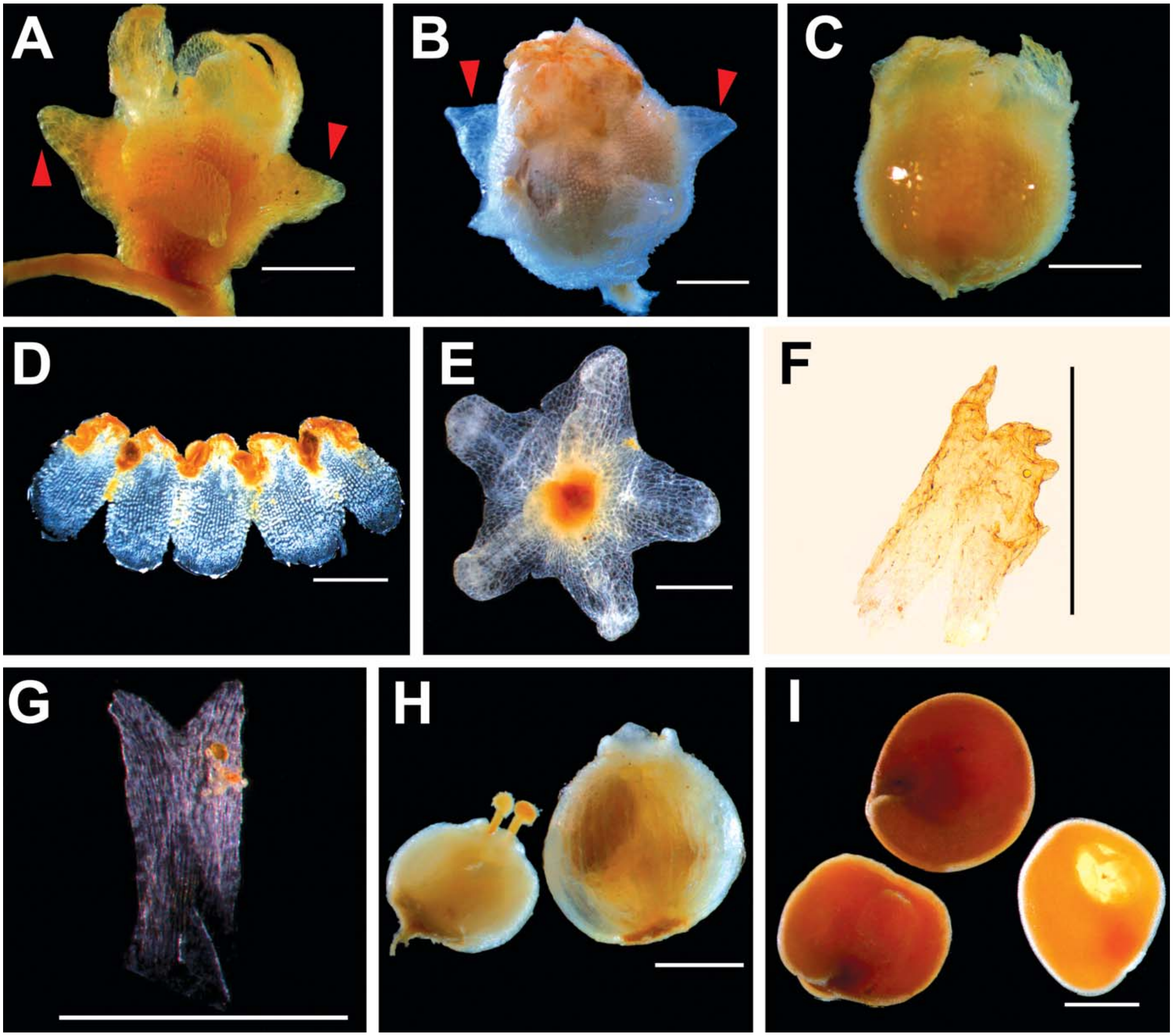

Fig. S7. Morphology of *Cuscuta warneri* reproductive structures. A–B. Flowers (red arrows show horn-like appendages with stomata on calyx lobe apices). C. Corolla 3D. D. Dissected corolla. E. Dissected calyx. F–G. Variation of infrastaminal scales (removed from corolla). H. Gynoecium and capsule. I. Seeds. Scale bars = 1 mm.

92°00’42”W, 3 Mar 2003, *Gutiérrez Báez 7673* (CICY); —San Luis Potosí: Vicinity of San Dieguito, 7–10 Jun 1905, *Palmer 640* (US); —Tabasco: Emiliano Zapata, 7 km NW of Chable. 17°54’13”N, 91°47’59”W, 21 Mar 2001, *Gutierrez Baez 7083* (CICY); —Tamaulipas: Vicinity of Tampico, 27-30 Mar 1910, *Palmer 333* (CAS) [**2780**]; —Zacatecas: Zacatecas, El Orito, 22.77236 N, 102.68501 W, 15 Nov 2012, *Valdez Ibarra 35670*12P0056623* (WLU) [**2830**]; **Paraguay.** Central Paraguay, 1888-1890, *Morong 259* (US); **USA.** —Arkansas: Ashley Co.: P.O Mist, 12 Aug 1938, *Demaree 18050* (CAS); Nevada Co.: Junction of Highways 24 & 30, 25 Jul 1970, *Demaree 62490* (UBC) [**1586**]; —Colorado: Pueblo Co.: Arkansas River bottoms, 4 mi SW of Pueblo, 4 Sep 1943, *Ewan 15327* (CAS)*; —Florida: Walkulla Co.: St. Marks Wildlife Refuge, 26 Jul 1957, *Godfrey 55747* (NCSC)*; —Louisiana: Lafourche Parish: S of LA 1/LA 3090 intersection on Hwy 3090, N of Port Fourchon, 29°08.32 N”, 90°11.05 W”, 20 Sep 2001, *Ferguson & Karaman-Castro 458* (LSU); —Oklahoma: Latimer Co.: Wilburton, 4 mi W and ½ mi N of Wilburton, 2 Aug 1968, *Means 3839* (OKLA); Pontotoc Co.: Ada, 15 mi S and 5 mi E of Ada, 7 Jul 1951, *McCoy 866* (OKLA); —Texas: *Clements 345* (CAS); Cameron Co.: 4 mi NW of Brownsville, bordering the military highway (48), 9 Jul 1941, *Runyon 2819* (NY) [**726**]*; Hill Co.: Cobb Creek at junction with Aquilla Creek, 9 Sep 1972, *Mahler & Flook 6991* (UA) [**993**].

“Cuscuta indecora *s.l.*”—

These two specimens were used only in the molecular study and could not be morphologically assigned to a variety because of insufficient biological material. **Argentina.** —Neuquén: Departmento Picún Leufú: Picún Leufú, on the banks of the Picún Leufú stream, 2 Jun 1982, *Cerana 308* (CORD) [**2446**]; **USA.** —Arizona: Apache Co.: Hwy 264, ~10 mi W of Hwy 191 (Burnside), 2019, *Stefanović SS-19-43* (TRTE) [**2386**].

Cuscuta warneri *Yunck.*: *USA.* —

Utah: Millard Co.: In vicinity of Flowell, 15 mi W of Fillmore, 10 Sep 1957, *Warner s.n.* (GH, RSA) [**Isotype 1551**, 890]; —New Mexico: Sierra Co.: Pedro Armendaris Grant, 15.6 mi N of Engle, east of Red Lake, 24 Sep 1998, *Peterson 98-699* (NMC) [662].

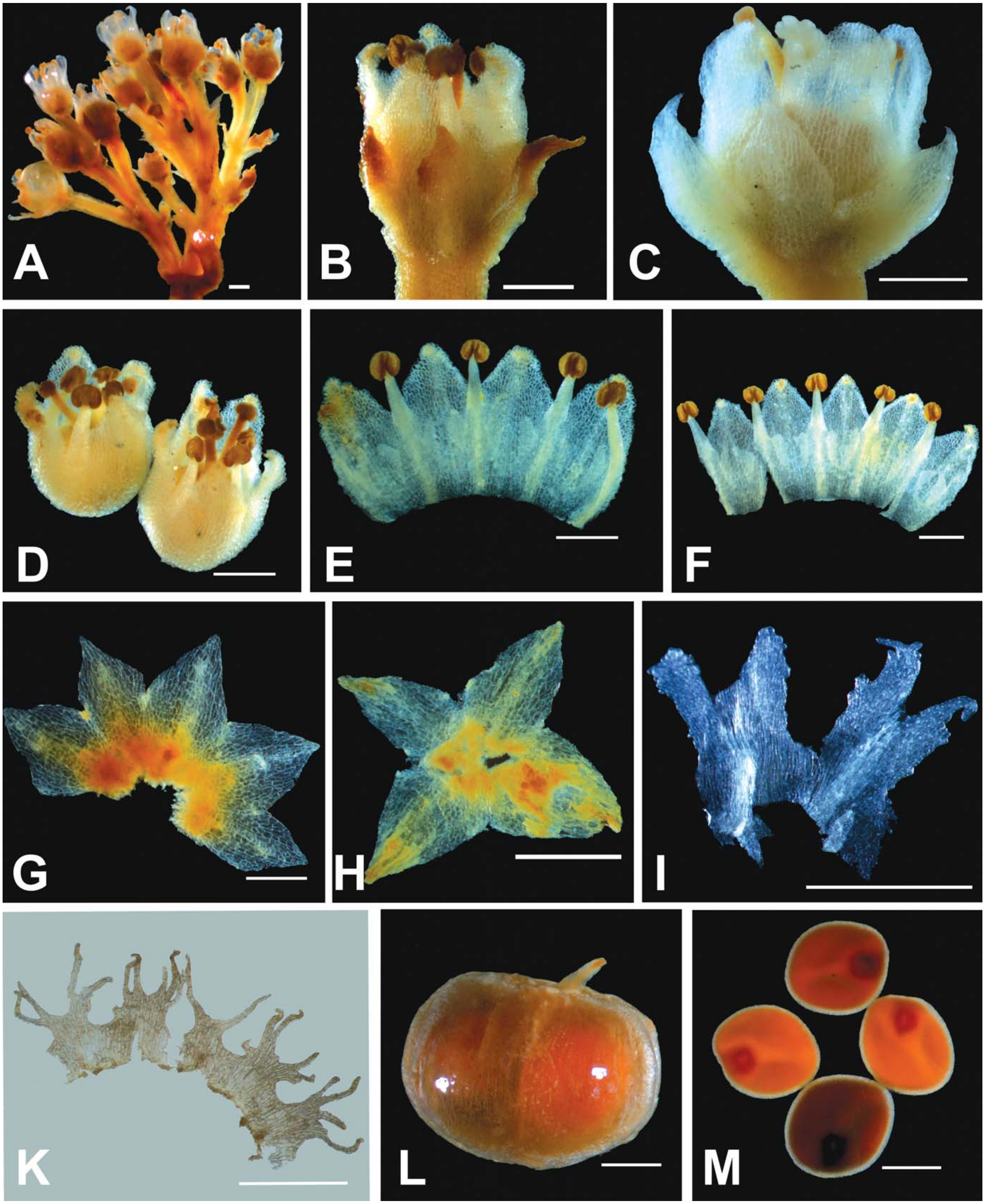

FIG. S8. Morphology of *Cuscuta coryli* reproductive structures. A. Inflorescence. B–C. Variation of flowers (four- and five-merous). D. Corollas 3D. E–F. Variation of corollas (dissected). G–H. Variation of calyces. I–K. Variation of infrastaminal scales (removed from corolla). L. Capsule. M. Seeds. Scale bars = 1 mm.

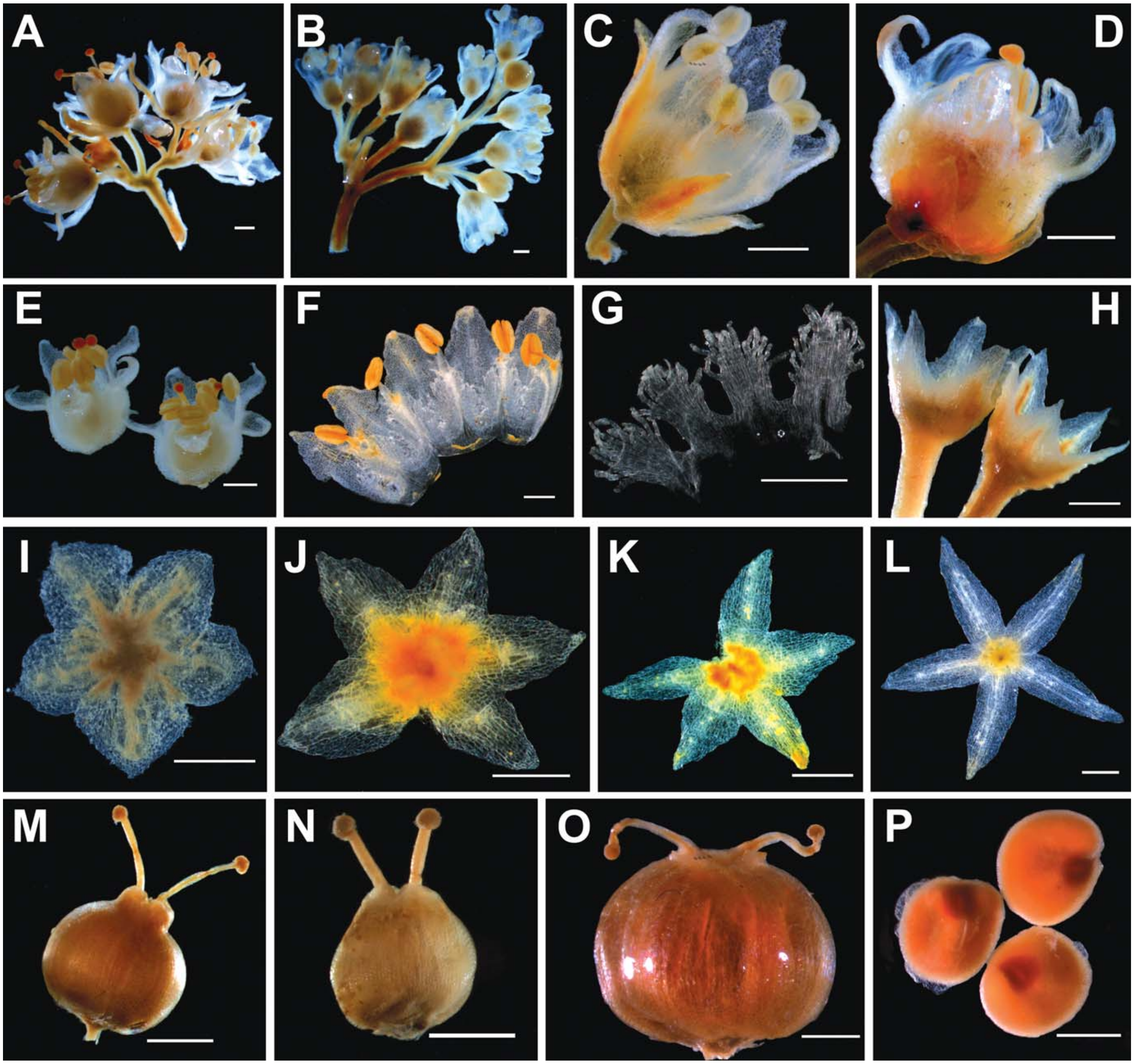

FIG. S9. Morphology of *Cuscuta indecora* s.l. reproductive structures. A–B. Variation of inflorescences. C–D. Variation of flowers. E. Corollas 3D. F. Dissected corolla. G. Infrastaminal scales (removed from corolla). H. Calyces 3D. I–L. Variation of calyces (dissected). M–N. Variation of gynoecium. O. Capsule. P. Seeds. Scale bars = 1 mm.

APPENDIX 2.

List of characters scored for morphometric study—

Continuous Characters. 1. Pedicel length (mm). Bract length (mm). 2. Bract width (measured at the base, mm). 3. Angle of bract apex (°). 4. Flower length (measured from the tips of corolla lobes to the receptacle base; mm). 5. Total calyx length (mm); Calyx lobe length (mm). 6. Maximum calyx lobe width (mm). 7. Middle calyx lobe width (mm). 8. Maximum calyx lobe length divided by maximum calyx lobe width. 9. Calyx tube length divided by total calyx length. 10. Angle of calyx lobe apex (°). 11. Calyx tube length (mm). 12. Circumference of calyx tube (mm). 13. Total corolla length (mm). 14. Corolla lobe length (mm). 15. Maximum corolla lobe width (mm). 16. Middle corolla lobe width (mm). 17. Corolla lobe apex width (mm). 18. Length of inflexed corolla lobe apex (mm). 19. Angle of corolla lobe apex (°). 20. Ratio of corolla lobe apex length divided by corolla lobe apex width. 21. Corolla tube length (mm). 22. Circumference of corolla tube at base of staminal filaments (mm). 23. Maximum infrastaminal scale length (mm). 24. Infrastaminal scale width at base (mm). 25. Maximum infrastaminal scale width (mm). 26. Length of free portion of infrastaminal scale (mm). 27. Infrastaminal scale bridge length (mm). 28. Length of longest infrastaminal scale fimbria (mm). 29. Number of infrastaminal scale fimbriae. 30. Stamen filament length (mm). 31. Anther length (mm). 32. Anther width (mm). 33. Length of longest style (mm). 34. Length of shortest style (mm); 36. Stigma width (mm); 35. Length of thickened apical portion of capsule (mm); 36. Capsule length (mm); 37. Capsule width (mm); 38. Seed length (mm); 39. Seed width (mm); 40. Hilum scar length (mm); 41. Vascular scar length (mm).

Binary Characters. 42. Flowers mostly 4-merous, rarely 3-merous: present (1), absent (0). 43. Flowers mostly 5-merous, rarely 4-merous present (1), absent (0). 44. Horn-like projections on calyx lobe apices: present (1), absent (0). 45. Corolla lobes connivent, not spreading or reflexed at full anthesis: present (1), absent (0). 46. Infrastaminal scale bifid: present (1), absent (0). 47. Capsule with distinct collar-like apex: present (1), absent (0).