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BRIEF COMMUNICATION

CUSCUTA JEPSONII (CONVOLVULACEAE): AN INVASIVE WEED OR AN EXTINCT ENDEMIC?[1]

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Despite their ecological significance, parasitic plants face more conservation challenges than do autotrophic plants. This is especially true for the groups that include weedy or invasive species such as *Cuscuta*. While approximately half of the *Cuscuta* (dodders) species may require conservation measures, the genus as a whole is sometimes posted on governmental lists of noxious or quarantine weeds. Our study challenges this stereotype and uses the case of *C. jepsonii* (Jepson's dodder) to illustrate the precarious biodiversity and conservation status faced by many dodder species. Until now, Jepson's dodder has been known only from its type collection. Consequently, its phylogenetic affinities, morphological variation, and ecology have remained unknown, and the species is currently ambiguously considered either synonymous to the invasive North American weed *C. indecora* or to an extinct endemic from California. Using molecular data from newly found collections, we infer that *C. jepsonii* belongs to *C. californica* species complex, instead of *C. indecora* clade. Also, we discuss the conservation of this species within the broader biological and ecological context of *Cuscuta* in general.

Key words: biodiversity; conservation; Convolvulaceae; *Cuscuta jepsonii*; dodders; ecology; extinct; invasive; parasitic plants; host specificity; phylogeny.

Parasitism has evolved independently at least 12 times in the angiosperms (Nickrent, 2009). Parasitic plants have been described as keystone species and ecosystem engineers because they impact multiple trophic levels and may even alter the abiotic environment (reviewed by Press and Phoenix, 2005). Yet the conservation of parasitic plants is fraught with more challenges than that of autotrophic plants (Marvier and Smith, 1997). Indeed, the slogan "equal rights for parasites" was coined by Windsor (1995) in an attempt to draw the attention of the scientific community to the bias against parasitic animals that pervades contemporary conservation biology. This situation applies particularly well to *Cuscuta* (dodders, Convolvulaceae), a genus of ca. 180 species of stem parasites with reduced scale-like leaves, and filiform stems that attach to the host through numerous haustoria (Yuncker, 1932; Kuijt, 1969).

Dodders are placed indiscriminately as *Cuscuta* spp. on Canadian provincial lists such as "noxious weeds" in British Columbia, Manitoba, Ontario, and Québec, and as "restricted weeds" (destroyed when found) in Alberta (Costea and Tardif, 2006; Rice, 2009). In the USA, "native and widely distributed species" are exempted from the federal noxious weed list (USDA, APHIS, 2006), despite the fact that some of these dodders (e.g., *C. campestris*) are invasive weeds (Parker and Riches, 1993; Holm et al., 1997; Costea and Tardif, 2006). Even so, the legislatures of Arizona, Arkansas, Massachusetts, Michigan, and Oregon contradict the U. S. federal provision and, similarly to the Canadian provinces, place dodders in bulk on lists such as "Prohibited Noxious Weeds", "Quarantine", or "Class A Noxious Weed" (Rice, 2009; USDA, NRCS, 2009). In the case of *Cuscuta*, the negative stereotype—parasites are dangerous and must be destroyed—is perpetuated by extrapolating the true danger posed by a limited number of species (~15 species considered as weeds worldwide; Parker and Riches, 1993; Dawson et al., 1994) to the scale of an entire genus, regardless of the fact that the vast majority of dodders are not weeds.

Similarly to other parasitic plants (e.g., *Rhinanthus*, Ameloot et al., 2006; Bardgett et al., 2006), *Cuscuta* species play an important role in the ecosystems. They have the capacity to reduce hosts' biomass and alter hosts' allocation patterns, as well as to significantly modify the structure of plant communities (Pennings and Callaway, 2002). For example, although it represents less than 5% of the total vegetation biomass, *C. salina* var. *major* from western North America plays a key role in maintaining diversity in salt marsh plant communities (Pennings and Callaway, 1996; Callaway and Pennings, 1998).

Despite their clear ecological significance, most studies of *Cuscuta* have focused on the detrimental species and methods for their eradication (reviewed by Dawson et al., 1994; Costea and Tardif, 2006), while natural history and/or systematic research has been comparatively overlooked. *Cuscuta jepsonii* Yunck. (Jepson's dodder) illustrates well the ambiguous status of many dodder species, from both taxonomic and biodiversity standpoints. Jepson's dodder, described by Yuncker (1921), has been known until now only from the holotype specimen collected by Willis Linn Jepson in 1892 in California. Because it has not been found again for more than a century, the California Native Plant Society (2009) assesses this species as presumably extinct (state rank: SH; global rank: GH) and includes it on List 3 ("plants about which we need more information"). On the

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other hand, *C. jepsonii* has been also widely accepted as a synonym of *C. indecora* Choisy var. *indecora* (Beliz, 1993; ITIS, 2009; USDA, NRCS, 2009), a common weed in the Americas (Prather et al., 1995; Costea et al., 2006a). Last, NatureServe (2009) ignores *C. jepsonii*. These contradictory treatments raise the question as to whether *C. jepsonii* is an invasive weed or a potentially extinct endemic from California.

During a survey of herbarium material from California, we discovered additional specimens of *C. jepsonii*. These specimens have allowed us to expand our knowledge about the morphological variation, ecology, and geographical distribution of *C. jepsonii* as well as to estimate its phylogenetic position using molecular data. The main objectives of this article are (1) to place *C. jepsonii* within the broad phylogenetic framework of *Cuscuta* subgenus *Grammica*, (2) to analyze evolutionary relationships with its closely related species, and (3) to discuss the conservation of this species in the larger biological and ecological context of *Cuscuta* in general.

MATERIALS AND METHODS

Morphology and micromorphology—Five new collections of *C. jepsonii* (Appendix 1) were discovered during our herbarium survey for the upcoming treatments of *Cuscuta* in the second edition of the *Jepson Manual* and *Flora of North America*. Flowers and fruits were rehydrated to document their morphology using a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 6.8 software (MIS, Villa Park, Illinois, USA). Micromorphology was studied with a scanning electron microscope (SEM) Hitachi (Tokyo, Japan) S-570 at 10 kV; samples were coated with 30 nm gold using an Emitech K 550 (Soquelec Ltd., Mississauga, Ontario, Canada) sputter coater (Costea et al., 2006a; Costea, 2007 onward). The conservation status was assessed using NatureServe (2009) ranks and criteria.

Phylogenetic analyses—Of five newly discovered collections of *C. jepsonii*, only one specimen (*Munz 16294*, RSA; Appendix 1) was deemed to be of sufficient quality and quantity for molecular studies. To infer the phylogenetic affinities of this species within *Cuscuta* subg. *Grammica*, we used multiple sequences from two plant genomes. From the plastid genome (ptDNA), we targeted a noncoding region containing the *trnL*-UAA intron, 3′ *trnL*-UAA exon, and intergenic spacer between this exon and *trnF*-GAA (hereafter called *trnL-F*) and the *rbcL* gene. We also obtained sequences from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (rDNA) as well as a ~950 bp portion at the 5′ end of the large nuclear ribosomal subunit (26S rDNA). DNA extractions, polymerase chain reaction (PCR) reagents and conditions, amplicon purifications, cloning, and sequencing procedures follow Stefanović et al. (2007) and Costea and Stefanović (2009). The sequences generated in this study have been submitted to GenBank (accessions FJ479697–FJ479700). Newly obtained sequences were incorporated into previously aligned matrices from all four regions (Stefanović et al., 2007; Costea and Stefanović, 2009; deposited in TreeBASE at http://treebase.org under study number S2126) using the program Se-Al version 2.0a11 (Rambaut, 2002). The gaps were scored automatically using the program SeqState version 1.32 (Müller, 2005), coded as simple indels (Simmons and Ochoterena, 2000), and appended to the sequence matrix as binary characters.

Two sets of phylogenetic analyses were conducted. The preliminary analyses were designed to place *C. jepsonii* in a broader context of *Cuscuta* subg. *Grammica* phylogeny and to test its proposed relationships with *C. indecora* in particular. These analyses were carried out on a large 100-species data set, comprising all major clades of *Cuscuta* subg. *Grammica* as defined by Stefanović et al. (2007) and using only *trnL-F* and ITS sequences. Once the placement of *C. jepsonii* was narrowed to clade A, more detailed analyses of its relationships within this group, informally referred to as the *C. californica* complex, were carried out using a 10-species data set (for details see Costea and Stefanović, 2009) and all four sequenced regions.

Parsimony searches were conducted in the program PAUP* version 4.0b10 (Swofford, 2002). For the broad-scale analyses, searches for most parsimonious (MP) trees were performed using a two-stage strategy. First, the search involved 1000 replicates with random stepwise addition (RAS) of taxa, tree-bisection-reconnection (TBR) branch swapping saving no more than 10 trees per replicate, and MULTREES option off. In the second stage, all trees in memory were analyzed with the same settings except the MULTREES option on. Given the smaller number of terminal units (46 accessions), the fine-scale parsimony analyses were run in a single step, with 1000 RAS, TBR branch swapping, but with MULTREES set to increase without limit. For both sets of analyses, the internal support for clades was inferred by nonparametric bootstrapping (Felsenstein, 1985) using 200 pseudoreplicates, each with 20 RAS, TBR branch swapping, and MULTREES option off (DeBry and Olmstead, 2000).

Bayesian Markov chain Monte Carlo (MCMC) phylogenetic inferences (Yang and Rannala, 1997) were conducted using the program MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003) on the *C. californica* complex data set only. For the details on the model of sequence evolution selection and Bayesian search settings, see Costea and Stefanović (2009). In brief, the analysis consisted of two runs of one million generations each, starting from a random tree, using the default priors and four Markov chains sampled every 100 generations and the TIM + G model of DNA evolution. Only the nodes receiving ≥0.95 posterior probabilities (PP) were considered to have statistically significant support (Rannala and Yang, 1996). Convergence of the chains was determined by examining the plot of all parameter values and –lnL scores against generation using the program Tracer version 1.3 (Rambaut and Drummond, 2004). Stationarity was assumed when all parameter values and the –lnL had stabilized.

RESULTS

The broad-scale parsimony analysis of *Cuscuta* subg. *Grammica* resulted in >100 000 equally parsimonious trees of 2796 steps each. A schematic consensus tree showing 15 well-supported major clades (labeled A–O) and the backbone relationships among them is presented in Fig. 1A (for detailed trees, see Stefanović et al., 2007). Independent (locus-specific) as well as combined (total-evidence) molecular analyses placed *C. jepsonii* firmly within clade A, with 100% BS, in disagreement with its previous tentative placement (based on limited morphological data, see Costea et al., 2006a) in proximity with *C. indecora* (clade M; Fig. 1A). An additional 74 steps are required to place *C. jepsonii* and *C. indecora* within the same clade. This length penalty does not come as a surprise given that multiple intervening nodes from total-evidence analysis had 100% BS support (Fig. 1A).

Both Bayesian runs carried out on a data set restricted to the members of the *C. californica* complex (Costea and Stefanović, 2009) plus *C. jepsonii*, converged on similar parameter values and –lnL scores and reached apparent stationarity at no later than 100 000 generations. The burn-in of data points, accumulated before asymptotic plateaus were reached, left a total of 18 000 combined trees (2 × 9000) that were summarized as a majority-rule consensus tree (Fig. 1B). The parsimony analysis using the same sequence matrix, but with the addition of gaps coded as binary characters, produced 2142 MP trees, each 994 steps in length (CI = 0.76; RI = 0.94). A strict consensus of all equally parsimonious trees (not shown) resulted in relationships topologically identical to those obtained using the Bayesian criterion (Fig. 1B).

According to our results, *C. jepsonii* is nested within the *C. californica* complex, a group that includes, for the most part, the species circumscribed by Yuncker (1932) in subsections *Californicae* and *Salinae*. In agreement with Yuncker's (1921, 1932) original suggestions, Jepson's dodder forms a well-supported (90% BS; ≥0.95 PP) sister lineage to the subclade that includes *C. californica*, *C. brachycalyx*, and *C. occidentalis* (Fig. 1B). Furthermore, *C. jepsonii* forms a distinct lineage within the *C. californica* complex, as highlighted by the long branch leading to it (Fig. 1B), comparable in length to other species in this complex.

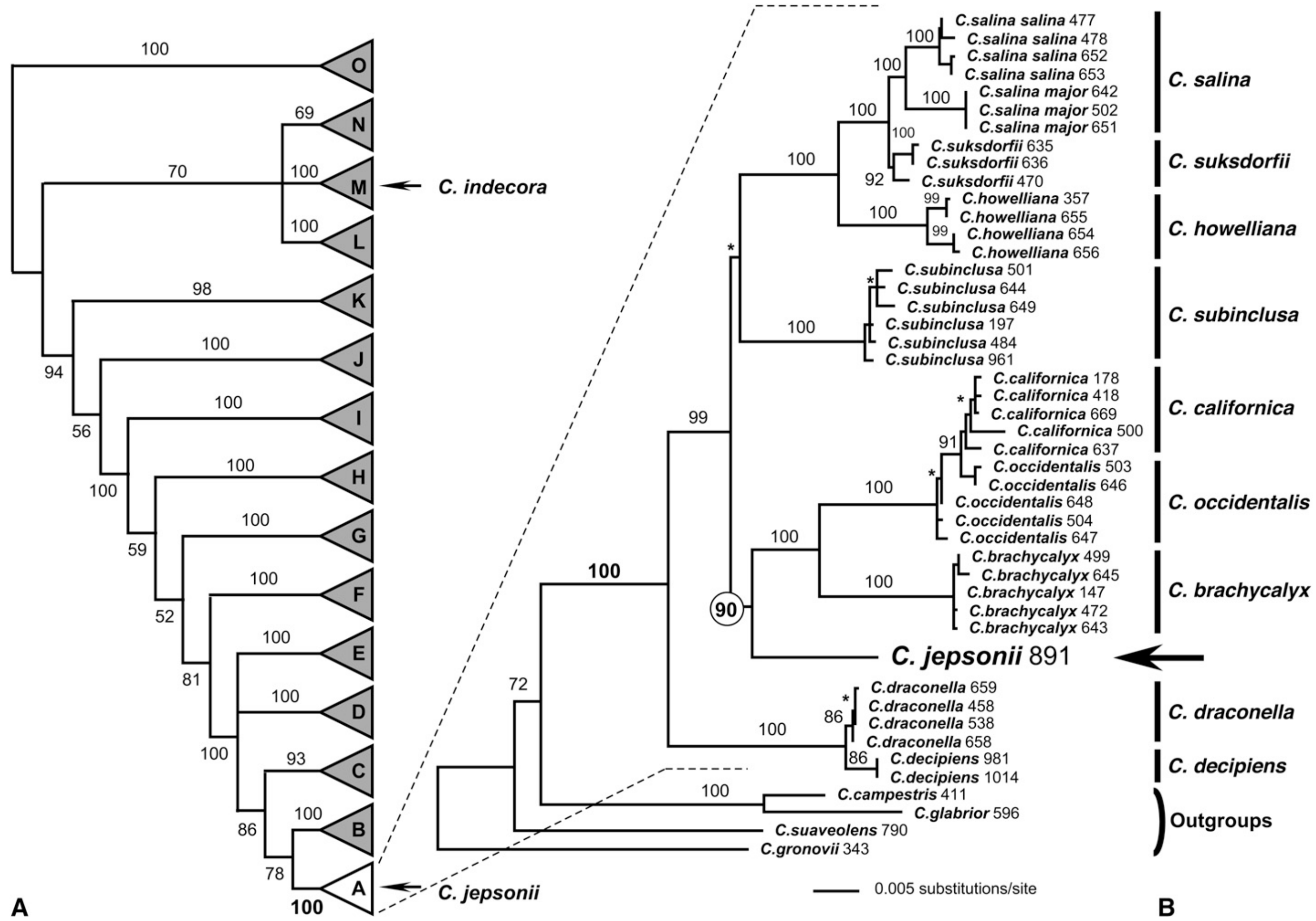

Fig. 1. Phylogenetic position of *Cuscuta jepsonii*. (A) Schematic overview of *Cuscuta* subg. *Grammica* phylogeny (strict consensus derived from the combined and *trnL-F* and ITS maximum parsimony analysis; see Stefanović et al., 2007 for details) depicting the relative positions of *C. jepsonii* and *C. indecora*. Fifteen major clades are labeled A–O; their bootstrap supports are indicated. (B) Majority-rule consensus tree with mean branch lengths from the Bayesian analysis of combined plastid (*trnL-F*, *rbcL*) and nuclear (ITS, 26S rDNA) data under the TIM + G model of DNA evolution showing fine-scale phylogenetic relationships of *C. jepsonii* with other species of *C. californica* complex (clade A). Bootstrap values are indicated for nodes supported at ≥50%. Asterisks indicate branches with Bayesian posterior probability <0.95; all other branches have posterior probability ≥0.95. Numbers following species names correspond to DNA accessions (see Costea and Stefanović, 2009).

In addition to resolving its phylogenetic placement, our results are consistent with the species status of *C. jepsonii*, as opposed to alternative taxonomic solutions that treated this entity as synonymous with either *C. californica* var. *papillosa* (Beliz, 1986) or *C. indecora* var. *indecora* (Beliz, 1993). Morphologically, *C. jepsonii* differs from all the species of the *C. californica* complex (Costea et al., 2006b) in having corolla lobes ca. 1/3 as long as the corolla tube (Fig. 2; in the other species of the clade, corolla lobes are equaling or longer than corolla tube). The previous descriptions of morphology based on the holotype alone (Yuncker, 1921, 1932; Costea et al., 2006a) are accurate except for the infrastaminal scales, which although generally reduced to ridges, were found to be shortly bifid at the apex in one collection (Fig. 2D). Pollen is 3(–4)-zonocolpate, 17–22 µm long, subspherical to prolate (the latter more common), rounded at the poles; tectum is granulate, imperforate, or with only a few puncta, 0.2–0.3 µm in diameter. Mature seeds, examined for the first time, are broadly elliptic to subround, 0.9–1.1 × 0.8–1 mm, dorsoventrally compressed, with a subterminal hilum.

DISCUSSION

***Distribution, ecology, and conservation status of* Cuscuta jepsonii**—Based on the information from the newly found collections (Appendix 1), the geographical distribution of Jepson's dodder in California spanned from the High North Coast Ranges and Mount Shasta to the Southern Sierra Nevada. Unfortunately, all these collections are old: the two most recent specimens were collected in the 1950s; the others are at least 100 years old (see Appendix 1). An extensive search on the southern slopes of Mount Shasta (Siskiyou Co., CA; the second most recent known collection site) in July 2008 failed to discover this species, although the suitable California lilac hosts (*Ceanothus*, Rhamnaceae; discussed later) were present. Nevertheless, *C. jepsonii* may not be extinct. First, this is a small species, much less conspicuous than others in this genus, and if it is not extinct, it is most likely rare ("uncommon", Munz and Keck, 1959; also see *Munz 16294* in Appendix 1). Second, most of the original collection sites are now part of extensive conservation

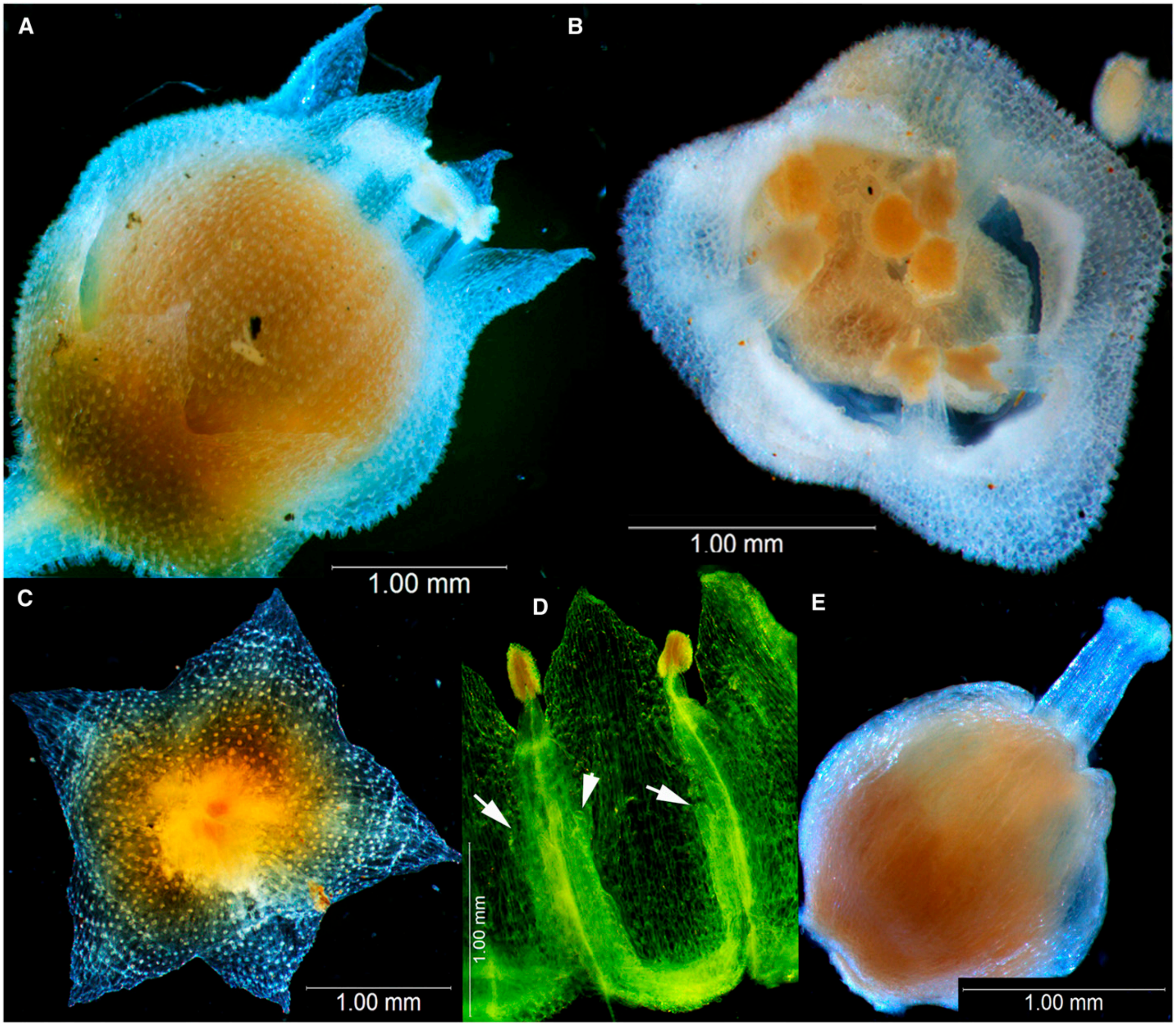

Fig. 2. Morphology of *Cuscuta jepsonii*. (A) Flower, lateral view. (B) Flower, view from above. (C) Calyx, dissected, dorsal view. Note that papillae on the calyx and corolla are arranged in rows similarly to *C. indecora*. (D) Corolla, dissected, showing stamens and reduced infrastaminal scales; arrows indicate short lateral fimbriae that make the scales bifid (fluorescent green is a digital manipulation created with Pax-it 6.8 to enhance contrast). (E) Gynoecium, lateral view. All images from *Heller 5981* (CAS, RSA, UC) except (E), which is from *Dudley 1774* (DS). Herbarium acronyms from Holmgren et al. (1990).

areas, e.g., Sanhedrin Mountain (proposed) and Yolla Bolly Middle Eel Wilderness Areas (parts of Mendocino National Forest), Shasta-Trinity National Forest, and Giant Sequoia National Forest. Finally, and perhaps most importantly, there have been no concerted efforts (besides our own) to locate this species. In brief, we suggest that *C. jepsonii* may be rediscovered, and we hope that the information presented here will provide the impetus to search for this species. Until then, the NatureServe (2009) conservation status category GH "Possibly Extinct—"Missing; known from only historical occurrences but still some hope of rediscovery"—is proposed for *C. jepsonii*.

The ecology of *C. jepsonii* was only mentioned briefly by Munz and Keck (1959) as "yellow pine forests," but more information can be inferred from its two known hosts: *Ceanothus prostratus* and *C. diversifolius*. The former species generally occurs in sunny, open sites on dry slopes and flats, in forests of *Pinus jeffreyi*, *P. ponderosa*, and *Pseudotsuga menziesii* at elevations ranging from 790 to 2700 m a.s.l. (Fross and Wilken, 2006; D. Burge, Duke University, unpublished data). *Ceanothus diversifolius* grows in more shaded places in relatively closed coniferous forests, often on cool but relatively dry ridges, flats, and drainages at elevations of 760–2300 m a.s.l. (Fross and Wilken, 2006; D. Burge, Duke University, unpublished data).

Host specificity: Conservation implications—Host specificity and host preference vary greatly among parasitic plants (Parker and Riches, 1993; Heide-Jørgesen, 2008), and host-race formation is an important evolutionary driver (e.g., Norton and Carpenter, 1998; Thorogood et al., 2008). Host specificity is also a crucial life history trait because it predefines the spatial limits within which a parasitic plant can occur and expand, both at the level of the ecosystem and at a geographical scale. The host–parasite interaction generates additional factors (e.g., host specificity and preference, host availability, host quality, host resistance to parasitism) that make the conservation of parasitic plants more challenging (Marvier and Smith, 1997).

Two empirical observations can be made about *Cuscuta* spp. from the point of view of their host specificity. First, the most successful dodders are the "generalists" that can parasitize plants from numerous families and genera. These *Cuscuta* spp. are usually weeds with a broad geographical distribution. Representatives of this category include: *C. campestris*, which is almost cosmopolitan in its distribution; *C. indecora* found across North and South America; *C. americana* from South America, West Indies, and parts of North America; *C. gronovii* in North America; as well as *C. reflexa* and *C. japonica*, mainly found throughout Asia, but locally introduced in other areas as well. The corollary of this observation is that dodders with conservation problems are "specialists," restricted to unique host genera or species. Among such species besides *C. jepsonii* are *C. warneri* on *Phyla* (Verbenaceae), *C. polyanthemos* on *Chamaesyce* (Euphorbiaceae), *C. attenuata* on *Iva annua* (Asteraceae), *C. veatchii* on *Schinus discolor* (Anacardiaceae) (for more examples, see Heide-Jørgesen, 2008). However, the host specificity for most of the *Cuscuta* spp. lies between these two extreme strategies because many dodders have adapted to parasitizing hosts that grow in a particular habitat from a certain geographical area.

The second observation is that specialized *Cuscuta* species are likely to become extinct before their hosts. For instance, *C. warneri* and *C. jepsonii* are both presumed to be extinct (Costea et al. 2006a). The former was known to parasitize *Phyla cuneifolia* and *P. nodiflora*, and the latter, *Ceanothus prostratus* and *C. diversifolius*, as indicated. These host species are all considered "secure—common; widespread and abundant" ("G5"), except for *C. diversifolius*, which has been assessed by NatureServe as having a conservation rank of "G3?" ("vulnerable?"). The same applies to all known hosts of *Cuscuta* species ranked G3 or rarer. In general, they have a substantially better conservation status than their *Cuscuta* parasites (NatureServe, 2009). The density of potential hosts represents a major limiting factor for *Cuscuta* populations that establish from seeds. Immediately after germination, the seedlings of *Cuscuta* have only 7–21 d to locate a host in their immediate proximity and establish a haustorial connection. If that does not occur, they will die (Dawson et al., 1994; Costea and Tardif, 2006). Therefore, any decline in the density or patchiness of the potential hosts will negatively impact the populations of *Cuscuta*. Cases in which the parasites are more likely to go extinct before their hosts have also been documented when the density of hosts modulates the success of infection (Lyles and Dobson, 1993).

Conclusions—The 1997 IUCN Red List of Threatened Species included 22 species of *Cuscuta* worldwide (Walter and Gillett, 1998), but this list has not been reevaluated against the more recent criteria (IUCN, 2007). Among the 37 species ranked by NatureServe (2009) from the USA and Canada, 14 are considered "at risk" (ranked G3 or rarer). According to these numbers, ~38% of the *Cuscuta* species north of Mexico are in need of conservation. As is, this value is probably an underestimation for two principal reasons. First, some rare species (e.g., *C. nevadensis*) or even potentially extinct species (e.g., *C. jepsonii*) are not present on the list from the NatureServe. Second, given that ~40 *Cuscuta* species (from a total of ~180 worldwide) are known only from a single herbarium specimen (their respective types) and an additional ~50 are represented by no more than 2–5 collections, it becomes apparent that the biology and natural history of approximately one half of the species in the genus is essentially unknown. This uncertainty extends to their conservation status, likely to be G3 or rarer. Attempts to include *Cuscuta* species in more recent red lists or inventories are hindered precisely by this gap of information. For example, the red list of endemic plants from Peru (León and Roque, 2006) listed seven potential species of *Cuscuta*, but because similarly to *C. jepsonii* these species are known only from their types, they could not be assessed and assigned a conservation rank.

For these reasons, the traditional focus on pests and their control methods must be complemented with more systematics and biodiversity-oriented studies. The potential of some dodder species to cause agricultural damage cannot be ignored, but at the same time a shift from the "bad parasite" stereotype associated with these ecologically important plants is necessary. Only in this way can we diminish inequalities in knowledge and conservation and create the foundations upon which some of the contemporary policies can be challenged. Hence, our demand: Equal rights for parasitic plants!

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Appendix 1. Voucher information for the type and newly found specimens of *C. jepsonii* (herbarium acronyms from Holmgren et al., 1990). All specimens were collected in California, and vouchers are listed by county of origin.

County—Collection locality, Host, Date, *Voucher* (Herbarium).

Lake Co.—Holotype: Big Horse Mountain, South Fork of Eel River, host *Ceanothus diversifolius*, 3 Aug 1892, *Jepson 5c* (JEPS, fragment NY); foothills south of Mt. Sanhedrin, midway between Potter Valley and Hullville, host *Ceanothus diversifolius*, 25 Jul 1902, *Heller 5981* (RSA, CAS, UC); Elk Mountain, 1220–1525 m, host *Ceanothus diversifolius*, 21 Jul to 16 Aug 1905, *Tracy 2349* (UC). **Shasta Co.**—South slope of Mount Shasta, in dry ashy, volcanic soil, ponderosa pine, Douglas firs, oaks, true firs, host *Ceanothus prostratus*, 6 Jul 1954, *McLeod s.n.* (OSU). **Tulare Co.**—Region of Sequoia National Forest, vicinity of Homer's Nose, 1525 m, host *Ceanothus diversifolius*, 11 Jul 1897, *Dudley 1774* (CAS). **Trinity Co.**—North Yolla Bolly Mountains, 2.5 mi NW of Stuart Gap, 1402 m, infrequent on *Ceanothus prostratus* in yellow pine forest, 17 Jul 1951, *Munz 16294* (RSA).