TAXONOMY OF THE *CUSCUTA PENTAGONA* COMPLEX (CONVOLVULACEAE) IN NORTH AMERICA

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ABSTRACT

Cuscuta pentagona, *C. campestris*, and *C. glabrior* are closely similar taxa recognized here at specific rank. Closely related to these are *C. runyonii*, *C. harperi*, *C. plattensis*, and *C. sandwichiana*, as well as *C. obtusiflora* var. *glandulosa* and *C. polygonorum*. *Cuscuta runyonii*, *C. harperi*, and *C. sandwichiana* are relatively narrow endemics, *C. plattensis* and *C. glabrior* have wider but apparently discrete ranges, while *C. obtusiflora* var. *glandulosa*, *C. polygonorum*, and especially *C. pentagona* and *C. campestris* are widespread and broadly sympatric in North America, at least in some regions. *Cuscuta campestris* is one of the most widespread species in the world, being additionally recorded from South America, Europe, Asia, Africa, and Australia. Comparisons among these nine species are presented as a key and as comparative descriptions. SEM images are provided for flowers, fruits, seeds, and pollen.

RESUMEN

Cuscuta pentagona, *C. campestris*, y *C. glabrior* son taxa fuertemente semejantes, reconocidos aquí como especies. Estrechamente relacionadas con éstas están *C. runyonii*, *C. harperi*, y *C. plattensis* así como también *C. obtusiflora* var. *glandulosa* y *C. polygonorum*. *Cuscuta runyonii*, *C. harperi* y *C. sandwichiana* son endémicas con áreas pequeñas, *C. plattensis* y *C. glabrior* tienen rangos geográficos más amplios pero aparentemente distintos, mientras que *C. obtusiflora* var. *glandulosa*, *C. polygonorum*, y especialmente *C. pentagona* y *C. campestris* son comunes y ampliamente simpátricas en Norteamérica, al menos en algunas regiones. *Cuscuta campestris* ocurre fuera de Norteamérica, siendo mencionada de Sudamérica, Europa, Asia, Africa, y Australia. Las comparaciones entre estos seis taxa se presentan en forma de clave y descripciones comparativas. Se ofrecen imágenes de SEM de las flores, frutos, semillas, y polen.

Engelmann (1859) distinguished three varieties of *Cuscuta pentagona* Engelm. in addition to the typical form: var. *calycina*, var. *verrucosa*, and var. *microcalyx*. Yuncker (1932, 1965) treated var. *calycina* and var. *verrucosa* at specific rank but provided a new name for each: *C. campestris* Yuncker (nom. nov.) and *C.*

glabrior (Engelm.) Yuncker (comb. nov.), respectively. He treated var. *microcalyx* as a synonym of typical *C. pentagona*. Recent studies have not recognized *C. campestris* at any rank (e.g., Beliz 1986; Gandhi et al. 1987), while *C. glabrior* has been regarded as a variety of *C. pentagona* (Gandhi et al. 1987) or as nomenclatural synonym of *C. indecora* Choisy var. *neuropetala* (Engelm.) Hitchc. (Beliz 1986). Three other species from North America, *C. harperi* Small, *C. plattensis* A. Nels., and *C. runyonii* Yuncker, were included by Yuncker in the same group (subsect. *Arvenses* Yuncker) with *C. pentagona* and *C. campestris* (Yuncker 1965). Although *C. runyonii* has been considered a good species by all authors, *C. harperi* and *C. plattensis* were treated by Beliz in her Ph.D. dissertation (1986) as nomenclatural synonyms of "*C. pentagona* var. *polygonorum*" and *C. indecora*, respectively.

The current paper is the second of several to present taxonomic analyses of *Cuscuta* species groups and complexes. The first (Costea et al. 2005) gave an assessment of *Cuscuta nevadensis* and *Cuscuta veatchii*; three others follow in this issue (Costea et al 2006a,b,c). Other two papers that are now in preparation will deal with the phylogeny of *Cuscuta* and its infrageneric taxonomy, including the formal delimitation of the groups of species treated in the four papers published in this issue. Evaluations of the status of all these taxa are necessary for the accounts of *Cuscuta* in the Flora of North America and the forthcoming revision of The Jepson Manual (California). The comments below on reproductive biology and taxonomy are in perspective of the whole genus.

REPRODUCTIVE BIOLOGY AND TAXONOMY OF *CUSCUTA*

Scarcity of information regarding the reproductive biology of *Cuscuta* species limits progress toward understanding the taxonomy and evolution of this genus. For example, a detailed study of floral biology is available only for *C. attenuata* Waterfall (Prather & Tyrl 1993), which is very closely related to to *C. indecora*. Although they may be sympatric over an extensive geographical range, species such as *C. campestris* and *C. pentagona* have never been found "growing together at the same site" (Musselman 1986). Apparently a single herbaceous host cannot support more than one parasite (often a single *Cuscuta* plant simultaneously parasitizes several different host plants), although it does not seem impossible that colonies of different *Cuscuta* species might exist side by side. Furthermore, although some species (e.g., *C. epithymum* Murray, *C. rostrata* Shuttlw. ex Engelm. & A.Gray) have been reported to be pollinated by insects (Beliz 1986; Musselman 1986; Holm et al. 1997), others such as *C. pentagona* and its relatives apparently are autogamous (Verdcourt 1948; Beliz 1986; Musselman 1986; Prather & Tyrl 1993; Dawson et al. 1994). In the *C. pentagona* complex, we observed that anthers dehisce longitudinally before flowers open, further substantiating previous observations of autogamy. The low pollen/ovule ratio (= 65) found by Beliz (1986) in *C. pentagona* (including *C.*

campestris) supports the idea that autogamy may be common (see Cruden 1977).

The occurrence of inbreeding may help explain the relatively high number of taxa (species and varieties) that are recognizable as morphological entities in *Cuscuta*. The existence of intermediate-like plants observed rarely in populations of the *C. pentagona* complex probably reflects populational variability in closely related taxa. Hybridization also is a possible explanation, but experimental attempts to produce hybrids (e.g. between *C. indecora* and *C. attenuata*) have failed (Prather & Tyrl 1993).

Seed dispersal of many *Cuscuta* species seems unspecialized (Kuijt 1969). "Natural" means of seed dispersal are unknown. Lyshede (1984) suggested that wind may play a significant role in dispersal because of the pits present on the seed coat of dry seeds. However, *Cuscuta* seeds do not possess "classical" adaptations for wind dispersal, and the alveolate/papillate seed coat seems more an adaptation related to the germination process (Costea & Tardif 2006). Kuijt (1969) mentioned that seeds remain viable while they pass through the digestive system of sheep, but Gómez (1994) in Sierra Nevada, Spain, reported that hosts infested with *C. epithymum* were avoided by the Spanish ibex, the main herbivore in the area. Herbivores may avoid plants infested with *Cuscuta* because of the yellowish color (Costea & Tardif 2006). Capsules and seeds of *Cuscuta* float, and although water dispersal has never clearly been documented, it may occur only in the species that prefer the vicinity of water, such as *C. gronovii* Willd. ex J. A. Schult. Dispersal over long distances of weed species such as *C. campestris* has been connected with anthropomorphic activities. The principal means of world-wide dispersal of *Cuscuta* weeds has been through contaminated seeds of forage legumes (alfalfa, clover, and lespedeza, especially *Lespedeza cuneata* (Dumont) G. Don; reviewed by Dawson et al. 1994; Costea & Tardif 2006). Furthermore, when wetted, the seed coat in *Cuscuta* species becomes papillose-gelatinous and adheres easily to soil particles, and seeds may thus be carried by farm machinery (Costea & Tardif 2006).

METHODS

Descriptions of morphology and micromorphology are based mostly on specimens from herbarium NY, which includes Yuncker's herbarium (Appendix 1). Measurements of floral parts except anthers were done on rehydrated herbarium material. Length of flowers was measured from the base of calyx to the tip of straightened corolla lobes. Pollen, anthers, seeds, and capsules were measured on SEM pictures taken with a scanning electron microscope Hitachi S-570 at 15 KV. Samples were coated with 30 nm gold using an Emitech K 550 sputter coater. Standard terminology for cell types and surface sculpturing patterns follows Barthlott et al. (1998); pollen terminology follows Hoen (1999). Conservation status was assessed using NatureServe (2005) ranks and criteria.

Identification of *Cuscuta* often is a lengthy process because rehydration of

flowers, dissection, and examination under a microscope are usually necessary. Variation may be expected on the same individual (e.g., Gandhi & Thomas 1983; Severova 1991). Furthermore, because flowers do not mature simultaneously, the size and ratios between different floral parts on the same plant may vary to some extent. A range of flowers, fruits, and seeds belonging to the same plant should be examined. The angled calyx of *C. pentagona* and *C. harperi* is best observed in flower and during early fructification; full development of capsules may obscure the character.

MICROMORPHOLOGY

Flowers and capsules.—**Laticifers**, **papillae**, and **multicellular protuberances** may occur on the floral parts and capsules and distinctions between these features can be important in recognizing members of the *C. pentagona* complex (magnification of 100× or more recommended). **Laticifers** are visible in the calyx and sometimes in the corolla and capsules of all taxa. Yuncker usually referred to them as "pellucid glandular-appearing cells" (Yuncker 1921, 1932, 1965). Laticifers may appear isolated, rotund, ovoidal or tangentially elongated, or they can be organized in rows (Fig. 1 c,e). Laticifers from the stems are perivascular, multinucleate, and articulated (Lyshede 1985). **Papillae** are more or less radially elongated cells, and they are present in the calyces, corollas, and capsules of *C. harperi*, *C. glabrior*, and *C. runyonii* (Fig. 1 e,f; 2 a,b,c). **Multicellular protuberances** are larger and they may occur in *C. runyonii* along the midveins of the calyx lobes (Fig. 2c). **Epicuticular wax** on the perianth, when present, is represented by longitudinally reticulated rodlets (Fig. 1f).

Pollen.—Pollen is relatively uniform among species. Grains are 3(-4)-zonocolpate (rarely 4-6 loxocolporate in aberrant grains), and they may be polymorphic in the same anther or flower, from spheroidal to prolate (Fig. 3). Ornamentation varies from tectum imperforatum or with a few puncta in *C. glabrior*, *C. runyonii*, and *C. plattensis*, to tectum perforatum in *C. pentagona*, *C. campestris*, *C. harperi*, and *C. obtusiflora* var. *glandulosa* (Fig. 3). The latter three species have sexine often persistent in punctum apertures (Fig. 3). *Cuscuta pentagona* and *C. obtusiflora* var. *glandulosa* have the largest puncta, up to 0.7 µm in diameter, sometimes approaching a microreticulate ornamentation (Fig. 3).

Seeds.—A striking feature of the seed coat epidermis is that when seeds dry, cells of the outer cell wall invaginate, which causes the seed surface to become alveolate (Fig. 4; see also Lyshede 1984; Knepper et al. 1990; Costea & Tardif 2006). Water uptake induces bulging of the invaginated epidermal walls, and epidermis cells become swollen and papillose (Fig. 4c). The diameter of seed coat epidermal cells is 17-50 µm in *C. pentagona*, *C. campestris*, *C. glabrior*, *C. runyonii*, and *C. harperi* and 15-20 µm in *C. plattensis*, *C. obtusiflora* var. *glandulosa*, and *C. polygonorum*. The seeds of *C. runyonii* and *C. polygonorum* have epicuticular wax organized as longitudinal rodlets (Fig. 4d), a feature not

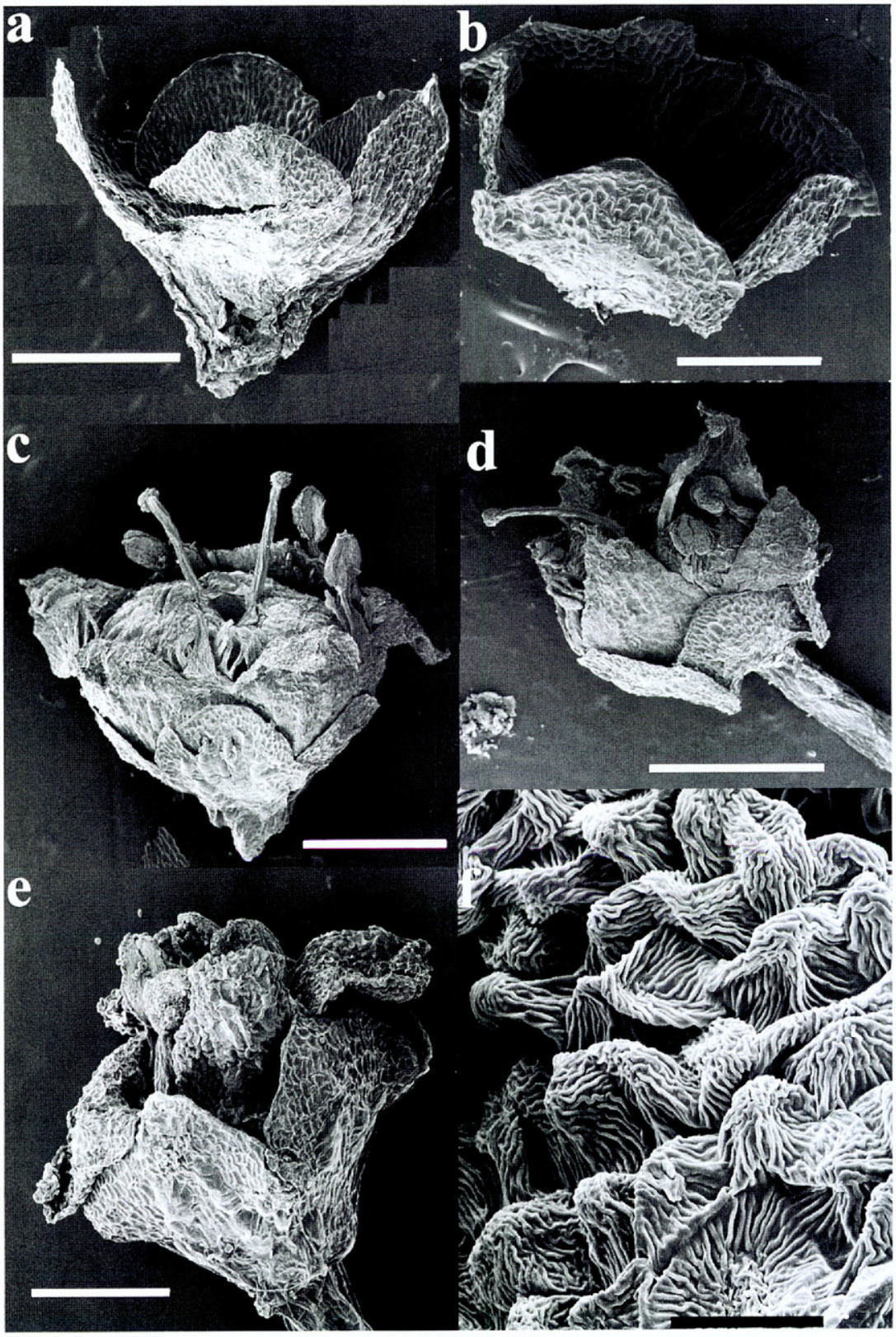

FIG. 1. **a.** Calyx of *C. campestris* (scale bar = 1 mm); **b.** Calyx of *C. pentagona* (scale bar = 0.5 mm); **c.** Flower with maturing capsule of *C. campestris* (scale bar = 1 mm); **d.** Flower of *C. pentagona* (scale bar = 0.75 mm); **e.** Flower of *C. harperi* (scale bar = 0.5 mm); **f.** Papillae on the corolla lobes of *C. harperi* (scale bar = 0.43 μm).

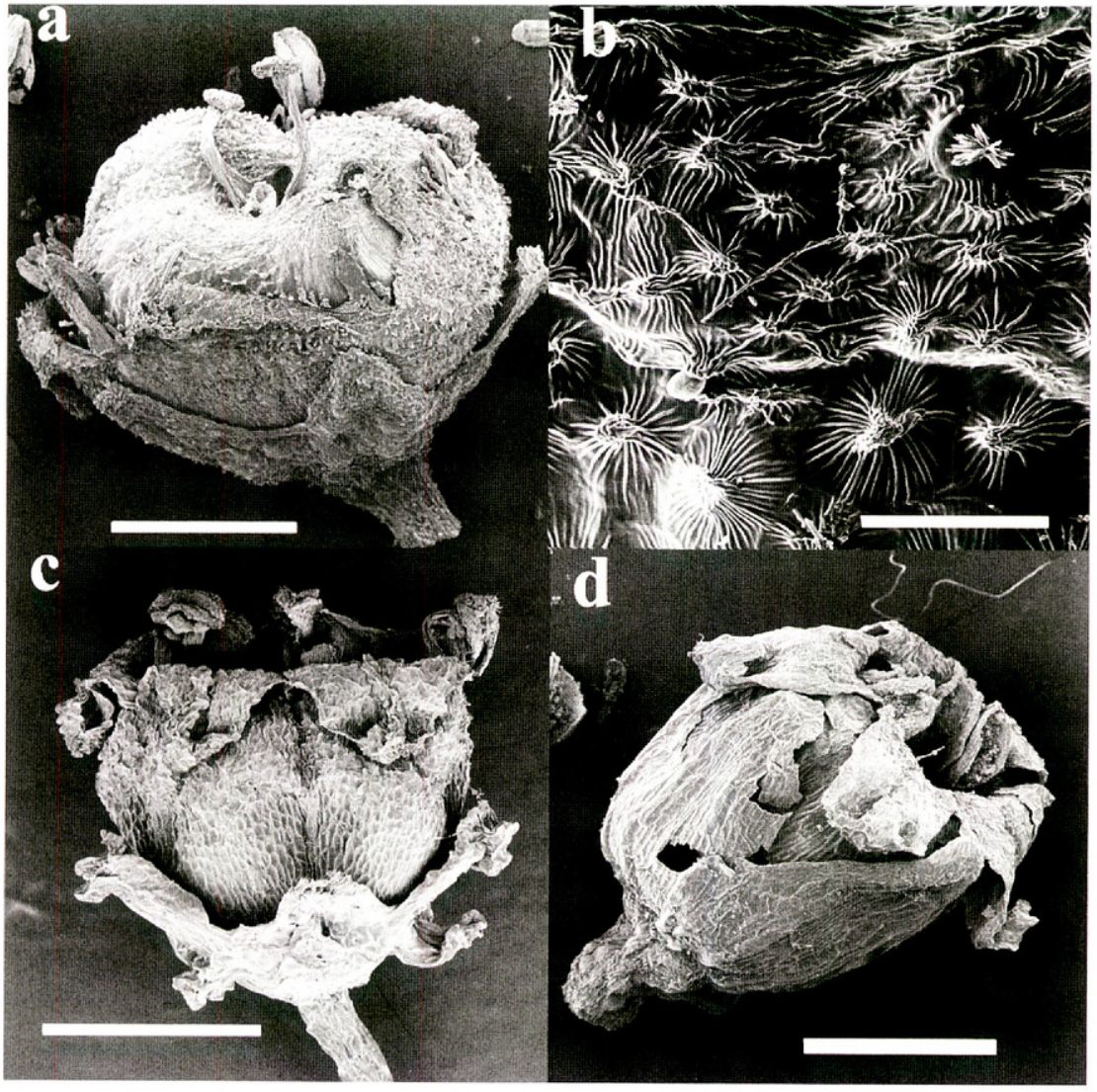

Fig. 2. **a.** Flower with maturing capsule of *C. glabrior* (scale bar = 1 mm); **b.** Papillae on the capsule of *C. glabrior* (scale bar = 0.75 μm); **c.** Flower of *C. runyonii*, arrows indicate multicellular projections; **d.** Flower of *C. plattenis* (scale bars = 1 mm).

observed in the other species. The hilum is round to broadly elliptic; the cells are smaller than in the rest of the seed coat and they are radially oriented around the vascular scar of the funiculum (Fig. 4 b,d). The vascular scar is linear, oblique to vertical (on broadest diameter of the seeds), 0.025–0.09 mm in *C. pentagona*, *C. campestris*, *C. glabrior*, *C. runyonii*, *C. harperi*, and *C. sandwichiana* and 0.125–0.25 mm in *C. plattensis*, *C. obtusiflora* var. *glandulosa*, and *C. polygonorum* (Fig. 4 a,e,f).

TAXONOMY

This group of species is characterized by globose or mostly depressed-globose capsules with relatively large interstylar apertures, which sometimes are thick-

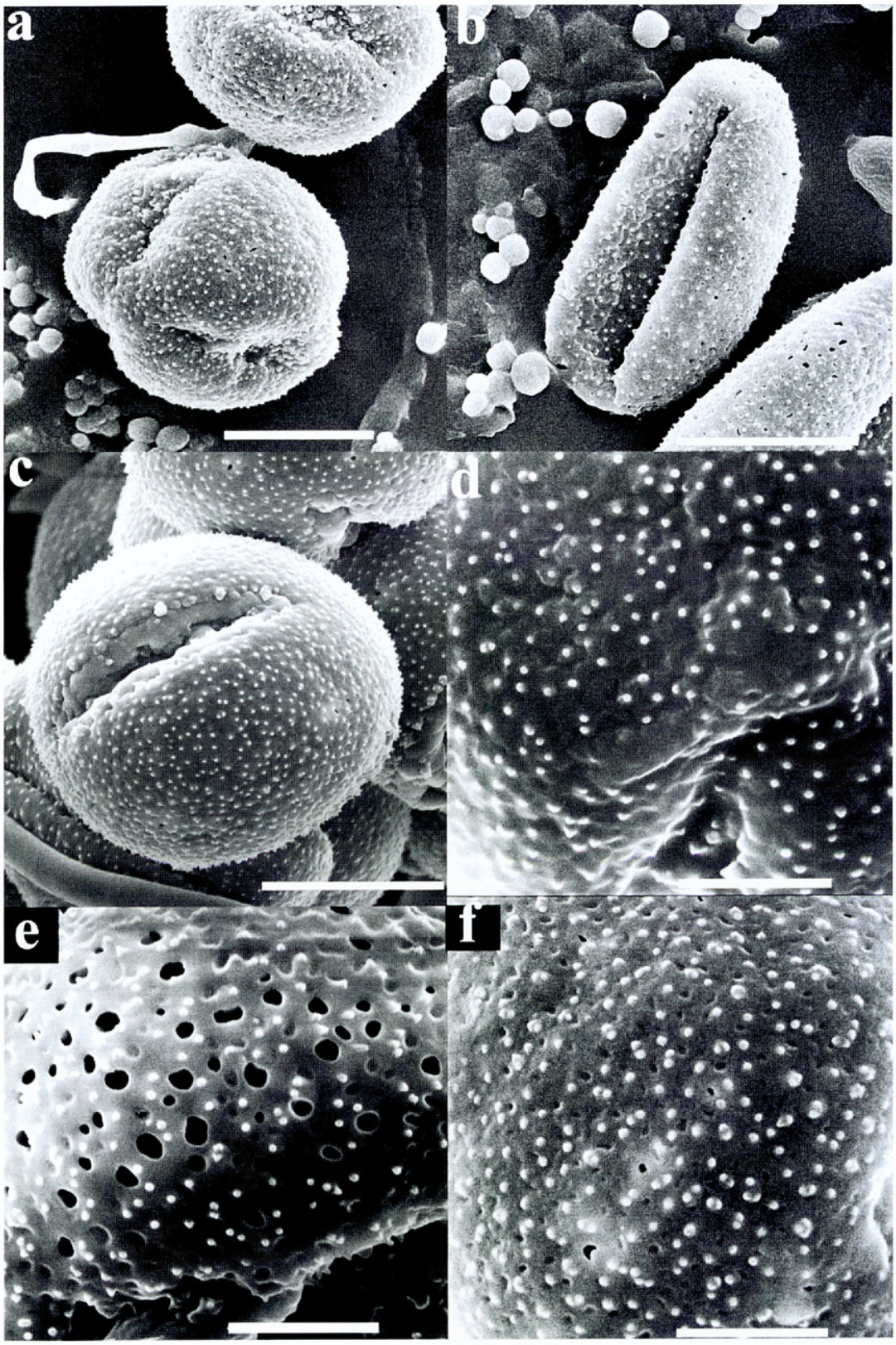

FIG. 3. Morphology of pollen. **a–b.** Polymorphic pollen grains of *C. harperi*; **c.** *C. plattensis* (scale bar = 8.6 μm); **d.** *C. plattensis*, tectum imperforatum; **e.** *C. pentagona*, tectum perforatum, **f.** *C. campestris*—tectum perforatum but sexine often persistent in puncta apertures (scale bars = 3 μm)

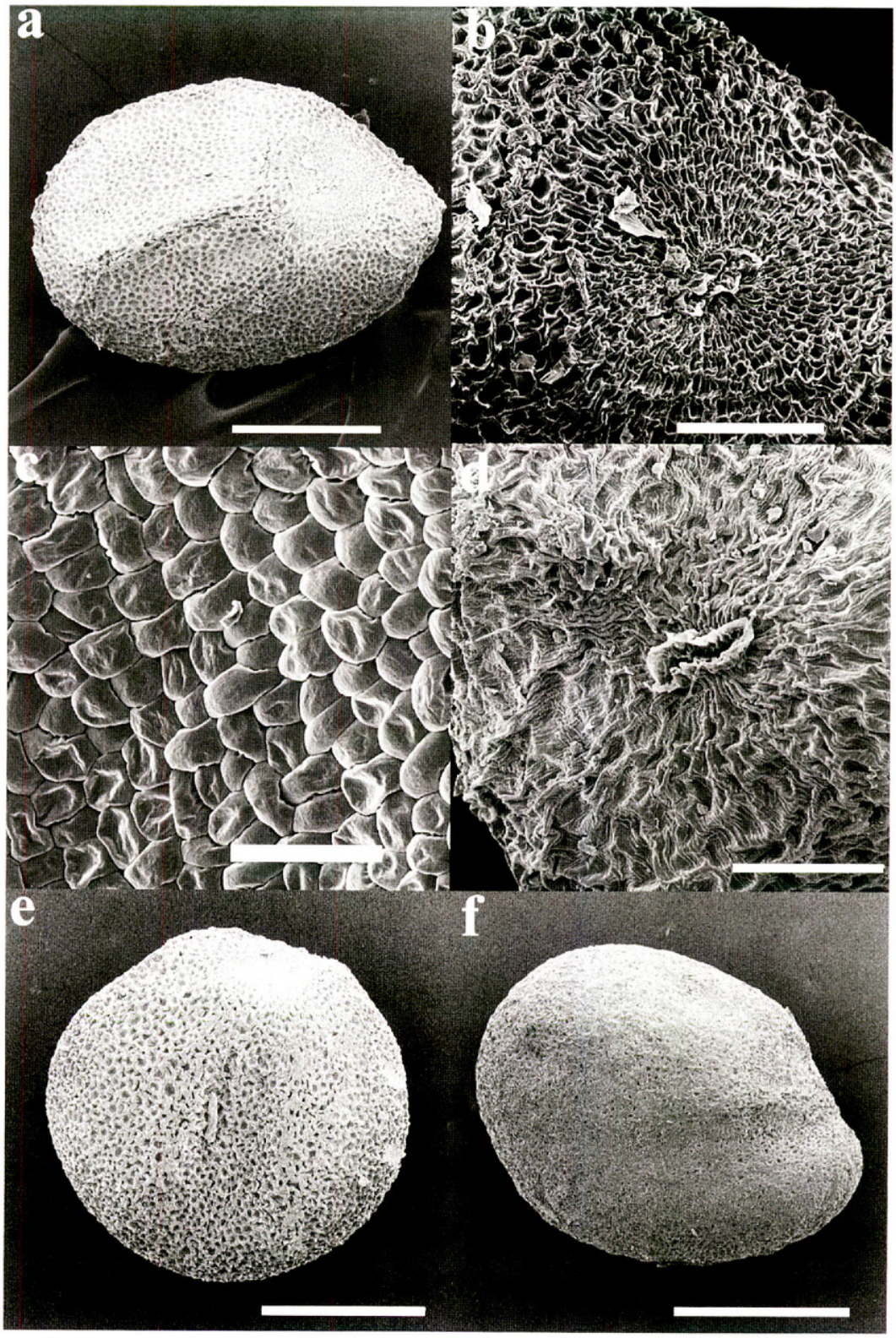

Fig. 4. Morphology of seeds. **a.** *C. campestris*, ventral view (scale bar = 0.5 mm); **b.** Hilum and alveolate seed coat of *C. campestris* (scale bar = 150 μm); **c.** Papillae on hydrated seed coat of *C. glabrior* (scale bar = 100 μm); **d.** Hilum of *C. runyonii* (scale bar = 120 μm); **e.** Seed of *C.* harperi, ventral view (scale bar = 0.43 mm); **f.** Seed of *C. plattensis*, ventral (scale bar = 0.5 mm).

ened but not raised to form a stylopodium. The corolla is persistent at the base of the capsules or surrounding them.

Cuscuta sandwichiana, a Hawaiian endemic, was placed by Yuncker (1932) in subsect. *Californicae* because it exhibits a reduction of the infrastaminal scales similar to the other species (*C. sandwichiana* was omitted in his 1965 treatment). This species, however, does not appear to be evolutionarily allied to *C. californica* complex. Beliz (1986) hypothesized that *C. sandwichiana* has evolved from *C. cephalanthi* Engelm., which is a member of the *C. gronovii* Willd. ex Roem. & Schult. complex. However, the stems of *C. sandwichiana* grow and branch as in species of the *C. pentagona* complex: the main and secondary stems grow continuously and never twine around the host. Instead, tendril-like branches produced from axillary buds of the rudimentary leaf-scales fix the parasite to the host. In *C. gronovii* and its relatives (e.g., *C. cephalanthi*, *C. umbrosa* Beyr. ex Hook., and *C. rostrata* Shuttlw. ex Engelm. & A. Gray), haustoria are formed as the main stem twines around the host, and no tendril-like axillary branches are generated (as first observed by Dawson 1984 in *C. gronovii*). The calyx and corolla of *C. sandwichiana* are relatively similar in morphology to those of *C. campestris*, although flowers are larger in *C. sandwichiana*. Seeds of *C. sandwichiana* are commonly angled, like those of *C. campestris*, and not dorsoventrally compressed as in *C. cephalanthi*.

Contrary to some relatively recent treatments (e.g. Austin 1986; Musselman 1986), *C. campestris* has not been accepted as a distinct taxon in modern North American overviews of the genus (Beliz 1986; Gandhi et al. 1987; Kartesz et al. 1999; USDA NRCS 2004). This judgment has been based on the allegedly variable morphology of the calyx, which was the main character used by Yuncker to differentiate this taxon from *C. pentagona* s. str. Beliz (1986) wrote: "The angled calyx (of *C. pentagona* s. str.) is not a constant feature, it is present in some flowers and absent on others in an individual; ... this feature may be an artifact created when flowers dry out." In contrast, we have found the angled calyx of *C. pentagona* to be a remarkably constant feature (Fig. 1b). Because the calyx lobes of *C. campestris* are overlapping, the calyx sometimes may appear angled in pressed flowers, but if the flowers are hydrated, the calyx usually appears "rounded" (Fig. 1a). The prominent angles of the calyx in *C. pentagona* are the result of a different morphology of the calyx lobes (Fig.1b). Furthermore, small but consistent differences in the size of floral parts, pollen, capsules, and seeds (see key below) usually separate the two taxa. Size overlap between the two taxa does occur, as well as intermediate-like plants, although the latter are uncommon. Austin (1979) discussed methods of pressing to avoid obscuring calyx traits in all species, but particularly in *C. pentagona* and *C. campestris*.

Four years before Yuncker formally recognized *Cuscuta campestris* as a separate species from *C. pentagona*, he was aware that his taxonomic solution might be received with reluctance. In a letter addressed to W.C. Ferguson, accom-

panying a collection of *C. campestris* sent to him for identification (*Ferguson 7795*, NY), Yuncker (1929) wrote: "I suspect I will be accused of various bad tendencies in the way of species making, but I think I have clarified the 'arvensis' situation somewhat." The assessment presented here also finds that *C. campestris* is consistently distinct from *C. pentagona*, although differences may seem subtle, and we believe their recognition as species best reflects the biological situation.

Similarly, *Cuscuta campestris* may be sometimes difficult to distinguish from *C. glabrior*, but the two taxa can be usually differentiated using a combination of features indicated in the key and descriptions. *Cuscuta runyonii* is most similar to *C. glabrior*, and *C. harperi* to *C. pentagona* (see descriptions; Yuncker 1932; 1942). *Cuscuta plattensis* does not appear to be evolutionarily allied to *C. indecora*, in contrast to the suggestion by Beliz (1986). Yuncker (1932, p. 140) considered *C. plattensis* to be "very closely related" to *C. campestris*. The morphology of seeds of *C. indecora* is different from the species of *C. pentagona* complex and more similar to that of *C. gronovii* and its relatives.

Two North American taxa previously treated within *Cuscuta* subsect. Platycarpae (Yuncker 1932), *C. obtusiflora* var. *glandulosa* Engelm. and *C. polygonorum* Engelm., are included here in subsect. *Arvenses* on the basis of their overall morphological similarity with the other species of this subsection. This close relationship was also emphasized by Beliz (1986), who referred to *C. polygonorum* as "*C. pentagona* var. *polygonorum*," within which *C. harperi* was included as a synonym. In contrast, we found that although *C. polygonorum* and *C. obtusiflora* var. *glandulosa* apparently are related to the species of subsect. *Arvenses*, each is clearly delimited morphologically. *Cuscuta australis* R. Br. from Australia and Asia, which is known only from one collection in North America (Jefferson Co., New York, 1926, *Muenscher s.n.*, NY), probably belongs to this group of species as well. This latter species has not been included in this taxonomic treatment limited in scope to North America.

In the *Cuscuta pentagona* complex, there are three relatively narrow endemics (*C. runyonii*, *C. harperi*, and *C. sandwichiana*), two with wider but apparently discrete ranges (*C. plattensis* and *C. glabrior*), and four species (*C. pentagona*, *C. campestris*, *C. polygonorum*, and *C. obtusiflora* var. *glandulosa*) widely distributed and broadly sympatric, at least in some regions. The exact North American distributions of *C. campestris* and *C. pentagona*, particularly, require additional floristic study. For additional synonymy see Yuncker (1932, 1965).

KEY TO SPECIES OF THE *CUSCUTA PENTAGONA* COMPLEX IN NORTH AMERICA

1. Infrastaminal scales well-developed, densely fringed or fimbriate.
   2. Corolla lobes obtuse, straight _____ **8. C. obtusiflora** var. **glandulosa**
   2. Corolla lobes acute, inflexed at apices.
      3. Calyx angled, loose around the corolla tube, 0.3–1.1 mm long; lobes broadly-ovate rhombic, ± auriculate, overlapping and forming prominent angles at

sinuses; flowers 0.9–2.5 mm long, corolla tube 0.5–1.2 mm; anthers 0.2–0.35 mm long; capsules 1.9–2.4 × 1.2–2.5 mm.

4. Flowers commonly 5-merous, 1.4–2.1(–2.5) mm long; calyx lobes not carinate and without rows of prominent laticifers along midveins (Fig. 1 b, d); seeds usually 4 per capsule, angled, subrotund to broadly elliptic, longitudinal groove absent _____ **1. C. pentagona**
4. Flowers commonly 4-merous, 0.9–1.1(–1.5) mm long; calyx lobes carinate or with rows of prominent laticifers along midveins (Fig. 1e); seeds usually 1 per capsule, almost spherical, with a longitudinal groove on the ventral face (Fig. 4e) _____ **2. C. harperi**

3. Calyx rounded, closely enclosing the corolla tube, 1–2.1 mm long; lobes ovate-triangular to triangular, not auriculate, overlapping or not and not forming prominent angles at sinuses; flowers 2.1–4.6(–5) mm long, corolla tube 1.1–2.5 mm; anthers 0.4–0.7 mm long; capsules 1.3–2.8 × 1.9–3.8 mm.
5. Calyx lobes about as wide as long, evidently overlapping (Fig.1a); persistent corolla enveloping 1/3 or less of the capsule (the basal portion) (Fig. 1c). _____ **3. C. campestris**
5. Calyx lobes longer than wide, not overlapping or only slightly so; persistent corolla enveloping 1/2 or more of the capsule.
6. Flowers (whole flowers or sometimes not obvious in the calyx) and capsules papillate; reddish-brown when dried, corolla campanulate-globose, saccate between the lines of stamen attachments; infrastaminal scales equaling corolla tube; seeds angled.
7. Calyx without multicellular projections (Fig. 2a) _____ **4. C. glabrior**
7. Base of calyx corresponding to each lobe with a reflexed spur-like multicellular projection 0.1–0.6 mm long, and often with smaller multicellular projections on the midveins of calyx lobes (Fig. 2c) _____ **5. C. runyonii**
6. Flowers (calyx, corolla, ovary) and capsules not papillate, creamy white when dried; corolla tube narrowly campanulate to cylindric-campanulate, not saccate between the lines of stamen attachments (Fig. 2d); infrastaminal scales shorter than corolla tube; seeds dorsoventrally compressed (Fig. 4f) _____ **6. C. plattensis**

1. Infrastaminal scales absent or reduced, bifid, or with a few distal teeth or fimbriae.
8. Flowers (4–)5-merous, 3–4(–5) mm; infrastaminal scales absent or reduced, truncate or triangular, bifid or distally with a few teeth or fimbriae; endemic to Hawaii _____ **7. C. sandwichiana**
8. Flowers (3–)4-merous, 2–2.7 mm; infrastaminal scales oblong, mostly shallowly bifid with 1–3 fimbriae on each side of the filament attachment or a few irregular fimbriae at the apex; widespread distribution in N America _____ **9. C. polygonorum**

1. **Cuscuta pentagona** Engelm., Amer. J. Sci. Arts 43:340. 1842. *Cuscuta arvensis* Beyr. ex Engelm. var. *pentagona* (Engelm.) Engelm., Trans. Acad. Sci. St. Louis 1:494. 1859. LECTOTYPE (Yuncker 1932): U.S.A. VIRGINIA: Norfolk, "On *Euphorbia* or *Tragia*," 1849, *Rugel s.n.* (MO).

Cuscuta pentagona Engelm. var. *microcalyx* Engelm., Amer. J. Sci. 45:76. 1843. LECTOTYPE (Yuncker 1921): U.S.A. ILLINOIS. [Cass Co.]: Beardstown, 1842, *Geyer s.n.* (MO). Engelmann cited only "Illinois."

Cuscuta arvensis Beyr. ex Engelm. in A. Gray, Man. Bot. (ed. 2) 336. 1856. *Epithymum arvense* (Beyr. ex Engelm.) Niewl. & Lunell, Amer. Midl. Naturalist 4:511. 1916. TYPE: Engelmann cited only "(in herb. Berlin)," perhaps referring to a Beyrich collection. As noted by Yuncker (1921, p. 51), a MO collection by Beyrich in 1845 from North Carolina may be "the type?" (an isotype). Evidently

Engelmann intended *C. arvensis* as a broad concept, since he noted that variants might be identified as *C. pentagona*, *C. pentagona* var. *microcalyx*, *C. pentagona* var. *calycina*, or *C. verrucosa*.

Stems 1.4–2.1(–2.5) mm in diameter, yellow to orange. **Inflorescences** dense, corymbiform to glomerulate of 3–15(–20) flowers; pedicels 0.5–3(–4.5) mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels, 0.4–2.2 × 0.2–1.3 mm, membranous, ovate, ovate-triangular to lanceolate, margins entire, apex acute. **Flowers** (4–)5-merous, 1.4–2.1(–2.5) mm (Fig. 1d), membranous, whitish when fresh, yellowish to brown when dried; **papillae** sometimes present on the corolla lobes; **laticifers** evident in the calyx and less obvious in the corolla and ovary/capsule, isolated or arranged in rows, ovoid or elongated; **calyx** yellow to brown, ± reticulate, shiny or not, angled, cupulate, ca. as long as the corolla tube, divided 1/2–2/3 the length, lobes overlapping and forming prominent angles at sinuses, broadly-ovate to rhombic, auriculate, not carinate, margins entire, apex rounded (Fig. 1b); **corolla** persistent; tube campanulate, 0.7–1.2 mm, not saccate between the lines of stamen attachments; lobes spreading, 0.65–1.1 mm long, triangular-lanceolate, margins entire, apex acute to acuminate, inflexed; **stamens** exserted, shorter than corolla lobes, anthers subrotund to broadly elliptic, 0.25–0.30 × 0.20–0.28 mm, filaments 0.3–0.4 mm; **pollen grains** 18–25.2 µm long; tectum perforatum; maximum diameter of puncta 0.6 µm; supratectal process granular to conical ± uniformly distributed (Fig. 3e); **infrastaminal scales** equaling corolla tube, oblong-ovate, rounded, ± uniformly, dense fimbriate; styles evenly filiform, 0.7–1.1 mm, ca. as long as the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose-depressed to ovoid, 1.9–2.4 × 1.6–2.5 mm, not thickened or raised around the medium to large interstylar aperture, translucent or not, persistent corolla at the capsule base. **Seeds** 4 per capsule, angled, subrotund to broadly elliptic, 0.9–1.1 × 0.8–1 mm, seed coat cells reticulate to alveolate/papillate, 18–35 µm in diameter; epicuticular wax absent; hilum region round 0.4–0.5 mm in diameter, vascular scar 0.07–0.09 mm long, vertical to slightly oblique. **2*n*** = 56 (Fogelberg 1938), ca. 44 (Pazy & Plitmann 1995).

Distribution and ecology.—**CANADA:** Manitoba (based on only 2 collections from DAO and MTMG, respectively). **U.S.A.:** Alabama, Arkansas, D.C., Delaware, Florida, Georgia, Kansas, Illinois, Indiana, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, New Jersey, New York, North Carolina, North Dakota, Oklahoma, Pennsylvania, South Carolina, South Dakota, Tennessee, Texas, Virginia, Washington. We have seen no evidence that *C. pentagona* has spread outside of North America, where it is less common than *C. campestris*. Isolated European records identified as this taxon (e.g., Buia 1938) are instead *C. campestris*. Flowering Jun–Nov. **Hosts:** numerous hosts (Gaertner 1950) growing in a wide variety of climates and soil types.

Conservation status.—G4G5 (apparently secure to secure) (G5, NatureServe 2005).

2. Cuscuta harperi Small, Fl. S.E. U.S. ed. 2, 1361, 1375. 1913. TYPE: U.S.A. GEORGIA: Altamaha Grit, between Peacocks and Harrison, on *Chondrophora virgata*, 20 Jul 1906, *Harper s.n.* (HOLOTYPE: NY, see Yuncker 1943; ISOTYPE: NY).

Stems 0.15–0.3 mm in diameter, orange-yellow. **Inflorescences** loose, corymbiform of 2–10(–15) subsessile or short pedicellate flowers; pedicels 0.5–2.5(–3) mm; bracts 1 at the base of clusters and absent (rarely present) at the base of pedicels, like those of *C. pentagona*. **Flowers** 4(–5)-merous, 0.9–1.1(–1.5) mm (Fig. 1e), fleshy, creamy-white when fresh, yellow to brownish when dried; **papillae** present on the corolla lobes (Fig. 1f); **laticifers** evident along midveins of calyx and less obvious in the corolla and ovary/capsule, isolated or in rows, elongated; **calyx** yellow-brownish, ± reticulate, rarely shiny, about as long as the corolla tube, angled, cupulate, lobes basally overlapping and forming prominent angles at sinuses, broadly-ovate rhombic, ± auriculate, ± carinate or with laticifers along midveins, margins entire, apex rounded; **corolla** persistent; tube campanulate, not saccate, 0.5–0.7 mm; lobes erect to reflexed, 0.4–0.7 mm, triangular-ovate, margins entire, apex subacute to acute, inflexed; **stamens** exserted, slightly shorter than corolla lobes, anthers subrotund to broadly elliptic, 0.2–0.25 × 0.15–0.18 mm, filaments 0.16–0.25 mm; **pollen** grains 17.5–25 μm long; tectum perforatum but sexine often persistent in puncta aperture; diameter of puncta 0.4 μm; supratectal process granular granular to conical ± uniformly distributed (Fig. 3 a,b); **infrastaminal scales** as long as the corolla tube, narrowly oblong, rounded, shortly and irregularly-dense fringed in the distal half; styles uniformly narrow terete to filiform, 0.5–0.9 mm, shorter than the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose to ovoid, 1.2–2.3 × 1.2–1.6 mm; not thickened around the small to moderately large interstylar aperture, almost translucent, with persistent corolla enveloping the 1/4–1/3 of the capsule bases. **Seeds** usually 1–2 per capsule, subglobose, with a longitudinal groove on the ventral face, 0.92–1.11 × 0.85–1.1 mm, seed coat cells alveolate/papillate, 35–50 μm in diameter; epicuticular wax absent; hilum region terminal, round, 0.14–0.16 mm in diameter, vascular scar 0.025–0.03 mm long, vertical to slightly oblique. **2*n*** = ?

Distribution and ecology.—**U.S.A.:** Alabama and Georgia. Flowering Sep–Nov. **Hosts:** *Bigelowia nuttallii*, *Croton willdenowii*, *Helianthus longifolius*, *Hypericum gentianoides*, *Liatris microcephala*, and other species of sandstone outcrops (see also Yuncker 1943).

Conservation status.—G1G2 (critically imperiled to imperiled) (G2, NatureServe 2005).

3. Cuscuta campestris Yuncker [nom. nov.], Mem. Torrey Bot. Club 18:138. 1932. Based on *Cuscuta pentagona* Engelm. var. *calycina* Engelm., Amer. J. Sci. 45:76. 1843 [1845]. *Cuscuta arvensis* Beyr. ex Engelm. var. *calycina* (Engelm.) Engelm., Trans. Acad. Sci. St. Louis 1:495. 1859. LECTOTYPE (Yuncker 1921): U.S.A. TEXAS: wet prairies, [no date], *Lindheimer 126* (MO).

Stems 0.3–0.5 mm in diameter, yellow to orange. **Inflorescences** dense,

corymbiform or glomerulate of (3-)6-25(-30) subsessile to short pedicellate flowers; pedicels 0.3-2.5(-3.5) mm; bracts 1 at the base of clusters and 0-1 at the base of pedicels, like those of *C. pentagona*. **Flowers** (4-)5-merous, (1.9-)2.1-3.6 mm (Fig. 1c), membranous, white-creamy when fresh, creamy or golden-yellow when dried; **papillae** absent; **laticifers** evident in the calyx and less obvious in the corolla and ovary/capsule, isolated or arranged in rows, rotund, ovoid or elongated; **calyx** yellow, reticulate, shiny, rarely obscurely angled, cupulate, about as long as corolla tube, divided 2/5-3/5 the length; lobes overlapping but not forming or rarely forming obscure angles at sinuses; ovate triangular, not carinate, margins entire, apex obtuse to rounded (Fig. 1a); **corolla** persistent; tube campanulate, not saccate, (1.1-)1.5-1.9 mm; lobes spreading, triangular-lanceolate, (1.1-)1.4-1.75 mm long, margins entire, apex acute to acuminate, inflexed; **stamens** exserted, shorter than corolla lobes, anthers broadly elliptic, (0.3-)0.4-0.5 × 0.25-0.3 mm, filaments 0.4-0.7 mm long; **pollen grains** 18.5-28 µm long; tectum perforatum but sexine often persistent in puncta aperture; maximum diameter of puncta 0.4 µm; supratectal process granular, often in groups of 2-4 (Fig. 3f); **infrastaminal scales** equaling or slightly exceeding corolla tube, oblong-ovate to spathulate, rounded, uniformly dense fimbriate; styles evenly filiform, 0.8-1.6 mm, ca. as long as the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose-depressed to depressed, 1.3-2.8 × 1.9-3.8 mm; not thickened or raised around the large interstylar aperture, sometimes translucent, persistent corolla enveloping 1/3 or less of the capsule base. **Seeds** 4 per capsule, angled, subrotund to broadly elliptic, 1.12-1.54 × 0.9-1.1 mm, seed coat cells alveolate/papillate, 32-40 µm in diameter; epicuticular wax absent; hilum region subterminal, round, 0.45-0.5 mm in diameter, vascular scar, 0.085-0.01 mm long, vertical or slightly oblique (Fig. 4 a,b). **2*n*** = 56 (Fogelberg 1938; Ward 1984).

Distribution and ecology.—**CANADA:** Alberta, British Columbia, Saskatchewan, Manitoba, Nova Scotia, Ontario and Québec. Darbyshire (2003) also mentioned it from NewFoundland, New Brunswick and Prince Edward Island. Although we found no herbarium collections, its presence in these provinces is possible. **U.S.A.:** Arizona, Arkansas, California, Colorado, Florida, Georgia, Idaho, Illinois, Indiana, Iowa?, Kansas, Kentucky, Louisiana, Massachusetts, Maryland, Michigan, Minnesota, Mississippi, Missouri, Montana?, Nebraska, Nevada, New Mexico, New Jersey, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, South Dakota, Tennessee, Texas, Utah, Virginia, Washington, West Virginia, Wisconsin, Wyoming. *Cuscuta campestris* is the second most common species in North America, after *C. gronovii* (Yuncker 1932), and perhaps the most successful and widespread *Cuscuta* weed worldwide, recorded from South America, Europe, Asia, Africa, and Australia (Holm et al. 1997). Flowering Jun-Nov. **Hosts:** numerous species from hundreds of genera in various families, including Hydrophyllaceae, Chenopodiaceae,

Verbenaceae, Convolvulaceae, Acanthaceae, Brassicaceae, Euphorbiaceae, Solanaceae, Urticaceae, Polygonaceae, Fabaceae, Asteraceae, and others (Gaertner 1950), growing in a wide variety of climates and soil types; reported *not* to survive on *Amaranthus retroflexus*, *Arctium lappa*, *Atriplex* spp., *Brassica nigra*, *Equisetum arvense*, *Glycine max*, selected cultivars of *Lycopersicon esculentum*, *Portulaca oleracea*, *Tanacetum vulgare*, *Vicia villosa*, Cyperaceae and Poaceae (Gaertner 1950; Parker & Riches 1993; Dawson et al. 1994; Costea & Tardif 2006).

Conservation status.—G5 (common) (the same assessment in NatureServe 2005).

4. Cuscuta glabrior (Engelm.) Yuncker, Mem. Torrey Bot. Club 18:140. 1932. *Cuscuta pentagona* Engelm. var. *glabrior* (Engelm.) Gandhi, Thomas, & Hatch, Sida 12:372. 1987. *Cuscuta verrucosa* Engelm. var. *glabrior* Engelm., Amer. J. Sci. 43:341. 1842. LECTOTYPE (Yucker 1932): U.S.A. TEXAS. [Harris Co.?]: dry sterile prairies west of Houston, *Lindheimer s.n.* (MO). The protologue noted that var. *glabrior* [was growing] "with the preceding variety [i.e., *C. verrucosa* var. *hispidula*], *F. Lindheimer*: on Petalostemon, *Drummond* (3rd collection, No. 247)." Choice of the Drummond collection (III, 247) as lectotype of *Cuscuta verrucosa* Engelm. var. *glabrior* has been associated with Yuncker (1921), but there Yuncker instead chose the Drummond type for *C. pentagona* var. *verrucosa*, citing *C. verrucosa* var. *glabrior* as a synonym.

Cuscuta verrucosa Engelm., Amer. J. Sci. 43:341. 1842 (nom. invalid., non Sweet 1823). *Cuscuta arvensis* var. *verrucosa* Engelm., Trans. Acad. Sci. St. Louis 1:495. 1859. *Cuscuta pentagona* Engelm. var. *verrucosa* (Engelm.) Yuncker, Illinois Biol. Monogr. 6:142. 1921. LECTOTYPE (Yuncker 1921): U.S.A. TEXAS: no other locality, *Drummond III 247* (MO; ISOLECTOTYPE: TEX). Engelmann described *C. verrucosa* and two varieties of it: var. *hispidula* (treated by us as *C. indecora* var. *indecora*) and var. *glabrior*. He cited collections associated with both varieties but none for *C. verrucosa* in its typical form. In 1859, in valid use of the epithet as *C. arvensis* var. *verrucosa*, he cited "Texas, Drummond! III. 247; Lindheimer! 127" and others as syntypes. Yuncker (1921, p. 52), under the combination *C. pentagona var. verrucosa*, indicated that "*Drummond III 247*" at MO was the type (lectotype).

Cuscuta arvensis Beyr. ex Engelm. var. *pubescens* Engelm., Trans. Acad. Sci. St. Louis 1:495. 1859. *Cuscuta pentagona* Engelm. var. *pubescens* (Engelm.) Yuncker, Illinois Biol. Monogr. 6:142. 1921. *Cuscuta glabrior* var. *pubescens* (Engelm.) Yuncker, Mem. Torrey Bot. Club 18:141. 1932. LECTOTYPE (Yuncker 1921): "Texas (... Lindheimer in 1847)" (MO). Engelmann's protologue cited "Western Texas, Lindheimer! Wright! 135 (574)."

Stems 0.35–0.5 mm in diameter, creamy. **Inflorescences** loose to compact, glomerulate or corymbiform of 3–25(–30) subsessile to pedicellate flowers; pedicels 0.8–4(–5) mm; bracts like in *C. campestris*. **Flowers** 5-merous, 1.4–2.1(–2.5) mm (Fig. 2a), membranous, white or commonly reddish when fresh, yellow to reddish-brown when dried; papillae present on the perianth, ovaries/capsules and sometimes on the pedicels (Fig. 2b); laticifers obvious in the calyx and less evident in the corolla and ovary/capsule, isolated or arranged in rows, rotund, ovoid or elongated; calyx yellow to reddish-brown, shiny, ± reticulate, cupulate, about as long as corolla tube; divided 1/2–2/3, lobes not overlapping, ovate triangular, not carinate, margins entire, apex obtuse to subacute; **corolla** persistent; tube campanulate-globose, saccate between the lines of stamen attachments, (1.1–)1.5–2.1 mm long; lobes spreading to reflexed, lobes 1.2–1.75 mm

long, triangular to sublanceolate, margins entire, apex acute to acuminate, inflexed; **stamens** exserted, shorter than corolla lobes, anthers broadly elliptic to elliptic-oblong, 0.44–0.67 × 0.22–0.3 mm, filaments 0.4–0.7 mm; **pollen grains** 18–22.6 µm long; tectum imperforatum or with a few puncta; maximum diameter of puncta 0.2 µm; supratectal process granular to conical ± uniformly distributed; **infrastaminal scales** reaching the filament bases, ovate to spatulate, rounded, uniformly dense fimbriate; styles evenly filiform, 0.9–1.6 mm, as long as or longer than the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose-depressed to depressed, 1.5–2.8 × 2.1–3.5 mm, not thickened or raised around the medium to large interstylar aperture, not translucent, persistent corolla enveloping 1/2–2/3 of the capsule. **Seeds** 4 per capsule, angled, subrotund to broadly elliptic, 0.95–1.15 × 0.85–1 mm, seed coat cells alveolate/papillate, 35–50 µm in diameter (Fig. 4c), epicuticular wax absent; hilum region subterminal, round, 0.13–0.2 mm in diameter, vascular scar 0.03–0.05 mm long, oblique. ***2n*** = ?

Distribution and ecology.—**U.S.A.:** Louisiana, New Mexico, Oklahoma, Texas, Utah; Mexico. Flowering Jun–Sep. **Hosts:** wide variety of herbaceous species, including *Amaranthus*, *Ambrosia*, *Amphiachyris*, *Asclepias*, *Convolvulus*, *Coreopsis*, *Croton*, *Dalea*, *Dyschoriste*, *Evolvulus*, *Gaura*, *Gilia*, *Hedeoma*, *Helenium*, *Lespedeza*, *Liatris*, *Machaeranthera*, *Medicago*, *Mimosa*, *Plantago*, *Prosopis*, *Tragia*, *Oenothera*, *Justicia*, *Polygonum*, *Ruellia*, *Solanum*, *Symphyotrichum*, *Thelesperma*, *Verbena*.

Conservation status.—G4G5 (the same assessment in NatureServe 2005).

According to Yuncker (1965, p. 6), *Cuscuta pentagona* var. *pubescens* (Engelm.) Yuncker "represents the extreme degree of papillation which covers the flower and extends down onto the pedicels. In var. *glabrior* the ovary and capsules are almost always more or less papillate while the corolla shows considerable variation in this character." We find continuous variation, and two varieties cannot be separated. Occasional plants that are hardly papillate can be distinguished from *C. campestris* by their calyx lobes, which are broadly triangular-lanceolate and not overlapping at the base and by the corolla enveloping the mature capsule (Fig. 2a).

5. Cuscuta runyonii Yuncker, Bull. Torrey Bot. Club 69:541. 1942. TYPE: U.S.A. TEXAS. Hidalgo Co.: La Joya, occasional, on dry hill tops, clay, 45 m, flowers cream white, hosts: *Coldenia canescens* and *Nama hispida*, 8 Jun 1941, *Runyon 2732* (HOLOTYPE: US; ISOTYPES: F, GH, MO, NY, TEX).

Stems 0.35–0.5 mm in diameter, yellow-orange. **Inflorescences** loose, ± umbellate of 2–15(–25) subsessile to pedicellate flowers; pedicels 0.8–4(–5) mm; bracts as in *C. campestris*. **Flowers** 5-merous, 2.5–3.5(–4) mm (Fig. 2c), white to creamy when fresh, reddish-brown when dried, membranous, **papillae** present on the perianth, ovary/capsules and sometimes on the pedicels; **laticifers** evident in

the perianth and less obvious in the ovary/capsule, isolated or arranged in rows, rotund, ovoid or tangentially elongated; **calyx** reddish-brown, ± reticulate, shiny, cupulate, shorter than corolla tube or about equaling it, divided 1/2–2/3 the length, lobes not basally overlapping, triangular, sometimes carinate, base of calyx corresponding to each lobe with a reflexed spur-like projection, 0.1–0.6 mm long (Fig. 2c), and often with smaller protuberances on the midveins of calyx lobes, margins entire, apex obtuse to subacute; **corolla** persistent; tube campanulate-globose, saccate between the lines of stamen attachments, (1.2–)1.6–2.3 mm, lobes reflexed, 1.2–2 mm, triangular-ovate to lanceolate, margins entire, apex acute to acuminate, inflexed; **stamens** exerted, shorter than corolla lobes anthers broadly elliptic to elliptic-oblong, 0.4–0.6 × 0.25–0.3 mm, filaments 0.4–0.6 mm long; **pollen grains** 18–23.8 μm long; tectum imperforatum or with a few puncta; maximum diameter of puncta = 0.3 μm; supratectal process granular to conical ± uniformly distributed; infrastaminal scales reaching the filament bases, oblong to spatulate, rounded, uniformly dense fimbriate; styles evenly filiform, 0.9–1.8 mm, equaling to longer than the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose-depressed, 1.6–3 × 2–3.4 mm; not thickened or raised around the large interstylar aperture large, not translucent, persistent corolla enveloping 1/2–1/1 of the capsule. **Seeds** 4 per capsule, angled, ovate to broadly elliptic, 0.95–1.40 × 0.85–1.1 mm, seed coat cells alveolate/papillate, 30–50 μm in diameter; epicuticular wax present with longitudinal; rodlets hilum region subterminal round to subrotund, 0.30–0.40 mm, vascular scar, 0.08–0.09 mm long, oblique (Fig. 4d). ***2n*** = ?

Distribution and ecology.—**U.S.A.:** Texas. Flowering Mar–Apr(–May, –July, –Oct). **Hosts:** species of *Dalea*, *Dyschoriste*, *Erigeron*, *Gutierrezia*, *Hymenoxys*, *Justicia*, *Linum*, *Melampodium*, *Oenothera*, *Nama*, *Spermolepis*, *Tetraneuris*, *Tiquilia*, *Thamnosma*, *Thelesperma*.

Conservation status.—G3 (vulnerable) (G4, NatureServe 2005).

6. Cuscuta plattensis A. Nels., Bull. Torrey Bot. Club 26:131. 1899. TYPE: U.S.A. WYOMING. [Carbon Co.?]: Platte Canyon, 27 Aug 1896, *A. Nelson 2768* (HOLOTYPE: RM; ISOTYPES: NY, US).

Stems 0.15–0.3 mm in diameter, yellow to pale orange. **Inflorescences** loose, paniculiform of 2–10(–15) subsessile to pedicellate flowers; pedicels 0.5–2.5(–3) mm.; bracts as in *C. campestris*. **Flowers** 5-merous, 3–4.6(–5) mm (Fig. 2d), membranous, white-creamy when fresh, whitish-yellow when dried; **papillae** absent; **laticifers** present in the calyx and less obvious in the corolla and capsule, isolated, ovoid to elongated; **calyx** yellow, reticulate, not shiny, cylindric-cupulate, ca. equaling the corolla tube, divided 1/2–2/3, lobes slightly basally overlapping, ovate triangular, not carinate, margins entire, obtuse to subacute; **corolla** persistent; tube narrowly campanulate to cylindric campanulate, not saccate, 1.9–2.5 mm, lobes spreading to reflexed, 1.4–2.2 mm long, triangular,

margins entire, apex narrowly acute, inflexed; **stamens** exserted, shorter than corolla lobes anthers subrotund, broadly elliptic to elliptic-oblong 0.4–0.7 × 0.3–0.4 mm, filaments 0.3–0.4 mm; **pollen grains** 18–26.3 µm long; tectum imperforatum or with a few puncta; diameter of puncta 0.2 µm; supratectal process granular ± uniformly distributed (Fig. 3c); **infrastaminal scales** 3/4–4/5 of the corolla tube, oblong-spathulate, rounded uniformly dense fringed to fimbriate; styles uniformly filiform, 1.3–1.6 mm, about as long as the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose to globose-depressed, 1.8–3.2 × 2.2–3.6 mm, not thickened or raised around the large intersylar aperture; not translucent, withered corolla persistent enveloping 1/2 or more of the capsule base. **Seeds** 1–4 per capsule, dorsoventrally compressed, broadly elliptic to obovate, 1.07–1.42 × 0.9–1.21 mm, seed coat cells alveolate/papillate, 15–20 µm in diameter; epicuticular wax absent; hilum region subterminal, subrotund, 0.30–0.35 × 0.28–0.30 mm, vascular scar 0.20–0.25 mm long, vertical to slightly oblique (Fig. 4f). ***2n*** **=** ?

Distribution and ecology.—**U.S.A.:** Nebraska, Washington, and Wyoming. Flowering Aug. **Hosts:** species of *Grindelia*, *Helianthus*, *Humulus Psoralea*, *Rubus*, *Solidago*.

Conservation status.—G1 (critically imperiled) (the same assessment in NatureServe 2005).

7. Cuscuta sandwichiana Choisy, Mem. Soc. Phys. Hist. Nat. Geneve 9:280. 1841.
TYPE: U.S.A. HAWAII. Sandwich Islands, 1830, *Gaudichaud-Beaupré 1* (HOLOTYPE: G-DC, fragment NY; ISOTYPE: P, fragment NY).

Stems, 0.2–0.5 mm, yellow-orange. **Inflorescence** loose, paniculiform of 3–7(–11) pedicellate flowers; pedicels 2–5 mm; bracts 1 at the base of clusters, usually lacking at the base of pedicels, membranous, narrow-triangular, 1–1.6 × 0.7–1 mm, margins entire, apex acute. **Flowers** (4–)5-merous, 3–4(–5) mm long (Fig. 5a), fleshy, white when fresh, yellow-brownish when dried; **papillae** absent; **laticifers** conspicuous in the corolla lobes, sometimes in the calyx and ovary/capsule as well, isolated or in rows, ovoid to elongated; **calyx** yellow-brown, not reticulate or shiny, cupulate, almost as long as corolla tube, divided 1/2–1/3 the length, lobes not basally overlapping, triangular-ovate, in some flowers carinate, margins entire, apex obtuse to subacute; **corolla** persistent; tube campanulate to globular, not saccate, 2–3 mm long, lobes erect to slightly spreading, 0.8–1.5 mm long, ovate-triangular, margins entire, apex obtuse to subacute with inflexed tips; **stamens** mostly included, shorter than corolla lobes, anthers broadly-elliptic 0.5–0.7 × 0.4–0.5 mm, filaments 0.2–0.7 mm; **pollen grains** 22–27.5 µm long; tectum imperforatum or with a few puncta; maximum diameter of puncta 0.3 µm; supratectal process granular to conical, ± uniformly distributed; **infrastaminal** scales absent or reduced, bifid, truncated or triangular, distally with a few teeth; styles uniformly stoutish, 0.5–1.1 mm, ca. as long as the

ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, globose to globose-depressed, 2.5–3.5 mm × 3.3–4 mm, ± thickened but not raised around the large interstylar aperture, not translucent, withered corolla surrounding the capsule. **Seeds** usually 2 per capsule, angled, elliptic to broadly-elliptic, 1.1–2 × 1–1.7 mm, seed coat cells alveolate/papillate, 35–50 µm in diameter, epicuticular wax absent; hilum region subterminal, round, 0.30–0.45 mm in diameter, vascular scar 0.19–0.25 mm long, vertical or slightly oblique (Fig. 5b). **2*n*** = ?

Distribution and ecology.—**U.S.A.:** Hawaii. Flowering summer–fall (Jun–Oct). **Hosts:** plants in seashores and arid habitats.

Conservation status.—G2 (imperiled) (the same assessment in NatureServe 2005).

8. Cuscuta obtusiflora Kunth var. **glandulosa** Engelm., Trans. Acad. Sci. St. Louis 1:492. 1859. *Cuscuta glandulosa* (Engelm.) Small, Fl. S.E. U.S. 969, 1337. 1903. LECTOTYPE (Yuncker 1921): U.S.A. GEORGIA. [Muscogee Co.]: Columbus, 1838, *Boykin s.n.* (MO). The protologue cited numerous collections in addition to the Boykin one.

Stems 0.25–0.4 mm in diameter, orange. **Inflorescences** dense, glomerulate of 5–18 sessile or subsessile flowers; pedicels absent to 1 mm; bracts 1 at the base of clusters and 0–1 at the base of pedicels/flowers, membranous, ovate, 0.5–1.3 × 0.2–1.1 mm, margins entire, apex acute to obtuse. **Flowers** 5-merous, 1.8–2.5 mm, membranous, creamy white when fresh, yellow-brown when dried; **papillae** absent; **laticifers** numerous, evident in the perianth and ovary/capsule, isolated, round to ovoid; **calyx** yellow-brownish not reticulate or shiny, shallowly cupulate, about equaling the corolla tube, divided ca. 1/2 the length, lobes barely basally overlapping, ovate, not carinate, margins entire, apex obtuse; **corolla** persistent; tube campanulate, not saccate, 1–1.5 mm, lobes erect to spreading, 0.8–1.5 mm long, ovate to ovate-oblong, margins entire, apex obtuse, straight; **stamens** exserted, shorter than corolla lobes, anthers ovate to broadly elliptic, 0.3–0.4 × 0.2–0.3 mm, filaments 0.4–0.6 mm; **pollen grains** (18–)20–24(–27) µm, tectum perforatum; maximum diameter of puncta 0.6 µm; supratectal process granular to conical ± uniformly distributed (Fig. 5c); infrastaminal scales reaching the filament bases, oblong, rounded, with a few basal fimbriae, densely fringed in the distal 3/4; styles uniformly stoutish, 0.4–1.1 mm, shorter than or equaling the ovary, stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, depressed-globose, 1.5–3 × 2.5–4 mm, not thickened or raised around the large interstylar aperture, not translucent, withered corolla persistent at the base. **Seeds** usually 4 per capsule, dorsoventrally compressed, broadly-ovate to broadly elliptic, 1.4–1.56 × 1.23–1.35 mm, seed coat cells alveolate/papillate, 20–30 µm in diameter, epicuticular wax usually present (Fig. 5d). **2*n*** = ?

Distribution and ecology.—**U.S.A.:** Alabama, Arkansas, Connecticut, Florida, Georgia, Kentucky, Louisiana, Minnesota, Mississippi, New York., Oklahoma.,

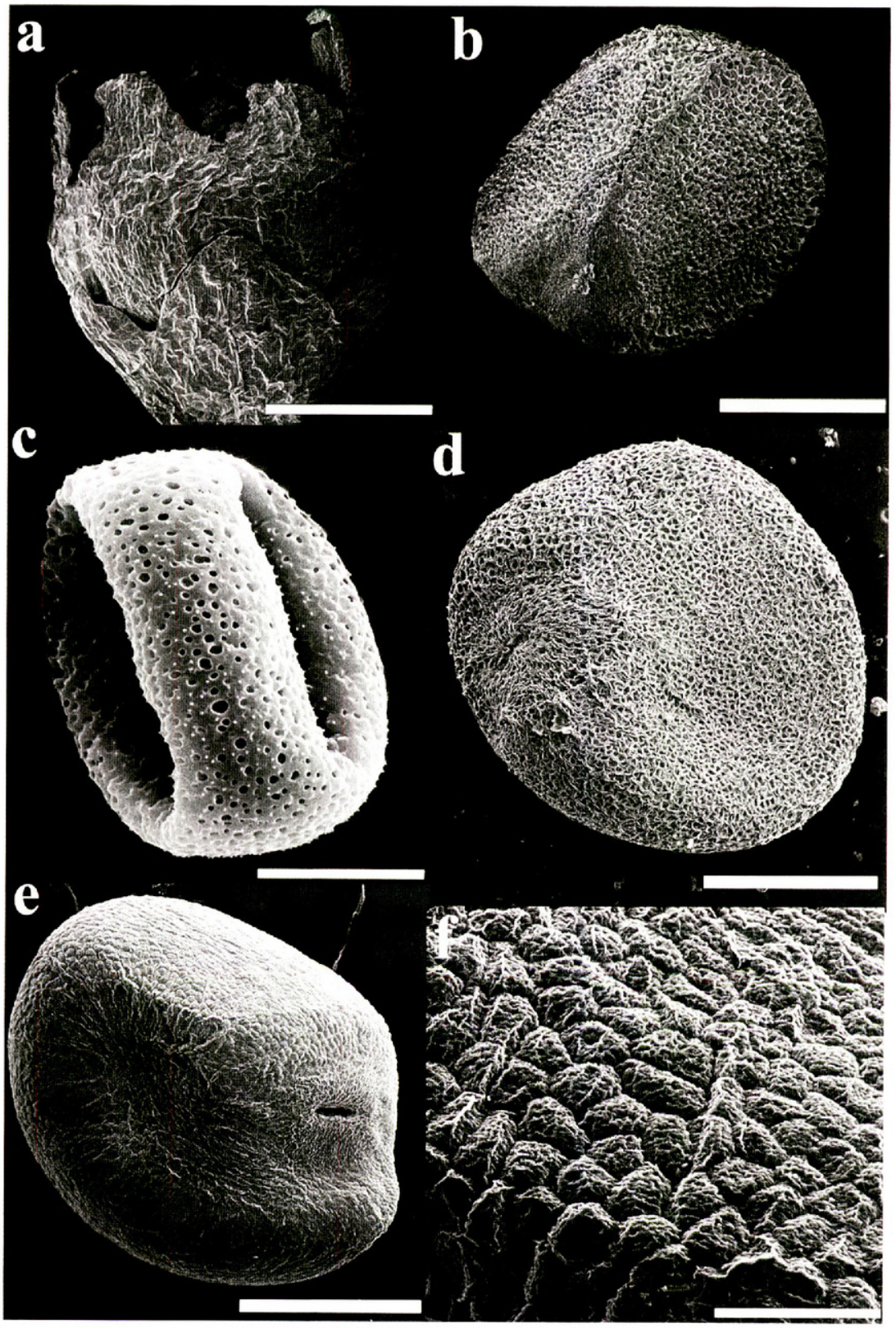

Fig. 5. *Cuscuta sandwichiana*. **a.** Flower (scale bar = 1 mm); **b.** seed (scale bar = 0.6 mm). *Cuscuta obtusiflora* var. *glandulosa*. **c.** Pollen (scale bar = 6 μm); **d.** seed (scale bar = 0.5 mm). *Cuscuta polygonorum*. **e.** Seed—general morphology (scale bar = 0.60 mm); **f.** seed—surface micromorphology (scale bar = 100 μm).

Pennsylvania, Texas; Mexico, West Indies (Puerto Rico, Cuba). Flowering Jul–Sep, –Oct. **Hosts:** species of *Alternanthera*, *Dalea*, *Hygrophila*, *Lythrum*, *Polygonum*, *Xanthium*.

Conservation status.—G3G4 (vulnerable to apparently secure) (G4, NatureServe 2005).

9. Cuscuta polygonorum Engelm., Amer. J. Sci. Arts 43:342. 1842. TYPE: U.S.A. MISSOURI: W of St. Louis, ["bottoms of sink-holes, or margins of ponds"], on *Polygonum*, Aug 1839, *Lindheimer s.n.* (HOLOTYPE: MO).

Stems 0.2–0.4 mm in diameter, yellow-orange. **Inflorescences** dense, glomerulate of 4–18 sessile to subsessile flowers; bracts 1 at the base of clusters and 0–1 at the base of pedicels, membranous, ovate-triangular to lanceolate, 0.3–1 × 0.2–0.9 mm, margins entire, apex acute; pedicels absent to 1 mm. **Flowers** (3–)4-merous, 2–2.7 mm, membranous, white when fresh, yellow-brown when dried; **papillae** absent; **laticifers** evident in the corolla and the ovary/capsule, isolated, round to ovoid; **calyx** yellow-brownish, not shiny or reticulate, cupulate, ca. equaling the corolla tube, divided 1/2–2/3 to the base, lobes not basally overlapping, triangular-ovate, not carinate, margins entire, apex obtuse to rounded; **corolla** persistent, tube cupulate to shallowly campanulate, not saccate, 1–1.4 mm, lobes erect, 1.1–1.6 mm long, triangular, margins entire, apex acute, straight; **stamens** exserted, shorter to nearly equaling corolla lobes, anthers ovate to broadly elliptic, 0.3–0.4 × 0.2–0.3 mm, filaments 0.4–0.7 mm; **pollen** grains (18–)21–24.5 (–26) µm long, tectum imperforatum or with a few puncta; maximum diameter of puncta 0.3 µm; supratectal process granular to conical ± uniformly distributed; **infrastaminal scales** usually reaching the filament bases, oblong, mostly shallowly bifid with 1–3 fimbriae on each side of the filament attachment or with a few irregular fimbriae at the apex; styles evenly subulate, 0.4–0.9 mm, shorter than the ovary; stigmas capitate, globose. **Capsules** indehiscent to irregularly dehiscent, depressed-globose, often appearing angled, 1.6–3 × 2.5–5 mm, not thickened or raised around the large interstylar aperture, not translucent, withered corolla persistent the capsule base. **Seeds** usually 4 per capsule, dorsoventrally compressed, subrotund, broadly ovate to broadly elliptic, 1.45–1.6 × 1.25–1.39 mm, seed coat cells alveolate/papillate or poliedric, 20–30 µm in diameter, epicuticular wax usually present; hilum region subterminal scar area slightly raised, elliptic, 0.45–0.6 × 0.3–0.35 mm; vascular scar 0.15–0.2 mm, vertical or slightly oblique (Fig. 5 e,f). ***2n*** = ?

Distribution and ecology.—**CANADA:** Ontario, Québec. **U.S.A.:** Arkansas, Connecticut, District of Columbia, Delaware, Iowa, Illinois, Indiana, Kansas, Kentucky, Louisiana, Massachusetts, Maryland, Maine, Michigan, Minnesota, Missouri, North Dakota, Nebraska, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, Rhode Island, Tennessee, Texas, Virginia, Wisconsin. Flowering

Jul–Oct. **Hosts:** usually *Polygonum* but occasionally also on *Impatiens*, *Ipomoea*, *Lycopus*, *Penthorum*, *Xanthium*, and others.

Conservation status.—G3 (vulnerable) (G5, NatureServe 2005).

APPENDIX 1.
VOUCHERS FOR THE SEM STUDY

Vouchers are from NY unless otherwise indicated.

1. **Cuscuta pentagona** (16 collections examined).—**U.S.A. DISTRICT OF COLUMBIA.** Eastern Branch near Mt. Hamilton, 2 Aug 1919, *Killip 6338*. **FLORIDA. Lake Co.:** 3 mi S of Sorrento, *Welch 1633*. **GEORGIA. Whitfield Co.:** field E of Dicks Ridge, 1000 ft, 27 Jul 1900, *Wilson s.n.* **INDIANA. Lawrence Co.:** 2 mi W of Bedford, flood plain of Salt Creek, 23 Aug 1934, *Kriebel 2518*. **KANSAS. Trego Co.:** 19 mi S and 2 mi W of Collier, 6 Aug 1952, *David & Harr 4136*. **MASSACHUSETTS. Middlesex Co.:** Winchester, Winter Pond, 22 Sep 1908, *Fernald & Weatherby s.n.* **MICHIGAN. Kalamazoo Co.:** Fort Custer, 12 Aug 1945, *Hanes 4541*. **MISSOURI. Phelps Co.:** Jerome, 27 Jul 1931, *Kellog s.n.* **NEW JERSEY. Ocean Co.:** Bay Head, 31 Jul 1910, *Mackenzie 4742*. **NEW YORK.** (no county given). Long Island, 8 Aug 1903, *Bicknell s.n.* **NORTH CAROLINA. Franklin Co.:** Franklin, 23 Jul 1888, *Johnson s.n.* **NORTH DAKOTA. Barnes Co.:** Eckelson, 15 Sep 1937, *Stevens s.n.* **Benson Co.:** Cranberry Lake, 8 Sep 1930, *Stevens s.n.* **TENNESSEE. Wayne Co.:** 4 mi W of Waynesboro, 10 Aug 1934, *Welch 1382*. **VIRGINIA. Arlington Co.:** 1/4 mi SE Hatfield, 9 Jul 1939, *Hermann 10391*; W of Williamsburg, 15 Aug 1921, *Weatherby 4230*.

2. **Cuscuta campestris** (23 collections examined).—**CANADA. QUÉBEC.** Montreal, Aug 1940, *Cartier s.n.* **ONTARIO. Waterloo Co.:** Galt, 26 Sep 1908, *Herriot s.n.* **Wellington Co.:** Guelph, 3 Aug 1943, *Howitt s.n.* **U.S.A. ARKANSAS. Craighead Co.:** Jonesboro, 260 ft, 6 Jun 1948, *Demaree 26643*. **Garland Co.:** Hot Springs, 500 ft, 17 Jul 1938, *Demaree 17932*. **CALIFORNIA. Los Angeles Co.:** Los Angeles, 10 Jul 1933, *Demaree 10533*. **IDAHO. Ada Co.:** Harrison Hollow on NE side of Boise, T4N R2E Sec 34 SENW, 2710 ft, 13 Aug 1980, *Ertter & Strachon 3951*. **FLORIDA. Dade Co.:** at 14000 SW 8th Road, Miami, 12 Nov 1974, *Corell 43759* (NY). **GEORGIA. Clarke Co.:** Athens, at 285 Hillcrest, 800 ft, 11 Nov 1946, *Cronquist 4209*. **INDIANA. Harrison Co.:** 4 mi SE of Central, 26 Aug 1945 *Deam s.n.*. **Wells Co.:** 5 mi NE of Bluffton, 26 Aug 1940, *Deam 59866*. **KENTUCKY. Fayette Co.:** Gentry-Thompson stockyards, Lexington, 2 Sep 1944, *McFarland s.n.* **MARYLAND. Wicomico Co.:** Willards, 4 Sep 1942, *Moldenke 13847*. **NEVADA. Douglas Co.:** Carson River, ca. 7 mi N of Minden, 4700 ft, 14 Sep 1969, *Howell 46198*. **NEW MEXICO. Grant Co.:** 1880–1881, *Rusby 295*. **NEW YORK. Onondaga Co.:** Syracuse, shore of Onondaga Lake, *Gaertner s.n.* **OREGON. Marion Co.:** Salem, Willamette River, 13 Jul 1922, *Nelson 4407*. **TENNESSEE. Knox Co.:** N of Knoxville, Wallace's Orchard, 6 Aug 1943, *Wilson 3007*. **TEXAS. Childress Co.:** 3.4 mi E of Childress, S of Hwy. 287, 6 Sep 1945, *Whitehouse 10715*. **Tom Green Co.:** South Caucho River, 8 mi N by E of Christoval, 29 Aug 1943, *Cory s.n.* **UTAH. Sanpete Co.:** T14S, R2E, SEC 22, 4 mi NE of Fountain Green on U-132, 9000 ft, 19 Jul 1977, *Neese & White 3682*. **VIRGINIA. Nansemond Co.:** Suffolk, 24 Jul 1893, *Heller s.n.*

3. **Cuscuta glabrior** (15 collections examined).—**U.S.A. OKLAHOMA. Murray Co.:** Sulphur, Platt National Park, 28 May 1935, *Merril 522*. **Pontotoc Co.:** 2 mi SW of Ada, near State Hwy. 12, 26 Jun 1947, *Robbins 2607*. **NEW MEXICO.** (no locality given) 1851–1852, *Wright 1635*. **TEXAS. Bell Co.:** Near Little River, 11 June 1930, *Wolff 2274*; Killen, 14 Aug 1931, *Wolff 3270*. **Bexar Co.:** 16 mi E of San Antonio, 27 Apr 1921, *Schulz 453*; San Antonio, 17 Apr 1911, *Clemens s.n.* **Burnet Co.:** along State Hwy. 29, 7 mi E of Burnet, *Webster & Rogers 6476*. **Coleman Co.:** 7 mi E of Santa Anna, 29 Jun 1958, *Correll & Johnston 19019*. **Dallas Co.:** Dallas, 30 Jun 1872, *Hall s.n.* **Edwards Co.:** 29 mi NW of Rocksprings, 27 Jun 1943, *Cory s.n.* **Ellie Co.:** above Red Oak Creek off Waco road, 10 Jun 1940, *Lundell & Lundell 9353*. **Neueces Co.:** Corpus Christi, 0–40 ft, 9–12 Apr 1894, *Heller s.n.* **Randall Co.:** Buffalo Lake National

Wildlife Refuge, 3 Aug 1975, *Higgins 9567*. **Terrell Co.:** low hills in upper big Canyon, ca. 30 mi N of Sanderson toward Sheffield, 2800 ft, *Warnock 14730*.

4. Cuscuta runyonii (5 collections examined).—**U.S.A. TEXAS. Duval Co.:** of Hyw. 44 NE of San Diego, 20 Apr 1949, *Lundell 14906*. **Hidalgo Co.:** 2 mi N of La Joy, 45 m, 13 Jul 1941, *Runyon 2825*. **Starr Co.:** Brownsville, 50 m, 27 Apr 1941, *Runyon 2622*. **Webb Co.:** ca. 21 mi from junction of Hwys. 81 & 83, along Hwy. 83, 1 Apr 1949, *Tharp & York 52-163*; 46 mi NE of Laredo, route #59, 17 Jul 1958, *Correll & Johnston 14906*.

5. Cuscuta harperi (5 collections examined).—**U.S.A. ALABAMA. Cherokee Co.:** Lookout Mt. at the edge of gorge of May's Gulf, *Harper s.n.* **De Kalb Co.:** Desoto State Park, above Fort Payne, in Little River Canyon, 8 Oct 1960, *Sherman et al. 27757*; Glades, 1200 ft, 13 Oct 1962, *Demaree 46295*; Lookout Mt., Jul 1898, *Ruth 473*. **Etowah Co.:** Black Creek just above Noccalula Falls, Lookout Mt., 31 Aug 1911, *Harper 147*.

6. Cuscuta plattensis (2 collections examined).—**U.S.A. WYOMING. Goshen Co.:** 3 mi NE of Torrington, T25N R60W Sec 31 S1/2 SW 1/4, 4200 ft, 15 Aug 1993, *Dorn 5470*. **Niobrara Co.:** near Newcastle, 24 Jul 1942, *Degener & Peiler 16242*.

7. Cuscuta sandwichiana (3 collections examined).—**U.S.A. HAWAII. Hawaii Co.:** East Maui, Makawao, Kaunauhae, La Perouse Bay, 30 Apr 1978, *Sylva & Rumel s.n.*; O'ahu, Ka'ena Pt., 29 Nov 1969, *Char 40*; O'ahu, Makapu'u Beach Park, 4 Oct 1960, *Fujiwara s.n.*

8. Cuscuta obtusiflora var. glandulosa (5 collections examined).—**U.S.A. ARKANSAS. Ashley Co.:** Lone Prairie, Prairies, 15 Sep 1940. *Demaree 21543*. **INDIANA. White Co.:** in the Tippecanoe River, ca. 1 mi below Monticello, 14 Aug 1925, *Deam 41990*. **OKLAHOMA. Haskell Co.:** stream ca. 5 mi S of the intersection of Hwy 2 with Hwy 31, 22 Jul 1967, *Mitchell 3387*. **TEXAS. Dallas Co.:** Bachmans Dam, bordering lake, wet area, 1 Sep 1942, *Lundell & Lundell 11717*; 24 Aug 1942, *Lundell 11626*.

9. Cuscuta polygonorum (7 collections examined).—**U.S.A. ARKANSAS. St. Francise Co.:** 5 mi S of Forrest City, 19 Sep 1959, *McDaniel 1419*. **INDIANA. Putnam Co.:** 2 mi E of Bainbridge, 20 Oct 1941, *Yuncker 10836*. **NEBRASKA. Otoe Co.:** extreme S part of SE1/4, NE1/4, Sec 25, T8N-R14E, 11 Sep 1974, *Sutherland 4096*. **NEW JERSEY, Somerset Co.:** Millstone, plaine de débordement de la rivière Millstone, 4 Aug 1956, *Lavoie 452* (QUE). **NEW YORK.** [county not indicated; **Nassau Co.?**] Long Island, Plattsdale, 19 Sep 1925, *Ferguson 4608*. **OHIO. Ottawa Co.:** Duck Club, Winous Pt., 4 Aug 1949, *Core & Anderson s.n.* **WISCONSIN. Winnebago Co.:** swampy area along the shore of lake Winnebago, N beyond the end of Hazel St., N of Murdock, in Oshkosh, 25 Jul 1965, *Arriman 598* (UNB).

ACKNOWLEDGMENTS

We thank directors and/or curators from ACAD, ALTA, ARIZ, ASU, BRIT, DAO, F, GH, HAM, MEXU, MICH, MT, MTMG, NFLD, NSPM, OAC, QFA, QUE, RBG, RSA, SASK, SFS, TEX & LL, TUP, UBC, UC & JEPS, UNB, UNM, US, USAS, UWO, UWPG, WAT, WIN, WIS, WTU, and XAL for loans to Costea. Dan Austin, Lytton Musselman and Alan Prather provided useful comments and suggestions for an earlier version of the manuscript. Thierry Deroin helped us with information about the type of *Cuscuta sandwichiana* and kindly donated all the *Cuscuta* fragments annotated by Yuncker (held in P) to WLU. Special appreciation goes to NY staff for approving and preparing the numerous voluminous loans. Alexandra Smith assisted us with the scanning electron microscope.

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