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

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ABSTRACT

The *Cuscuta indecora* complex (*Cuscuta* subsect. *Indecorae*) in North America is characterized by fleshy, papillose flowers, corolla lobes with inflexed tips, and capsules with a thickened stylopodium. It includes *C. indecora*, *C. coryli*, *C. warneri*, and *C. jepsonii*. Recent taxonomists have proposed to treat the latter three taxa at varietal rank within *C. indecora* or as synonyms of it. We maintain *C. warneri* and *C. jepsonii* at specific rank because of their distinctive morphology, even though the latter is known only from the type collection and the former from a very limited number of specimens. *Cuscuta indecora* includes var. *indecora*, var. *longisepala*, and **C. indecora** var. **attenuata** (Waterfall) Costea, comb. et stat. nov. *Cuscuta indecora* vars. *bifida* and *neuropetala* are treated as synonyms of *C. indecora* var. *indecora*. *Cuscuta warneri* and *C. coryli* are reported as new floristic records from New Mexico and Québec, respectively.

RESUMEN

El complejo *Cuscuta indecora* (*Cuscuta* subsect. Indecorae) en América del Norte está caracterizado por flores papilosas y suculentas, lóbulos de la corola con puntas inflexionadas, y cápsulas con un estilopodio engrosado. El complejo incluye *C. indecora*, *C. coryli*, *C. warneri*, y *C. jepsonii*. Recientemente algunos taxónomos han propuesto tratar las últimas tres variedades dentro de la categoría *C. indecora* o como un sinónimo del mismo. Mantenemos que *C. warneri* y *C. jepsonii* están en una categoría especial por su morfología distinta, a pesar de que la última se conoce sólo por la colección del tipo, y la primera es conocida mediante un número de especimenes muy limitado. *Cuscuta indecora* incluye var. *indecora*, var. *longisepala*, y **C. indecora** var. **attenuata** (Waterfall) Costea, comb. et stat. nov. *Cuscuta indecora* vars. *bifida* y *neuropetala* son tratadas cómo sinónimos de *C. indecora* var. *indecora*. *Cuscuta warneri* y *C. coryli* figuran como nuevas citas florísticas de Nuevo México y Quebec, respectivamente.

Cuscuta subsect. *Indecorae* Yuncker is characterized by fleshy, papillose flowers, corolla lobes with inflexed tips, and capsules with a thickened stylopodium

SIDA 22(1): 209 – 225. 2006

(Yuncker 1932, 1965). In Yuncker's view, it included three North American species (*C. indecora* Choisy, *C. coryli* Engelm., and *C. warneri* Yuncker) and one from South America (*C. stenolepis* Engelm.). A fifth species, *C. attenuata* Waterfall, was added to subsect. *Indecorae* by Prather and Tyrl (1995), although Waterfall (1971) had suggested that *C. attenuata* resembled *C. compacta* Juss. of subsect. *Lepidanche* Engelm. *Cuscuta attenuata* is closely similar to *C. indecora*, but Prather and Tyrl (1995) maintained both at specific rank, emphasizing their apparent reproductive isolation. *Cuscuta warneri* was treated by Beliz in her Ph.D. thesis (1986) as a variety of *C. indecora*; this unpublished combination has been included in some recent North American overviews (e.g., Kartesz 1999). *Cuscuta jepsonii* Yuncker, which was initially treated in subsect. *Californicae* Yuncker (Yuncker 1932), has been recently considered conspecific with *C. indecora* (Beliz 1993, 2002). The taxonomic status and relationships of these taxa are reevaluated here, based on morphology and micromorphology of flowers, capsules, seeds, and pollen.

METHODS

Descriptions of morphology are based on samples from specimens from NY, which includes Yuncker's herbarium (Appendix 1). Measurements and pictures were 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. Terminology regarding the micromorphology of flowers, seeds and capsules, and pollen were described in detail in the first paper published in this issue (Costea et al. 2006). Conservation status was assessed using NatureServe (2005) ranks and criteria.

TAXONOMY

Cuscuta indecora and C. coryli.—*Cuscuta indecora* is a highly variable and common species both in North America and South America (Engelmann 1859; Yuncker 1921, 1932, 1965; Beliz 1986; Prather & Tyrl 1995). *Cuscuta coryli* is less variable and is sympatric with *C. indecora* over a significant geographic area (see below). Yuncker (1932) mentioned that *C. coryli* "is closely related to *C. indecora*, but is distinguished by its often 4-parted flowers which are commonly smaller (ca. 2 mm long), rudimentary scales and shape of fruit." We find that flowers of *C. coryli* may be both 4-merous and 5-merous on the same specimen, and sometimes even 3-merous. Engelmann (1843) noted "flowers frequently 5-parted" for *C. coryli*, but he later (1859) modified this observation to flowers "mostly 4-parted." Although the type and many collections of *C. coryli* apparently have more 4-merous than 5-merous flowers, 5-merous flowers predominate in some specimens. Ranges of variation in floral size in *C. indecora* and *C. coryli* are closely similar. *Cuscuta indecora* has small flowers, 2.1–2.7 mm long,

with the corolla tube 0.9–1.5 mm long; flowers of *C. coryli* are 1.7–2.6(–3) mm long, with the corolla tube (0.7–)1–1.4 mm long.

Such observations perhaps led Beliz (1987–1988, in herb. NY, GH) to consider *Cuscuta coryli* conspecific with *C. indecora*. Although they are clearly related and sometimes overlapping in several character states, the two taxa can be usually distinguished using a combination of characters (see key and descriptions below) and their recognition as separate species is appropriate.

Description of infrastaminal scales in these two species has been confusing. For example, in *Cuscuta coryli*, Engelmann was consistent, describing the infrastaminal scales as "appressed, bifid, consisting of a few teeth ... one or two teeth on each side of the filament (1942) ... or lobes laterally adhering to the lower (attached) part of the filament" (1859). Yuncker (1921, 1932) added "scales rudimentary, bifid, toothed, ordinarily reduced to toothed wings on either side of filament attachment." Figure 42e (1921) depicted one bifid infrastaminal scale with 1 or 2 fimbria on the each side of the staminal filament, while in Fig. 39 (1932), these lateral fimbria are replaced by dentate lobes (wings). In his 1965 treatment, Yuncker removed the term "bifid" from the description of infrastaminal scales of *C. coryli* and applied it to *C. indecora* var. *bifida* Yuncker, which was described as identical in other respects to *C. indecora* var. *indecora*. We find that the infrastaminal scales of var. *bifida* are not truly bifid, but rather the spathulate scales may have 2 or 3(–4) deeper apical incisions, which create 2 or 3(–4) lobes that are further fringed. "Normal" scales may occur in the same flower together with lobed ones. Such plants are regarded here as populational variants of *C. indecora* var. *indecora*. Bifid scales, as pointed out by Engelmann (1842, 1859), are characteristic of *C. coryli*.

The varieties of *C. indecora* and the status of *Cuscuta attenuata*.—Yuncker (1965) treated *Cuscuta indecora* with three varieties (var. *indecora*, var. *bifida*, and var. *longisepala*): as noted below, we tentatively maintain var. *longisepala* but var. *bifida* is not appropriately recognized. *Cuscuta indecora* var. *neuropetala* (Engelm.) Hitchc., distinguished by its relatively larger flowers, has been accepted in recent overviews of the genus (Beliz 1993, 2002; Kartesz 1999). We find that although var. *neuropetala* can be often identified, its connection to var. *indecora* by a series of intermediates makes taxonomic recognition unfeasible.

Prather and Tyrl (1995) observed that *Cuscuta attenuata* is morphologically similar to *C. indecora*. Indeed, Yuncker annotated (in herb. NY) some collections of *C. attenuata* as *C. indecora* var. *longisepala*. The present study substantiates the similarities, which extend to the morphology and micromorphology of perianth, seeds, pollen, and capsules. The geographic range of *C. attenuata* lies completely within that of var. *indecora*, but preliminary evidence suggests that *C. attenuata* may have a narrower host preference. In UPGMA and principal components analyses by Prather and Tyrl, *C. attenuata* is part of a single

cluster with *C. indecora* var. *indecora* and var. *longisepala*; univariate analyses separated these three taxa, although they were broadly overlapping in morphology. Prather and Tyrl (p. 456) concluded that "*C. attenuata* is a distinct species albeit morphologically similar to *C. indecora*. In the absence of reproductive isolation we might treat *C. attenuata* as a variety of *C. indecora*." Experimental crosses by Prather and Tyrl between *C. attenuata* and both varieties of *C. indecora* produced neither fruits nor seeds, while populations of *C. attenuata* were interfertile. Whether var. *indecora* and var. *longisepala* were interfertile was not reported.

For consistency with the degree of morphological difference between other *Cuscuta* species (as we are recognizing them), *C. attenuata* is treated here at varietal rank within *C. indecora*. In view of its apparent reproductive isolation and host specialization, it is a more strongly defined entity than var. *longisepala*, which also is broadly sympatric with var. *indecora*. Var. *longisepala* is tentatively maintained here, until its biology and evolution may be better understood.

Cuscuta warneri.—This species is a strikingly distinct dodder. Each calyx lobe is apically prolonged into a conical spur-like projection (Fig. 4 a,b,d), infrastaminal scales are oblong with truncate and dentate apex, and capsules have a collar-like apex and very short styles (Fig. 4d). The calyx spurs are accrescent, relatively small in flower and reaching maximum size in fruit, when they detach easily (at least on dry material). *Cuscuta warneri* shows strong similarity to *C. indecora* in morphology and micromorphology of perianth, capsules, seeds, and pollen (as also observed by Yuncker 1960). Beliz (1986) wrote that "critical studies, however, indicate that *C. warneri* is probably an abnormal specimen of *C. indecora* ... and until more material is available for studies, *C. warneri* is recognized as a variety of *C. indecora*." Our observations, in contrast, do not indicate that *C. warneri* is teratological. Flowers have all the components and they are fertile, each capsule usually with 2 seeds in which the embryos appear to develop normally. The fact that *C. warneri* is known only from the type locality and a collection from New Mexico (see bellow) indicates that its distribution is localized, but its morphological distinction justifies continuing recognition at specific rank.

The spur-like projections of the perianth of *Cuscuta warneri* have an unknown biological role. Similar morphology also is encountered in other, more distantly related species: *C. runyonii* Yuncker, *C. applanata* Engelm., *C. boldinghii* Urban, and *C. chapalana* Yuncker.

Cuscuta jepsonii.—This species was described and included by Yuncker (1921, 1933) in subsect. *Californicae* because infrastaminal scales are absent or reduced to ridges. Beliz (1986) initially considered it to be a synonym of *C. californica* Hook. & Arn. var. *papillosa* Yuncker, but she later (1993) treated it as a synonym of *C. indecora* var. *indecora*. She did not provide substantiating evidence for these decisions. The species is known only from the UC holotype.

Based on study of this collection, we confirm that *C. jepsonii* may belong to subsect. *Indecorae*, where it represents an extreme case of infrastaminal scale reduction. The 5-merous flowers and papillae morphology are similar to *C. indecora*, from which it differs by very small anthers, 0.2–0.3 mm long, which are more like those of *C. coryli*.

Infrastaminal scales vary to some extent in many *Cuscuta* species. Nevertheless, we know of no instance of complete reduction of infrastaminal scales in a species where scale development is characteristically normal, even if variable. For this reason, and until additional material can be studied, *C. jepsonii* is maintained as a distinct species.

KEY TO THE SPECIES OF *CUSCUTA* SUBSECT. *INDECORAE* IN NORTH AMERICA

1. Infrastaminal scales absent or reduced to ridges _____ **4. C. jepsonii**
1. Infrastaminal scales present.
   2. Calyx lobes with an apical spur-like projection; infrastaminal scales dentate at apex _____ **3. C. warneri**
   2. Calyx lobes without spur-like projections; infrastaminal scales fimbriate.
      3. Flowers commonly 5-merous, 2–5.3 mm long, infrastaminal scales united with the corolla tube for 1/3–1/2 (rarely 3/4) of their length, subspathulate to spathulate, rarely 2–3 lobed, apex rounded rarely truncate, with (6–)20–35(–50) fimbria; capsule yellowish and ± semi-transparent when dried, globose, subglobose to slightly depressed-globose, 0.8–1.5 times wider than long, the suture lines between the 2 carpels not or only slightly depressed _____ **1. C. indecora**
      3. Flowers (3–)4–5-merous, 1.7–2.6(–3) mm long; infrastaminal scales united with the corolla tube for most of their length, oblong, bifid with 1–3 fimbria on each side of filament attachment, rarely ± truncate with 3–6 fimbria; capsule brown and not semi-transparent when dried, initially globose, becomes depressed, 1.6–2.4 times wider than long, the suture lines between the 2 carpels depressed, forming a longitudinal groove on the opposed sides of capsule _____ **2. C. coryli**

1. Cuscuta indecora Choisy, Mém. Soc. Phys. Genéve 9:278, t.3, f.5. 1842 (**Fig. 1, Fig. 3a,d,e,g,h**). *Cuscuta decora* Choisy ex Engelm. var. *indecora* (Choisy) Engelm., Trans. Acad. Sci. St. Louis 1:502. 1859. *Grammica indecora* (Choisy) W.A. Weber, Southw. Naturalist 18:319. 1973. *Epithymum indecorum* (Choisy) Nieuwl. & Lunell, Amer. Midl. Naturalist 4:511. 1916. TYPE: MEXICO. [TAMAULIPAS]: "Mexicum ad Matamoros," *Berlandier 2285-865* (HOLOTYPE: G-DC; ISOTYPES: MO, P).

Stems 0.4–0.7 mm thick, yellow to orange. **Inflorescences** loose to dense, paniculate-cymose clusters, sometimes originating endogenously; pedicels 0.5–6 mm long, papillate-hispid to glabrous; bracts one (rarely 0) at the pedicel base, ovate to lanceolate. **Flowers** (4–)5-merous, 2–5.3 mm long fleshy, translucent-white when fresh, of the same color or dark-brownish when dried; epidermal cells arranged in rows, fleshy, with anticlinal walls convex (dome-like), additionally with cylindric-conical papillae 40–80 µm long; when flowers dry up, rows of dehydrated epidermal cells are usually easily discernible; epicuticular wax represented by longitudinally reticulated rodlets; laticifers isolated or in

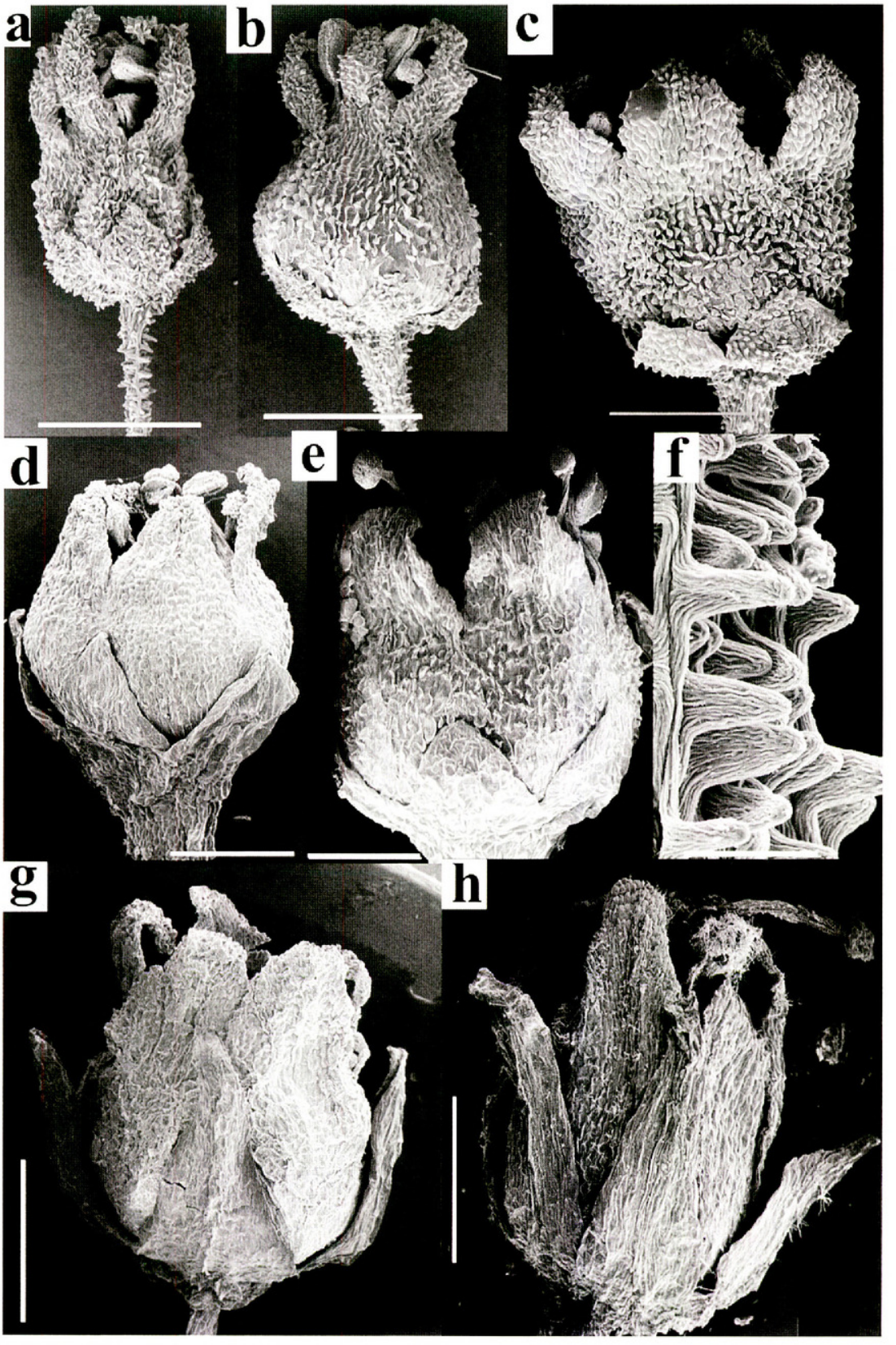

FIG. 1. Floral variation in *C. indecora*: **a**–**e.** var. *indecora* (scale bar = 1 mm); **f.** Papillae on the calyx of var. *indecora* (scale bar 75 μm); **g.** var. *longisepala*; **h.** var. *attenuata* (scale bar = 1 mm).

longitudinal rows, ovoidal to elongated, present in the perianth along the midveins, ovary and capsules often running longitudinally and yellowish-orange colored. **Calyx** cupulate, 1/2 to somewhat longer than the corolla tube, divided 1/2–2/3 of the length, lobes triangular-ovate to lanceolate, acute to attenuate, more or less overlapping at the base. **Corolla** tube campanulate, campanulate-cylindric, subglobose or suburceolate, 1–3.2 mm long, lobes 0.7–1.5 mm long triangular-ovate, acute, ca. 1/3 to equaling corolla length, suberect to erect, apically inflexed. **Stamens** barely exserted or enclosed; anthers elliptic to oblong, (0.5–)0.6–0.9(–1.2) × 0.3–0.5 mm long; filaments equaling or longer than anthers; pollen 3(–4)-zonocolpate, subprolate to prolate, 24–36 µm long, tectum imperforatum or with a few isolate puncta, sexine scabrate with isolated granules. **Infrastaminal scales** reaching the filaments, united with the corolla tube for 1/3–1/2 (rarely 3/4) of their length; subspathulate to spatulate, apex rounded, rarely truncate or 2–3(–4) lobed, with (6–)20–35(–50) fimbria. **Styles** distinct, 1–2.5 mm long, ± unequal, evenly filiform, suberect or weakly divergent; stigmas capitate, globose. **Capsules** yellowish to light-brown and ± semi-transparent when dried (pericarp thin), glabrous, subglobose, globose, to slightly depressed-globose, 0.9–1.5 wider than long, narrowed and thickened around the style bases, indehiscent or irregularly dehiscent, surrounded or capped by the withered corolla; pericarp epidermis smooth. **Seeds** 2–4 per capsule, 1.42–1.86 × 1.25–1.6 mm, shape heterogeneous on the same plant: dorsoventrally compressed to weakly angled, broadly elliptic to transversely oblique, hilum subterminal, rarely almost terminal, broadly elliptic, 0.40–0.45 × 0.32–0.36 mm; vascular scar linear, 0.15–0.18 mm, vertical; seed surface variable: a) epidermis cells more or less polygonal and puzzle-like, b) alveolate when dry and papillose when wet, and c) only some cells are papillose and the rest are ± puzzle-like; size of epidermal cells 20–50 µm in diameter.

KEY TO THE VARIETIES OF *CUSCUTA INDECORA*

1. Calyx lobes ovate triangular, reaching ca. 1/2 of the corolla tube _____ **a. C. indecora** var. **indecora**

1. Calyx lobes lanceolate mostly longer than the corolla tube.
   2. Calyx lobes acute; flowers in loose clusters; parasitic on a wide range of species _____ **b. C. indecora** var. **longisepala**
   2. Calyx lobes attenuate; flowers in dense clusters; parasitic primarily on *Iva annua* _____ **c. C. indecora** var. **attenuata**

a. Cuscuta indecora var. **indecora. (Fig. 1 a,b,c,d,e).** *Cuscuta neuropetala* Engelm., Amer. J. Sci. Arts 45:75. 1843. *Cuscuta indecora* Choisy var. *neuropetala* (Engelm.) Hitchc., Contr. U.S. Natl. Herb. 3:549. 1896. TYPE: U.S.A. TEXAS. [Harris Co.]: in wet prairies near Houston, on different Compositae, such as *Liatris*, *Solidago*, *Helianthus*, *Rudbeckia*, and on *Myrica cerifera*, Aug 1843, *Lindheimer 124* (HOLOTYPE: MO; ISOTYPES: NY, US).

Cuscuta neuropetala Engelm. var. *littoralis* Engelm., Boston J. Nat. Hist. 5:223. 1845. LECTOTYPE (here designated; Beliz 1986, in herb.): U.S.A. TEXAS. [Galveston Co.]: Galveston, Apr 1843,

Lindheimer s.n. (MO; ISOLECTOTYPE: NY). The protologue noted "Seashore of Galveston Island, on *Lycium carolinianum*, *Borrichia frutescens*, *Iva frutescens*, etc. Flowers in May."

Cuscuta verrucosa Engelm. var. *hispidula* Engelm., Amer. J. Sci. Arts 43:341. 1842. *Cuscuta indecora* var. *hispidula* (Engelm.) Yuncker, Illinois Biol. Monogr. 6:148. 1921. TYPE: U.S.A. TEXAS. [Harris Co.]: "in dry and sterile prairies, west of Houston, on *Euthamia*, *Schrankia*, *Aster*, *Ambrosia*, *Evolvulus*, and other low herbs, flowering in April and May, *F. Lindheimer*" s.n. (HOLOTYPE: MO, presumably). Yuncker (1921) cited *Berlandier 2285-MO* as the type of *C. indecora* var. *hispidula*, but that collection is interpreted here as the holotype of *C. indecora* (var. *indecora*).

Cuscuta hispidula Engelm., Amer. J. Sci. Arts 45:75. 1843. TYPE: U.S.A. TEXAS. [Harris Co.]: Engelmann did not cite a collector but noted "in dry and sterile prairies west of Houston. Flowering in April and May," apparently referring to the same Lindheimer collection typifying *C. verrucosa* var. *hispidula* (above). *Cuscuta hispidula* apparently was not intended by Engelmann to be a new combination based on the earlier *C. verrucosa* Engelm. var. *hispidula*, as he wrote "*Cuscuta hispidula* n. sp." and "Compare the remarks made in Vol. XLIII p. 341, under *C. verrucosa*."

Cuscuta indecora var. *bifida* Yuncker, Illinois Biol. Monogr. 6:149. 1921. LECTOTYPE (designated here): U.S.A. NEVADA. Twin Springs, May-Oct, *Purpus 6343* (UC 124538). Two sheets at UC are marked as "isotype" of var. *bifida*: the other is *Purpus s.n.*, without date (UC 124541).

Distribution and ecology.—**CANADA:** Saskatchewan. **U.S.A.:** Alabama, Arkansas, Arizona, California, Colorado, Connecticut, Florida, Georgia, Idaho, Iowa, Illinois, Kansas, Kentucky, Louisiana, Maryland, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, Nevada, New Jersey, New Mexico, North Carolina, North Dakota, Oklahoma, South Carolina, South Dakota, Tennessee, Texas, Utah, Virginia, Washington, West Virginia, Wyoming. **MEXICO; WEST INDIES; SOUTH AMERICA.** It is probably the third most common dodder in North America, after *C. gronovii* and *C. campestris*. It is listed as a "locally" important weed in the U.S.A. and Argentina (Parker & Riches 1993). Flowering Jul–Nov. **Hosts:** wide range of herbaceous and woody species, e.g., *Agalinis*, *Baccharis*, *Borrichia*, *Chenopodium*, *Eupatorium*, *Helianthus*, *Heterotheca*, *Hypericum*, *Ipomoea*, *Iva*, *Kosteletzkya*, *Lepidium*, *Ligustrum*, *Myrica*, *Pluchea*, *Polygonum*, *Rhynchosia*, *Solidago*, *Suaeda*, *Symphyotrichum*, *Tephrosia*, *Vernonia*.

Conservation status.—G5 (common) (NatureServe 2005). ***n*** = 15 (Pinkava et al. 1974); **2*n*** = 30 (Pazy & Plitmann 1995).

b. Cuscuta indecora var. **longisepala** Yuncker, Illinois Biol. Monogr. 6:149, Fig. 44, 97. 1921 (**Fig. 1g**). TYPE: U.S.A. TEXAS. On the Blanco, *Wright s.n.* (HOLOTYPE: MO).

Distribution and ecology.—**U.S.A.:** Texas. **MEXICO; SOUTH AMERICA.** Flowering summer–fall. **Hosts:** herbaceous and woody species. Conservation status: T2T1 (imperiled to critically imperiled) (not yet assessed by NatureServe 2005).

c. Cuscuta indecora var. **attenuata** (Waterfall) Costea, comb. & stat. nov. (**Fig. 1h**). *Cuscuta attenuata* Waterfall, Rhodora 73:575. 1971. TYPE: U.S.A. OKLAHOMA. McCurtain Co.: Waterfall Creek, 8 mi S and 2 mi E of Idabel, *Waterfall 17157* (HOLOTYPE: OKLA; ISOTYPE: GH).

Distribution and ecology.—**U.S.A.:** Kansas, Oklahoma, Texas (Prather & Tyrl 1993).

Conservation status.—imperiled (G2) (Natureserve 2004). Flowering late Aug–Oct. **Hosts:** *Iva annua*, rarely *Symphyotrichum* spp., mudflats, floodplains, and disturbed areas.

Conservation status.—T2T1 (imperiled to critically imperiled) (G2, Natureserve 2005). ***2n*** = 30 (Prather & Tyrl 1993).

2. Cuscuta coryli Engelm., Amer. J. Sci. Arts 43:337. 1842. (**Fig. 2, Fig. 3 b, c, f).**
TYPE: U.S.A. MISSOURI. [St. Louis Co.]: "on *Corylus* near St. Louis," Sep 1841, *Engelmann s.n.* (HOLOTYPE: MO; ISOTYPE: GH). The protologue reads "on *Corylus*, in the barrens west of St. Louis, in August and September."

Cuscuta coryli Engelm. var. *stylosa* Engelm., Amer. J. Sci. 43:337. 1842. TYPE: U.S.A. MISSOURI. [St. Louis Co.]: "on *Solidago*, St. Louis," Sep 1841, *Engelmann s.n.* (HOLOTYPE: MO; ISOTYPES: GH, US). The protologue reads "On *Solidago*, in dry prairies near St. Louis."

Cuscuta inflexa Engelm., Trans. Acad. St. Louis 1:502. 1859 [nom. invalid.]. Apparently a renaming of *Cuscuta coryli*, as the latter was cited immediately and first in synonymy (other names at specific rank also were cited). A number of collections were cited in the protologue.

Stems 0.30–0.50 mm thick, yellow to orange. **Inflorescences** usually dense (sometimes loose), paniculate-cymose clusters, sometimes originating endogenously; pedicels 0.5–3 mm long, glabrous; bracts one at the pedicel base, ovate to lanceolate. **Flowers** 4–5-merous (rarely 3-merous), 1.7–2.6(–3) mm long, fleshy, white when fresh, commonly dark-brownish when dried; epidermal cells fleshy, organized in rows with anticlinal walls convex (dome-like); papillae like those described in *C. indecora* usually absent; when flowers dry up, rows of dehydrated epidermal cells are more or less inconspicuous; epicuticular wax present represented by longitudinally reticulated rodlets; laticifers isolated or in longitudinal rows, ovoidal to elongated, present in the perianth midveins, ovary and capsules. **Calyx** cupulate, equaling or somewhat longer than corolla tube, rarely in some flowers shorter than corolla tube, divided 1/2–2/3 of the length, lobes triangular-ovate, acute, not or only slightly overlapping at the base. **Corolla** tube campanulate to suburceolate, 0.5–1.3(–1.5) mm long, lobes 0.8–1.2(–1.5) mm long, triangular-ovate, acute, ca. 1/3 to equaling corolla length, suberect to erect, apically inflexed. **Stamens** barely exserted or enclosed; anthers (0.2–)0.3–0.45 × 0.19–0.25 mm long; filaments equaling or longer than anthers; pollen as in *C. indecora*. **Infrastaminal scales** ca. reaching the filaments, united with the corolla tube for most of their length, oblong, bifid, with short dentate wings or 1–3 fimbria on each side of filament attachment, rarely truncate with 3–6 fimbria. **Styles** distinct, 0.7–1.5 mm long, ± unequal, evenly filiform, strongly divergent in capsule; stigmas capitate, globose. **Capsules** dark-brown and not semi-transparent when dried (pericarp thick), glabrous, initially globose later become evidently depressed, 1.6–2.4 times wider than long; the former suture lines between the 2 carpels forming a longitudinal groove on opposed sides of capsule; depressed and thickened around the style bases, indehiscent or irregularly dehiscent, surrounded or capped by the withered corolla; pericarp epidermis with

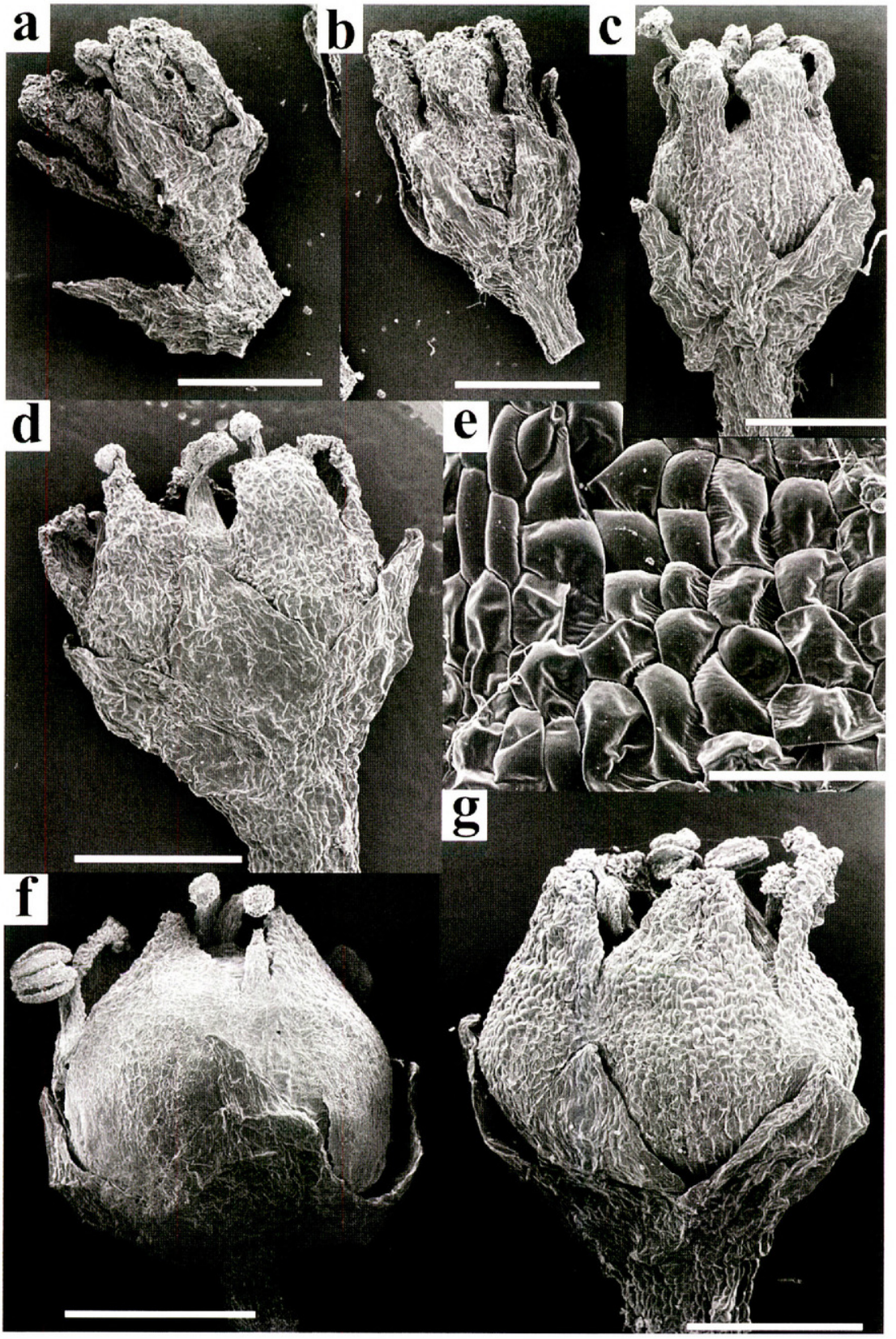

FIG. 2. Floral variation in *C. coryli*: **a–g.** excepting e (scale bar = 1 mm); **e.** Convex fleshy epidermis cells in the corolla (scale bar = 150 μm).

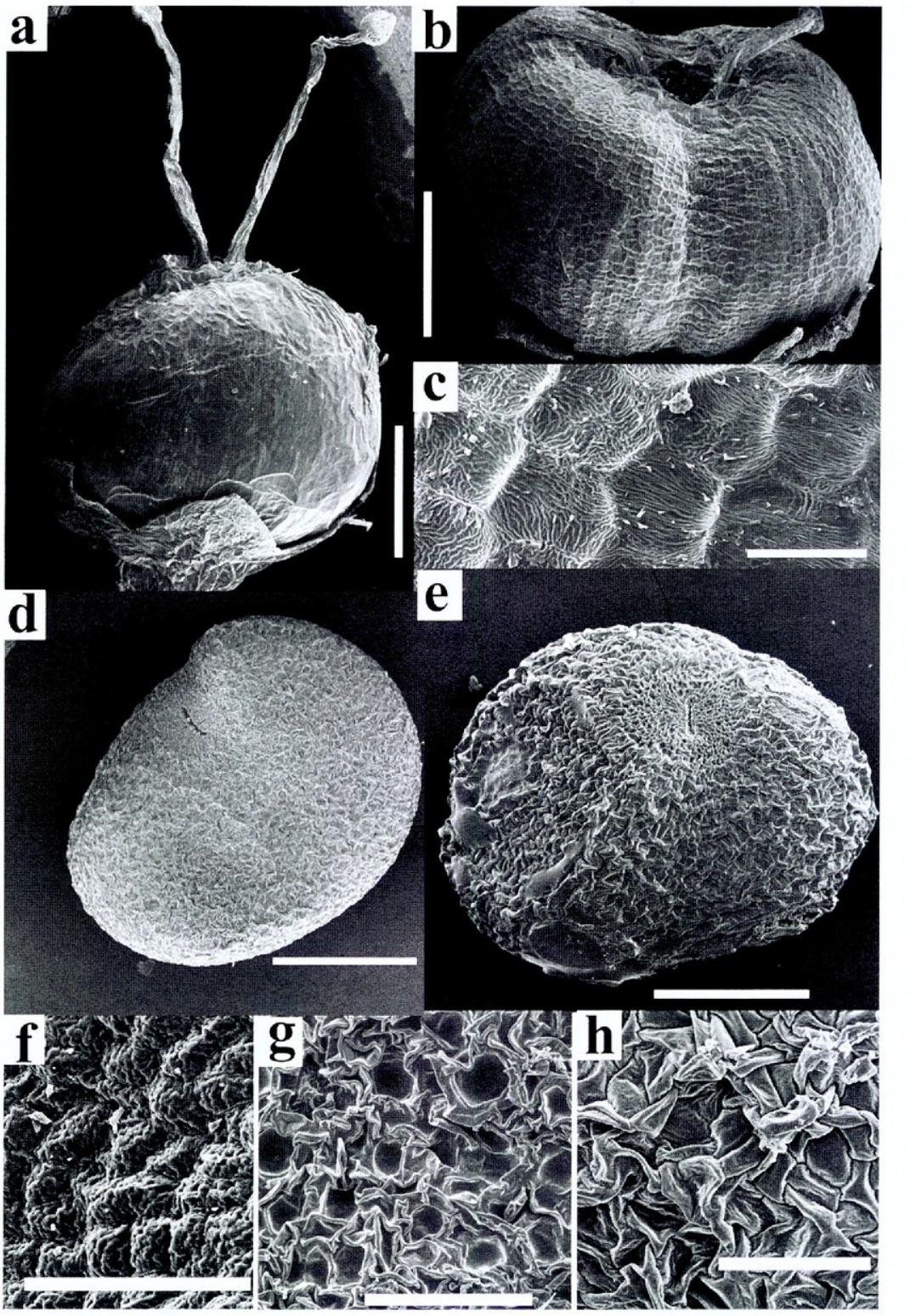

FIG. 3. Capsules and seeds of *C. indecora* and *C. coryli*. **a.** Capsule of *C. indecora* (scale bar = 1 mm); **b.** Capsule of *C. coryli* (scale bar = 1 mm); **c.** Surface of capsule of *C. coryli* (scale bar = 70 μm); **d–e.** Variation of seeds of *C. indecora*: **d.** Dorsoventrally compressed; **e.** More or less angled (scale bar = 0.60 mm); **f–g.** Surface of dry seeds: **f.** *C. coryli*, polygonal with epicuticular wax; **g–h.** *C. indecora*: **g.** Alveolate; **h.** Polygonal with groups of papillose cells (scale bars =200 μm).

a prominent pattern of polygonal cells. **Seeds** 3–4 per capsule, 1.32–1.65 × 1.25–1.4 mm, similar to those of *C. indecora*; additionally seed coat with polygonal epidermal cells may have epicuticular wax as in Fig. 3f. **2*n*** = ?

Distribution and ecology.—"Throughout the United States east of Rocky Mountains, but less common southward and westward" (Yuncker 1965). **CANADA:** Manitoba, Ontario, Québec, Saskatchewan. **U.S.A.:** Alabama, Arkansas, Arizona, Connecticut, District of Columbia, Delaware, Iowa, Illinois, Indiana, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Virginia, Wisconsin, West Virginia.

The floristic record from Québec is new, based on a single collection: QUÉBEC, Chambly Co.: St. Lambert, 9 Aug 1935, *Terrill 884* (MTMG). The species is considered "critically imperiled" (S1) in Canada (Argus & Pryer 1990; NatureServe 2004). Flowering Aug–Oct. **Hosts:** wide range of herbaceous and woody species, including *Aster*, *Ceanothus*, *Corylus*, *Helianthus*, *Monarda*, *Rhus*, *Rubus*, *Solidago*.

Conservation status.—S2S3 (imperiled to vulnerable) in the U.S.A. (not yet assessed by NatureServe 2004); critically imperiled (N1) in Canada (Argus & Pryer 1990; NatureServe 2005).

3. Cuscuta warneri Yuncker, Brittonia 12:38. 1960 (**Fig. 4.**). TYPE: U.S.A. UTAH. Millard Co.: vicinity of Flowell, 15 mi W of Fillmore, on *Phyla cuneiformis*, 10 Sep 1957, *Warner s.n.* (HOLOTYPE: UTC; ISOTYPES: DAO, DPU, GH, NY, OSC, RSA, US, WSU).

Stems 0.30–0.50 mm thick, yellow. **Inflorescences** of subsessile flowers on glabrous pedicels, 0.5–1 mm, in few-flowered glomerules; bracts one at the base of pedicels, ovate to lanceolate. **Flowers** 5-merous, 2.1–4 mm long, slightly fleshy, white-creamy, papillate-hispidulous, corolla epidermis with papillae 30–50μm long oriented in rows; epicuticular wax consisting from longitudinally reticulated rodlets; laticifers isolated or in longitudinal rows as in *C. indecora*. **Calyx** campanulate-cupulate, ca. 1/2 the corolla length, divided ca 1/2, lobes triangular-ovate, carenate, each apically enlarged to form a large, prominent, divergent, horn-like projection, 0.5–0.75 mm long, and sometimes basally with a smaller multicellular projections; not overlapping. **Corolla** tube campanulate-urceolate, 1.7–2.5 mm long, lobes triangular-ovate, more or less auriculate, acute, 0.5–0.7 mm long, 1/3–1/4 the corolla length, suberect, apically inflexed and basally overlapping. **Stamens** included, incurved over the ovary, anthers broadly elliptical 0.4–0.7 × 0.3–0.4 mm; filaments about as long as the anthers; pollen as in *C. indecora*. **Infrastaminal scales** ca. reaching the filaments, united with the corolla tube for ca. 1/2 of their length, oblong, shallowly and irregularly toothed at the truncate apex. **Styles** distinct, 0.2–0.4 mm, evenly filiform, barely longer than the collar-like stylopodium; stigmas globose, capitate. **Capsules**

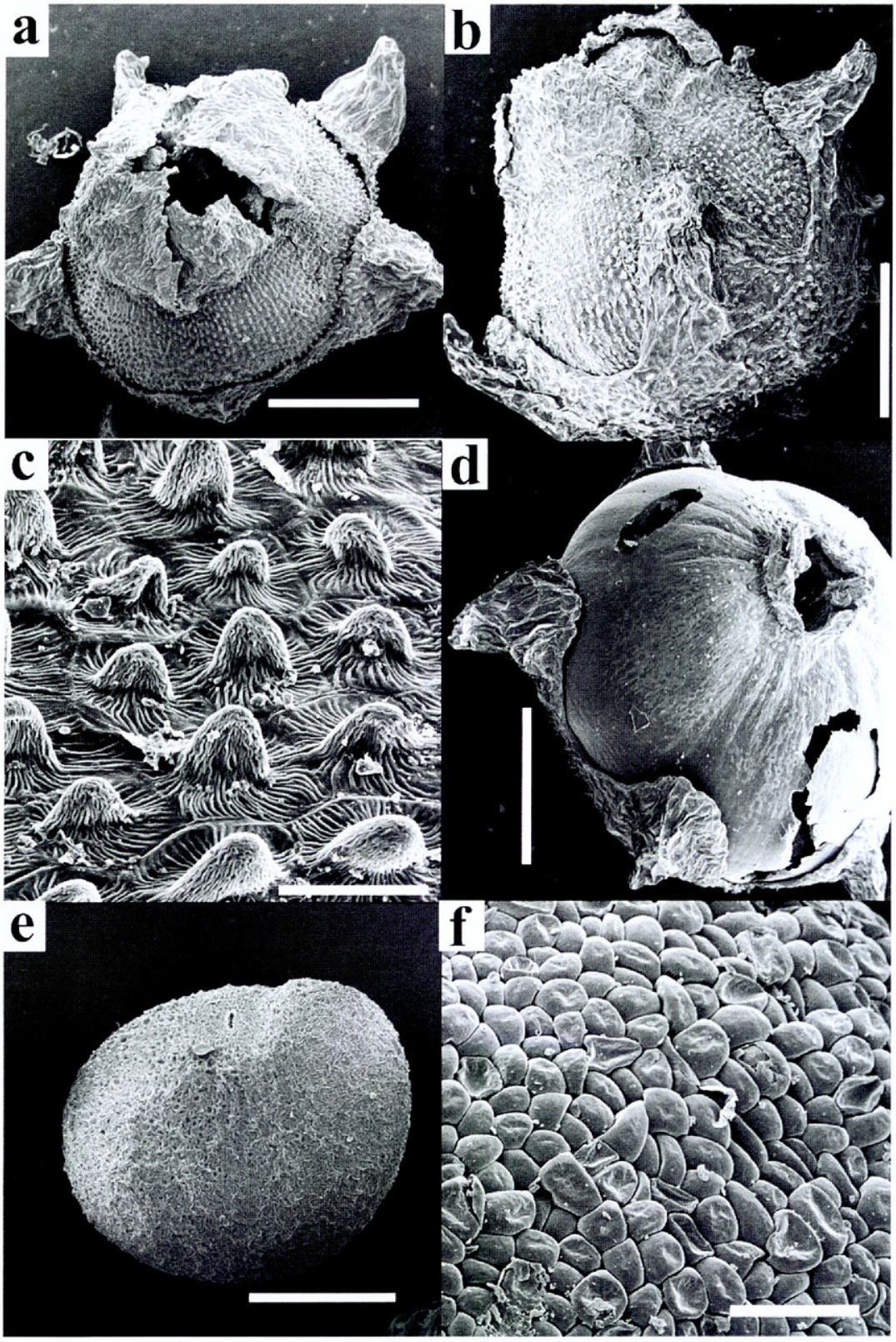

FIG. 4. *Cuscuta warneri*. **a–b.** Morphology of flowers: **a.** Apical view; **b.** Lateral view (scale bars = 1 mm); **c.** Papillae on corolla (scale bar = 75 μm); **d.** Capsule with persistent calyx at base (scale bar = 1 mm); **e–f.** Morphology of seeds: **e.** Seed, ventral view (scale bar = 0.60 mm); **f.** Surface of hydrated seed epidermis (scale bar 75 μm).

yellowish, ± semi-transparent when dried, more or less papillose, globose, 0.9–1.2 wider than long, the suture line between the 2 carpels not depressed; thickened and raised around the style base, indehiscent or irregularly dehiscent, enveloped by the corolla; pericarp epidermis smooth, with scattered papillae 10–20 µm long. **Seeds** 2 per capsule, 1.33–1.56 × 1.26–1.40 mm, dorsoventrally compressed, subround to broadly-elliptic, hilum subterminal, round 0.15–0.18 mm in diameter, vascular scar, 0.04–0.08 mm long, linear, oblique; surface of the seed coat alveolate when dry and papillose when wet, seed epidermis cells 0.26–0.40 µm in diameter. $2n = ?$

Distribution and ecology.—**U.S.A.:** The species has been considered "possibly extinct" because despite repeated search it has never been found again at the type locality in Utah (Reveal & Cronquist 1984; NatureServe 2005). However, we have found one more collection from southern New Mexico (Sierra Co.: Pedro Armendaris Grant, 15.6 mi N of Engle, E of Red Lake, 4800 ft, on *Phyla incisa*, 24 Sep 1998, *Peterson 98-699* (NMC)). The species has also been mentioned from Arizona (NatureServe 2005), but we are not aware of any herbarium vouchers. Albeit clearly extremely rare and endangered, this species might be potentially distributed at a low frequency over a larger geographic range, spanning Utah, Arizona, and New Mexico. Flowering and fruiting Jul–Sep. **Hosts:** known only from *Phyla* sp.

Conservation status.—T1 (critically imperiled) (GH, presumed extinct, NatureServe 2005).

4. Cuscuta jepsonii Yuncker, Illinois Biol. Monogr. 6:149. 1921. **(Fig. 5).** TYPE: U.S.A. CALIFORNIA: Big Horse Mountain, South Fork of Eel River, 3 Aug 1892, *W.L. Jepson 5c* (HOLOTYPE: JEPS, fragment NY).

Stems 0.30–0.40 mm thick, pale-yellow. **Inflorescences** of short-pedicellate flowers in cymose clusters; bracts one at the pedicel base, ovate to lanceolate. **Flowers** 5-merous, 2–2.7(–3) mm long, fleshy, white-cream; epidermal cells arranged in rows, fleshy, with anticlinal walls convex (dome-like), additionally with cylindric-conical papillae 40–70 µm long; when flowers dry up, rows of dehydrated epidermal cells are usually easily discernible; epicuticular wax represented by longitudinally reticulated rodlets; laticifers isolated ovoidal to elongated, or arranged in longitudinal rows, present in the perianth along the midveins, ovary and capsules often running longitudinally and yellowish-orange colored. **Calyx** shallowly cupulate, ca. 1/2 as long as the corolla tube, divided ca. 1/2 the length, lobes triangular, acute, not basally overlapping. **Corolla** tube campanulate-globular, becoming suburceolate, 1.3–2 mm long, lobes triangular, acute, less than 1/2 as long as the tube, erect, with inflexed apices. **Stamens** mostly included, anthers broadly elliptical 0.2–0.3 × 0.1–0.2 mm long; filaments about as long as the anthers; pollen as in *C. indecora*. **Infrastaminal scales** lacking or represented only by ridges and short bridges. **Styles** 0.4–0.8

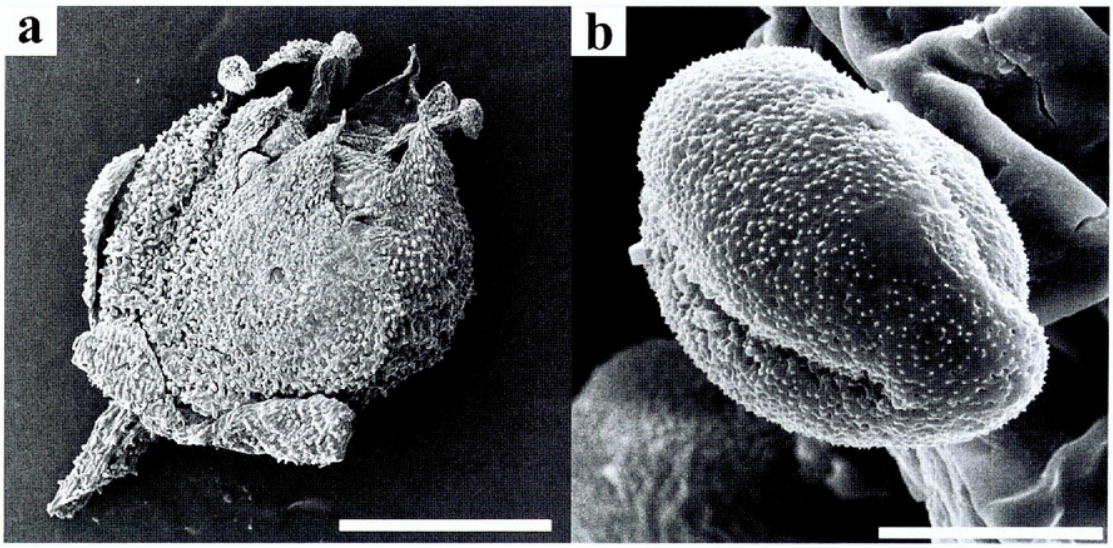

FIG. 5. *Cuscuta jepsonii*. **a.** Flower (scale bar = 1 mm); **b.** Pollen (scale bar = 10 μm).

mm long, ± unequal, somewhat subulate, erect or divergent in capsule; stigmas capitate, globose. **Capsules** light-brown ± semi-transparent when dried (pericarp thin), glabrous, subglobose, globose, to slightly depressed-globose, 1–1.5 wider than long, narrowed and thickened around the style bases, indehiscent or irregularly dehiscent, surrounded by the withered corolla. **Seeds** (no mature seeds were seen) 2–4 per capsule. ***2n*** = ?

Distribution and ecology.—Known only from the type collection. Flowering summer–early fall (Jul–Sep). **Hosts:** *Ceanothus*.

Conservation status.—GH (presumed extinct) (not mentioned in NatureServe 2005).

APPENDIX 1.—VOUCHERS FOR THE SEM STUDY (NY, EXCEPT *C. WARNERI* FROM GH AND *C. JEPSONII* FROM UC)

1a. Cuscuta indecora var. indecora (19 collections examined).—**U.S.A. ARIZONA. Pinal Co.:** Superior, Gloke Hwy, July 1926, *Moore s.n.* **CALIFORNIA. Kern Co.:** Bakersfield, 400 ft, 6 Jul 1920, *Fisher s.n.* **San Bernardino Co.:** San Bernardino Mts., lower edge of Upper Sonoran Zone, 4000 ft, 9 Nov 1932, *Wolf 4392*. **COLORADO. Larimer Co.:** Fort Collins, 5000 ft, 25 Aug 1896, *Baker s.n.* **FLORIDA. Putnam Co.:** 2.5 mi S of San Mateo, 26 Jul 1961, *Godfrey & Reinert 61139a*. **IDAHO. Gooding Co.:** Hagerman Valley, 13/E, 7S, 21 Aug 1941, *Davis 4306*. **Elmore Co.:** 2 mi E of Glenns Ferry, 23 Aug 1940, *Christ 11779*. **LOUISIANA. Terrebone Parish**: around Louisiana Universities Marine Consortium lab buildings and along La. 56 in Cocodrie, S of Houma, T21S, R18E, 12 Aug 1989, *Thomas 111952*. **MISSISSIPPI. Harrison Co.:** Ship Island, 15 Jun 1952, *Demaree 31920*. **NEBRASKA. Arthur Co.:** Arapaho Prairie, T18N R39W Sect 31, 32, ca. 1200 m, 27 Jul 1977, *Vescio & Kruse 174*. **NEVADA. Nye Co.:** Rt. 52 near Rt. 16 junction, 2600 ft, 26 Sep 1970, *Beatley s.n.* **NEW MEXICO. Chaves Co.:** Bottomless Lakes State Park at the edge of Pasture Lake, 5 Oct 1966, *Crutchfield 2319*. **Eddie Co.:** a few m N of Texas border ca. 0.5 mi SE of Hwy. 62-180, ca. 3900 ft, 1 Sep 1985, *Spellenberg & Spurrier s.n.* **OREGON. Umatilla Co.:** near Hermiston, 29 Jul 1944, *Peck 22633*. **TEXAS. Angelina Co.:** near Shawnee, 10 Sep 1942, *Lundell & Geiser 11905*. **El Paso Co.:** along Hwy. 62-180, 4 mi E of junction with Hwy 659, ca

4000 ft, 23 Oct 1983, *Worthington 11583*. **Llano Co.:** hills above Inks Dam, 21 May 1940, *Lundell & Lundell 9025*. **UTAH. Utah Co.:** T10S, Sec. 4, 0.5 mi E of Genola turnoff on Hwy 50-6, 4650 ft, 8 Sep 1984, *Baird et al. 1513*. **Weber Co.:** Howel Experimental Fruit Farm, Pleasant View, N Ogden, 7 Sep 1967, *Nye s.n.*

1b. Cuscuta indecora var. longisepala (2 collections examined).—**TEXAS. Chambers Co.:** Anahuac, 3 ft, 10 Jun 1933, *Fisher s.n.* **Cameron Co.:** 4 mi NW of Brownsville, bordering the Military Hwy, 10 m, 9 Jul 1941, *Runyon 2819*.

1c. Cuscuta indecora var. attenuata (3 collections examined).—**KANSAS. Republic Co.:** 2 mi N and 2 mi W of Wayne, 13 Sep 1952, *Horr 4410*. **TEXAS. Cameron Co.:** Robb's Ranch, 0.5 mi N of Ranch house, bordering the road, 10 Aug 1941, *Runyon 2873*. **Dallas Co.:** Dallas, Sep 187(?4), *Reverchon s.n.*

2. Cuscuta coryli (17 collections examined).—**CANADA. ONTARIO(?)**: St. Clair River (?), Squirrel Island, 16 Sep 1920, *Farwell 5692*. **U.S.A. ARIZONA. (no county given):** Grand Canyon, 7 Sep 1886, *Eggert s.n.* **ILLINOIS.** Menard(?), no date, *Hall s.n.* **INDIANA. Lake Co.:** just S of Pine, 19 Sep 1926, *Deam 43763*. **Nobble Co.:** 4 mi N of Kendallville, 23 Aug 1928, *Deam 46128*. **MARYLAND. Montgomery Co.:** wood near Widewaters, 26 Aug 1934, *Killip 31293*. **MICHIGAN. Kalamazoo Co.:** 4 mi NE of Schoolcraft, 6 Sep 1938, *Hanes 548*. **MISSOURI.** St. Louis, Sep 1842, *Engelmann s.n.* **Bush Co.:** Eagle Rock, 28 Sep 1896 and 14 Aug 1905, *Bush 202 and 3244*. **NEBRASKA. Richardson Co.:** woods of Lee's Ranch, 1.5 mi NW of Fargo, 1000 ft, 15 Sep 1940, *Reynolds 2727*. **NEW JERSEY. Somerset Co.:** Second Mountain, Watchung, 29 Aug 1937, *Moldenke 10086*; Little Snalie Hill, Sep 1915, *MacKenzie 6772*. **NEW YORK. Tioga Co.:** Campville, 20 Sep 1895, *collector illegible (F.E. Fr...) 296*; Long Island, Sea Cliff, 24 Sep 1928, *Ferguson 7181*; Staten Island, 24 Oct 1891, *Vail s.n.* **TENNESEE. Carter Co.:** Roan Mountain Station, 28 Aug 1908, *Rydberg 8179*. WISCONSIN. Madison, no date, *Watson s.n.*

3. Cuscuta warneri (1 collection examined).—**U.S.A. NEW MEXICO. Sierra Co.:** Pedro Armendaris Grant, 15.6 mi N of Engle, E of Red Lake, 4800 ft, on Phyla incise, 24 Sep 1998. *Peterson 98-699* (NMC). **UTAH.** The type collection (GH).

4. Cuscuta jepsonii (1 collection examined).—**U.S.A. CALIFORNIA.** The type collection (UC).

ACKNOWLEDGMENTS

We thank directors/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. Special thanks to NY staff for approving and preparing the four voluminous loans containing the herbarium of T.G. Yuncker. Dan Austin, Alan Prather and Lytton Musselman provided valuable comments and suggestions for an earlier version of the manuscript. Special appreciation goes to Therry Deroin (P) for sending the fragments of the *Cuscuta indecora* type and to Barbara Ertter (UC) and Emily Wood and Walter Kittredge (GH) for permission for SEM study of the types of *C. jepsonii* and *C.* warneri. Alexandra Smith assisted us with the scanning electron microscope. Elma Schweigert translated the abstract into Spanish.

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