TAXONOMY OF CUSCUTA GRONOVII AND CUSCUTA UMBROSA (CONVOLVULACEAE)

Mihai Costea (corresponding author)

Department of Biology Wilfrid Laurier University 75 University Avenue West Waterloo, Ontario N2L 3C5, CANADA mcostea@wlu.ca Guy L. Nesom

Botanical Research Institute of Texas 509 Pecan Street Fort Worth, Texas 76102-4060, U.S.A. gnesom@brit.org

Saša Stefanović

Department of Biology University of Toronto at Mississauga 3359 Mississauga Road Mississauga, Ontario L5L 1C6, CANADA

ABSTRACT

Cuscuta umbrosa is the correct name for the species often recognized as *C. megalocarpa*. It apparently intergrades in some features with *C. gronovii*, but the two are generally distinct across a broad region of sympatry. Three varieties are recognized within *C. gronovii*: var. *gronovii* is widespread; var. *latiflora* is broadly sympatric with var. *gronovii* but is maintained because relationships with *C. gronovii* var. *gronovii* and *C. cephalanthi* are not clear; var. *calyptrata* is more distinct and narrowly restricted in range, although it also is sympatric with var. *gronovii*.

RESUMEN

Cuscuta umbrosa es el nombre correcto para la especie reconocida recientemente como C. megalocarpa. Es ampliamente simpátrica y algo intergradada con C. gronovii, pero las dos especies son generalmente claras. Se reconocen tres variedades dentro de C. gronovii: var. gronovii que está muy esparcida; var. latiflora es ampliamente simpátrica con la var. gronovii pero se mantiene debido a la relación con C. gronovii var. gronovii y C. cephalanthi no está clara; la var. calyptrata es más clara y estrechamente restringida en su distribución geográfica, aunque sea también simpátrica con la var. gronovii.

The original concept of *Cuscuta umbrosa* Beyr. ex Hook. (1840) included *C. gronovii* Willd. ex Roem. & Schult. (1820) in typical form as well as a variant plant, based on the specimens cited in the protologue. Engelmann (1859) clarified the typification of *C. umbrosa*, distinguishing it from *C. gronovii*, and described the variant as *C. gronovii* var. *curta* Engelm. Yuncker recognized the variant taxon at specific rank, at first (1921, 1932) using the name *C. curta* (Engelm.) Rydb. but later (1943, 1965) adopting *C. umbrosa* as the earliest legitimate name. We find that recently *C. umbrosa* either has been accepted as a species under yet another name, *C. megalocarpa* Rydb. (1901) (Kartesz 1999;

Darbyshire 2003; USDA, NRCS 2004), or else it has not been recognized at any taxonomic rank (Beliz 1986-1987, in herb; Crins & Ford 1988).

Cuscuta gronovii and C. umbrosa, as recognized here, are similar and apparently closely related to C. cephalanthi Engelm. and C. rostrata Shuttlw. ex Engelm. & A. Gray. These four species, which were placed by Yuncker (1965) in two subsections (Platycarpae and Cephalanthae), have the same pattern of stem growth and branching: haustoria are formed as the main stem twines around the host and no tendril-like axillary branches are generated. This pattern was first observed by Dawson (1984) in C. gronovii. The evolutionary and taxonomic status of C. umbrosa is reevaluated here, especially with regard to its relationship with C. gronovii.

METHODS

Descriptions of morphology are based on samples from specimens from DAO, NY, and SMU (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

Yuncker (1932, 1965) characterized Cuscuta gronovii as having "styles about equaling the ovary or somewhat shorter," in contrast to those of C. umbrosa, which are "very short, about one fourth the length of the ovary." Other contrasts between these taxa emphasized by Yuncker are in the morphology of infrastaminal scales and the size of capsules and seeds. According to him, C. *umbrosa* has infrastaminal scales about half the length of the corolla tube, broad, of ten truncate and bifid, and capsules and seeds are larger. In contrast, C. gronovii has infrastaminal scales about equaling the corolla tube, oblong and not truncate or bifid, and capsules and seeds are comparatively smaller. We find that C. gronovii and C. umbrosa usually are morphologically distinguishable, but C. gronovii may show character states similar to C. umbrosa even when it occurs outside the geographical range of the latter. For example, C. gronovii from Ontario and Québec may occasionally have more or less truncate infrastaminal scales one-third the length of the corolla tube, or short stigmas, or comparably large seeds (Crins & Ford 1988) and capsules. Commonly only one state character of *C. umbrosa*, or rarely a combination of two (e.g., large capsules and seeds), occurs in C. gronovii. Such plants of C. gronovii may be separated from C. umbrosa using the character combinations in the following key. Other differences can be found in pollen morphology: C. gronovii has pollen grains with tectum

imperforatum or a few puncta, while *C. umbrosa* has tectum perforatum or almost microreticulate (Fig. 1).

Cuscuta gronovii has a wide geographic distribution in North America and is broadly sympatric with *C. umbrosa*. The former is more common in central and northeastern regions (Yuncker 1932), while the latter is primarily a prairie species. *Cuscuta gronovii* usually is distinct from *C. umbrosa* by a greater morphological gap than are the varieties of *C. gronovii* among themselves (see key below).

Within *Cuscuta gronovii*, Yuncker (1965) recognized three varieties: var. *gronovii*, var. *latiflora* Engelm., and var. *calyptrata* Engelm. Variety *latiflora* and variety *gronovii* are broadly sympatric across their geographic range, they show no distinct preferences toward hosts, and morphological intermediates occur. Var. *calyptrata* is more narrowly restricted in range (Texas and Louisiana) but is sympatric with the widespread var. *gronovii*. Continued recognition of sympatric varieties within *Cuscuta gronovii* is unusual. It reflects the observations that (1) a close morphological similarity exists among the varieties, (2) each of the varieties usually is morphologically distinct although intermediates may be relatively common, and (3) each of the non-typical varieties shows features suggesting that it might be more closely related to species of the *Cuscuta cephalanthi-rostrata* group or at least that genetic interchange among taxa of this broader group may have influenced the variation patterns within *C. gronovii*. We consider it premature to discard the varieties as formally recognized taxonomic entities until relationships involving all these taxa are clarified.

Cuscuta gronovii Willd. ex Roem. & Schult., Syst. Veg. 6:205. 1820 (Fig. 1 a, c, f). Epithymum gronovii (Willd. ex Roem. & Schult.) Nieuwl. & Lunell, Amer. Midl. Naturalist 4:511. 1916. Type (see Yuncker 1943): North America, unspecified locality, Willdenow 3160-10 (B, a photo seen).

Stems medium to coarse, yellow to orange. **Inflorescence** of pedicellate (1–4.5 mm) flowers in loose or dense, paniculate cymose clusters, sometimes endogenously formed; each flower with one ovate to broadly triangular bract at the pedicel base, and sometimes 1–2(–4) bracteoles on the pedicels. **Flowers** 5-merous (sometimes 3- or 4-merous), 2–4(–4.7) mm long, not papillose, white-cream, with a few to many isolated, round to ovoid translucent laticifers in the calyx, corolla, and ovary. **Calyx** cupulate, campanulate to narrow-campanulate, reaching to ca. the middle of the corolla tube or the corolla sinuses, divided ca. 1/2–2/3

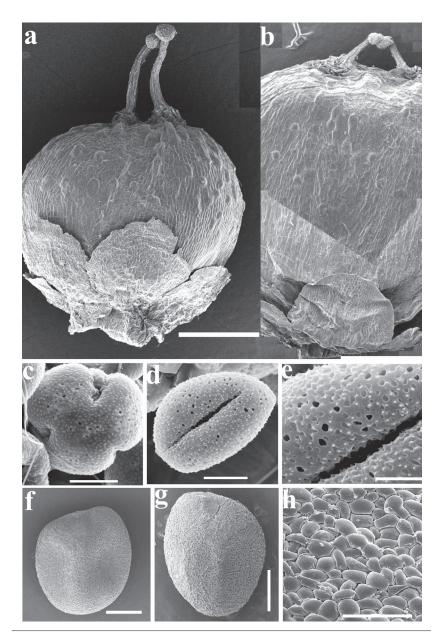


Fig. 1. **a**-**b**. Capsules with calyx at the base: **a**. Cuscuta gronovii var. gronovii; **b**. Cuscuta umbrosa (assembled from two pictures) (scale bar = 1 mm); **c**-**e**. Morphology of pollen. **c**. Cuscuta gronovii (scale bar = 7.5 μ m); **d**-**e**. Cuscuta umbrosa (scale bar = 8.5 and 3 μ m, respectively); **f**-**h**. Morphology of seeds: **f**. C. gronovii; **g**. C. umbrosa (scale bar = 0.6 mm); **h**. Hydrated seed coat of C. umbrosa (scale bar = 120 μ m).

the calvx length, lobes ovate to suborbicular or oblong, apex rounded or obtuse, more or less basally overlapping, margins entire to serrulate; corolla tube campanulate, broadly- or narrow campanulate (1-)1.5-2.5(-3) mm long, lobes mostly ovate, rounded-obtuse, commonly 1/3 the tube corolla tube, sometimes 1/2 to equaling the corolla tube, spreading or reflexed; epicuticular wax absent or reduced to a few reticulated rodlets; **stamens** exserted, anthers on filaments equaling or longer than anthers; **pollen** 3(-4)-zonocolpate, (18-)19-24(-27) µm long, rounded or truncated at poles, polymorphic in the same anther or flower, from spheroidal to subprolate (the former shape more frequent); tectum imperfortatum with a few puncta, rarely tectum perforatum with puncta 0.3-0.5 µm in diameter; sexine scabrate usually with isolated granules; **infrastaminal** scales oblong or broadly-oblong, rounded or truncate and bifid, deeply fringed distally, shorter than the corolla tube or reaching the filament bases; styles distinct, slender, thickened at the base or occasionally slightly subulate, (0.6-)1.2-2.2 mm long; stigmas capitate, globose. **Capsules** globose, ovoid to globose-conic or subobpyriform, thickened at the top, interstylar opening relatively small, sometimes with a short and broad but discernible neck, $2.5-4.5(-5.2) \times 2-4(-5)$ mm, indehiscent or irregularly dehiscent, surrounded or capped by the withered corolla. **Seeds** 2-4 per capsule, $1.35-1.7(-2.4) \times 1.2-1.5(-1.6)$, dorsoventrally compressed to obscurely angled, subrotund to broadly-ovate; hilum subterminal, subrotund, $0.33-0.39 \times 0.30-0.33$ mm, vascular scar of funiculum linear, 0.20-0.25 mm long, vertical to slightly oblique. Surface of seed epidermis variable: alveolate when dry and papillate when hydrated (cells 20-50 um in diameter), or cells more or less polygonal and puzzle-like, with epicuticular wax organized as reticulated rodlets. 2n = 60 (Fogelberg 1938).

KEY TO VARIETIES OF CUSCUTA GRONOVII

- a. Cuscuta gronovii Var. gronovii. Cuscuta vulgivaga Engelm., Amer. J. Sci. Arts 43:338. 1842.
 Cuscuta gronovii Willd. ex Roem. & Schult. var. vulgivaga (Engelm.) Engelm., Trans. Acad. Sci.
 St. Louis 1:508. 1859. Engelmann (1842) described three varieties within the species and cited
 specimens for each of the three (as below), but he did not specify which variety was typical
 for the species nor did he cite any specimens pertinent to the typical expression of the species, exclusive of varieties. In 1859, he noted for C. gronovii var. vulgivaga that "It is Willdenow's
 original C. gronovii, in his Hb. nro. 3160" (thus equating var. vulgivaga with var. gronovii).

Cuscuta vulgivaga Engelm. var. [_] laxiflora Engelm., Amer. J. Sci. Arts 43:338. 1842. LECTOTYPE (designated here): U.S.A. Alabama: [Oct] 1824, Buckley s.n. (MO). Engelmann cited three (or four?) collections: "Western New York on Decodon, Dr. A. Gray; Missouri on Cephalanthus and Amphicarpaea, and Georgia, on ____? [sic], J. Carey; Alabama, on Salix and Aster, S.B. Buckley." The lectotype sheet has a branch of Salix nigra and one of Symphyotrichum sp., each hosting Cuscuta.

- Cuscuta vulgivaga Engelm. var. [_] glomerata Engelm., Amer. J. Sci. Arts 43:338. 1842. LECTOTYPE (designated here): U.S.A. VERMONT: On Leersia, [no date], John Carey s.n. (MO). Engelmann noted that "my specimens are from Vermont on Leersia, and New Hampshire, on Solidago, both from Mr. J. Carey." The lectotype specimen has a small branch of the host with Cuscuta and a packet with dissected flowers. Mounted on the same sheet is a fragment packet with a Carey specimen of Cuscuta "on Solidago" from New Hampshire. It appears likely that both specimens are fragments of the original collections.
- Cuscuta vulgivaga Engelm. var. [_] tetramera Engelm., Amer. J. Sci. Arts 43:338. 1842. Type: U.S.A: Engelmann noted only "Connecticut, on *Urtica*, J. Carey" (HOLOTYPE: MO, presumably, not located).

Distribution and ecology.—The most common and widespread dodder in North America (Engelmann 1859; Yuncker 1965). CANADA: Alberta, British Columbia, Manitoba (only a few collections), Ontario, New Brunswick, Nova Scotia, Prince Edward Island, Québec, Saskatchewan (only a few collections). U.S.A.: Alabama, Arkansas, Arizona, Colorado, Connecticut, District of Columbia, Florida, Georgia, Iowa, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska., New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin, Wyoming. West Indies (Yuncker 1965) and Europe along water courses (Feinbrun 1972). Growing in a wide variety of climates but apparently preferring shaded and/or wet environments, sometimes occurring as a weed, e.g., in cranberries and grapevine (Parker & Riches 1993). Flowering Jun-Nov. **Hosts**: numerous species from hundreds of genera of herbaceous and wood plants in various families, including Acanthaceae, Anacardiaceae, Apiaceae, Asteraceae, Bignoniaceae, Brassicaceae, Caprifoliaceae, Commelinaceae, Convolvulaceae, Cornaceae, Balsaminaceae, Betulaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Polygonaceae, Primulaceae, Rosaceae, Rubiaceae, Solanaceae, Urticaceae, Verbenaceae, Vitaceae, and others (see also Gaertner 1950). Conservation status: G5 (common) (the same assessment in NatureServe 2005).

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

Louis, on *Saururus*, Sep 1841, *Geyer s.n.* (MO). Engelmann also cited "Alabama, Dr. A. Prout; Texas, on *Boehmeria*, *Polygonum*, &c., F. Lindheimer."

Variety *latiflora* is variable and intermediates with var. *gronovii* are relatively common. In seemingly intermediate specimens, on a single plant flowers can be found with the calyx about equaling the corolla tube or somewhat shorter. Apparently, the corolla tube may grow to some extent after fertilization occurs, thus modifying the ratio between calyx length and corolla tube. In var. *gronovii* all the flowers have the calyx about half the corolla tube length. The size of flowers and capsules in var. *latiflora* is similar to *C. cephalanthi*, but the latter differs in its 4-merous flowers and capsules capped by the withered corollas.

Forms of var. *latiflora* with corolla lobes as long as the corolla tube are comparable in floral morphology to *Cuscuta obtusiflora* var. *glandulosa*, which differs mostly in its depressed-globose capsules with large intersylar apertures. Engelmann (1842) also pointed out that var. *latiflora* bears some affinities with *C. polygonorum*, which is closely similar to *C. obtusiflora*.

Distribution and ecology.—The same distribution and hosts as var. *gronovii* but less common. Flowering Sep-Nov.

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

c. Cuscuta gronovii var. calyptrata Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859.
Cuscuta calyptrata (Engelm.) Small, Fl. S.E. U.S. 969. 1903. LECTOTYPE (Yuncker 1921): U.S.A.
Western Louisiana, [no date], J. Gregg s.n. (MO). Engelmann also cited "Texas, Lindheimer!"

The only differences between var. *calyptrata* and var. *gronovii* apparently are in corolla size and the way the corolla is shed. In var. *calyptrata*, as the capsule expands, the corolla breaks transversely more or less regularly from the base and a permanently narrowed portion of the tube holds the proximal portion of the corolla (including the styles and remnants of the stamens) coherent as it is lifted atop the capsule. In var. *gronovii*, the corolla breaks irregularly, transversely and longitudinally, as the capsule expands and it remains at the capsule base. In the few plants studied that might be intermediate, the corolla tube is not apically narrowed and breaks irregularly but is lifted at the top of the capsule at least in some flowers. Variety *calyptrata* is the most narrowly distributed entity of the *C. gronovii* complex and perhaps the most sharply defined. However, var. *calyptrata* is very similar to *C. cephalanthi* in the unique way corolla caps the mature capsule, but the latter differs in commonly 4-merous flowers, narrower infrastaminal scales, and depressed-globose capsules. The relationships between these three taxa need further study.

Distribution and ecology.—**U.S.A.:** Louisiana, Texas. Flowering Aug-Oct. **Hosts:** woody and herbaceous species.

Conservation status.—T1T2 (critically imperiled to imperiled) (T2, NatureServe 2005).

2. Cuscuta umbrosa Beyr. ex Hook., Fl. Bor. Amer. 2:78. 1840. (Fig. 1 b, d, g, h). Grammica umbrosa (Beyr. ex Hook.) W.A. Weber, Southwest. Naturalist 18:319. 1973. LECTOTYPE (designated here): "Northwestern America," Douglas s.n. (K). Among three collections, Hooker cited "N.W. Coast of America, Douglas." The interpretation of C. umbrosa has been intertwined with that of C. gronovii var. curta (below), apparently obscuring an unequivocal lectotypification of the earlier name from Hooker's publication. Engelmann (1859) placed "C. umbrosa Hook. l.c. in part" in synonymy of C. umbrosa var. curta, and he cited "Northwestern America, Douglas! Fremont!" Yuncker (1965) treated Cuscuta gronovii var. curta as a synonym of C. umbrosa but noted only that the type locality of C. umbrosa was "Northwestern America."

- Cuscuta gronovii Willd. ex Roem. & Schult. var. curta Engelm., Trans. Acad. Sci. St. Louis 1:508. 1859. Cuscuta curta (Engelm.) Rydb., Bull. Torrey Bot. Club 40:466. 1913. LECTOTYPE (Yuncker 1921): "Northwest America (Fremont's 3rd Exped. 79), the type, in the Engelmann Herb. (MO). For C. curta (with C. umbrosa as a synonym), Yuncker (1932) later cited "Northwestern America, (Douglas, a specimen in the Kew Herbarium)" as the "type."
- Cuscuta megalocarpa Rydb, Bull. Torrey Bot. Club 28:501. 1901. LECTOTYPE (formally designated here, Reveal in herb. 1977): U.S.A. COLORADO: Cucharas Creek, near La Veta, 7000 ft, 15 Sep 1900, Vreeland 670 (NY). Rydberg also cited Tweedy 2278, a collection from Sheridan Co., Wyoming.

Stems medium to coarse, yellow to orange. **Inflorescence** of pedicellate (1–7 mm) flowers commonly in dense, paniculate cymose clusters; each flower with one ovate to broadly triangular bract at the pedicel base. Flowers 5-merous (sometimes 4-merous), 2-3.5(-4.4) mm long, not papillose, white-cream, with a few to many isolated, round to ovoid translucent laticifers in the calyx, corolla and ovary. Calvx campanulate reaching to ca. the middle of the corolla tube, divided ca. 1/2-2/3 the calyx length, lobes ovate, apex rounded or obtuse, basally overlapping, margins entire to serrulate; **corolla** tube campanulate, 1.7–2.3(–2.7) mm, lobes mostly ovate to broadly-triangular ovate, rounded-obtuse, 1/3-1/4 the tube corolla tube, spreading or reflexed; epicuticular wax absent or reduced to a few reticulated rodlets; stamens exserted, anthers on filaments equaling or longer than anthers; **pollen** 3(-4)-zonocolpate, (18-)20-25(-28) µm long, rounded or truncated at poles, polymorph in the same anther or flower, from spheroidal to subprolate (the former shape more frequent); usually tectum perforatum to almost microreticulate, puncta 0.4-0.7 µm in diameter, rarely tectum imperforatum; sexine scabrate with isolated granules; infrastaminal **scales** infrastaminal scales broadly-oblong, and apically truncate to slightly bilobed, fringed, 1/2(-1/3) as long as the tube; **styles** distinct, slender, thickened at the base 0.3-0.7(-0.9) mm long; stigmas capitate, globose. Capsules subglobose, ovoid to globose-conic or subobpyriform, thickened at the top, interstylar oppening relatively small, sometimes with a short and broad but discernible neck, $3.5-6.5(-7) \times 3-5(-6)$ mm, indehiscent or irregularly dehiscent. **Seeds** 3-4 per capsule, $(1.8-)2-2.5(-2.8) \times 1.5-1.65$ mm, dorsoventrally compressed to obscurely angled, broadly-elliptic to obovate; hilum subrotund, 0.40- 0.60×0.39 -0.46 mm, vascular scar of funiculum linear, 0.20-0.25 mm long,

vertical to slightly oblique. Surface of seed epidermis alveolate when dry and papillate, with cells $20\text{--}50\,\mu m$ in diameter.

Cuscuta umbrosa is similar in some aspects of flower, fruit, and seed morphology to *C. rostrata*. Both have infrastaminal scales shorter than the corolla tube and large capsules and seeds. *Cuscuta rostrata* is recognizable by the narrower infrastaminal scales and especially by the prominently beaked ovary and capsule. *Cuscuta umbrosa*, however, sometimes produces capsules with a short and broad neck, which may indicate homology with the beaked capsules of *C. rostrata*. **2n** = ?

Distribution and ecology.—CANADA: Alberta., Manitoba, NW Ontario (only one collection), Saskatchewan. U.S.A.: Colorado, Kansas, Minnesota, Montana, Nebraska, New Mexico, New York (as reported by Mitchell and Tucker 1997; possibly a waif), North Dakota, Oklahoma, South Dakota, Utah, Wyoming. Flowering Jul-Oct. Growing in shaded and/or wet environments. Hosts: species of Salix, Ampelopsis, Symphoricarpos, Clematis, Epilobium, Convolvulus, Scutellaria, Linum, and other genera.

 ${\it Conservation status.} - G4G5 (apparently secure to secure) (G5, Nature Serve~2005).$

APPENDIX 1. VOUCHERS FOR THE SEM STUDY

1a. Cuscuta gronovii var. gronovii (16 collections examined). CANADA. ONTARIO. Leeds Co.: Rear of Leeds Twp., 1 km N of Oak Leaf, 6 km SE of Delta, 44∞35'20"N 76∞02'55"N, 3 Sep 1990, Catling 5111 (DAO). NOVA SCOTIA. Lunenburg Co.: Wentzell Lake, 17 Aug 1921, Fernald & Long 24402 (NY). U.S.A. ALABAMA. Montgomery Co.: Alabama River Bottoms. 4 mi N of Montgomery. 31 Oct 1943, Kpeooer et al.s.n. (NY). ARKANSAS. Hot Springs Co.: Magnet Cove, 470 ft, 2 Oct 1938, Hale 2062 (NY). FLORIDA. Taylor Co.: vicinity of Adams Beach, 16 Oct 1961, Godfrey & Honk 61565 (NY). GEORGIA. Fulton Co.: Atlanta, 1164 Clifton Rd., 1 Oct 1956, Burbanck s.n. (NY). INDIANA. Franklin Co.: bank of river 4 mi S of Laurel, 12 Oct 1924, Deam 41026 (NY). MAINE. Knox Co.: seashore Martinsville, 14 Aug 1952, Friesner s.n. (NY). MASSACHUSETTS. Barnstable Co.: 26 Aug 1928, Fernald et al., Exiccatae Grayane 480 (NY). MICHIGAN. Kent Co.: 7 mi N of Lowell, 28 Aug 1931, Yuncker & Welch 3792 (NY). MISSISSIPPI. Noxubee Co.: 3 mi of Macon, 22 Oct 1960, McDaniel 2276 (NY). MIS-**SOURI. Jefferson Co.:** 6.5 mi W of DeSoto, 38∞07'30"N 90∞40'30", 25 Aug 1991, *Raven & Raven* 27930 (NY). Saint Louis Co.: near Saint Louis, 1878, Eggert s.n. (NY). NEW JERSEY. Middlesex Co.: opposite New Brunswick, Oct 1918, Mackenzie s.n. (NY). OHIO. Ottawa Co.: Turtle Creek, Ottawa National Wildlife Refuge, 570 ft, 22 Aug 1996, Hill 28542 (NY). PENNSYLVANIA. York Co.: near McCall's Ferry, 9 Sep 1893, Heller & Halbach 1357 (NY). WISCONSIN. Waushara Co.: 2.5 mi SSW of Borth, 15 Aug 1984, Bewick 100 (NY).

1b. Cuscuta gronovii var. latiflora (12 collections examined). U.S.A. INDIANA. Daviess Co.: 1.5 mi SE of Newberry, 21 Sep 1932, *Deam 53259* (NY). Pasey Co.: 12 mi SW of Mt. Vernon, 20 Aug 1922, *Deam 37712* (NY). Sullivan Co.: along Busseron Creek, 2 mi E of Sullivan, 3 Oct 1931, *Deam 51395* (NY). IOWA. Wapello Co.: Cliffland, NW1/4 Sec. 11,T-71N, R-13W, 30 Sep 1954, *Davidson 4051* (NY). MARYLAND. (no county given): at mouth of Little Gunpowder River, 2 Sep 1902, *Shull 289* (NY). MICHIGAN. Kalamazoo Co.: Portage Twp., 20 Jul 1936, *Hanes s.n.* (NY). NEW JERSEY. Mercer Co.: Duck Island, below Trenton, 21 Aug 1921, *Mackenzie s.n.* (NY). NEW YORK. Nassau Co.: Long

Island, Oyster Bay, 11 Sep 1926, Ferguson 6091 (NY). **Suffolk Co.:** Long Island, Water Mill, 10 Aug 1925, Ferguson 4293 (NY). **Wayne Co.:** Lake Ontario, Fairbanks Point, Williamson Twp., 246 ft, 10 Aug 1939, Hinkey 4484 (NY). **TEXAS. Wood Co.:** Lake Ellis, 3 Sep 1942, Lundell 11750 (NY). **VIRGINIA. Princess Anne Co.:** along North Landing River, near Creed's, 9 Sep 1935, Fernald et al. 5011 (NY).

1c. Cuscuta gronovii var. calyptrata (1 collection examined). **U.S.A. TEXAS. Rockwall Co.:** 3.25 mi NW of Rockwall, 22 Oct 1946, *Cory 52529* (SMU).

2. Cuscuta umbrosa (14 collections examined). CANADA. ALBERTA: Lethbridge, 30 Aug 1971, Allen 150 (DAO). MANITOBA: Aweme (?), 9 Aug (no year), Criddle s.n. (DAO); Delta, S13-T14-R7, 20 Aug 1953, Löve & Löve 6199 (DAO); Delta Marsh, University Field Station, 50°11'N 98° 24'W, 9 Aug 1984, Szumigalski 18 (DAO); Otterburne, 13 Aug 1954, Bernard 497 (DAO); Winnipeg, Mulvey Avenue, Sep 1975, Fields s.n. (DAO). SASKATCHEWAN: Carnduff, 20 Aug 1948, Budd & Lodge 1197 (DAO); 10 mi S of- and 0.5–1 mi E of Gainsborough, Hutler River Valley, NE1/4 Sec. 9 T1 R30 W1, 29 Jul 1988, Harms 39594 (DAO). U.S.A. COLORADO. Teller Co. (?).: Manitou (Experimental Forest?), 31 Aug 1892, Mulford s.n. (NY). MINNESOTA. Carlton Co.: 3 mi SW of Fond du Lac, 22 Aug 1945, Moore & Huff 18199 (DAO). NORTH DAKOTA. Cass Co.: Fargo, 9 Sep 1950, Stevens 1228 (DAO). SOUTH DAKOTA. Potter Co.: Forest City, Sep 1892, Griffiths & Glosser s.n. (NY). UTAH. Salt Lake Co.: City Creek Canyon, 8000 ft, 10 Aug 1883, Leonard 250 (NY).

ACKNOWLEDGMENTS

Dan Austin, Lytton Musselman and an anonymous reviewer provided valuable comments and suggestions that improved an earlier version of the manuscript. 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. Special appreciation is extended to NY staff for approving and preparing the numerous voluminous loans. Robert Vogt and Meine Jutta (B) provided helpful information regarding the type collection of *Cuscuta gronovii*, and Kaj Vollesen (K) provided information regarding the type collection of *Cuscuta umbrosa*. Alexandra Smith assisted us with the scanning electron microscope and Elma Schweigert checked the translation of the Spanish abstract.

REFERENCES

- Costea, M., G.L. Nesom, and S. Stefanović. 2006. Taxonomy of the *Cuscuta pentagona* complex (subsect. *Arvenses*: Convolvulaceae) in North America. Sida 22:151–175.
- Crins, W.J. and B.A. Ford. 1988. The parasitic dodders (*Cuscuta*: Cuscutaceae) in Ontario. Canad. Field-Nat. 102: 209–215.
- Darbyshire, S.J. 2003. Inventory of Canadian agricultural weeds. Agriculture and Agri-Food Canada, Research Branch, Ottawa, ON. 396 pp. Electronic Publication: http://res2.agr.ca/ecorc/weeds_herbes/title-titre_e.htm.
- Dawson, J.H. 1984. A vegetative character that separates species of *Cuscuta*. Proc. 3rd Interntl. Symposium on Parasitic Weeds. Pp. 184–187.

- ENGELMANN, G. 1842. A monograph of the North American Cuscutineae. Amer. J. Sci. 43: 333–346.
- ENGELMANN, G. 1859. Systematic arrangement of the species of the genus *Cuscuta* with critical remarks on old species and descriptions of new ones. Trans. Acad. Sci. St. Louis 1:453–523.
- Feinbrun, N. 1972. *Cuscuta* L. In:T.G. Tutin, V.H. Heywood, N.A. Burges, D.M. Moore, D.H. Valentine, S.M. Walters, D.A. Webb, eds. Flora Europaea, Vol. 3, Diapensiaceae to Myoporaceae. Cambridge University Press. Pp. 74–77.
- FOGELBERG, S.O. 1938. The cytology of *Cuscuta*. Bull. Torrey Bot. Club. 65:631–645.
- Gaertner, E.E. 1950. Studies of seed germination, seed identification, and host relationships in Dodders, *Cuscuta* spp. Mem. Cornell Agric. Exp. Sta. 294:1–56.
- Kartesz, J. T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. First edition. In: Kartesz, J.T. and C.A. Meacham. 1999. Synthesis of the North American Flora, Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC.
- MITCHELL, R.S. and G.C. Tucker. 1997. A checklist of New York state plants (rev. ed.). New York State Bull. 490. New York State Museum, Albany.
- NatureServe. 2005. NatureServe Explorer: An online encyclopedia of life [web application]. Version 4.0. NatureServe, Arlington, Virginia. http://www.natureserve.org/explorer (Accessed: November 16, 2005).
- Parker, C. and C.R. Riches. 1993. Parasitic weeds of the world. Biology and control. CAB International, Wallingford, UK.
- USDA, NRCS. 2004. The PLANTS database. National Plant Data Center, Baton Rouge, LA. Electronic Publication, Version 3.5: http://plants.usda.gov>
- YUNCKER, T.G. 1921. Revision of the North American and West Indian species of *Cuscuta*. Illinois Biol. Monogr. 6:91–231. Reprinted 1970, Johnson Reprint Company, N.Y.
- YUNCKER, T.G. 1932. The genus Cuscuta. Mem. Torrey Bot. Club 18:113–331.
- YUNCKER, T.G. 1943. Nomenclatural changes in the genus *Cuscuta* and notes on some American species. Bull. Torrey Bot. Club 70:61–67.
- YUNCKER, T.G. 1965. Cuscuta. North American Flora, ser. 2, 4:1–51.