

A Phylogenetically Based Infrageneric Classification of the Parasitic Plant Genus *Cuscuta* (Dodders, Convolvulaceae)

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Abstract—*Cuscuta* (dodders, Convolvulaceae) is one of the largest and most economically important lineages of parasitic plants. The genus has a sub-cosmopolitan distribution with more than 75% of the species diversifying in the New World. The last monograph, published by Truman George Yuncker in 1932, provided a solid species-level taxonomic foundation. However, as revealed by recent phylogenetic studies, its infrageneric classification has been in great need of a taxonomic reappraisal, mainly because the morphological characters used in the previous classifications have been greatly affected by convergent evolution. Several recent phylogenetic and character evolution studies with broad sampling, as well as species-level revisions, have illustrated the deficiencies of previous classifications and provided an explicit and robust phylogenetic framework. Here we propose a new phylogenetic classification that places all 194 currently accepted species of *Cuscuta* into four subgenera and 18 sections. Sections have a strong morphological and biogeographical predictive value and include from one to 31 species. Thirteen section names are new or applied for the first time at the sectional rank: *Babylonicae* (Yunck.) M. A. García, *Subulatae* (Engelm.) Costea & Stefanović, *Obtusilobae* (Engelm.) Costea & Stefanović, *Prismaticae* (Yunck.) Costea & Stefanović, *Ceratophorae* (Yunck.) Costea & Stefanović, *Umbellatae* (Yunck.) Costea & Stefanović, *Gracillimae* Costea & Stefanović, *Californicae* (Yunck.) Costea & Stefanović, *Indecorae* (Yunck.) Costea & Stefanović, *Oxycarpae* (Engelm. ex Yunck.) Costea & Stefanović, *Racemosae* (Yunck.) Costea & Stefanović, *Partitae* Costea & Stefanović, and *Denticulatae* (Yunck.) Costea & Stefanović. An identification key to sections is included together with an overview of morphology, geographical distribution, taxonomic notes, and lists of included species.

Keywords—Molecular phylogeny, morphology, systematics, taxonomy.

Cuscuta (dodder) is a genus of nearly 200 species of stem parasites that has evolved within Convolvulaceae (reviewed by Stefanović and Olmstead 2004, 2005). Dodder embryos lack cotyledons; their radicle is devoid of apical meristems and degenerates a few days after germination (Truscott 1966; Sherman et al. 2008). Another distinctive characteristic of this parasitic lineage is the diversity of photosynthetic capabilities and plastome reductions at clade and at species levels, which accompanied transitions from hetero- to holoparasitism (reviewed by Braukmann et al. 2013). The genus is nearly cosmopolitan, but the majority of species (ca. 75%) are native to North and South America. Dodders occur in a great variety of habitats, from temperate to tropical, desert to riparian, littoral to high mountains, grasslands, forests, saline, and disturbed habitats. Similarly to other parasitic plants, dodders act as keystone species in their ecosystems (Press and Phoenix 2005). Approximately 15–20 *Cuscuta* sp. worldwide are agricultural and horticultural pests (Dawson et al. 1994; Costea and Tardif 2006), and in most countries the control and quarantine measures target the genus as a whole, ignoring the fact that more species may be endangered or even threatened with extinction (Costea and Stefanović 2009a).

Remarks about the peculiar morphology of *Cuscuta* and its parasitic nature date back to the Babylonian Talmud and Dioscorides, while the etymology of the generic name can be retraced to Aramaic and/or ancient Hebrew (Costea and Tardif 2004). As a distinct group, *Cuscuta* had been recognized before Linnaeus by Bauhin (1623), Ray (1682), and Tournefort (1694). In 1753, Linnaean *Cuscuta* included only two species: *C. europaea* (including *C. europaea* var. *epithimum*) and *C. americana* (Linnaeus 1753). Choisy (1841) published the first monograph of *Cuscuta*, in which he increased the number of known species to 38 and provided the first infrageneric classification based on the shape of stigmas. His “*Sectio prima*” with acute/clavate stigmas and “*Sectio secunda*” with globose-capitate stigmas circumscribe the major infrageneric groups known today as subgenera *Cuscuta* and *Grammica*, respec-

tively. The next monograph of the genus was provided by Engelmann (1859), who added 57 new species and used style and stigma characters to delimit three major (unranked) “Groups” of dodders: *Cuscuta*, with two styles and elongated stigmas; *Grammica* with two styles and capitate stigmas; and *Monogynella* with one style and variously shaped stigmas. Subsequent botanists and scholars of *Cuscuta* (e.g. Peter 1891; Mirande 1900; Yuncker 1921, 1932, 1965; Hunziker 1949, 1950) endorsed this delimitation with three subgenera, which have been universally accepted until today. In contrast to the definition of subgenera, the separation of infrageneric taxa below the rank of subgenus has varied considerably from author to author. Engelmann (1859) defined nine sections and six subsections. Yuncker (1932) proposed an intricate infrageneric classification with eight sections and 32 subsections. Finally, Hunziker, in treatments of *Cuscuta* from Argentina and Uruguay (Hunziker 1949, 1950), added two new subsections to Yuncker’s classification of subgenus *Grammica*.

During the last decade, our understanding of *Cuscuta* systematics has been substantially enhanced by molecular studies aimed at unraveling evolutionary relationships at different taxonomic levels, character evolution, and biogeography. Two broad-level molecular phylogenetic studies based on plastid (pt) *trnL-UAA/trnF-GAA* and nuclear ribosomal (nr) ITS sequences tested the monophyly of subgenera *Cuscuta* and *Grammica* and provided the relationships among their major infrageneric clades (García and Martín 2007; Stefanović et al. 2007). Similar results were also obtained in a study by McNeal et al. (2007), which was less comprehensive in terms of taxon sampling but included representatives from across the entire genus as well as additional pt sequences (*rps2* and *matK*). Finally, in the most comprehensive phylogenetic study to date we expanded our previous sampling and existing matrices to the entire genus using coding plastid and nuclear sequence data (*rbcl* and nrLSU, respectively) from a wide taxonomic sampling and covering its morphological, physiological, and geographical diversity (García et al. 2014). While these recent

studies have largely confirmed the three major groups/subgenera proposed by Engelmann, the delimitation of a fourth major lineage, “*Pachystigma*”, which includes South African species, emerged as a necessity. Subgenus *Cuscuta* was found to be paraphyletic, with the South African members of this subgenus (sect. *Pachystigma*) more closely related to subgenus *Grammica*, as previously suggested by McNeal et al. (2007) based on a limited sampling. In addition, much more substantial changes were revealed at a sectional level, particularly in the largest infrageneric group, subgenus *Grammica* (153 species; $\sim 3/4$ of species diversity of the genus). In contrast to Yuncker’s classification of subg. *Grammica* with 2 sections and 24 subsections, our results have indicated the existence of 15 well-supported major clades (labeled informally A–O in Stefanović et al. 2007, Stefanović and Costea 2008; García et al. 2014). Moreover, the species make-up of these groups diverges significantly from the taxonomic arrangements of Engelmann (1859) and Yuncker (1932). Also, a series of focused studies explored in depth the species-level evolutionary relationships within nine of the 15 major *Grammica* clades (Costea et al. 2005, 2006a, b, c, 2008a, 2009, 2011a, b, 2013; Costea and Stefanović 2009b, 2010). All of these studies emphasized the necessity for a new infrageneric classification and nomenclatural scheme for *Cuscuta*. Thus the main objective of this study is to incorporate all of the above mentioned phylogenetic results into a new formal infrageneric classification of this genus, in conjunction with a re-evaluation of traditional taxonomic characters.

MATERIALS AND METHODS

This infrageneric classification is based on the molecular phylogenetic framework provided primarily by the studies of García and Martín (2007), Stefanović et al. (2007), and García et al. (2014). The infrageneric taxa proposed, four subgenera and 18 sections, are all monophyletic (Fig. 1). The smallest section is monotypic and the largest includes 31 species. To maximize nomenclatural stability, whenever possible, we retained the available infrageneric names, although especially in subg. *Grammica* most of these names are applied for the first time at the sectional rank. For this purpose, all the previous infrageneric names were typified. In the case of Rafinesque’s generic names, the problem is not strictly typification, because at least one species was indicated by the author for each genus (Rafinesque 1836), but rather determining the identity of these *Cuscuta* species. Yuncker (1921, 1932) and Manitz (1976) elucidated the identity of most of these species names, and we proposed *Cuscuta* synonyms for the remaining ones.

Three hybrid species, each involving parents from two different clades of subgenus *Grammica*, *C. sandwichiana*, *C. bifurcata*, and *C. xanthochortos* (Stefanović and Costea 2008; García et al. 2014), were assigned to one of their respective “progenitor” clades based on their morphological affinities. The classification included all the accepted species even if some of them could not be studied in previous molecular studies. The latter species are often known only from the type specimen(s), and a provisional placement was proposed based on their morphology. These species are indicated with an asterisk (“*”) in the “included species” of each section. A few remaining species with an uncertain status were also considered and their placement discussed separately. Thus, this study also represents the most accurate species count of genus *Cuscuta* to date.

Cuscuta collections from the following herbaria were studied and annotated: AAU, ABH, ALTA, ARAN, ARIZ, ASU, B, BAB, BC, BCN, BM, BOL, BORD, BR, BRIT, CAL, CANB, CAS, CEN, CHR, CHSC, CIIDIR, CIMI, COI, CTES, DAO, E, F, FT, G, GH, H, HUFU, HUJ, IAC, IEB, IND, J, JACA, JE, JEPS, K, L, LAU, LD, LE, LL, LP, LPB, LPS, M, MA, MACB, MAF, MEL, MERL, MEXU, MGC, MICH, MO, MPU, MSTR, NAP, NBG, NMC, NY, OAC, OKLA, OSC, OXF, P, PACA, PRE, QCNE, QFA, RB, RNG, RSA, S, SALA, SAM, SASK, SD, SEV, SGO, SI, SPF, TEX, TRT, TRTE, UA, UB, UBC, UCR, UCT, UNB, UNM, UPRRP, UPS, US, VAL, W, WTU, and XAL.

Morphological characters used to define subgenera and sections are based on Engelmann (1859), Yuncker (1932, 1965), a series of recent species-level systematic studies (see introduction), and several character evo-

lution studies of the pollen, perianth, infrastaminal scales, and gynoecium in *Cuscuta* (Welsh et al. 2010; Wright et al. 2011, 2012; Riviere et al. 2013; García et al. 2014). Morphological characteristics of subgenera and sections are shown in Figs. 2, 3, 4. Stereomicroscopy images were taken from rehydrated flowers of herbarium specimens using a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 7.5 software (MIS Inc., Villa Park, Illinois, released 2014). For scanning electron microscopy (SEM), we used hexamethyldisilazane (HMDS) as an alternative for critical point drying (Costea et al. 2011a, b). Examination, measurements and pictures were taken at 10 kV using a Hitachi SU1510 variable pressure scanning electron microscope. Thousands of photographs that illustrate details of the floral parts, pollen, and fruit morphology are available on the *Digital Atlas of Cuscuta* (Costea 2007-onwards).

DISCUSSION

Convergent Evolution Hindered Previous Section-level Classifications in *Cuscuta*—Similarly to other parasitic plants (Kuijt 1969), evolution to parasitism in *Cuscuta* was accompanied by a drastic reduction of the vegetative organs (e.g. stems and leaves) and a diversification of the floral parts and breeding systems (Wright et al. 2011, 2012). Therefore, previous classifications of *Cuscuta* (e.g. Engelmann 1859; Yuncker 1932) had to rely entirely on flower and fruit characteristics. However, recent systematic investigations at the species level (see introduction) and character evolution studies revealed that the majority of morphological characters in *Cuscuta* are significantly affected by convergent evolution. Such characters include: perianth features (Wright et al. 2012); shape, size, and reduction of infrastaminal scales (Riviere et al. 2013); pollen morphology (Welsh et al. 2010); shape/size of gynoecium/capsule parts (Wright et al. 2011; García et al. 2014); and fruit dehiscence/indehiscence (García et al. 2014). For example, Yuncker (1932) considered fruit dehiscence/indehiscence to be of paramount significance and hypothesized that dehiscent capsules have evolved from indehiscent ones. Accordingly, he divided subgenus *Grammica* into two sections: *Eugrammica* with dehiscent capsules, and *Cleistogrammica* with indehiscent capsules. In contrast, we found that capsule dehiscence is the plesiomorphic condition while the apomorphic indehiscence has evolved multiple times, sometimes with reversals to dehiscence (García et al. 2014). Thus convergent evolution has obscured the natural infrageneric groups, particularly at the section level and in the species-rich subgenus *Grammica*, and as a result, neither the two subsections nor the 24 subsections proposed by Yuncker (1932) for the latter subgenus are monophyletic (Fig. 1).

In some cases, entire clades/sections of subg. *Grammica* from different continents converge morphologically, in others, only certain species belonging to different clades share strong morphological affinities. Convergent evolution within the largest clades/sections also took place. For example, *Lobostigmae* and *Subulatae* are the largest infrageneric groups of subg. *Grammica* (18 and 31 species, respectively); the former group is North American and the latter South American, but both clades have in common large, fleshy flowers, thick styles, and large or lobed stigmas. These floral characteristics likely evolved in association with the tendency towards xenogamy observed in most species of these two clades (Wright et al. 2012). Similarly, sect. *Oxycarpae* from North America and *Racemosae* from South America are difficult to separate morphologically, and their species have comparable mixed-mating breeding systems in common (Wright et al. 2012).

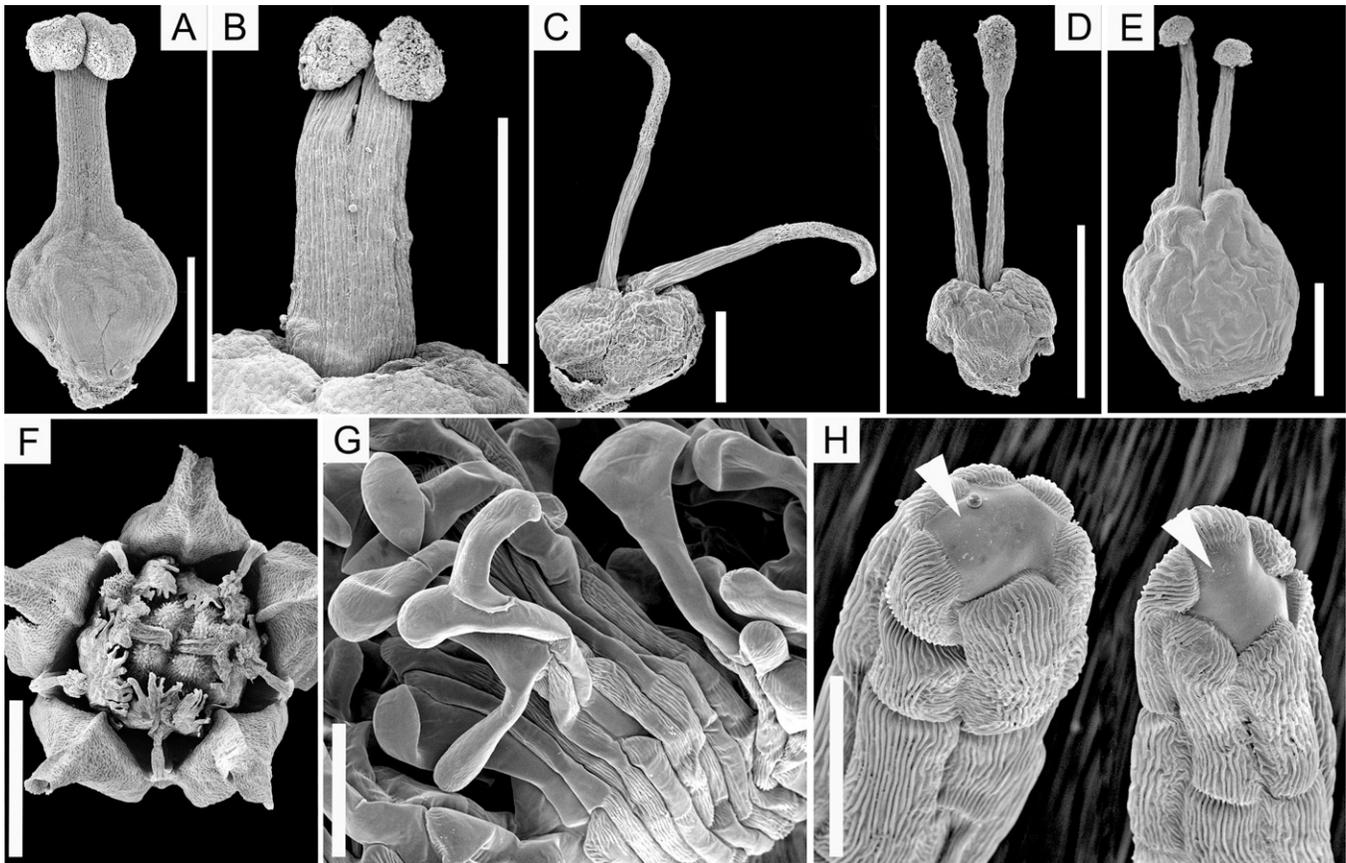


FIG. 2. Morphological characteristics of *Cuscuta* subgenera. A–B. Subgenus *Monogynella*, one style gynoecium. A. *C. japonica*. B. *C. exaltata*, style distally bifid. C. Subgenus *Cuscuta*, gynoecium with two equal styles having a \pm similar diameter as the cylindrical stigmas, *C. epithymum*. D. Subgenus *Pachystigma*, gynoecium with two equal or unequal styles, thinner than the clavate stigmas, *C. angulata*. E. Subgenus *Grammica*, gynoecium with two unequal styles and capitate stigmas, *C. gronovii*. F–H. Infrastaminal scales (IFS). F. General position in the flower, *C. argentinana*. G. IFS fimbriae in subgenus *Monogynella*, *C. reflexa*. H. IFS fimbriae in subgenera *Cuscuta*, *Pachystigma*, and *Grammica*, *C. campestris*. Arrows indicate laticifers (the smooth cells). Scale bars. A–F = 1 mm; G–H = 50 μ m.

(e.g. by Engelmann, Yuncker, Hunziker), have been validated by modern studies; therefore, morphology is a strong predictor of species lineages within each section.

In conclusion, because of convergent evolution it was unavoidable that some morphological overlap would occur among the sections of subgenus *Grammica*. Even so, the morphological predictive value of these new infrageneric groups is high, in addition to the molecular, biogeographical, and probably biochemical characters.

***Cuscuta*: One Versus Several Genera**—Even though a single genus concept has dominated botanical literature, historically *Cuscuta* was also considered to consist of several distinct genera. For example, Loureiro (1790) described genus *Grammica*. Rafinesque (1836) thought that *Cuscuta* included “at least” 10 other genera, which he defined based on characters that are currently considered appropriate at the species level (*Cuscuta* s. s., *Anthanema*, *Aplostylis*, *Dactylepis*, *Eronema*, *Kadula*, *Kadurias*, *Lepimenes*, *Nemepis*, and *Pentake*). The definition of a monotypic family Cuscutaceae by Dumortier (1829) further stimulated the description of new genera. Note that the different classifications of *Cuscuta*, either as multiple genera of Cuscutaceae or as groups/subgenera of a unified genus (with the exception of Rafinesque 1836), have always been based on various interpretations of the morphology of styles and stigmas (Wright et al. 2011). For example, Pfeiffer (1845) treated *Cuscuta* as a family with three genera:

Cuscuta with linear stigmas, *Epilinella* with clavate stigmas, and *Engelmannia* with capitate stigmas. Des Moulins (1853) segregated the family into five genera: *Cuscuta* (stigma fili-form), *Epilinella* (stigma claviform), *Monogynella* (styles fused), *Cassutha* [J. Bauh.] (stigma capitate), and *Succuta* (stigma fili-form). Most recently, Hadač and Chrtek (1970) proposed a classification with four genera: *Cuscuta* s. s., *Grammica*, *Monogynella*, and *Kadurias*, and published in this and subsequent articles a great number of nomenclatural combinations: 119 in *Grammica*, 25 in *Monogynella*, and five in *Kadurias* (IPNI 2014). Since none of these multi-generic nomenclatural innovations were accompanied by systematic studies, they were in general not accepted. The characters used, with the exception of the historical gynoecium characters, vary considerably across the genus (e.g. the number of chromosomes and number of coils in the embryo). More recent character evolution studies have found that *Monogynella*, the sister group to the rest of *Cuscuta*, is quite distinct morphologically compared to other lineages, *Pachystigma*, *Cuscuta*, and *Grammica* (e.g. Wright et al. 2011; Riviere et al. 2013). However, a monogeneric concept of *Cuscuta* is backed up by its consistent and strongly supported monophyly within Convolvulaceae (Stefanović and Olmstead 2004). This approach is also practical, considering the minute morphological differences between the major groups of *Cuscuta*, which are treated as subgenera in this article.

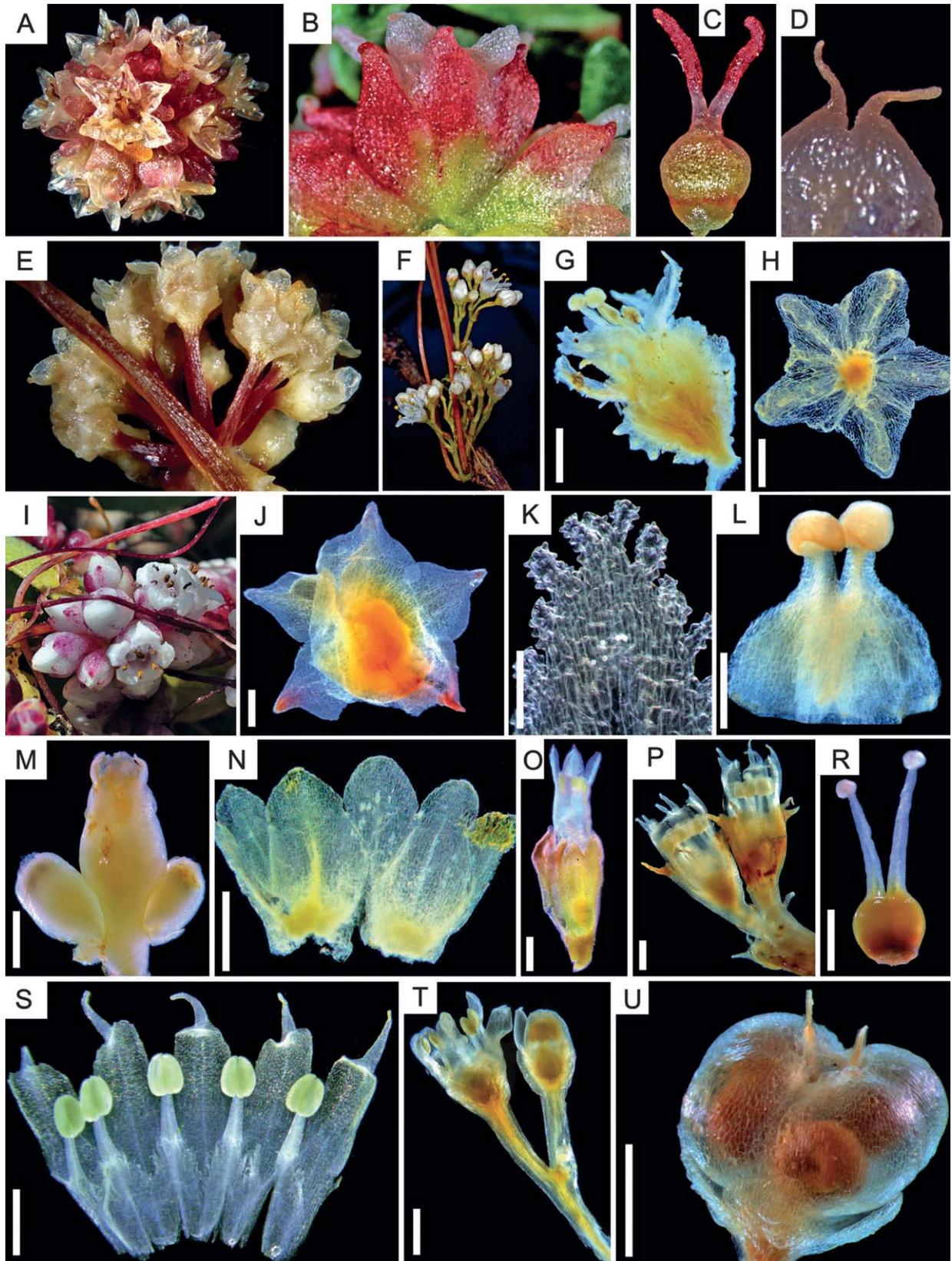


FIG. 3. Examples of morphological characteristics of *Cuscuta* sections. A–C. Sect. *Cuscuta*. A. inflorescence, *C. approximata* subsp. *macranthera*. B. Flower, *C. epithymum* subsp. *kotschyi*. C. gynoecium, *C. epithymum* subsp. *epithymum*. D. Sect. *Epistigma*, gynoecium, *C. kotschyana*. E. Sect. *Babylonicae*, inflorescence, *C. babylonica*. F. Subg. *Pachystigma*, inflorescence, *C. africana*. G–H. Sect. *Grammica*. G. Flower, *C. alata*. H. Dissected calyx, *C. chinensis* subsp. *chinensis*. I–L. Sect. *Subulatae*. I. Inflorescence/flowers, *C. purpurata*. J. Dissected calyx, *C. foetida*. K. Papillate infrastaminal scale fimbriae, *C. rubella*. L. Gynoecium, *C. odorata*. M–N. Sect. *Obtusilobae*. M. flower, *C. americana*. N. Dissected calyx, *C. americana*. O. Sect. *Prismaticae*, flower, *C. prismatica*. P–S. Sect. *Ceratophorae*. P. Flowers, *C. boldinghii*. R. Gynoecium, *C. boldinghii*. S. Dissected corolla, *C. boldinghii*. T–U. Sect. *Umbellatae*. T. Inflorescence fragment, *C. umbellata*. U. Capsule, *C. umbellata*. Scale bars = 1 mm.

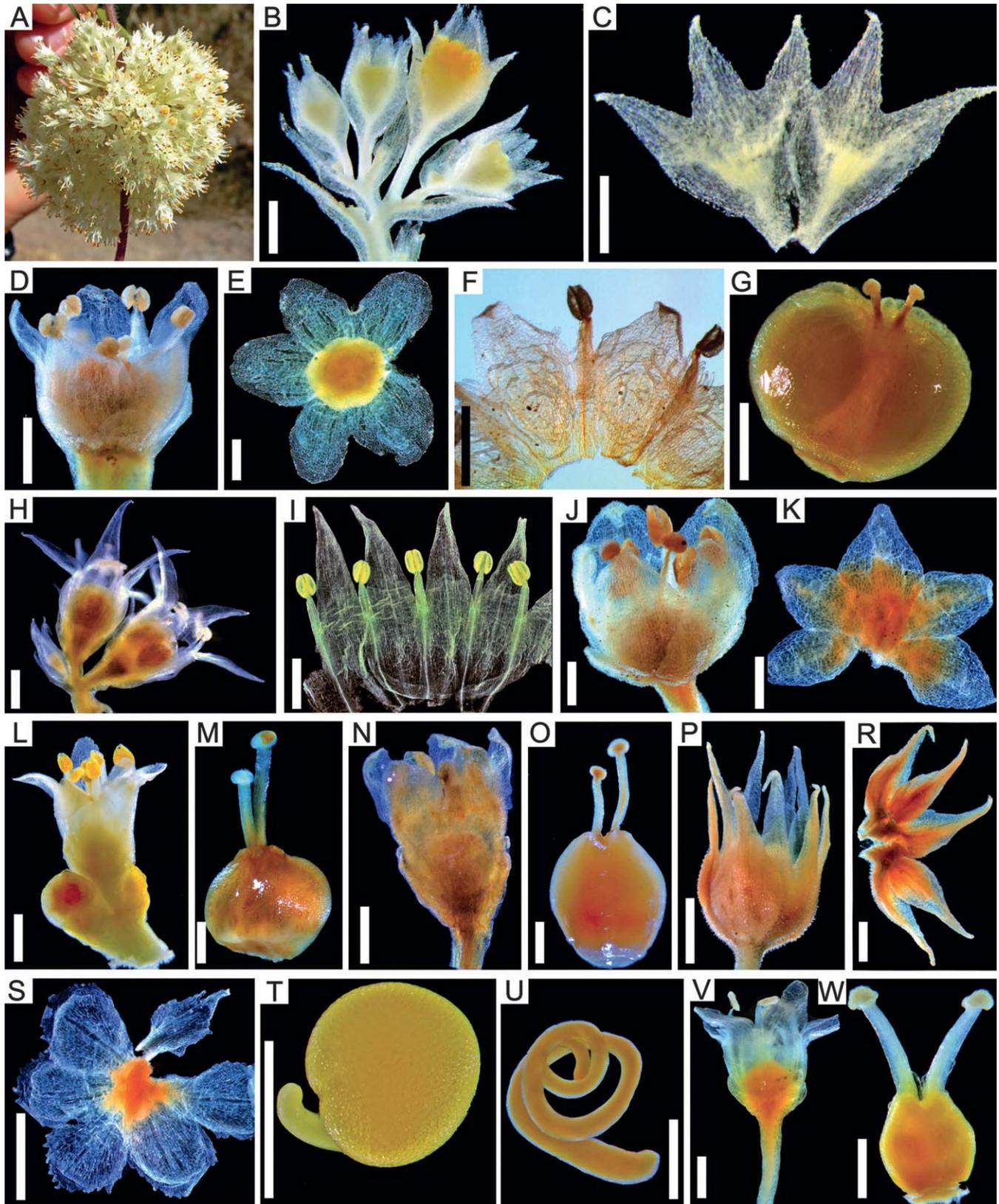


FIG. 4. Examples of morphological characteristics of *Cuscuta* sections. A–C. Sect. *Gracillimae*. A. Inflorescence, *C. gracillima*. B. Flowers, *C. gracillima*. C. Dissected calyx, *C. gracillima*. D–G. Sect. *Cleistogrammica*. D. Flower, *C. obtusiflora*. E. Dissected calyx, *C. obtusiflora*. F. Dissected corolla, *C. campestris*. G. Capsule, *C. campestris*. H–I. Sect. *Californicae*. H. Flowers, *C. californica*. I. Dissected corolla, *C. californica*. J–K. Sect. *Indecorae*. J. Flower, *C. indecora* var. *indecora*. K. Dissected calyx, *C. indecora*. L–M. Sect. *Oxycarpae*. L. Flower, *C. gronovii* var. *gronovii*. M. Capsule, *C. gronovii* var. *gronovii*. N–O. Sect. *Racemosae*. N. Flower, *C. racemosa*. O. Capsule, *C. racemosa*. P–R. Sect. *Partitae*. P. Flower, *C. burrellii*. R. Dissected calyx, *C. burrellii*. S–T. Sect. *Denticulatae*. S. Dissected calyx, *C. denticulata*. T. Embryo, *C. denticulata*; U–W. Sect. *Lobostigmae*; U, 'typical' *Cuscuta* embryo included as a comparison for sect. *Denticulatae*, *C. woodsonii*. V. Flower, *C. tasmanica*. W. Gynoecium, *C. tasmanica*. Scale bars = 1 mm.

How Many Species of Cuscuta are Known to Exist?—Yuncker (1932) included 158 species in his monograph. Subsequent overview works commonly mentioned “about 150” species even if more species were described after 1932 (e.g. many included in Hunziker 1949, 1950; Yuncker 1965). It is unclear why GBIF (2014), EOL (2014), and the many sources following them, report a vague 100–170 number of species for this genus. Similarly, The Plant List (2014) included 127 *Cuscuta* species

with “medium confidence” and 77 with “low confidence” (not even a single binomial has “high confidence” according to this source). This level of uncertainty is unacceptable in the case of *Cuscuta*, which unlike other genera has received a lot of attention from a systematic point of view, both past and present. To eliminate any ambiguity, we emphasize that we accepted 194 species, with more likely to be discovered in the future. In order to be useful, biodiversity lists must be based on systematics.

TAXONOMIC TREATMENT

KEY TO THE SUBGENERA OF *CUSCUTA*

1. Gynoecium with 1 style, sometimes distally bifid; fimbriae of infrastaminal scales are glandular trichomes with the secretory cells completely exposed I. Subg. *Monogynella*
1. Gynoecium with 2 styles; fimbriae of infrastaminal scales with secretory cells [internal laticifers(s)] protected by an epidermis 2
2. Stigmas elongate: conical, cylindrical, terete or clavate 3
2. Stigmas capitate IV. Subg. *Grammica*
 3. Stigmas ± as thick as the styles II. Subg. *Cuscuta*
 3. Stigmas thicker than the styles III. Subg. *Pachystigma*

Cuscuta L., Sp. Pl.: 124. 1753.—TYPE: *Cuscuta europaea* L. (N. L. Britton et A. Brown, Ill. Fl. N. U. S. ed. 2. 3: 48. 1913; Hitchcock, Prop. Brit. Bot. 126. 1929). *Cassytha* S. F. Gray, Nat. Arr. Brit. Pl. 2: 345. 1821, nom. illeg. non L., 1753.

Hemi- to holoparasitic herbs, annual or perennating through haustorial tissue left inside the host. Stems filiform, greenish, yellow, orange, or purple, trailing or dextrorsely twining and attached to the host by numerous small haustoria. Leaves rudimentary, alternate, scales. Inflorescence units monochazial cymes further grouped in thyrses or cymose inflorescences. Flowers bisexual, radial, (3–)4–5-merous, more or less fleshy, white, white-creamy, sometimes yellow or pink to purple; laticifers commonly present in all the flower organs, isolated or articulated, conspicuous or not; calyx and corolla gamopetalous; stamens alternating with the corolla lobes, anthers longitudinally dehiscent; pollen heteromorphic, commonly 3-zonocolpate (sometimes 5–12-zonocolpate), exine imperforate, perforate, microreticulate or reticulate; infrastaminal scales with secretory role usually present, scale-like appendages alternating with the corolla lobes, variously fimbriate, fused at the base and adnate with the base of the corolla tube; ovary superior, 2-locular, each locule with 2 anatropous ovules; styles 1 or 2, terminal, stigmas capitate to linear. Fruits capsules, circumscissile by a ± regular line near the base, irregularly dehiscent or indehiscent. Seeds 1–4 per capsule; hilum terminal or subterminal; endosperm nuclear; embryo uniformly slender, without cotyledons, 1–3-coiled, rarely globose-enlarged.

I. CUSCUTA SUBG. MONOGYNELLA (Des Moul.) Peter, Engl. & Prantl, Nat. Pflanzenfam. 4(3): 38. 1891. *Monogynella* Des Moul., Étud. Cuscut. 65. 1853. *Cuscuta* [“Group”] *Monogynella* Engelm., Trans. Acad. Sci. St. Louis 1: 460. 1859, nom. inval. *Cuscuta* subg. *Monogynella* (Engelm.) Yunck., Mem. Torrey Bot. Club 18: 248. 1932, comb. superfl.—TYPE: *Monogynella vahliana* (Vahl.) Des Moul. (*Cuscuta monogyna* Vahl). Peter made no reference to Des Moulins’s *Monogynella* but indicated that the taxonomic arrangement follows Engelmann. Since Engelmann stated that his “Group” *Monogynella* is based on Des Moulins’s (genus) *Monogynella*, the basionym can be attributed unequivocally to Des Moulins. Figures 2A–B, G.

Aplostylis Raf., Fl. Tellur. 4: 91. 1838.—TYPE: *Aplostylis lupuliformis* (Krock.) Raf. (≡ *Cuscuta lupuliformis* Krock.).

Kadurias Raf., Fl. Tellur. 4: 91. 1838.—TYPE: *Kadurias reflexa* (Roxb.) Raf. (≡ *Cuscuta reflexa* Roxb.).

Cuscuta sect. *Callianche* Engelm., Trans. Acad. Sci. St. Louis 1: 518. 1859.—TYPE: *Cuscuta reflexa* Roxb.

Cuscuta sect. *Monostylos* Maxim., Prim. Fl. Amur.: 200. 1859.—TYPE: *Cuscuta systyla* Maxim. (= *Cuscuta lupuliformis* Krock.).

Inflorescences ± loose thyrses: spiciform, racemiform or paniculiform; bracts 1 at the base of cymes, 0–2 at the base of- and sometimes on the pedicels; pedicels absent to 10 mm long; infrastaminal scale fimbriae are glandular hairs with the secretory cells entirely exposed; pollen 25–37.2 μm long, 3–6(7)-colpate, tectum microreticulate to reticulate (exception: imperforate in *C. monogyna*); style 1, sometimes distally bifid; stigmas variable: globose, depressed-globose, flattened, ellipsoid, ovoid, obovoid, rectangle-shaped or conical. Capsules circumscissile dehiscent, interstylar aperture absent. Seeds dorso-ventrally compressed, with seed coat cells ± rectangular and puzzle-like arranged, not alveolate/papillatae. Chromosome numbers: $2n = 28, 30, 32, 42, 48$ (Vasudevan 1975; Kaul and Bhan 1977; Pazy and Plitmann 1995; García and Castroviejo 2003).

Note—Molecular data indicate that the recognition of sections in subg. *Monogynella* is unwarranted. Although *Monogynella* has relatively few species (see below), the diversity of its flower morphology is comparable with that of the much larger subg. *Grammica* (e.g. for pollen, Welsh et al. 2010; gynoecium, Wright et al. 2012; and infrastaminal scales, Riviere et al. 2013). This suggests that *Monogynella* species have experienced a high degree of transgressive segregation at the same time with the adaptive radiation that followed the evolution to parasitism in *Cuscuta*.

Included species—This section includes 15 species: *C. bucharica** Palib. ex Fedschenko, *C. cassytoidea* Nees, *C. convallariiflora** Pavlov, *C. engelmannii** Korsh, *C. exaltata* Engelm., *C. japonica* Choisy, *C. gigantea* Griff., *C. lehmanniana* Bunge, *C. lophosepala** Butkov, *C. lupuliformis* Krock., *C. macrolepis* R. C. Fang & S. H. Huang*, *C. monogyna* Vahl, *C. pamirica** Butkov, *C. reflexa*

Roxb., and *C. violacea* Rajput & Syeda. *Cuscuta chittagongensis* Sengupta, M. Salar Khan & Huq described from Bangladesh (Sengupta et al. 1983) is a teratological form of *C. reflexa*. The most recent species described in this subgenus, *Monogynella tiricensis* (Chrtek 1997) from North Pakistan, appears to be closely related to *C. gigantea* Griff. In general, further research is necessary to test species limits and reveal evolutionary relationships within subg. *Monogynella*.

Distribution—Most species of subg. *Monogynella* are Eurasian; however, *C. cassytoides* is African and Southeastern Asian, while *C. exaltata* is North American. *Cuscuta japonica* and *C. reflexa* have been introduced recently elsewhere through seeds used in traditional medicinal products imported from Asia.

II. CUSCUTA SUBG. CUSCUTA. *Cuscuta* ["Group"] *Cuscuta* Engelm., Trans. Acad. Sci. St. Louis 1: 459. 1859, nom. inval. *Cuscuta* subg. *Genuina* Hunz., Revista Fac. Ci. Exact. 13 (1): 239. 1950, nom. inval.—TYPE: *Cuscuta europaea* L.

Lepimenes Raf., Fl. Tellur. 4: 91. 1838.—TYPE: *Lepimenes epithimum* Raf. (= ?*Cuscuta europaea* L.)

Epilinella Pfeiff., Bot. Zeit. 3: 673. 1845.—TYPE: *Epilinella cuscutoides* Pfeiff. (≡ *Cuscuta epilinum* Weihe).

Epithimum Opiz, Sezman: 40. 1853.—TYPE: *Epithimum cuscutoides* Opiz (≡ *Cuscuta epithimum* (L.) L.).

Succuta Des Moul., Étud. Cuscut.: 74. 1853. *Cuscuta* subg. *Succuta* (Des Moul.) Yunck., Ill. Biol. Monogr. 6: 111. 1921.—TYPE: *Succuta alba* (C. Presl.) Des Moul. (= *Cuscuta epithimum* (L.) L.).

Inflorescences dense, glomerulate; bracts 1 at the base of the inflorescences, usually absent at the base of pedicels; pedicels absent to 4.0 mm long; infrastaminal scales fimbriae with internal laticifer(s); pollen grains 18–27 μm long, 3(12)-colpate, tectum imperforate (rarely perforate); styles 2, ± equal or stigmas sessile (lacking styles); stigmas cylindrical, terete or clavate, ± of the same thickness as the styles; capsules irregularly or circumscissile dehiscent or indehiscent; interstylar aperture small or inconspicuous; seeds angled to subglobose, seed coat cells alveolate when dry and papillose when hydrated. Chromosome numbers: $2n = 8, 10, 14, 16, 18, 20, 26, 28, 30, 32, 36, 42$ (Pazy and Plitmann 1995; García and Castroviejo 2003). Figure 2C.

Subgenus *Cuscuta* includes 21 species (see sections below).

KEY TO THE SECTIONS OF CUSCUTA SUBG. CUSCUTA

1. Styles absent or stigmas on short apical ovary projections (rostrum) Sect. *Epistigma*
1. Styles present 2
 2. Calyx not truncated, with well-developed lobes more than 0.5 mm long Sect. *Cuscuta*
 2. Calyx truncated, without lobes or reduced to a short mucro up to 0.5 mm long Sect. *Babylonicae*

1. CUSCUTA SECT. CUSCUTA. *Cuscuta* sect. *Eucuscuta* Engelm., Trans. Acad. Sci. St. Louis 1: 460. 1859, nom. inval. *Cuscuta* subsect. *Leptostylae* Rouy, Fl. France 10: 355. 1908, nom. inval. *Cuscuta* subsect. *Europaeae* Yunck., Mem. Torrey Bot. Club 18: 274. 1932, nom. inval.—TYPE: *Cuscuta europaea* L.

Cuscuta subsect. *Eu epilinella* Rouy, Fl. France 10: 354. 1908, nom. inval.—TYPE.—*Epilinella cuscutoides* Pfeiff. (≡ *Cuscuta epilinum* Weihe.)

Cuscuta subsect. *Planiflorae* Yunck., Mem. Torrey Bot. Club 18: 280. 1932.—TYPE: *Cuscuta planiflora* Ten.

Inflorescence a dense or umbellate glomerule, with a single basal bract, generally with more than 2 flowers. Flowers 1.4–5.0 mm long, sessile or on pedicels up to 4.0 mm long; calyx cupulate to urceolate, shorter to longer than the corolla tube, divided 1/4 to nearly to the base, lobes broadly ovate to obovate, occasionally somewhat keeled, margins entire, apex subulate to obtuse or with a terminal or subterminal multicellular conical or subconical protuberance; corolla campanulate, tubular or urceolate, lobes shorter to longer than the tube, from broadly ovate to obovate, margins entire, apex subulate to obtuse, sometimes cucullate or with a terminal or subterminal multicellular conical or subconical protuberance; infrastaminal scales present, shorter to longer than corolla tube; pollen grains 3-colpate to 12-pantocolpate, 18–27 μm long, tectum imperforate (rarely perforate); styles cylindrical or somewhat subulate; stigmas cylindrical, terete or clavate, ± of the same thickness as the styles. Capsule circumscissile dehiscent (indehiscent in *C. triumvirati*) globose to globose-depressed with a small to intermediate interstylar aperture. Figures 3A–C.

Note—Yuncker (1932) divided sect. *Cuscuta* in three subsections: *Babylonicae*, “*Europaeae*” and *Planiflorae*. Whereas subsect. *Babylonicae* is accepted here as a different monotypic section (see below), *Europaeae* and *Planiflorae* are not recognised because they were based on highly homoplasious characters. The phylogeny of García and Martín (2007) showed that neither of the latter subsections was monophyletic, but three major clades were resolved for species of sect. *Cuscuta*. One of them included species distributed in Tropical Africa and SW of the Arabian Peninsula. A second clade included *C. europaea*, *C. approximata*, and *C. balansae*, and the rest of the species formed the third monophyletic group. The relationships between and within these three groups are discussed in García and Martín (2007) and more detailed revisions of particular groups within subg. *Cuscuta* can be found in García (1998, 1999, 2001).

Included Species—Section *Cuscuta* includes 15 species: *C. abyssinica* A. Rich., *C. approximata* Bab., *C. balansae* Boiss. & Reut., *C. castroviejoii* M. A. García, *C. epilinum* Weihe, *C. epithimum* (L.) L., *C. europaea* L., *C. nivea* M. A. García, *C. palaestina* Boiss., *C. planiflora* Ten., *C. pretoriana* Yunck., *C. rausii* M. A. García, *C. rhodesiana* Yunck., *C. somaliensis* Yunck., *C. triumvirati* Lange. *Cuscuta mesatlantica* Dobignard described from Morocco (Dobignard 2009) also belongs to this section but we could not examine the type or other specimens to confirm its validity. According to the description it may be a synonym of *C. epithimum* or *C. approximata*. Other species that have been recognized in local taxonomic treatments of the genus (e.g. Butkov 1953; Feinbrun 1972; Plitmann 1978) are here considered as synonyms. More detailed studies, however, may suggest the recognition of *C. pellucida* Butkov, *C. kurdica* Engelm., and *C. maroccana* Trab., which we considered synonyms of *C. planiflora*,

C. europaea, and *C. epithymum*, respectively. *Cuscuta obtusata* Engelm. and *C. letourneuxii* Trab., species accepted by Yuncker (1932), are known only from the type collections and lack clear distinctive morphological characters.

Distribution—Section *Cuscuta* evolved in Europe, Africa, and Asia, except the South East and Indian subcontinent. Species such as *C. approximata*, *C. epithymum*, and *C. planiflora* have been introduced and naturalized in the Americas, Australia, and New Zealand.

2. *CUSCUTA* SECT. *EPISTIGMA* Engelm., Trans. Acad. Sci. St. Louis 1: 471. 1859.—TYPE: *Cuscuta pedicellata* Ledeb., here designated.

Cuscuta sect. *Clistococca* Engelm., Trans. Acad. Sci. St. Louis 1: 473. 1859.—TYPE: *Cuscuta capitata* Roxb.

Inflorescence in a more or less dense or umbellate glomerule, with a single basal bract, generally with more than 2 flowers. Flowers 2.0–5.5(–6.5) mm long, sessile or on pedicels up to 5.0 mm long; calyx rotate or campanulate to urceolate, shorter to longer than the corolla tube, entire or divided 2/3 to the base, lobes broadly ovate to triangular or absent (calyx truncate in *C. haussknechtii*), somewhat keeled and fleshy to the apex, margins entire or slightly denticulate, apex subulate to obtuse; corolla campanulate, tubular or urceolate, lobes shorter to longer than the tube, from broadly ovate to obovate, margins entire, apex subulate to obtuse; infrastaminal scales present, shorter to longer than corolla tube; pollen data not available; styles lacking; stigmas cylindrical or subulate. Capsule irregularly dehiscent (indehiscent in *C. capitata*) globose to globose-depressed with a small to intermediate interstylar aperture. Figure 3D.

Note—This section includes *C. capitata*, which Engelm. (1859) and Yuncker (1932) included in a monotypic section, *Clistococca*, based on its indehiscent fruits. Fruit dehiscence is highly homoplastic in *Cuscuta* and indehiscent fruits are also present in other species of the type subgenus, such as in *C. triumvirati*. At a superficial examination, the styles of *C. capitata* appear developed but their conical morphology, together with the pyriform shape of the ovary indicate that they are apical projections of the ovary (rostrum) rather than true styles. Moreover, a similar morphology of the upper part of the ovary is present in other species traditionally included in sect. *Epistigma*, such as *C. pedicellata* or *C. kotschyana*. Given the topology of the phylogenetic trees obtained by García and Martín (2007) and García et al. (2014) we consider *C. capitata* as a member of sect. *Epistigma*.

Included Species—Section *Epistigma* includes five species: *C. capitata* Roxb., *C. haussknechtii* Yunck., *C. kotschyana* Boiss., *C. pedicellata* Ledeb., *C. pulchella* Engelm.

Distribution—Section *Epistigma* is distributed in Central and Southwest Asia, as well as in Northeast Africa.

3. *Cuscuta* sect. *Babylonicae* (Yunck.) M. A. García, stat. nov.
Cuscuta subsect. *Babylonicae* Yunck., Mem. Torrey Bot. Club 18: 273. 1932.—TYPE: *Cuscuta babylonica* Aucher ex Choisy.

Inflorescence a loose umbellate glomerule, with a single basal bract, generally with 1–4 (–15) flowers. Flowers 2.5–3.5 mm long, on pedicels up to 7 mm long; calyx obconic or campanulate, shorter or as long as the corolla tube, truncated and entire, lobes absent or reduced to acute and erect-spreading projections up to 0.5 mm long; corolla tubular

or campanulate in anthesis and urceolate in fruit, lobes about as long as the tube, ovate to oblong, obtuse, margins entire; infrastaminal scales present, shorter than corolla tube, with very short or almost absent fimbriae; pollen grains 3(4)-colpate, 17–19 μm long, tectum imperforate; styles cylindrical or somewhat subulate; stigmas long subulate or subcylindrical, \pm of the same thickness as the styles. Capsule irregularly dehiscent, subglobose to globose-depressed with a small to intermediate interstylar aperture. Figure 3E.

Note—The ITS phylogeny obtained by García and Martín (2007) placed *C. babylonica* sister to the species of sect. *Epistigma*. This relationship was not resolved in the *trnL* intron phylogeny in the same study but the forced topology of this species as sister to the species of sect. *Cuscuta* was not rejected by a Shimodaira-Hasegawa test (García and Martín 2007). Some characters, such as the development of the first buds of the glomerules into floral branches instead of flowers and the fruit dehiscent by an irregular line, suggest a relationship of this species with sect. *Epistigma*. However, the developed styles which characterize sect. *Cuscuta* bring *C. babylonica* closer to this latter group of species. Its characteristic morphology and the unclear phylogenetic relationships are the reasons to propose a monotypic section for this species. *Cuscuta babylonica* has the lowest chromosome number known in the genus ($2n = 8$) and the longest chromosomes known in subg. *Cuscuta* (up to 8 μm ; Pazy and Plitmann 1987).

Included Species—Sect. *Babylonicae* is monotypic including only *C. babylonica* Aucher ex Choisy.

Distribution—*Cuscuta babylonica* is distributed in Central and West Asia but more common in Iraq.

III. *CUSCUTA* SUBGEN. *PACHYSTIGMA* (Engelm.) Baker & C. H. Wright, Thiselton-Dyer (ed.), Fl. Cap. 4(2): 84. 1904.
Cuscuta sect. *Pachystigma* Engelm., Trans. Acad. Sci. St. Louis 1: 474. 1859. *Cuscuta* subsect. *Africanae* Yunck., Mem. Torrey Bot. Club 18: 263. 1932.—TYPE: *Cuscuta africana* Willd. *Cuscuta* subsect. *Cucullatae* Yunck., Mem. Torrey Bot. Club 18: 263. 1932.—TYPE: *Cuscuta cucullata* Yunck. (= *Cuscuta gerrardii* Baker).

Inflorescence \pm loose paniculiform, bracts 1 at the base of clusters, 1 at the base of pedicels; pedicels to 8 mm long; infrastaminal scales fimbriae with internal laticifer(s); pollen grains 3(4)-colpate, 22–30 μm long, tectum imperforate to perforate; styles 2, equal or slightly unequal, cylindrical, oblong or conical, thicker than the styles. Capsules circumscissile, interstylar aperture inconspicuous; seed coat cells commonly alveolate when dried and papillose when hydrated. Figures 2D, 3F.

Note—Although *Pachystigma* was proposed as a subgenus by Baker and Wright (1904) more than a century ago, this is the first time it is accepted (see Introduction). No morphological characters have been found to further divide this small subgenus into different sections. The tree topologies obtained by García et al. (2014) also indicate that the recognition of sections in subg. *Pachystigma* is unnecessary. Yuncker (1932) recognized the monotypic subsect. *Cucullatae* based on the indehiscent fruits of *C. cucullata*. Yuncker mentioned that *C. gerrardii* may also belong to that subsection. After studying the types and a few more recent collections we consider that *C. cucullata* and *C. gerrardii* are conspecific.

Included Species—Subgenus *Pachystigma* includes five species: *C. africana* Willd., *C. angulata* Engelm., *C. gerrardii* Baker, *C. natalensis* Baker, *C. nitida* E. Mey. ex Choisy.

Distribution—Subgenus *Pachystigma* is confined to South Africa and it is more common in the coastal regions of Western Cape, Eastern Cape, and Natal provinces. *Cuscuta gerrardii* also occurs in Swaziland.

IV. CUSCUTA SUBG. GRAMMICA (Lour.) Peter, Engl. & Prantl, Nat. Pflanzenfam. 4(3): 38. 1891. *Grammica* Lour. Fl. Cochinch. 170. 1790 ["Grmmica"].—TYPE: *Grammica aphylla* Lour. (= *Cuscuta chinensis* Lam.).

Anthanema Raf., Fl. Tellur. 4: 90. 1838.—TYPE: *Anthanema paradoxa* (Raf.) Raf. (= *Cuscuta paradoxa* Raf.; designated by Manitz 1976)

Dactylepis Raf. Fl. Tellur. 4: 125. 1838.—TYPE: *Dactylepis brownei* Raf. (= ?*Cuscuta americana* L.; Yuncker 1932)

Eronema Raf. Fl. Tellur. 4: 125. 1838.—TYPE: *Eronema robinsoni* Raf. (= ?*Cuscuta americana* L.; Yuncker 1932)

Kadula Raf., Fl. Tellur. 4: 90. 1838.—TYPE: *Kadula corymbosa* (Ruiz & Pav.) Raf. (= *Cuscuta corymbosa* Ruiz & Pav.).

Nemepis Raf., Fl. Tellur. 4: 91. 1838.—TYPE: *Nemepis odorata* (Ruiz & Pav.) Raf. (= *Cuscuta odorata* Ruiz & Pav., designated by Manitz 1976)

Pentake Raf., Fl. Tellur. 4: 90. 1838.—TYPE: *Pentake chinensis* (Lam.) Raf. (= *Cuscuta chinensis* Lam.).

Lepidanche Engelm., Amer. J. Sci. Arts 43: 343. 1842.—TYPE: *Lepidanche compositarum* Engelm. (= *Cuscuta glomerata* Choisy).

Engelmannia Pfeiff., Bot. Zeitung (Berlin) 3: 673. 1845.—TYPE: *Engelmannia migrans* Pfeiff. (= *Cuscuta suaveolens* Ser.).

Cuscutina Pfeiff., Bot. Zeitung (Berlin) 4: 492. 1846.—TYPE: *Cuscutina suaveolens* Pfeiff. (= *Cuscuta suaveolens* Ser.). Also proposed as a substitute name for *Engelmannia*.

Pfeifferia Buching. in Ann. Sci. Nat., Bot., sér. 3, 5: 88. 1846.—TYPE: *Pfeifferia suaveolens* Buching. (= *Cuscuta suaveolens* Ser.).

Buchingera F. W. Schultz, Jahrb. Pract. Pharm. Verwandte Fächer 14: 170. 1847.—TYPE: *Buchingera suaveolens* F.W. Schultz. (= *Cuscuta suaveolens* Ser.). *Buchingera* was proposed as a substitute name both for *Engelmannia* Pfeiff. 1845, non A. Gray ex Nuttall 1840 (Asteraceae) and for *Pfeifferia* J. D. Buchinger 1846, non *Pfeifferia* Salm-Dyck 1845 (Cactaceae).

Cuscuta ["Group"] *Grammica* Engelm., Trans. Acad. Sci. St Louis 1(3): 459. 1859, nom. inval.

Inflorescences dense to loose, glomerulate, paniculiform, umbelliform, corymbiform, fasciculate or racemiform; bracts 1–3 at the base of the clusters, 0–10 at the base of and on the pedicels; pedicels absent to 12 mm; infrastaminal scales fimbriae with internal laticifer(s), very variable, sometimes entirely reduced; pollen grains 13–30 μ m long, 3(4)-colpate, tectum imperforate, perforate, microreticulate (7–8-colpate and reticulate in some species of sect. *Subulatae*); styles 2, \pm unequal; stigmas capitate (globose, depressed, flattened or ellipsoid); capsules circumscissile dehiscent or indehiscent; interstylar aperture inconspicuous to large; seeds globose to ovoid, angled or dorsoventrally compressed; seed coat cells commonly alveolate when dried and papillose when hydrated. Chromosome numbers: $2n = 28, 30, 32, 38, 44, 56, 60$ (Fogelberg 1938; Pazy and Plitmann 1995; García and Castroviejo 2003). Figures 2E–F, H.

Subgenus *Grammica* includes 153 species (see sections below).

KEY TO THE SECTIONS OF SUBGENUS GRAMMICA

1. Embryo spherically enlarged Sect. *Denticulatae*
1. Embryo filiform, not spherically enlarged 2
2. Styles thick, 0.3–0.9 mm in diameter, cylindrical or subulate; pollen grains with microreticulate or reticulate exine (exceptions with imperforate or tectum perforate are possible); stigmas large (0.25–0.6 mm in diameter) and/or lobed 3
3. Calyx and/or corolla lobes with conical or cylindrical subterminal, dorsal multicellular appendages Sect. *Ceratophorae*
3. Corolla lobes without conical or cylindrical appendages; when appendages are present on the calyx, they are crest-like along the midvein/carena of lobes 4
4. Fimbriae of infrastaminal scales often papillatae; S America (2 sp. in Africa) Sect. *Subulatae*
4. Fimbriae of infrastaminal scales not papillatae; N America (2 sp. in Australia) Sect. *Lobostigmae*
2. Styles thin, 0.1–0.2 mm in diameter, cylindrical; pollen grains with perforate or imperforate tectum; stigmas small (0.1–0.25 mm in diameter), not lobed 5
5. Flowers elongated; calyx and corolla divided ca. 1/4 the length 6
6. Calyx cylindrical viewed in cross-section; infrastaminal scales 3/4 to equalling corolla tube Sect. *Obtusilobae*
6. Calyx pentagonal viewed in cross-section; infrastaminal scales 1/2 of the corolla tube Sect. *Prismaticae*
5. Flowers more or less spherical or wider than long; calyx and corolla divided 1/2 to the base (if flowers are elongated, calyx and corolla are deeply divided) 7
7. Capsules dehiscent [indehiscent in *C. vandevenderi*, *C. columbiana* (sect. *Gracillimae*), *C. acuta*, and *C. membranacea* (sect. *Umbellatae*); *C. yucatanana* (sect. *Grammica*)] 8
8. Inflorescence glomerulate (umbellate in *C. yucatanana* but fruit indehiscent) Sect. *Grammica*
8. Inflorescences umbellate or corymbiform (glomerulate in *C. punana*, sect. *Gracillimae*; *C. odontolepis*, sect. *Umbellatae*). 9
9. Stems disappear at flowering time and inflorescences seem to emerge from the host's stems Sect. *Gracillimae*
9. Some stems persist at flowering time and bear inflorescences Sect. *Umbellatae*
7. Capsule indehiscent (dehiscent in *C. partita* of sect. *Partitae*) 10
10. Calyx lobes acute 11
11. Flowers with numerous bracts Sect. *Oxycarpae* (in part)
11. Flowers with 0–1 bracts 12
12. Corolla lobes inflexed Sect. *Indecorae*
12. Corolla lobes straight 13
13. Calyx divided nearly to the base; S America Sect. *Partitae*
13. Calyx divided 1/2–2/3; Western N America Sect. *Californicae*

10. Calyx lobes obtuse or rounded 14
 14. Inflorescence glomerulate; corolla lobes inflexed; capsule depressed-globose,
 not narrowed distally, with conspicuous interstyler aperture Sect. *Cleistogrammica*
 14. Inflorescence paniculiform; corolla lobes straight; capsule globose narrowed
 or thickened apically; interstyler aperture inconspicuous 15
 15. North America Sect. *Oxycarpae* (in part)
 15. South America Sect. *Racemosae*

4. *CUSCUTA* SECT. *GRAMMICA*. *Cuscuta* sect. "*Eugrammica*" Engelm., Trans. Acad. Sci. St. Louis 1: 476. 1859, in part, nom. inval.—TYPE: *Grammica aphylla* Lour. (= *Cuscuta chinensis* Lam.).

Cuscuta subsect. *Obtusilobae* Engelm., Trans. Acad. Sci. St. Louis 1: 476. 1859, in part.—TYPE: *Cuscuta americana* L., here designated.

Cuscuta subsect. *Tinctoriae* Yunck., Mem. Torrey Bot. Club 18: 208. 1932, in part (only *C. chinensis* Lam.).—TYPE: *Cuscuta tinctora* Mart.

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part (*C. dentatasquamata* Yunck., *C. potosina* W. Schaffn. ex Engelm.).—TYPE: *Cuscuta odontolepis* Engelm.

Cuscuta subsect. *Acutae* Yunck., Mem. Torrey Bot. Club 18: 152. 1932, in part (*C. palustris* Yunck. and *C. yucatanana* Yunck.).—TYPE: *Cuscuta acuta* Engelm.

Inflorescence glomerulate (umbellate in *C. yucatanana*). Flowers 1.5–4 mm long; calyx cupulate, ca. as long as the corolla tube, divided 1/2–2/3 to the base, lobes broadly triangular-ovate, carinate or with stomatiferous multicellular protuberances along mid-veins, margins entire, apex acute to ± obtuse; corolla campanulate; lobes equaling the tube, apex acute to ± obtuse, not inflexed; infrastaminal scales present, equaling or longer than corolla tube; pollen grains 3(4)-colpate, tectum imperforate; styles cylindrical, thin (0.1–0.2 mm in diameter); stigmas globose (0.1–0.25 mm in diameter). Fruit dehiscent (indehiscent in *C. yucatanana*) globose to globose-depressed (ovoid in *C. potosina*), with small interstyler aperture. Figures 3G–H.

Note—The composition of this group is essentially new because its species were included by Yuncker (1932, 1965) in three different subsections (Fig. 1): *C. applanata* and *C. chinensis* in subsect. *Tinctoriae*; *C. potosina* in subsect. *Odontolepisae* (both subsections classified in sect. *Eugrammica*; Yuncker 1932), and *C. yucatanana* in subsect. *Acutae* (sect. *Cleistogrammica*; Yuncker 1932). Costea et al. (2011b) added to this clade a new species, *C. azteca*, and reinstated *C. alata*, previously considered synonymous to *C. applanata* (Yuncker 1932, 1965). Moreover, Costea et al. (2011b) found *C. chinensis* and *C. applanata* to represent one single species.

Included Species—Section *Grammica* includes seven species: *C. alata* Brandegee, *C. azteca* Costea & Stefanović, *C. chinensis* Lam., *C. dentatasquamata* Yunck.*, *C. palustris* Yunck.*, *C. potosina* W. Schaffn. ex Engelm., and *C. yucatanana* Yunck.

Distribution—Section *Grammica* is distributed in Southern U. S. A. and Mexico, with *C. chinensis* var. *chinensis* having a disjunct distribution in Australia and Asia, most likely as a result of relatively recent long-distance dispersal (Costea et al. 2011b).

5. *Cuscuta* sect. *Subulatae* (Engelm.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Subulatae* Engelm., Trans. Acad. Sci. St. Louis 1: 476. 1859, in part (all the species

except *C. jalapensis*).—TYPE: *Cuscuta grandiflora* Kunth, here designated. *Cuscuta* subsect. *Grandiflorae* Yunck., Mem. Torrey Bot. Club 18: 183. 1932.—TYPE: *Cuscuta grandiflora* Kunth

Cuscuta subsect. *Odoratae* Yunck., Mem. Torrey Bot. Club 18: 188. 1932.—TYPE: *Cuscuta odorata* Ruiz & Pav.

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part (*C. cockerellii* and *C. hitchcockii*).—TYPE: *Cuscuta odontolepis* Engelm.

Cuscuta subsect. *Acutilobae* Yunck., Mem. Torrey Bot. Club 18: 201. 1932, in part (all spp. except *C. xanthochortos* Mart.).—TYPE: *Cuscuta acutiloba* Engelm.

Cuscuta subsect. *Oxycarpae* Engelm., Acad. Sci. St. Louis 1: 499. 1859, in part (only *C. cristata* Engelm.).—TYPE: *Cuscuta gronovii* Willd., here designated.

Cuscuta subsect. *Platycarpae* Engelm. ex Yunck., Mem. Torrey Bot. Club 18: 124. 1932, in part (only *C. cristata* Engelm.).—TYPE: *Cuscuta obtusiflora* Kunth, here designated.

Cuscuta subsect. *Lepidanchiopsis* Yunck., Ill. Biol. Monogr. 6: 119. 1921, in part (all spp. except *C. strobilacea* Liebm.).—TYPE: *Cuscuta bracteata* Engelm., here designated.

Cuscuta subsect. *Denticulatae* Yunck., Mem. Torrey Bot. Club 18: 170. 1932, in part (only *C. microstyla* Engelm.).—TYPE: *Cuscuta denticulata* Engelm.

Inflorescences glomerulate (fasciculate or umbellate in *C. grandiflora*, *C. argentinana*, *C. friesii*). Flowers are among the largest in subg. *Grammica*, 4–9 mm, often fleshy, thick and sometimes fragrant (exceptions: *C. argentinana* and *C. microstyla* have relatively small flowers, 2–3 mm long); calyx cupulate to campanulate, 1/4 to equaling corolla tube, divided 1/2–2/3, with lobes acute to rounded, overlapping or not; corolla cupulate, globose or cylindrical with lobes acute to rounded; infrastaminal scales diverse (absent in *C. grandiflora*), commonly with papillae on the fimbriae; pollen grains 3(4) or 6–7-colpate, tectum imperforate, perforate, microreticulate, or reticulate; styles cylindrical, thick (0.2–0.9 mm in diameter), stigmas large (0.25–0.6 mm in diameter), usually lobed; fruit dehiscent (indehiscent in *C. cristata*). Figures 3I–L.

Note—*Subulatae* is the largest section of subg. *Grammica* and of *Cuscuta* in general. The group included in Engelmann's view all the species with thick and/or subulate styles regardless of the shape of their calyx/corolla lobes. With the exception of *C. jalapensis* which does not belong to this clade (see section *Lobostigmae*), this is also largely the species composition of clade O that resulted from our phylogenetic studies (Stefanović et al. 2007; García et al. 2014). Yuncker (1932), however, left *C. jalapensis* in subsection *Subulatae* together with several newly described related species with subulate styles from Mexico, which belong to section *Lobostigmae*, and redistributed the species of Engelmann's subsect. *Subulatae* among three new subsections (*Grandiflorae*,

Odoratae, and *Acutilobae*; Fig. 1). Several species with numerous bracts at the base of the flower, a morphological trait that also evolved in the sections *Ceratophorae* and *Obtusilobae*, were grouped by Yuncker (1921) in a new section, *Lepidanchopsis*. *Cuscuta cristata*, which is also a part of sect. *Subulatae*, was included by both Engelm. (1859) and Yuncker (1932) in sect. *Cleistogrammica* because of its indehiscent capsules.

Included Species—Section *Subulatae* includes 29 species and possibly two additional ones that need confirmation (see below): *C. acutiloba* Engelm.*, *C. alatoloba* Yunck.*, *C. argentinana* Yunck., *C. bella* Yunck., *C. boliviana* Yunck., *C. bracteata* Engelm.*, *C. chilensis* Ker Gawl., *C. cockerellii* Yunck., *C. cristata* Engelm., *C. foetida* Kunth, *C. friesii* Yunck., *C. flossdorfii* Hicken, *C. goyaziana* Yunck.*, *C. hitchcockii**, *C. kilimanjari* Oliv., *C. grandiflora* Kunth, *C. globiflora* Engelm., *C. lucidicarpa* Yunck., *C. microstyla* Engelm., *C. odorata* Ruiz & Pav., *C. orbiculata* Yunck., *C. paitana* Yunck., *C. parodiana* Yunck., *C. pycnantha* Benth., *C. purpurata* Phil., *C. rotundiflora* Hunz., *C. rubella* Yunck., *C. serrata* Yunck.*, *C. tucumana* Yunck.*. Based on their morphology, *C. blepharolepis* Welw. ex Hiern*, *C. rustica* Hunz., known only from their types, may also be a part of this clade but we were not as confident about their placement as in the case of the rest of the species.

Distribution—Section *Subulatae* is South American except for *C. kilimanjari* and possibly *C. blepharolepis*, which are African. Biogeographical scenarios of long-distance dispersal in subg. *Grammica* were discussed by García et al. (2014).

6. ***Cuscuta* sect. *Obtusilobae*** (Engelm.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Obtusilobae* Engelm., Trans. Acad. Sci. St. Louis 1: 479. 1859, in part.—TYPE: *Cuscuta americana* L., here designated. *Cuscuta* subsect. *Americanae* Yunck., Mem. Torrey Bot. Club 18: 217. 1932.—TYPE: *Cuscuta americana* L.

Inflorescences glomerulate or dense paniculiform. Flowers 3–7 mm long; calyx cylindrical (round in cross-section), 3/4 to equalling corolla tube, divided ca. 1/4 the length, with rounded lobes; corolla cylindrical, lobes ca. 1/4 of the corolla tube, rounded; infrastaminal scales 3/4 to equaling corolla tube; pollen grains 3(4)-colpate, tectum imperforate (perforate in *C. macrocephala*); styles cylindrical, thin; stigmas small. Fruit dehiscent, globose to ovoid. Figures 3M–N.

Note—Engelm. (1859) circumscribed Subsect. *Obtusilobae* to include many more species; our delimitation approaches his informal (unranked) subgroup of taxa with “elongated flowers”. Yuncker (1932) maintained this core of species as a subsection, *Americanae* (Fig. 1).

Included Species—Section *Obtusilobae* includes four species: *C. americana* L., *C. cozumeliensis* Yunck., *C. globulosa* Benth., and *C. macrocephala* W. Schaffn. ex Yunck.

Distribution—The section is distributed in the U. S. A. (Florida), Mexico, West Indies, Central and South America.

7. ***Cuscuta* sect. *Prismaticae*** (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Prismaticae* Yunck., Mem. Torrey Bot. Club 18: 225. 1932.—TYPE: *Cuscuta prismatica* Pav. ex Choisy.

Inflorescences glomerulate or dense paniculiform. Flowers 4–7 mm long; calyx campanulate-cylindrical, angled (pentagonal in cross-section), 1/2–3/4 of the corolla tube, divided ca. 1/4 of its length, with rounded or acute lobes; corolla cylindrical, lobes ca. 1/4 of the corolla tube, rounded or acute; infrastaminal scales ca. 1/2 of the corolla tube;

pollen grains 3(4)-colpate, tectum imperforate; styles cylindrical, thin; stigmas small. Fruit dehiscent, globose. Figure 3O.

Note—Subsection *Prismaticae* included originally only *C. prismatica* (Yuncker, 1932). We have found that this species is closely related to *C. corymbosa*, not to *C. americana* (Stefanović et al. 2007; García et al. 2014) and its relatives as suggested by both Engelm. (1859) and Yuncker (1932). This section resembles morphologically sect. *Obtusilobae* but differs in the pentagonal calyx (lobes are flat forming the faces of a pentagonal prism) and infrastaminal scales ca. 1/2 the length of the corolla tube.

Included Species—Section *Prismaticae* includes only two species: *C. corymbosa* Ruiz & Pav. and *C. prismatica* Pav. ex Choisy.

Distribution—Members of this section are distributed in Mexico, Central, and South America.

8. ***Cuscuta* sect. *Ceratophorae*** (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Ceratophorae* Yunck., Ill. Biol. Monogr. 6: 116. 1921.—TYPE: *Cuscuta boldinghii* Urban (= *C. ceratophora* Yunck.).

Cuscuta subsect. *Lepidanchopsis* Yunck., Ill. Biol. Monogr. 6: 119. 1921, in part (only *C. strobilacea* Liebm.).—TYPE: *Cuscuta strobilacea* Liebm., here designated.

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part. (*C. costaricensis* Yunck., *C. ortegana* Yunck.).—TYPE: *C. odontolepis* Engelm.

Cuscuta subsect. *Tinctoriae* Yunck., Mem. Torrey Bot. Club 18: 208. 1932, in part (*C. mexicana* Yunck.).—TYPE: *Cuscuta tinctoria* Mart.

Inflorescences glomerulate to corymbiform. Flowers 3–7 mm long; calyx cupulate, campanulate or tubular ca. 1/2 to longer than corolla tube, divided nearly to the base, with entire or variously denticulate lobes; corolla tube campanulate to cylindrical (ovoid to urceolate in *C. carnosa*), lobes acute to rounded. Both calyx and corolla lobes commonly with dorsal, subterminal conical or cylindrical multicellular appendages with stomata (absent on the corolla of *C. carnosa*); infrastaminal scales diverse; pollen grains 3(4)-colpate, tectum imperforate, perforate or microreticulate; gynoecea with thick, subulate or cylindrical styles and large, globose stigmas. Fruit dehiscent. Figures 3P–S.

Note—In the past, subsect. *Ceratophorae* comprised only four species: *C. chapalana*, *C. erosa*, *C. boldinghii*, and *C. blepharolepis* (Yuncker 1921; 1932). *Cuscuta blepharolepis*, known only from its type, could not be sampled for the molecular studies but based on its morphology is more likely to be a member of section *Subulatae*. Our results have shown that four other species, *C. strobilacea*, *C. mexicana*, *C. costaricensis*, and *C. ortegana*, previously included by Yuncker (1932, 1965) in the subsections *Lepidanchopsis*, *Tinctoriae*, and *Odontolepisae*, are also members of sect. *Ceratophorae* (Fig. 1; Stefanović et al. 2007), together with two new species, *C. bonafortunae* and *C. carnosa* (Costea et al. 2011a).

Included Species—Section *Ceratophorae* comprises nine species: *C. boldinghii* Urb., *C. bonafortunae* Costea & I. García, *C. carnosa* Costea and Stefanović, *C. chapalana* Yunck., *C. costaricensis* Yunck., *C. erosa* Yunck., *C. mexicana* Yunck., *C. ortegana* Yunck., and *C. strobilacea* Liebm.

Distribution—The section is distributed in Southern U. S. A., Mexico, West Indies, Central America, and Northern South America.

9. *Cuscuta* sect. *Umbellatae* (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Umbellatae* Yunck., Mem. Torrey Bot. Club 18: 234. 1932, in part (see Note)—TYPE: *Cuscuta umbellata* Kunth.

Cuscuta subsect. *Leptanthae* Yunck., Mem. Torrey Bot. Club 18: 242. 1932.—TYPE: *Cuscuta leptantha* Yunck.

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part (*C. odontolepis* Engelm.).—TYPE: *Cuscuta odontolepis* Engelm.

Cuscuta subsect. *Acutae* Yunck., Mem. Torrey Bot. Club 18: 152. 1932, in part (*C. acuta* Engelm. and *C. membranacea* Yunck.).—TYPE: *Cuscuta acuta* Engelm.

Inflorescences umbelliform or fasciculate. Flowers 2–5 mm long (to 7.5 mm in *C. polyanthemos*); calyx campanulate to cylindrical, 1/4 to equaling the length of the corolla tube, divided 1/3–1/2 the length, with acute lobes; corolla tube campanulate to cylindrical with acute lobes; infrastaminal scales commonly equalling corolla tube (absent in *C. hyalina*); pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit dehiscent (indehiscent in *C. acuta* and *C. membranacea*). Figures 3T–U.

Note—The evolutionary history of this section involved hybridization and long-distance dispersal (Stefanović and Costea 2008; Costea and Stefanović 2010). Section *Umbellatae* includes in our view a part of the former subsect. *Umbellatae* in which Yuncker (1932, 1965) grouped nine species characterized by umbellate inflorescences and dehiscent capsules (*C. umbellata*, *C. deltoidea*, *C. desmouliniana*, *C. fasciculata*, *C. gracillima*, *C. hyalina*, *C. lacerata*, *C. macvaughii*, *C. saccharata*, and *C. serruloba*). Phylogenetic studies indicated a need for radical reorganization of this group. First, *C. gracillima*, *C. sidarum* (= *C. saccharata*), and *C. deltoidea* (= *C. serruloba*) form a separate infrageneric group (see sect. *Gracillimae*; Stefanović et al. 2007; Costea et al. 2008a). Second, five other species previously included in various sections and subsections of subg. *Grammica* are also a part of this clade/section (Stefanović et al. 2007; Costea and Stefanović 2010; Fig. 1). Two of these, *C. acuta* and *C. membranacea*, have indehiscent capsules (previously included in sect. *Eugrammica*, subsect. *Acutae*; Yuncker 1932; Hunziker 1949), while the rest have circumscissile capsules: *C. odontolepis* (formerly in sect. *Eugrammica*, subsect. *Odontolepisae*; Yuncker 1932), *C. tuberculata*, *C. leptantha*, and *C. polyanthemos* (formerly in sect. *Eugrammica*, subsect. *Leptanthae*; Yuncker 1932). Finally, two new species, *C. liliputana* and *C. legitima*, were recently described from southern U. S. A. and Mexico (Stefanović and Costea 2008; Costea and Stefanović 2010). *Cuscuta appendiculata* from South Africa was included by Yuncker (1932) in subsection *Acutae*. To date, in subg. *Grammica*, only the sections *Subulatae* and *Umbellatae* are known to have representatives in Africa. Morphologically, *C. appendiculata* may belong to sect. *Umbellatae* but we could not sample it for the molecular studies. A closer examination of the specimens used by Stefanović et al. (2007) for *C. appendiculata* revealed that they belong to *C. gerrardii* (García et al. 2014).

Included Species—Section *Umbellatae* comprises 13 species: *C. acuta* Engelm., ?*C. appendiculata* Engelm.*, *C. desmouliniana* Yunck., *C. hyalina* Roth, *C. lacerata* Yunck.*, *C. legitima* Costea & Stefanović, *C. leptantha* Engelm., *C. liliputana* Costea & Stefanović, *C. membranacea* Yunck., *C. odontolepis* Engelm.,

C. polyanthemos W. Schaff. ex Yunck., *C. tuberculata* Brandegee, and *C. umbellata* Kunth.

Distribution—Section *Umbellatae* is distributed in Southern U. S. A., Mexico, and West Indies (8 sp.); South America (3 sp.); Asia, East and Southeast Africa (*C. hyalina* and possibly *C. appendiculata*).

10. *Cuscuta* sect. *Gracillimae* Costea & Stefanović, sect. nov.—TYPE: *Cuscuta gracillima* Engelm.

Cuscuta subsect. *Umbellatae* Yunck., Mem. Torrey Bot. Club 18: 234. 1932, in part (see Note).—TYPE: *Cuscuta umbellata* Kunth

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part (only *C. choisiana* Yunck.).—TYPE: *Cuscuta odontolepis* Engelm.

Cuscuta subsect. *Californicae* Yunck., Mem. Torrey Bot. Club 18: 156. 1932 (in part, only *C. insquamata* Yunck.).—TYPE: *Cuscuta californica* Choisy.

Resembling morphologically sect. *Umbellatae* but differing in its stems that disappear at flowering stage when the parasite is often represented only by the spherical umbelliform inflorescences that emerge directly from the host's stem.

Inflorescences umbelliform or corymbiform. Flowers 1.6–5.5 mm long; calyx campanulate to cylindrical, equaling or exceeding the corolla tube, divided 1/3–1/2 the length, lobes acute; corolla tube campanulate to cylindrical with acute lobes; infrastaminal scales equalling or exceeding corolla tube; pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit dehiscent (indehiscent in *C. vandevederi*). Figures 4A–C.

Note—Section *Gracillimae* is a segregate of the former subsect. *Umbellatae* (see above; Yuncker 1932; Costea et al. 2008a). The position of *C. macvaughii* remained unresolved in our phylogeny (García et al. 2014): while the parsimony analysis placed this species as sister to sect. *Gracillimae*, a sister relationship with sect. *Indecorae* was recovered in Bayesian and maximum likelihood trees, however, in all cases with low support (García et al. 2014). Morphologically, this species shares strong affinities with both sections but the morphology of inflorescences brings *C. macvaughii* closer to section *Gracillimae*.

Included Species—Section *Gracillimae* includes nine species: *C. choisiana* Yunck.*, *C. gracillima* Engelm., *C. colombiana* Yunck., *C. deltoidea* Yunck., *C. insquamata* Yunck.*, *C. macvaughii* Yunck., *C. punana* Costea & Stefanović, *C. sidarum* Liebm., *C. vandevederi* Costea & Stefanović.

Distribution—Members of sect. *Gracillimae* are distributed in Mexico, Central, and South America.

11. CUSCUTA SECT. CLEISTOGRAMMICA Engelm. [“Clistogrammica”], Trans. Acad. Sci. St Louis 1: 490. 1859. *Cuscuta* subsect. *Platycarpae* Engelm. ex Yunck., Mem. Torrey Bot. Club 18: 124. 1932, in part (all spp. except *C. cristata* Engelm. and *C. victoriana* Yunck.).—TYPE: *Cuscuta obtusiflora* Kunth, here designated. *Cuscuta* subsect. *Obtusiflorae* Hunz., Revista Fac. Ci. Exact. 12 (4): 1124–1125. 1949.—TYPE: *Cuscuta obtusiflora* Kunth

Cuscuta subsect. *Arvenses* Yunck., Mem. Torrey Bot. Club 18: 134. 1932.—TYPE: *Cuscuta pentagona* Engelm., here designated.

Cuscuta subsect. *Indecorae* Yunck., Mem. Torrey Bot. Club 18: 161. 1932, in part (only *C. stenolepis* Engelm.).—TYPE: *Cuscuta indecora* Choisy

Cuscuta subsect. *Californicae* Yunck., Mem. Torrey Bot. Club 18: 156. 1932 (in part, only *C. sandwichiana* Choisy).—TYPE: *Cuscuta californica* Choisy.

Inflorescences glomerulate to dense paniculiform or corymbiform. Flowers 2–4 mm long; calyx cupulate to campanulate, equalling corolla tube, divided 1/2–2/3 the length; lobes obtuse or rounded; corolla campanulate, corolla lobes obtuse to acute, inflexed or cucullate; infrastaminal scales equalling or exceeding corolla tube (undergoing a reduction trend in *C. australis*); pollen grains 3(6)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit indehiscent, depressed-globose or globose with the withered corolla remaining around it, or at the base. Figures 4D–G.

Note—Engelmann's (1859) delimitation of sect. *Cleistogrammica* included all the *Grammica* species with indehiscent capsules with the exception of *C. tasmanica*. In its current composition, this section groups together most of the species placed by Yuncker (1932) in two subsections: *Platycarpae* and *Arvenses* (Fig. 1). The evolution of this group involved hybridization and long-distance dispersal (Stefanović et al. 2007; Stefanović and Costea 2008; García et al. 2014).

Included Species—Section *Cleistogrammica* comprises 15 species: *C. australis* R. Br., *C. bifurcata* Yunck., *C. campestris* Yunck., *C. harperi* Small, *C. glabrior* (Engelm.) Yunck., *C. gymnocarpa* Engelm., *C. karatavica* Pavl.*, *C. pentagona* Engelm., *C. plattensis* A. Nelson, *C. polygonorum* Engelm., *C. runyonii* Yunck., *C. obtusiflora* Kunth, *C. sandwichiana* Choisy, *C. schlechteri* Yunck., and *C. stenolepis* Engelm. (the latter thought by Yuncker 1932 to belong to section *Indecorae*).

Distribution—*Cleistogrammica* is the section of subg. *Grammica* with the most complex biogeography. While most of its species are North American (Costea et al. 2006a; Stefanović et al. 2007; García et al. 2014), long-distance dispersal was documented on all the other continents: South America (*C. gymnocarpa*, *C. stenolepis*, and in part *C. obtusiflora*), Africa (*C. bifurcata* and *C. schlechteri*), Asia, Australia and Europe (*C. australis*, *C. karatavica*). In addition, *C. campestris* has been recently dispersed worldwide as a seed contaminant of forage legume crops (Costea and Tardif 2006).

12. *Cuscuta* sect. *Californicae* (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Californicae* Yunck., Mem. Torrey Bot. Club 18: 156. 1932.—TYPE: *Cuscuta californica* Choisy.

Cuscuta subsect. *Subinclusae* Yunck., Mem. Torrey Bot. Club 18: 165. 1932, in part (all species except *C. micrantha* Choisy).—TYPE: *Cuscuta subinclusa* Dur. & Hilg.

Cuscuta subsect. *Racemosae* Yunck., Mem. Torrey Bot. Club 18: 143. 1932, in part (only *C. decipiens* Yunck.).—TYPE: *Cuscuta racemosa* Mart.

Inflorescences glomerulate to umbelliform. Flowers 2–7 mm long; calyx campanulate to cylindrical 1/2 to equalling or exceeding corolla tube, divided 1/3–1/2 the length, lobes acute (rounded in *C. decipiens*); corolla campanulate, cylindrical or globose, lobes acute (rounded in *C. decipiens*); infrastaminal scales show a reduction trend from well-developed in *C. decipiens* and *C. draconella* to absent in *C. californica*, *C. brachycalyx*, *C. jepsonii*, and *C. occidentalis*; pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit indehiscent, globose to ovoid. Figures 4H–I.

Note—The current delimitation of section *Californicae* amalgamates Yuncker's (1932) subsections *Californicae* and *Subinclusae* (Fig. 1). *Cuscuta micrantha*, placed by Yuncker (1932) in subsect. *Subinclusae*, belongs to sect. *Racemosae* (Stefanović et al. 2007; García et al. 2014). Two new species, *C. draconella* and *C. pacifica*, and a species formerly included by Yuncker (1932) in subsection *Racemosae*, *C. decipiens*, were also placed by molecular studies in this section (Costea and Stefanović 2009b).

Included Species—Section *Californicae* has 11 species: *Cuscuta brachycalyx* Yunck., *C. californica* Hook. & Arn., *C. decipiens* Yunck., *C. draconella* Costea & Stefanović, *C. howelliana* P. Rubtsoff, *C. jepsonii* Yunck., *C. occidentalis* Millsp., *C. pacifica* Costea & M. A. R. Wright, *C. salina* Engelm., *C. subinclusa* Durand & Hilg., *C. suksdorfii* Yunck.

Distribution—Members of this section are confined to Southwestern North America.

13. *Cuscuta* sect. *Indecorae* (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Indecorae* Yunck., Mem. Torrey Bot. Club 18: 161. 1932, in part (all species except *C. stenolepis* Engelm.).—TYPE: *Cuscuta indecora* Choisy

Inflorescences paniculate or corymbiform. Flowers 2–5 mm long, fleshy because of dome-like epidermal cells (papillae also commonly present); calyx campanulate, equalling or exceeding corolla tube, divided 1/2–2/3 of the length, lobes acute; corolla campanulate, urceolate or globose, corolla lobes acute with inflexed tips; infrastaminal scales equalling corolla tube or showing a reduction trend (e.g. *C. warneri*); pollen grains 3(4)-colpate, tectum imperforate; styles cylindrical, thin; stigmas globose, small. Fruit indehiscent, globose to depressed, with a thickened apex or interstyler aperture. Figures 4J–K.

Included Species—Section *Indecorae* includes three species: *C. indecora* Choisy, *C. coryli* Engelm., *C. warneri* Yunck.

Distribution—The species of this section are North American. *Cuscuta indecora* has been further dispersed as a weed of forage legumes in South America.

14. *Cuscuta* sect. *Oxycarpae* (Engelm. ex Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Oxycarpae* Engelm. ex Yunck., Mem. Torrey Bot. Club 18: 172. 1932.—TYPE: *Cuscuta gronovii* Willd., here designated.

Cuscuta subsect. *Cephalanthae* Yunck., Mem. Torrey Bot. Club 18: 123. 1932.—Type: *Cuscuta cephalanthi* Engelm.

Lepidanche Engelm., Amer. J. Sci. Arts 43: 343, 1842. *Cuscuta* subsect. *Lepidanche* (Engelm.) Engelm., Trans. Acad. Sci. St. Louis 1(3): 509. 1859.—TYPE: *Lepidanche compositarum* Engelm. (= *Cuscuta glomerata* Choisy)

Inflorescences paniculiform to glomerulate or sometimes rope-like; numerous bracts similar to calyx lobes present in some species at the base of the flowers (*C. compacta*, *C. cuspidata*, *C. glomerata*, *C. squamata*). Flowers 2–6 mm; calyx campanulate, 1/2 to equalling corolla tube, divided 1/2–2/3 (or nearly to the base in the sp. with multiple bracts); lobes obtuse to acute; corolla campanulate to cylindrical, lobes obtuse to acute straight; infrastaminal scales 1/2 to equalling corolla tube, with very long fimbriae; pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit indehiscent, globose (depressed-globose in *C. cephalanthi*), commonly narrowed/thickened distally. Figures 4L–M.

Note—Yuncker (1932) limited subsect. *Oxycarpae* of Engelm. (1859) to include only *C. gronovii*, *C. rostrata*, and *C. umbrosa*. Our phylogenetic results (Stefanović et al. 2007; García et al. 2014) also placed in this group several species with multiple bracts (*C. compacta*, *C. cuspidata*, *C. squamata*, and *C. glomerata*), which were initially considered to form a distinct genus, *Lepidanthe* (Engelmann 1842), and later a subsection of section *Cleistogrammica* (Engelmann 1859; Yuncker 1932). In addition, *C. cephalanthi*, thought by Yuncker (1932) to form a monotypic subsection (*Cephalanthae*), is an integral part of this group.

Included Species—Section *Oxycarpae* includes eight species: *C. cephalanthi* Engelm., *C. compacta* Juss., *C. cuspidata* Engelm., *C. glomerata* Choisy, *C. gronovii* Willd., *C. rostrata* Shuttlew. ex Engelm. & A. Gray, *C. squamata* Engelm., and *C. umbrosa* Beyr. ex Hook.

Distribution—The group is North American; *C. gronovii* var. *gronovii* was also introduced but not naturalised in West Indies and West Europe.

15. **Cuscuta** sect. **Racemosae** (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Racemosae* Yunck., Mem. Torrey Bot. Club 18: 143. 1932.—TYPE: *Cuscuta racemosa* Mart.

Cuscuta subsect. *Subinclusae* Yunck., Mem. Torrey Bot. Club 18: 166. 1932, in part (*C. micrantha* Choisy).—TYPE: *Cuscuta subinclusa* Dur. & Hilg.

Cuscuta subsect. *Tinctoriae* Yunck., Mem. Torrey Bot. Club 18: 208. 1932, in part (only *C. corniculata* Engelm. and *C. incurvata* Prog.).—TYPE: *Cuscuta tinctoria* Mart.

Cuscuta subsect. *Acutilobae* Yunck., Mem. Torrey Bot. Club 18: 201. 1932, in part (only *C. xanthochortos* Mart.).—TYPE: *Cuscuta acutiloba* Engelm.

Cuscuta subsect. *Acutae* Yunck., Mem. Torrey Bot. Club 18: 152. 1932, in part (only *C. globosa* Ridl.).—TYPE: *Cuscuta acuta* Engelm.

Inflorescences paniculiform, corymbiform or fasciculate. Flowers 1.5–4 mm long; calyx campanulate to cylindrical, 1/2 to equaling corolla tube, divided 1/2–3/4, lobes acute or obtuse/rounded; corolla campanulate to cylindrical, lobes acute to obtuse; infrastaminal scales equalling corolla tube; pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit globose, indehiscent, commonly narrowed or thickened apically. Figures 4N–O.

Note—New additions to subsect. *Racemosae* of Yuncker (1932) based on molecular results (Stefanović et al. 2007; García et al. 2014) are: *C. micrantha* (subsect. *Subinclusae*, Yuncker 1932), *C. corniculata*, *C. incurvata* (subsect. *Tinctoriae*, Yuncker 1932), *C. globosa*, and *C. werdermannii* (the latter included in subsect. *Acutae* by Hunziker 1949).

Included Species—Section *Racemosae* comprises 15 species: *C. andina* Phil.*, *C. corniculata* Engelm., *C. globosa* Ridl.*, *C. incurvata* Prog., *C. micrantha* Choisy, *C. parviflora* Engelm., *C. pauciflora* Phil.*, *C. peruviana* Yunck.*, *C. platyloba* Prog., *C. racemosa* Mart., *C. suaveolens* Ser., *C. taimensis* Ferreira & Dettke*, *C. werdermannii* Hunz., *C. xanthochortos* Mart. ex Engelm., and *C. yunckeriana* Hunz.*

Distribution—All the species of sect. *Racemosae* are South American. *Cuscuta suaveolens* was introduced at the end of the 19th century in North America, Europe, Africa, and

Australia with seeds of alfalfa but it did not naturalize on these continents.

16. **Cuscuta** sect. **Partitae** Costea & Stefanović, sect. nov.—TYPE: *Cuscuta partita* Choisy

Inflorescences corymbiform or paniculiform. Flowers 2–5 mm long; calyx campanulate, equalling to exceeding corolla tube, divided almost to the base, lobes linear to lanceolate acute; corolla globose to campanulate; lobes linear to lanceolate, entire; infrastaminal scales equalling or exceeding corolla tube; pollen grains 3(4)-colpate, tectum imperforate or perforate; styles cylindrical, thin; stigmas globose, small. Fruit dehiscent or indehiscent, globose or globose-depressed. Figures 4P–R.

Note—*Cuscuta partita* and *C. haughtii* were thought by Yuncker (1932) to belong to subsections *Odontolepisae* and *Acutae*, respectively. *Cuscuta burrellii* and *C. longiloba* are among the last species *Cuscuta* described by Yuncker (1957, 1961), and the author was undecided about their placement either in subsection *Odontolepisae* or *Acutae*.

Included Species—Section *Partitae* includes five species: *C. burrellii* Yunck., *C. longiloba* Yunck., *C. haughtii* Yunck., *C. partita* Choisy, *C. rojasii* Hunz.*

Distribution—Section *Partitae* is South American.

17. **Cuscuta** sect. **Denticulatae** (Yunck.) Costea & Stefanović, stat. nov. *Cuscuta* subsect. *Denticulatae* Yunck., Mem. Torrey Bot. Club 18: 170. 1932, in part (all spp. except *C. microstyla* Engelm.).—TYPE: *Cuscuta denticulata* Engelm.

Cuscuta subsect. *Subinclusae* Yunck., Mem. Torrey Bot. Club 18: 165. 1932, in part (only *C. salina* var. *apoda* (Yunck.) Yunck. = *C. nevadensis* I. M. Johnst.).—TYPE: *Cuscuta subinclusa* Dur. & Hilg.

Inflorescences glomerulate to umbelliform. Flowers 2–3 mm long; calyx cylindrical-campanulate, ca. equalling corolla tube, divided ca. 2/3 the length, lobes rounded to acute; corolla campanulate, lobes rounded to acute; infrastaminal scales equalling corolla tube; pollen grains 3(4)-colpate, tectum imperforate; styles cylindrical, thin; stigmas globose, small. Fruit indehiscent, globose-ovoid to ovoid, 1-seeded; embryo spherically enlarged. Figures 4S–T.

Note—Yuncker (1932) placed in this group *C. denticulata*, *C. veatchii*, and a South American species, *C. microstyla* (Yuncker 1932); however, the latter belongs to Sect. *Subulatae* (Stefanović et al. 2007; García et al. 2014).

Included Species—Section *Denticulatae* has three species: *C. denticulata* Engelm., *C. nevadensis* I. M. Johnst., and *C. veatchii* Brandege.

Distribution—*Cuscuta denticulata* and *C. nevadensis* are distributed in Western U. S. A. while *C. veatchii* grows in the Central Desert of Baja California, Mexico.

18. **Cuscuta** sect. **Lobostigmae** Engelm. [“Lobostigma”], Trans. Acad. Sci. St. Louis 1: 512. 1859. *Cuscuta* subsect. *Lobostigmae* (Engelm.) Yunck., Mem. Torrey Bot. Club 18: 142. 1932.—TYPE: *Cuscuta tasmanica* Engelm., here designated.

Cuscuta subsect. *Tinctoriae* Yunck., Mem. Torrey Bot. Club 18: 208. 1932, in part (only *C. tinctoria* Mart.).—TYPE: *Cuscuta tinctoria* Mart.

Cuscuta subsect. *Subulatae* Engelm. ex Yunck., Mem. Torrey Bot. Club 18: 195. 1932, in part (only *C. jalapensis*)—TYPE: *Cuscuta grandiflora* Kunth.

Cuscuta subsect. *Americanae* Yunck., Mem. Torrey Bot. Club 18: 217. 1932, in part (only *C. floribunda* Kunth).—TYPE: *Cuscuta americana* L.

Cuscuta subsect. *Odontolepisae* Yunck., Mem. Torrey Bot. Club 18: 226. 1932, in part (only *C. purpusii* Yunck.).—TYPE: *Cuscuta odontolepis* Engelm.

Cuscuta subsect. *Platycarpae* Engelm. ex Yunck., Mem. Torrey Bot. Club 18: 124. 1932, in part (only *C. victoriana* Yunck.).—TYPE: *C. obtusiflora* Kunth

Inflorescences glomerulate to corymbiform. Flowers commonly large and thick, 4–9 mm long (1.5–2.5 mm in *C. victoriana*); Calyx campanulate to globose, 1/2 to equalling corolla tube, divided 1/2–1/4 the length, lobes acute to rounded; corolla campanulate to globose, lobes acute to rounded; infrastaminal scales equalling corolla tube; pollen grains 3 (4)-colpate, tectum imperforate, perforate, or microreticulate; styles cylindrical or subulate, thick (0.2–0.9 mm in diameter), stigmas large (0.25–0.6 mm in diameter), usually lobed. Fruit dehiscent (indehiscent in *C. tasmaniana* and *C. victoriana*). Figures 4V–W.

Note—Both Engelmann (1859) and Yuncker (1932) included in the section/subsection *Lobostigmae* only *C. tasmanica*. Phylogenetic results showed that *C. tasmanica* is a part of the second largest infrageneric group of subg. *Grammica* (Costea et al. 2013). Most of these species (*C. jalapensis*, *C. mitriformis*, *C. rugosiceps*, *C. lindsayi* and *C. woodsonii*) were placed by Yuncker (1932) in subsect. *Subulatae*, while others were originally included in other subsections: *Tinctoriae* (*C. tinctoria* vars. *tinctoria* and *aurea*), *Odontolepisae* (*C. purpusii*), *Americanae* (*C. tinctoria* var. *floribunda*), and *Platycarpae* (*C. victoriana*) (Fig. 1). In addition, seven new species from this clade were recently described (Costea et al. 2008b; Costea et al. 2013).

Included Species—Section *Lobostigmae* includes 18 species: *C. cotijana* Costea & I. García, *C. durangana* Yunck*, *C. iguanella* Costea & I. García, *C. insolita* Costea & I. García, *C. jalapensis* Schldtl., *C. lindsayi* Wiggins, *C. mitriformis* Engelm. ex Hemsl. [“mitraeformis”], *C. montana* Costea & Stefanović, *C. purpusii* Yunck., *C. rugosiceps* Yunck., *C. tasmanica* Engelm., *C. tatei* Yunck*, *C. timida* Costea & Stefanović, *C. tinctoria* Mart. ex Engelm., *C. tolteca* Costea & Stefanović, *C. victoriana* Yunck., *C. volcanica* Costea & I. García, and *C. woodsonii* Yunck.

Distribution—Section *Lobostigmae* is distributed in Mexico and the adjacent areas (Southern U. S. A. and Central America); as an exception, *C. tasmanica*, *C. tatei*, and *C. victoriana* have a disjunct distribution in Australia.

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