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Short Communication

Disentangling parasitic vines in the tropics: taxonomic notes for an accurate identification of *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae)

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Abstract

Parasitic plants are often associated with agricultural, forestry and grassland economic losses, but they are also keystone species in their natural ecosystems. *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae) are parasitic plants which have evolved similar stem habit and morphology, rendering them remarkably similar during the vegetative stage. Since both genera are common in the tropics, misidentifications are frequent, which is detrimental for understanding their geographical distribution, biology and ecology, as well as to the development of adequate control or conservation practices. We here present a practical identification guide for a clear and accurate distinction between *Cuscuta* and *Cassytha,* using stems and reproductive structures of both fresh plants and herbarium specimens, aimed at taxonomists and agricultural experts. An identification key, a comparative table, detailed descriptions and illustrations are included to facilitate genus recognition. The current practice of macroscopic observation of the filiform stems, on which many professionals rely, may not be enough to distinguish the two genera. The analysis of stem micromorphology, and/or of the flower or fruit morphology, are necessary for a conclusive identification.

Keywords: dodders, invasive species, love vine, morphology, weeds.

Resumo

Plantas parasitas são frequentemente associadas a perdas agrícolas e silvo pastoris. Entretanto, elas são espécies chave na dinâmica dos ecossistemas. Os gêneros *Cuscuta* (Convolvulaceae) e *Cassytha* (Lauraceae) são ambos parasitas filiformes que têm evoluído em habitats similares, sendo a morfologia dos seus ramos notavelmente similar durante sua fase vegetativa. Devido ao fato de ambos os gêneros serem comuns nos trópicos, erros de identificação são frequentes, o que prejudica a compreensão de suas distribuições geográficas, biologia, e ecologia, bem como o desenvolvimento de medidas de controle ou práticas de manejo e conservação adequadas. Esse estudo oferece um detalhado guia de identificação para taxonomistas e cientistas agrários, usando ramos vegetativos e estruturas reprodutivas de representantes dos dois gêneros, tanto de coleções vivas como herborizadas. Estão incluídas uma chave de identificação, uma tabela comparativa, descrições detalhadas, fotografias e ilustrações como subsídio para as identificações. A atual prática de observação macroscópica dos ramos filiformes, na qual muitos profissionais se apoiam, mostra-se insuficiente para distinguir os dois gêneros. A análise micro morfológica dos ramos e/ ou das flores ou frutos é necessária para uma identificação conclusiva.

Palavras-chave: cipó-chumbo, plantas invasoras, fios-de-ovos, morfologia, plantas daninhas.

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Parasitic plants are often overlooked in floristic studies although they are common in many natural ecosystems and may have a significant detrimental economic impact as agricultural pests or noxious weeds (Parker & Riches 1993; Costea & Tardif 2006; Teixeira-Costa 2016). As agricultural pests, the infestation by some parasitic plants can lead to severe yield losses, increased harvesting costs and contamination of commercial seed lots (Parker & Riches 1993; Dawson *et al*. 1994, Costea & Tardif 2006; Ashigh & Marquez 2010). At an organismal scale, they directly or indirectly affect the physiology of their hosts (Dawson *et al.* 1994, Nelson 2008); cause behavioral modifications in herbivores (Gómez 1994) and animal poisoning (Barcellos 1990); and are involved in pathogen transmission (Dawson *et al*. 1994; Nelson 2008). In natural plant communities, parasitic plants act as ecosystem engineers and keystone species, increasing the diversity of species in plant communities and modifying abiotic factors (*e.g*., Pennings & Callaway 1996; Watson 2009). Another positive aspect of parasitic plants is their wide use in traditional medicine systems, for example in Asia (Visaka *et al.* 2010; Donnapee *et al.* 2014), Bahamas, West Indies and Polynesia (Nelson 2008). In recent years, some parasitic plants have been proposed as biological control agents for green invasive plants (Nelson 2008; Yu *et al.* 2008; Cirocco *et al.* 2018).

Cuscuta L. and *Cassytha* L. are the only parasitic lineages that evolved within Convolvulaceae and Lauraceae, respectively (Stefanović & Olmstead 2004, APG IV 2016, Nickrent 2020). Although the genera are very distantly related to one another (APG IV 2016; Nickrent 2020), they evolved a similar habit as stem parasitic vines and represent a remarkable example of convergent evolution (Heide-Jørgensen 2008, Nickrent 2020): their leaves are reduced to minute scales, and stems are filiform, greenish, yellow, orange or reddish, dextrorsely twining around the stems of the hosts, and eventually covering them. Haustoria develop on the inner side of the stem coils (Dawson *et al*. 1994; Heide-Jørgensen 2008). The confusion between *Cuscuta* and *Cassytha,* due to their morphological similarities, is reflected in these two genera sharing in the tropics the vernacular name "love vine".

The two genera overlap geographically in the southern hemisphere, namely in tropical regions, where numerous species of *Cuscuta* have diversified (Yuncker 1932; Costea *et al*. 2015) and one species of *Cassytha* in particular, *C. filiformis* L., is ubiquitous (Weber 1981). Especially during the vegetative stage, their morphologically similar stems, either fresh or dried, can make the genus separation challenging (Heide-Jørgensen 2008; Tennakoon *et al*. 2016). Indeed, we have often noted that in tropical herbaria more than half of the *Cuscuta* specimens are misidentified as *Cassytha*. The frequent confusion between the two genera has hindered the adequate delimitation of their geographical distribution ranges (*e.g*., Nelson 2008), understanding their biology and ecology (including host ranges), and ultimately developing appropriate pest control management protocols.

Guidelines to assist both taxonomists and agricultural or forestry experts to correctly identify these two genera are not available. Some taxonomic works focusing on one or both genera have briefly mentioned some diagnostic features (Schroeder 1967; Kuijt 1969; Weber 1981; Dawson *et al.* 1994; Baitello 2003; Heide-Jørgensen 2008; Kropf *et al*. 2015). However, even in more comprehensive works (*e.g*., Dawson *et al.* 1994; Heide-Jørgensen 2008; Nelson 2008; Tennakoon *at al*. 2016), no comparative morphological details were provided for the separation of the two genera, especially when using (dried) herbarium specimens, which are routinely used in systematic, floristic and biogeographic studies. Therefore, our objective is to provide a detailed guide for the accurate identification of *Cuscuta* and *Cassytha*, supporting research studies and agroforestry management strategies.

Morphological data were generated from fieldwork, conducted between 2010 and 2020, in Brazil (Bahia, Minas Gerais, Piauí, Rio de Janeiro, and São Paulo) and Mexico (Nayarit, Colima, Jalisco, Michoacán, Puebla, Oaxaca, Veracruz). In addition, thousands of herbarium specimens were examined and annotated from the following institutions: 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, DIAM, E, ESA, F, FT, G, GH, H, HB, HRCB, HUEFS, HUFU, HUSC, HUJ, IAC, IEB, IND, J, JACA, JE, JEPS, K, L, LAU, LD, LE, LIL, LL, LP, LPB, LPS, M, MA, MACB, MAF, MBM, MEL, MERL, MEXU, MGC, MICH, MO, MPU, MSTR, NAP,

NBG, NMC, NY, OAC, OKLA, OSC, OXF, P, PACA, PMSP, PRE, QCNE, QFA, R, RB, RNG, RSA, S, SALA, SAM, S, SD, SEV, SGO, SI, SJRP, SP, SPF, SPSF, TEX, TRT, TRTE, UA, UB, UBC, UCR, UCT, UEC, UNM, UPCB, UPRRP, UPS, US, USAS, VAL, W, WTU, and XAL (Herbaria acronyms follow Thiers 2018-continuously updated).

Macromorphological characters were photographically documented during fieldwork. Micromorphological features were characterised by study of herbarium specimens, with structures analysed in both dried and rehydrated conditions, and imaged under Light and Scanning Electron Microscopy. For observations and photographic records under Light Microscopy, Zeiss Opticam Stemi SV6 and Nikon SMZ1500 stereomicroscopes were used, with application of Extended Depth of Focus (EDF). Scanning Electron Microscopy measurements and photographs were taken using a Hitachi SU1510 variable pressure scanning electron microscope, at 10 kV. Prior to examination, samples were sputter-coated with 30 nm of gold using an Emitech K550 (Emitech, Ltd. Ashfort, UK).

A comparison table was prepared which includes both vegetative and reproductive characters (Tab. 1), and identification keys that can be used for different ontogenetic stages were prepared. Full morphological descriptions of the genera are also provided, to assist in the preparation of floristic and taxonomic works.

Identification Key

Fresh sample in vegetative state (magnification 30× or more required). (For additional details see Tab. 1).

1. Stems greenish to orange with fine longitudinal rugae or ridges; trichomes present or absent .... *Cassytha*
1'. Stems yellowish to orange or reddish-purple (greenish in seedlings), usually smooth (see Table 1); trichomes absent ..... *Cuscuta*

Dry or fresh sample at reproductive stage (magnification 30× or more required)

1. Inflorescences racemose (usually spike), few-flowered. Flowers white-creamy or greenish, 3-merous with perianth elements free. Stamens 9; staminodes may occur..... *Cassytha*
1'. Inflorescences monochazial cymes with numerous flowers, usually compound and forming dense aggregations of flowers. Flowers white, white-creamy, yellowish, pink to reddish, 4-5-merous (rarely 3-merous), with perianth elements fused. Stamens 4-5, all fertile ..... *Cuscuta*

Table 1 – Comparison of the macro- and micromorphological characteristics of *Cassytha* and *Cuscuta*.

	***Cassytha* (Figs. 1 a-i; 2 a-c)**	***Cuscuta* (Figs. 1 j-p; 2 d-g)**	**Observations**
Life form	Perennial, hemiparasitic vines (Heide-Jørgensen 2008, Tennakoon *et al.* 2016), occurring mainly in coastal areas of pantropical regions (Nelson 2008).	Annual or perennial, hemiparasitic to holoparasitic vines, present in many habitats, ranging from coastal areas to high elevations, with sub-cosmopolitan distribution (Costea *et al.* 2015).	*Cuscuta* species exhibit a range of plastome reductions (Braukmann *et al.* 2013).

	***Cassytha* (Figs. 1 a-i; 2 a-c)**	***Cuscuta* (Figs. 1 j-p; 2 d-g)**	**Observations**
Stem morphology, micromorphology and anatomy	Filiform, 0.4-3 mm thick with fine longitudinal rugae or ridges; glabrous or occasionally presenting trichomes, forming a puberulent indumentum cover; epidermis cuticle with waxy plaques; stomata numerous, in parallel rows; stomata guard cells at right angles with the longitudinal axis of the stems (Heide-Jørgensen 2008). Stem coils producing haustoria similar to the rest of the stem (Figs.1b,e; 2a-c). Anatomically, stems exhibit secondary growth and their wood has bordered pits with a torus; fibers develop in the phloem (Heide-Jørgensen 2008).	Filiform, 0.3-2.4 mm thick, smooth and glabrous; epidermis cuticle without epicuticular deposits; stomata very few, irregularly distributed; stomata guard cells oriented in parallel with the longitudinal axis of stems (Yuncker 1943; Fig. 1j, k; Fig. 2d-e). Stem coils producing haustoria (haustorial stems) often develop multicellular projections with stomata, as in species of subg. *Grammica* (Fig. 2f-g) Stems lack secondary growth and fibers (wood is absent as well) (Clayson *et al.* 2014).	When broken, fresh stems of *Cassytha* are usually scented which is due to the presence of secretory tissues with essential oils (Weber 1981, Tennakoon *et al.* 2016). *Cuscuta* stems have laticifers, but the latex secreted is inodorous (Clayson *et al.* 2014). Dry stems of *Cassytha* are very rigid, while stems of *Cuscuta* are more flexible.
Stem color	Generally greenish-olive but, occasionally becoming yellowish or orange (Fig. 1e-f,h).	Yellowish, orange, reddish or purple, rarely greenish (Fig.1o-p).	In both genera, stems become (dark) brown upon drying, but in *Cuscuta* they may preserve better their original yellowish-orange color (Fig.1j).
Leaves	Alternate, reduced to inconspicuous scales, sessile, sometimes pubescent (Weber 1981).	Alternate, reduced to microscopic scales, glabrous.	Sometimes it is possible to observe the leaf scales of *Cassytha* at the stem apex.
Inflorescences	Spikes, less frequently racemes or panicles (Weber 1981, Kropf 2015); the few flowers widely spaced along the inflorescence axis (Fig.1a,e).	Monochazial cymes (rarely thyrses), generally compound, dense and with numerous flowers (Fig.1j, l,p).	Some *Cuscuta* species may have few-flowered inflorescences, in which case flower pedicels are usually conspicuous, while in *Cassytha* flowers are sessile or subsessile (Fig.1 e,h).
Flowers	3-merous (Fig.1f-g); perianth elements free.	4-5-merous (rarely 3-merous) (Fig.1m,o); perianth elements fused.	Flowers are bisexual and radial in both genera.
Stamens	9, arranged in 3 whorls; anthers open by two flaps (Fig.1f-g)	4-5 on one cycle, alternating with the corolla lobes; anthers open by longitudinal slits (Fig.1o)	As in other Convolvulaceae, the stamens of *Cuscuta* are fused with the corolla tube.
Staminodes	Present in the 4th whorl.	Staminodes absent.	
Pollen	Apolar; inaperturate; spheroidal, 25-60 mm in diameter, exine verrucate or spinuloid; (Van der Merwe *et al.* 1990).	Colpate, commonly 3(4)-zonocolpate, sometimes 5-6 (8)-colpate; prolate, spheroidal to oblate; 12-42 mm long; tectum imperforate to reticulate; exine with rounded or acute processes (Welsh *et al.* 2010).	Pollen grains in *Cassytha* are uniform while in *Cuscuta* they are polymorphic, variable as number of colpi within the same anther and flower.

	***Cassytha* (Figs. 1 a-i; 2 a-c)**	***Cuscuta* (Figs. 1 j-p; 2 d-g)**	**Observations**
Appendices	A pair of glands is associated with the staminal filaments of the 3rd whorl (Weber 1981).	Infra-staminal scales are associated with the base of staminal filaments, with great morphological diversity within the genus (Riviere *et al.* 2013).	In some species of *Cuscuta*, infra-staminal scales are completely reduced (e.g., *Cuscuta grandiflora* Kunth.; Riviere *et al.* 2013).
Ovary	Globose-elliptic, 1 locule with 1 ovule (Weber 1981).	Globose, depressed-globose, ovoid or obovoid, 2 locules, 2 ovules per locule (Wright *et al.* 2011).	Pollen/ovule ratios have been used to estimate breeding systems in *Cuscuta* (Wright *et al.* 2012).
Style(s)	1, terminal, conic (Fig.3c).	1 or 2, terminal, cylindrical or subulate (Fig.3i).	
Stigma	1, narrow, inconspicuous (Endress & Igersheim 1997).	2, conspicuous, elongated, globose, flattened (other shapes are also possible, Wright *et al.* 2011).	
Fruit	Drupe, 4-10 x 3-7 mm (Fig.1a,d,i).	Membranous capsule; dehiscent, indehiscent, or irregularly dehiscent (Ho & Costea 2018) usually smaller than 0.5 cm (Fig.1n).	In *Cassytha,* usually only a few fruits can be observed along the stems; *Cuscuta* often exhibits dense infructescences.
Seeds	1 per fruit, glabrous; embryo not coiled, with 2 large cotyledons (Sastri 1962).	1-4 per fruit, glabrous, embryo filiform 1-4 times coiled; cotyledons absent Olszewski *et al.* (2020).	

Genus description

Cassytha L. Species Plantarum 1: 35. 1753. Type: *Cassytha filiformis* L. INDIA: Type: Osbeck s.n. (LINN n.v.). Figs. 1a-g; 2a-c; 3a-e.

Perennial hemiparasitic; stems filiform, greenish, or orange, glabrous to tomentose. Leaves alternate, reduced to scales, more evident at stem apices. Inflorescences axillary, few-flowered, racemose, commonly spikes, sometimes racemes or panicles, often reduced to heads. Flowers bisexual, 3-meous, sessile or short-pedicellate; 1 bract and 2 ovate bracteoles with ciliate apex; perianth ovoid to urceolate, distally contracted after anthesis; perianth elements 6, in 2 whorls: outer 3 smaller, inner 3, larger. Stamens 9, arranged in 3 whorls, rarely those of the second whorl reduced to staminodes; filaments of 3rd whorl with 2 subsessile glands; anthers 2-locular; cells of 1st and 2nd whorls introrse, those of the 3rd whorl extrorse, dehiscing via flaps (apically hinged valves); staminodes 3, in a 4th whorl. Ovary globose-elliptic, glabrous. Fruit a drupe, enclosed in the persistent and dilated floral tube, presenting a small apical opening; seeds 1 per fruit, with 2 fleshy cotyledons (Weber 1981; Baitello 2003; Nelson 2008; Tennakoon *et al*. 2016, *pers. obs.*).

Distribution: The genus is predominantly distributed in the Southern Hemisphere (Chanderbali *et al*. 2001). Most species are Australian, some also occurring in Africa and Asia. *Cassytha filiformis* has a pantropical distribution (Baitello 2003).

Cuscuta L. in Species Plantarum 1: 124. 1753. Type: *Cuscuta europaea* L. FRANCE. PARIS. Dalib 53 (LT n.v.). Figs. 1i-n; 2d-g; 3f-j.

Annual to perennial, hemi-parasitic to holo-parasitic; stems filiform, yellowish, orange, purple or reddish, smooth and glabrous. The coiled stems producing haustoria (haustoria stems) of subg. *Grammica* exhibit multicellular protuberances with stomata. Leaves alternate, reduced to scales. Inflorescences axillary; the units are monochazial cymes which are further aggregated in thyrses or compound, dense cymes; bracts and bracteoles 1–15. Flowers bisexual 4–5-merous (rarely 3-merous); sepals and petals connate; infra-staminal scales usually present, variously dentate or fimbriate; stamens 4–5 on one whorl, alternating with the corolla lobes; filaments fused with the

Figure 1 – Morphological characterization of *Cassytha* and *Cuscuta,* using living and dried specimens, imaged with stereomicroscopy. a-i. *Cassytha filiformis* - a. fragment of herbarium specimen; b. rehydrated stem from herbarium specimen, note longitudinal ridges (white arrows indicate lines of stomata); c. dried flower; d. dried fruit; e. inflorescence of living plant showing pubescent peduncle (also note the greenish color of stems); f. top overview of 3-merous flower; g. rehydrated flower viewed under stereomicroscope; h. side view of flower in the field. i. Fresh, immature fruits; j. *Cuscuta racemosa* var. *miniata* - fragment of herbarium specimen. k. rehydrated stem of *Cuscuta gronovii* (note the absence of hairs and scarce stomata indicated with asterisks); l. *Cuscuta platyloba* - dried inflorescence. m-p. *Cuscuta racemosa* var. *miniata* - m. dried flower; n. capsule; o. top view of 5-merous flower; p. habit. (a. *A. Macedo 4166*; b. *O.J. Pereira 410*; c. *E.S.G. Guarino & B.M.T. Walter 579*; d. B. *Stannard & T. Silva 52807*; j. *I. Cordeiro et al. CFSC 8211*; k. *M. Costea s.n.*; l. *A.A. Conceição 893*; m. *H.F. Leitão-Filho 27718*; n. *E. Pereira 1517*). Images: a, c, d. S.S. Silva 2018; b, g, k, M. Costea; e. R. Simão-Bianchini; f, g. S.E. Martins 2007; i. M.L. Brotto 2016; j, l-p. S.S. Silva 2018-2019. Scale bars- a, i. 1 cm; b. 0.5 mm; c, d, l. 2 mm; g. 1 mm; k. 0.5 mm; m, n. 1 mm.

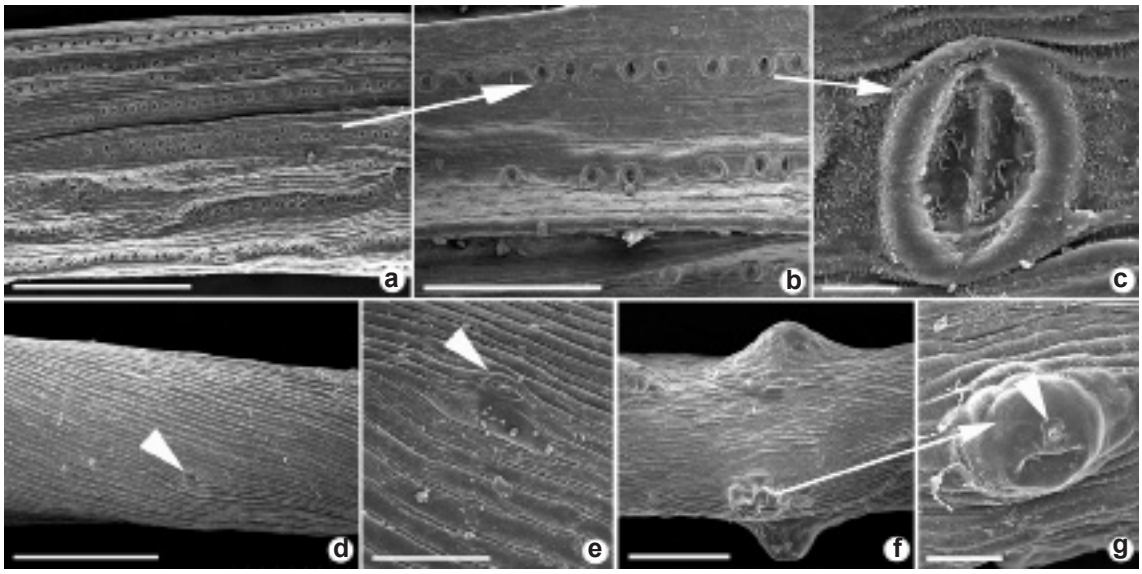

Figure 2 –- Micromorphology of *Cassytha* and *Cuscuta* stems, using rehydrated herbarium specimens and imaging under scanning electron microscopy. a-c. *Cassytha filiformis* - a. stem at low magnification, showing longitudinal ridges and lines of stomata; b. detail of stomata rows; c. stoma and epicuticular wax. d-g. *Cuscuta gronovii*. D. general view, note the smooth epidermis and only one stoma present (indicated with arrow); e. epidermis surface and stoma detail; f-g. haustorial stems with multicellular protuberances bearing stomata; f. general view; g. multicellular protuberance viewed from the top (arrow indicates stoma). (a-c *M.R.R. Vidal 325*; d-g *Costea s.n.*). Scale bars - a. 0.5 mm; b. 200 mm; c. 15 mm; d. 0.4 mm; e, g. 100 mm; f. 0.5 mm.

corolla tube; anthers opening via longitudinal slits. Ovary depressed-globose, ovoid to obovoid, glabrous to papillose, in species with two styles, an interstylar aperture is present; styles 1–2; stigmas elongate, capitate. Fruit a capsule, dehiscent, in which case circumscissile, indehiscent, or irregularly dehiscent. Seeds 1–4 per capsule; embryo filiform, 1–4-coiled, cotyledons absent (Yuncker 1932, Riviere *et al*. 2013, Costea *et al*. 2015, *pers. obs*.).

Distribution: A relatively reduced number of species (~15) are common agricultural invasive weeds (Costea & Stefanović 2009) that have been dispersed world-wide as seed contaminants (Olszewski *et al*. 2020). The remaining ~185 species have more restricted geographical distributions but are encountered on all continents (Yuncker 1932; Costea *et al.* 2015). Subgenus *Grammica* accounts for over 75% of the genus diversity and has evolved in the New World (Stefanović *et al.* 2007).

Even though *Cuscuta* and *Cassytha* are morphologically similar due to convergent evolution of their habit and life form, it is possible to accurately distinguish them during both their vegetative and reproductive stages, using either fresh or dry, herbarium specimens. The confusion between the two genera is likely to occur when only stems are available and examination is superficial, with the naked eye. However, stem micromorphological characters (Table 1) allow the reliable separation of the two genera even when only small stem fragments are available. The identification of *Cuscuta* and *Cassytha* using reproductive traits should pose no problem due to the markedly contrasting floral/fruit morphologies; however, the use of a magnifier is recommended for the flowers.

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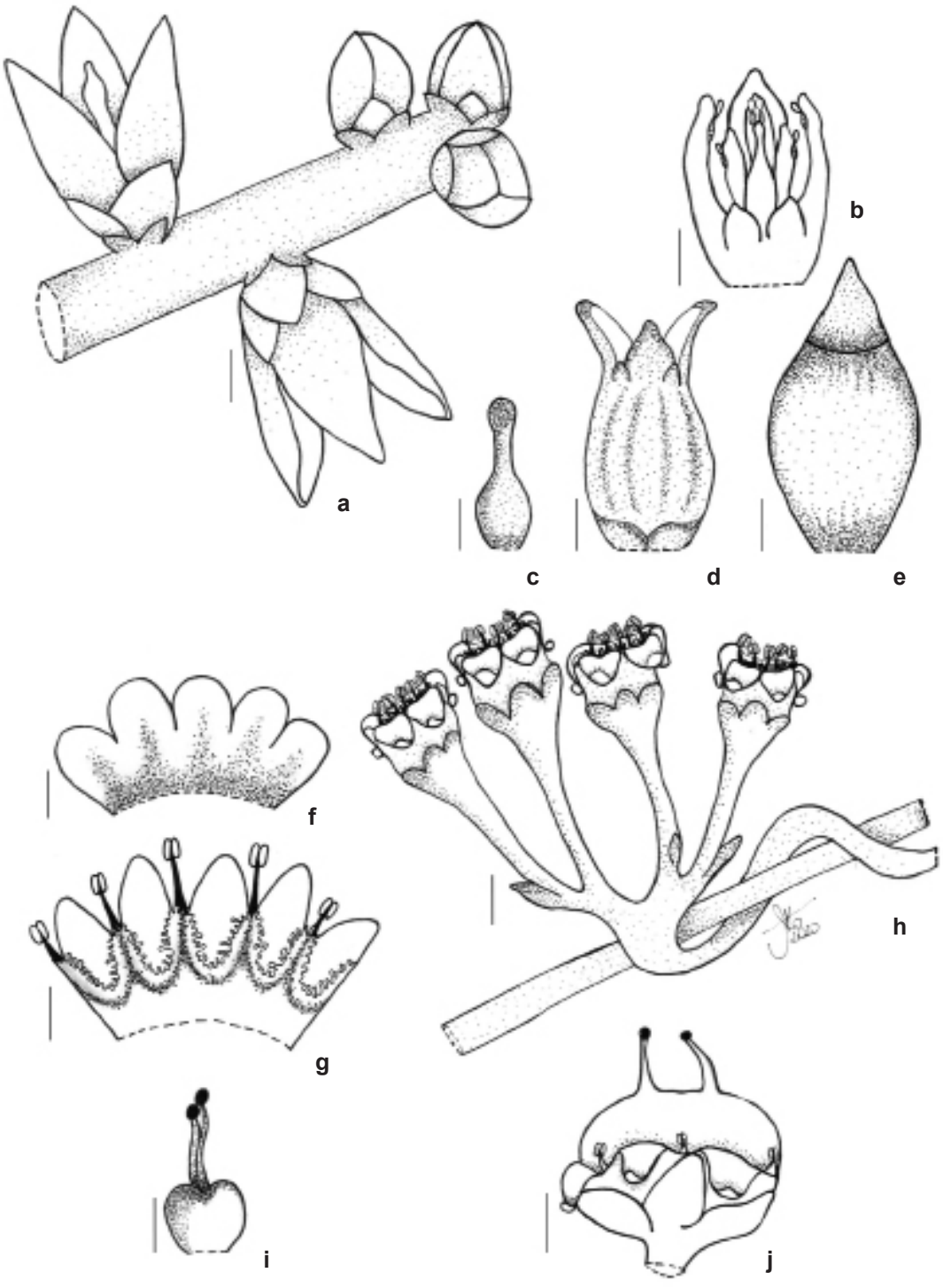

Figure 3 – Schematic representation of the main diagnostic reproductive characteristics of *Cassytha* and *Cuscuta*. a-e. *Cassytha filiformis*. a. inflorescence. b. longitudinal section through a flower, showing the disposition of androecium and gynoecium. c. ovary. d. fruit covered by the hypanthium. e. fruit. f-j. *Cuscuta racemo*sa. f. dissected calyx. g. dissected corolla showing infra-staminal scales. g-h. part of an inflorescence. i. ovary. j. fruit with persistent corolla and calyx. (a-e *E.S.G. Guarino & B.M.T. Walter 579*; f-j *G. Hashimoto 1950*). Scale bars 1mm. Illustration by Stephanie Karoline de Oliveira (2020).

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Literature cited

APG IV - Angiosperm Phylogeny Group IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1-20.

Ashigh J & Marquez E (2010) Dodder (*Cuscuta* spp.) biology and management. NM State University, Cooperative Extension Service, College of Agricultural, Consumer and Environmental Sciences, New Mexico. 4p.

Baitello JB (2003) *Lauraceae*. *In*: Wanderley MGL *et al.* (eds.) Flora Fanerogâmica do estado de São Paulo. Instituto de Botânica, São Paulo. Vol. 3, pp. 149-224.

Barcellos JM (1990) A cultura da alfafa. Embrapa Cerrados-Comunicado Técnico (INFOTECA-E), Planaltina. 12p.

Braukmann T, Kuzmina M & Stefanović S (2013) Plastid genome evolution across the genus *Cuscuta* (Convolvulaceae): two clades within subgenus *Grammica* exhibit extensive gene loss. Journal of Experimental Botany 64: 977-989.

Cartwright DK & Templeton GE (1989) Preliminary evaluation of a dodder anthracnose fungus from China as a mycroherbicide for dodder control in the US. Journal of the Arkansas Academy of Science 43: 15-18.

Chanderbali AS, Werff H & Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. Annals of Missouri Botanical Garden 88: 104-134.

Cirocco RM, Facelli JM & Watling JR (2018) A native parasitic plant affects the performance of an introduced host regardless of environmental variation across field sites. Functional Plant Biology 45: 1128-113.

Clayson C, García-Ruiz I & Costea M (2014) Diversity, evolution, and function of stomata bearing structures in *Cuscuta* (dodders, Convolvulaceae): From extrafloral nectar secretion to transpiration in arid conditions. Perspectives in Plant Ecology, Evolution and Systematics 16: 310-321.

Costea M & Tardif FJ (2006) The biology of Canadian weeds. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe. Canadian Journal of Plant Science 86: 293-316.

Costea M & Stefanović S (2009) *Cuscuta jepsonii* (Convolvulaceae): An invasive weed or an extinct endemic? American Journal of Botany 96: 1744-1750.

Costea M, García MA & Stefanović S (2015) A phylogenetically based infrageneric classification of the parasitic plant genus *Cuscuta* (Dodders, Convolvulaceae). Systematic Botany 40: 269-285.

Dawson JH, Musselman LJ, Wolswinkel P & Dörr I (1994) Biology and control of *Cuscuta*. Reviews of Weed Science 6: 265-317.

Donnapee S, Li J, Yang X, Ge AH, Donkor PO, Gao XMY & Chang YX (2014) *Cuscuta chinensis* Lam.: A systematic review on ethnopharmacology, phytochemistry and pharmacology of an important traditional herbal medicine. Journal of Ethnopharmacology 157: 292-308.

Endress PK & Igersheim A (1997) Gynoecium diversity and systematics of the Laurales. Botanical Journal of the Linnean Society 125: 93-168.

Gómez JM (1994) Importance of direct and indirect effects in the interaction between a parasitic angiosperm (*Cuscuta epithymum*) and its host plant (*Hormathophylla spinosa*). Oikos 71: 97-106.

Heide-Jørgensen H (2008) Parasitic flowering plants. Brill.

Ho A & Costea M (2018) Diversity, evolution and taxonomic significance of fruit in *Cuscuta* (dodder, Convolvulaceae); the evolutionary advantages of indehiscence. Perspectives in Plant Ecology, Evolution and Systematics 32: 1-17.

Kuijt J (1969) The biology of parasitic flowering plants. The biology of parasitic flowering plants. University of California Press, Berkeley. 246p.

Parker C & Riches CR (1993) Parasitic weeds of the world. Biology and control. CAB International, Wallingford. 332p.

Pennings SC & Callaway RM (1996) Impact of a parasitic plant on the structure and dynamics of Salt Marsh vegetation. Ecology 77: 1410-1419.

Mehannaa ET, El-sayedb NM, Ibrahimc AK, Ahmedc SA & Abo-Elmattya DM (2018) Isolated compounds from *Cuscuta pedicellata* ameliorate oxidative stress and upregulate expression of some energy regulatory genes in high fat diet induced obesity in rats. Biomedicine & Pharmacotherapy 108: 1253-1258.

Kropf MS, Quinet A & Andreata RHP (2015) Lauraceae das restingas do estado do Rio de Janeiro, Brasil. Iheringia Série Botânica 70: 287-308.

Nelson SC (2008) *Cassytha filiformis*. Plant Desease 42: 1-10.

Nickrent DL (2020) Parasitic angiosperms: How often and how many? Taxon 69. Available at < https://onlinelibrary.wiley.com/doi/abs/10.1002/tax.12195>. Access on 24 May 2020. DOI: <https://doi.org/10.1002/tax.12195>.

Olszewski M, Dilliott M, García-Ruiz I, Bendarvandi B & Costea M (2020) *Cuscuta* seeds: diversity and evolution, value for systematics/identification and exploration of allometric relationships. PLOS One (accepted).

Riviere S, Clayson C, Dockstader K, Wright MA & Costea M (2013) To attract or to repel? Diversity, evolution and role of the "most peculiar organ" in the *Cuscuta* flower (dodder, Convolvulaceae)—the infrastaminal scales. Plant Systematics and Evolution 299: 529-552.

Sastri RLN (1962) Studies in Lauraceae. III. Embryology of *Cassytha*. Botanical Gazette 123: 197-206.

Schroeder CA (1967) The stem parasite *Cassytha filiformis* a botanical relative of avocado. California Avocado Society 51: 159-160.

Stefanović S & Olmstead RG (2004) Testing the phylogenetic position of a parasitic plant (*Cuscuta*, Convolvulaceae, Asteridae): Bayesian Inference and the Parametric Bootstrap on data drawn from three genomes. Systematic Biology 53: 384-399.

Stefanović S, Kuzmina M & Costea M (2007) Delimitation of major lineages within *Cuscuta* Subgenus *Grammica* (Convolvulaceae) using plastid and nuclear DNA sequences. American Journal of Botany 94: 568-589.

Teixeira-Costa L (2016) Plantas parasitas. *In* Peña EMH (org.) Botânica no inverno. Instituto de Biociências da Universidade de São Paulo, São Paulo. Pp. 131-137.

Tennakoon KU, Rosli R & Le QV (2016) Biology of aerial parasitic vines in Brunei Darussalam: *Cuscuta* and *Cassytha*. Scientia Bruneiana 15: 58-64.

Thiers B [continuously updated]: Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at: <http://sweetgum.nybg.org/science/ih/>. Access on 24 February 2020.

Van der Merwe JJM, Van Wyk AE & Kok PDF (1990) Pollen types in the Lauraceae. Grana 29: 185-196.

Vikasa K, Udaya PS, Raj BH, Amar R & Kamaruz ZM (2010) Pharmacognostical evaluation of *Cuscuta reflexa* Roxb. Pharmacognosy Journal 2: 74-82.

Watson DM (2009) Parasitic plants as facilitators: more Dryad than Dracula? Journal of Ecology 97: 1151-1159.

Weber JZ (1981) A taxonomic revision of *Cassytha* (Lauraceae) in Australia. Journal of the Adelaide Botanic Garden 3: 187-262.

Welsh M, Stefanović S, & Costea M (2010). Pollen evolution and its taxonomic significance in *Cuscuta* (dodders, Convolvulaceae). Plant Systematics and Evolution 285: 83-101.

Wright MA, Welsh M & Costea M (2011) Diversity and evolution of the gynoecium in *Cuscuta* (dodders, Convolvulaceae) in relation to their reproductive biology: two styles are better than one. Plant Systematics and Evolution 296: 51-76.

Wright MA, Ianni MD & Costea M (2012). Diversity and evolution of pollen-ovule production in *Cuscuta* (dodders, Convolvulaceae) in relation to floral morphology. Plant Systematics and Evolution 298: 369-389.

Yu H, Yu FH, Miao SL & Dong M (2008) Holoparasitic *Cuscuta campestris* suppresses invasive *Mikania micrantha* and contributes to native community recovery. Biological Conservation 141: 3653-2661.

Yuncker GT (1932) The genus *Cuscuta*. Memoirs of the Torrey Botanical Club 18: 109-331.

Yuncker TG (1943) Observations on the presence of stomata in some species of *Cuscuta*. Proceedings of the Indiana Academy of Science 53: 100-104.

Selected specimens examined** of **Cassytha filiformis: AUSTRALIA. NICHOLSON: Mittiebah, 26.III.1981, fl. e fr., *T.S Henshall 3479* (NT, SP). BRAZIL. BAHIA: Abaíra, Garimpo do Bicota, 13°20'N, 41°51'W, 24.III.1992, fr., *B. Stannard & T. Silva 52087* (CEPEC, HUEFS, K, SP). CEARÁ: Aiquiraz, Prainha, 13.XI.2001, fl. e fr., *A. Heringer et al. 2301* (HEPH, SPSF). GOIÁS: Distrito Federal, Barro Alto, Córrego Pombal e Rio das Almas (margem direita), 16.VII.1992, fl., *B.M.I. Walter et al. 1696* (CEN, SPSF); Campo próximo ao Riacho Fundo, 15°52' 00"N, 48°W, 1100m, 10.I.2001, fl., *E.S.G. Guarino & B.M.T. Walter 579* (SPSF); Reserva Ecológica do Guará, 26.I.1994, fr., *G.P. da Silva 2221* (CEN, SPSF). ESPÍRITO SANTO: Guarapari, 8.II.1985, fl., *O.J. Pereira 410* (SP, VIES). SÃO PAULO: Suzanápolis, Estância Califórnia, 4.VIII.1995, fr., *M.R. Pereira-Noronha et al. 1531* (SPF, SPSF, UEC); Conceição da Barra, área da Aracruz Celulose, 20.V.1994, fl. e fr., *O.J. Pereira et al. 3556* (VIES, SPSF). MINAS GERAIS: Ituiutaba, 15.I.1956, fl. e fr., *A. Macedo 4166* (SP); Jardim Botânico, 6.III.1933, fr., *A.J. de Sampaio 7329* (R); Uberlândia, Rio Uberabinha, 22.VII.1956, fr., *A. Macedo 4558* (SP). PARÁ: Marabá, Serra dos Carajás, 18.IV.1970, fr., *P. Cavancante & M. Silva 2654* (MG, SPSF). RIO DE JANEIRO: Armação de Búzios, Praia de Una, 18.VIII.1998, fr., *D. Fernandes et al. 07* (R); Guaratiba, praia Grumari, 06.VIII.1973, *M.R.R. Vidal 325* (RB). SÃO PAULO: Álvares Florence, 5 km do trevo de Álvares Florence, 2.XI.1994, fl., *M.R. Silva 1381* (SJRP). TOCANTINS: Cristalândia, Fazenda São Sebastião, 10°33'58"S, 49°34'40"W, 19.III.2010, fl. e fr., *F.C.A. Oliveira et al. 1692* (IBGE, SP); Lizarda, Estrada Lizarda/ TO para Alto Parnaíba/ MA, 12.VIII.2016, fl., *E.R. Santos et al. 283* (R).

Selected specimens examined** of **Cuscuta: ***Cuscuta americana***: BRAZIL. CEARÁ: Crato, 7°09'35"S, 39°35'03"W, 11.VIII.1948, fl., *I.A. Duarte 1413* (RB). PARAÍBA: Areia, Escola de Agronomia do Nordeste, 14.IX.1944, fl., *J. M. Vasconcellos 631* (IAC). ***Cuscuta burrellii***: BRAZIL. GOIÁS: Alto Paraíso, Fazenda São Bento, 23.II.1991, fl., *D. Alvarenga et al. 766* (SP). ***Cuscuta campestris***: PORTUGAL. ALTO ALANTEJO: Monte da Vinha, margem do Guadiana, 10.VIII.1965, fr., *A.B. de Tovar 12* (IAC). ***Cuscuta gronovii***: CANADA. ONTARIO: Waterloo, Grand River, 43°30'12.02'N, 80°29'37.97'W, 12.VIII.2012, fl., *M. Costea s.n.* (WLU). ***Cuscuta obtusiflora***: ARGENTINA. BUENOS AIRES: San Vicente, 26°59'48"S, 54°28'51"W, 23.XII.1926, fr., *A.T. Hunziker 3964* (CORD, SP). ***Cuscuta orbiculata***: BRAZIL. PIAUÍ: Caracol, Estrada para Serra Grande, 18.VII.2011, fl. e fr., *E. Melo et al. 10139* (HUEFS, SP). ***Cuscuta parviflora***: BRAZIL. GOIÁS: Distrito Federal, Cia Fercal, 19.IX. 1964, fl., *H.S. Irwin & T.R. Soderstrom 6279* (UB, SP). BAHIA: Mucugê, Guiné, 1400m, 25.XI.2000, fl., *A.A. Conceição 893* (SPF, WLU). ***Cuscuta racemosa***: BRAZIL. RIO DE JANEIRO: Paraty, Fazenda Goura Vrindavana, 7.VI.2003, fl., *D. Mello 26* (R). SÃO PAULO: Piracicaba, 22.V.1990, fl. e fr., *L. Capillari Jr.* (ESA, SP 292458); São Paulo, Ponte Grande, 21.V.1950, fl. e fr. *G. Hashimoto 1950* (SP). ***Cuscuta racemosa* var. *miniata***: BRAZIL. MINAS GERAIS: Santana do Riacho, Conceição do Mato Dentro, ao longo da Rodovia Belo Horizonte, 18°55'S, 43°54'W, 24.III.1982, fl. e fr., *I. Cordeiro et al. CFSC 8211* (SPF, WLU); Diamantina, Estrada Diamantina-Medanha, 10.XII.1992, fl., *H.F. Leitão-Filho 27718* (UEC); 25.V.1955, fl., *E. Pereira 1517* (RB, WLU).

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