

CUCUMIS (CUCURBITACEAE) MUST INCLUDE CUCUMELLA, DICOELOSPERMUM, MUKIA, MYRMECOSICYOS, AND OREOSYCE: A RECIRCUMSCRIPTION BASED ON NUCLEAR AND PLASTID DNA DATA

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SUMMARY

Recent molecular studies have revealed that the genus *Cucumis* in its current circumscription is paraphyletic. To become monophyletic, *Cucumis* must include five genera of the subtribe Cucumerinae, namely *Cucumella*, *Dicoelospermum*, *Mukia*, *Myrmecosicyos*, and *Oreosyce*, already regarded as closely related by earlier workers based on morphology. The 19 species in the five genera are here formally transferred to *Cucumis*, resulting in 14 new combinations, two changes in status, and three new names (*Cucumis indicus*, *C. kirkbrideana*, and *C. oreosyce*). A description of the genus and a key to its 52 species are given, and the subgenera and sections are recircumscribed to reflect monophyletic groups. Subgenus *Humifructus*, with a haploid chromosome number of 12, contains only *C. humifructus* and *C. hirsutus*, while subgenus *Cucumis*, with $n = 12$ or $n = 7$, contains the remainder of the species. The latter is further divided into the sections *Aculeatosi*, *Cucumella*, *Cucumis*, *Metuliferi*, and *Sagittati*.

Key words: Cucurbitaceae, *Cucumis*, *Cucumella*, *Dicoelospermum*, *Mukia*, *Myrmecosicyos*, *Oreosyce*.

INTRODUCTION

The following recircumscription of the genus *Cucumis* L. is based on molecular studies in which the author took part (Kocyan et al., in press; Renner et al., provisionally accepted). Although numerous specimens were studied during herbarium visits (E, FT, K, KUN, L, M, P, W, WAG, WU), species concepts here follow Kirkbride (1993, 1994) and De Wilde & Duyfjes (2007). Phylogenetic analyses of plastid and nuclear DNA sequences (Kocyan et al., in press; Renner et al., provisionally accepted) show that *Cucumis* in its current circumscription is paraphyletic and needs to include five genera of the subtribe Cucumerinae Pax to become monophyletic, namely *Cucumella* Chiov., *Dicoelospermum* C.B. Clarke, *Mukia* Arn., *Myrmecosicyos* C. Jeffrey, and *Oreosyce* Hook.f. Based on leaf, flower and pollen morphology, De Wilde & Duyfjes (2007) already combined *Dicoelospermum* with *Mukia*. All five of these genera were treated as close relatives of *Cucumis* in earlier morphological classifications of the Cucurbitaceae: Jeffrey (1980) placed them together with *Cucumis* in his broadly circumscribed tribe Melothrieae Endl. (34 genera) and mentions them explicitly as the closest relatives of

Cucumis. In revised classifications (Jeffrey, 1990, 2005), he recognized a more narrowly circumscribed subtribe, Cucumerinae, which nevertheless still included *Cucumeropsis* Naudin, *Melancium* Naudin, *Melothria* L., *Muellerargia* Cogn., *Posadaea* Cogn., and *Zehneria* Endl. All but one of these genera are placed far from *Cucumis* based on the molecular data of Kocyan et al. (in press). The Australasian–African genus *Muellerargia* is the sister group to a monophyletic *Cucumis* (as recircumscribed formally herein).

CUCUMIS

- Cucumis* L. (1753) 1011. — Type: *Cucumis sativus* L. (lecto (Britton & Wilson, 1925)).
Melo Mill. (1754) (no pagination). — Type: *Cucumis melo* L. (lecto (Swart, 1979)).
Mukia Arn. in Wight (1840) 50. — *Melothria* L. sect. *Mukia* (Arn.) Cogn. (1881) 622. — Type: *Mukia scabrella* (L.) Arn. (= *Mukia maderaspatana* (L.) M. Roem.).
Oreosyce Hook.f. (1871) 548. — Type: *Oreosyce africana* Hook.f.
Dicoelospermum C.B. Clarke (1879) 630 ('*Dicaelospermum*', correction Von Post & Kuntze (1903)). — Type: *Dicoelospermum ritchiei* C.B. Clarke.
Hymenosicyos Chiov. (1911) 62. — Type: *Hymenosicyos membranifolius* (Hook.f.) Chiov. (= *Oreosyce africana* Hook.f.).
Cucumella Chiov. (1929) 183. — Type: *Cucumella robecchii* Chiov. (= *Cucumella kelleri* (Cogn.) C. Jeffrey).
Myrmecosicyos C. Jeffrey (1962) 357. — Type: *Myrmecosicyos messorius* C. Jeffrey.

Plants small to medium-sized climbers or trailers; annual or with perennial rootstock (rarely tubers) and herbaceous or perennial, woody shoots, usually hispid or scabrid-hairy. *Tendrils* present or rarely absent, solitary or rarely in groups of 5–8, simple or rarely bifid. *Leaves* simple, unlobed or palmately lobed, petiolate, margin entire or serrate. *Flowers* small to medium-sized, monoecious or rarely dioecious. Petals 5, yellow, disc free from the receptacle-tube. Male flowers solitary or in up to 19-flowered groups, sessile or pedicellate, rarely subtended by a bracteole; receptacle-tube infundibular to campanulate, sepals 5, rarely 4, small, long-triangular, linear, subulate or filiform; petals elliptic or (ob)ovate, free or united at base. Stamens 3, two double 2-theous, 1 single 1-theous, inserted near the middle of the receptacle-tube, filaments shorter than the anthers, glabrous; thecae lateral, straight (sometimes apically hooked) or sigmoid (triplicate), connective narrow, glabrous or papillate, puberulous to hairy, disc obconic or depressed globose, basal, free from the tube. Female flowers solitary or in fascicles of up to 6, usually separate from male flowers, pedicellate; ovary hairy, globose to oblong; ovules several to many, horizontal; perianth as in male flowers; style terete, thick, glabrous; stigma entire, sublobate or 3-lobed; lobes carnosose, papillose, often with 1–9 finger-like projections on the margin; staminodes often present, three, subulate; disc annular, surrounding base of style, free from tube. *Fruit* fleshy, thin or rather firm-walled, indehiscent or rarely expelling seeds explosively, solitary or clusters of up to 6, subsessile or short-pedicelled, (sub)globose or ellipsoid, cylindrical, (ob)ovoid, or spindle-shaped, smooth and glabrous or pubescent or with dense to scattered fleshy spines, pustules or tubercles, that end in a hyaline bristle, sometimes beaked or fusiform, yellow, orange, red or greenish to brownish when ripe, often with longitudinal pale stripes, rarely maturing underground. *Seeds* small to medium-sized, few to many, globose or lenticular compressed, light-coloured, ovate or elliptic in outline, often ornamented, glabrous or rarely puberulent, margin often distinct, usually

unwinged. Chromosome numbers $n = 7, 12$ (also polyploids with $n = 24$ or 36 (Den Nijs & Visser, 1985) and apparently aneuploid cultivars of *C. melo* with $n = 20$ or 22 (Chandola et al., 1965).

CUCUMIS subgenus **HUMIFRUCTUS** H. Schaefer, *nom. nov.*

CUCUMIS series **HUMIFRUCTOSI** J.H. Kirkbr. (1993) 77. — Type: *Cucumis humifructus* Stent (Species 1, 2)

1. **Cucumis hirsutus** Sond. in Harv. & Sond. (1862) 497. — Type: *C.L.P. Zeyher 581* (lecto MEL, n.v. (Kirkbride, 1993)), South Africa, Inter Wonderfontyn & Moojerivier.
2. **Cucumis humifructus** Stent (1927) 356. — Type: *S.M. Stent s.n.* (holo PRE, n.v.), South Africa, Transvaal, Pretoria, grown from seed sent by E.E. Galpin, Naboomspruit, Waterberg (*Galpin M. 719*), 13.02.1925.

CUCUMIS subgenus **CUCUMIS** (Species 3–52)

CUCUMIS section **CUCUMIS** (Species 3–11)

3. Cucumis gracilis (Kurz) H. Schaefer, *comb. nov.*

Basionym: *Mukia maderaspatana* (L.) M. Roem. var. *gracilis* Kurz (1877) 104. — *Mukia scabrella* (L.) Arn. var. *gracilis* (Kurz) C.B. Clarke (1879) 623. — *Melothria maderaspatana* (L.) Cogn. var. *gracilis* (Kurz) Cogn. (1881) 624. — Type: *Wallich Cat. 6714* (iso K), Myanmar, Pagamew.

4. **Cucumis hystrix** Chakrav. (1952) 896. — Type: *N.E. Parry 859* (holo K), India, Meghalaya, Garo Hills, Tura Mt, 04.11.1929; Paratype: *Griffith 2554* (K), India, Arunachal Pradesh, Mishmee Hills.

5. Cucumis javanicus (Miq.) H. Schaefer, *comb. nov.*

Basionym: *Karivia javanica* Miq. (1856) 661. — *Melothria javanica* Cogn. (1881) 625. — *Mukia javanica* (Miq.) C. Jeffrey (1969) 3, t. 3661. — Type: *Horsfield s.n.* (holo U, n.v.), Indonesia, Java.

6. Cucumis leiospermus (Wight & Arn.) H. Schaefer, *comb. nov.*

Basionym: *Bryonia leiosperma* Wight & Arn. (1834) 345. — *Mukia leiosperma* (Wight & Arn.) Wight (1840) 50. — *Melothria leiosperma* (Wight & Arn.) Cogn. (1881) 622. — Type: *Wight 1112* (lecto K (Jeffrey, 1969)), India, Madras, Palni Hills.

7. Cucumis maderaspatanus L. (1753) 1012

Synonym: *Mukia maderaspatana* (L.) M. Roem. (1846) 47. — *Melothria maderaspatana* Cogn. (1881) 623. — Type: t. 170, f. 2 in L., Plukenet, Almag. 1696, South Afrika (lecto (Meeuse, 1962); epitype: Herb. *Plukenet 201* (BM, n.v.)).

8. **Cucumis melo** L. (1753) 1011. — Type: Sweden. Plant cultivated at Uppsala (lecto LINN, sheet number 1152.8, n.v. (Meeuse, 1962)).

9. *Cucumis ritchiei* (C.B. Clarke) H. Schaef., *comb. nov.*

Basionym: *Dicoelospermum ritchiei* C.B. Clarke (1879) 630 ('*Dicaelospermum*', correction Von Post & Kuntze (1903)). — *Mukia ritchiei* (C.B. Clarke) W.J. de Wilde & Duyfjes (2007). — Type: *Ritchie 316* (lecto K (De Wilde & Duyfjes, 2007)), India, Western.

Note — See *Cucumis indicus* (47) for a comment on nomenclature.

10. *Cucumis rumphianus* (Scheff.) H. Schaef., *comb. nov.*

Basionym: *Melothria rumphiana* Scheff. (1876) 25. — *Mukia rumphiana* (Scheff.) W.J. de Wilde & Duyfjes (2007). — Type: *Teijsmann 7496* (lecto n.v. (De Wilde & Duyfjes, 2007)), Indonesia, Ternate.

11. *Cucumis sativus* L. (1753) 1012. — Type: *J. Burser vol. 17, no. 97* (lecto UPS, n.v. (Ten Pas et al., 1985)), Europe. Cultivated plants.

CUCUMIS section ACULEATOSI J.H. Kirkbr. (1993) 27. — Type: *Cucumis dipsaceus* Ehrenb. ex Spach (Species 12–35)

12. *Cucumis aculeatus* Cogn. (1896a) 209. — Type: *G.L.A. Volkens 1972* (lecto BR, n.v. (Kirkbride, 1993)), Tanzania, Moshi Distr., Kilimanjaro, 1200 m, 08.03.1894.

13. *Cucumis africanus* L.f. (1782) 423. — Type: Hermann, *Parad. bat. Tab. 134, 1698* (holo n.v.).

14. *Cucumis anguria* L. (1753) 1011. — Type: Sweden, plant cultivated at Uppsala (lecto LINN, sheet number 1152.6, n.v. (Kirkbride, 1993)).

15. *Cucumis baladensis* Thulin (1991) 541. — Type: *Thulin, Hedrén & Abdi Dahir 7464* (holo UPS, n.v.), Somalia, Shabeellaha Dhexe reg., 16 km N of Muqdisho along road to Balcad, 15.05.1990.

16. *Cucumis canoxyi* Thulin & A.N. Al-Gifri (1994) 315. — Type: *M. Thulin, Eriksson, Gifri, Langstroem 8299* (holo UPS, n.v.; iso Aden Univ., E, K), Yemen, Hadramaut.

17. *Cucumis carolinus* J.H. Kirkbr. (1993) 43. — Type: *M.G. Gilbert & M. Thulin 1116* (holo K), Kenya, Wajir Distr., 4 km SW Habaswein, 240 m, 27.04.1978.

18. *Cucumis dipsaceus* Ehrenb. ex Spach (1838) 211. — Type: *G. Ehrenberg & Hemprich s.n.* (holo B†, lecto MPU, n.v. (Kirkbride, 1993)), Saudi Arabia, Wadi Kamme east of al-Qunfidha, Febr. 1825.

19. *Cucumis ficifolius* A. Rich. (1847) 294. — Type: *R. Quartin-Dillon & A. Petit s.n.* (lecto P (Jeffrey, 1967)), Ethiopia, Sholoda.

20. *Cucumis hastatus* Thulin (1991) 535. — Type: *M. Thulin, Hedrén & Abdi Dahir 7765* (holo UPS, n.v.), Somalia, Bay reg., 52 km from Yaaq Bari Weyne to Buurhakaba, 23.05.1990.

21. ***Cucumis heptadactylus*** Naudin (1859) 24. — Type: *C. Zeyher 591* (lecto P (Kirkbride, 1993)), South Africa, Colesberg.
22. ***Cucumis insignis*** C. Jeffrey (1985) 209. — Type: *Gilbert & Jefford 4656* (holo K), Ethiopia, Sidamo, 39 km from Yavello on new road to Agree Mariam, c. 1 km S of village of Sorupa, 1580 m.
23. ***Cucumis jeffreyanus*** Thulin (1991) 539. — Type: *W. Burger 3214* (holo K), Ethiopia, Harere reg. N of Erer-Gota near Idorra, 31.08.1963.
24. ***Cucumis kalahariensis*** A. Meeuse (1962) 70. — Type: *R. Story 5320* (lecto PRE, n.v. (Kirkbride, 1993)), South Africa, cultivated at Roodeplaat from seed collected in Namibia at Nama Pan (26.08.1955), Apr. 1957.
25. ***Cucumis meeusei*** C. Jeffrey (1965) 218. — Type: *B. de Winter 3713* (holo K), Namibia, bed of Omuramba Omatako at Karahuwisa, 27.11.1955.
26. ***Cucumis messorius*** (C. Jeffrey) H. Schaefer, *comb. nov.*
Basionym: *Myrmecosicyos messorius* C. Jeffrey (1962) 357. — Type: *Bogdan 980* (holo K), Kenya, Nakuru Distr., Elmenteita, Soysambu Estate.
27. ***Cucumis myriocarpus*** Naudin (1859) 22. — Type: *J.H. Bowker s.n.* (lecto K (Kirkbride, 1993)), South Africa, Cape Province, Somerset.
28. ***Cucumis prolatior*** J.H. Kirkbr. (1993) 53. — Type: *J.B. Gillett & F.N. Gachathi 20478* (holo K), Kenya, Eastern, Kitui Distr., Nairobi-Garissa road, 3 km SW of Mwingi, 08.05.1974.
29. ***Cucumis prophetarum*** L. (1755) 33. — Type: *F. Hasselquist s.n.* (holo LINN, n.v.), Middle East.
30. ***Cucumis pubituberculatus*** Thulin (1991) 538. — Type: *M. Thulin, Hedrén & Abdi Dahir 7288* (holo UPS, n.v.), Somalia, Galgudud reg., Ceeldheer, just E of town, 07.05.1990.
31. ***Cucumis pustulatus*** Naudin ex Hook.f. (1871) 544. — Type: *G.H. Schimper 835* (lecto K (Jeffrey, 1967)), Ethiopia, 31.06.1862.
32. ***Cucumis quintanilhae*** R. Fern. & A. Fern. (1963) 269. — Type: *R.B. Drummond 6025* (holo SRGH, n.v.), Zimbabwe, turn off to Limpopo Ranches, 10 miles north of Beitbridge, 25.03.1959.
33. ***Cucumis rigidus*** E. Mey. ex Sond. in Harv. & Sond. (1862) 497. — Type: *J.F. Drège s.n.* (lecto K (Kirkbride, 1993)), South Africa, Cape Prov., on the Gariep River.
34. ***Cucumis thulinianus*** J.H. Kirkbr. (1993) 56. — Type: *C.F. Hemming 2011* (holo K), Somalia, Northern reg., Erigavo, 1722 m, 05.10.1960.

- 35. *Cucumis zeyheri*** Sond. in Harv. & Sond. (1862) 496. — Type: *C. Zeyher* 582 (lecto BM, n.v. (Kirkbride, 1993)) South Africa, Cape Prov., Gamka River, May 1840.

CUCUMIS section **SAGITTATI** H. Schaef., *sect. nov.* — Type: *Cucumis sagittatus* Peyr. (Species: 36, 37)

- 36. *Cucumis globosus*** C. Jeffrey (1965) 215. — Type: *A. Harwood* 19 (holo K), Tanzania, Mbeya Distr., about 1 km southeast of Ilomba local court, 27.02.1963.

- 37. *Cucumis sagittatus*** Peyr. in Wawra & Peyr. (1860) 567. — Type: *H. Wawra* 263 (lecto W, n.v. (Kirkbride, 1993)), Angola, prope Benguelam.

CUCUMIS section **METULIFERI** (J.H. Kirkbr.) H. Schaef., *stat. nov.* — Species 38–40

Basionym: *Cucumis* ser. *Metuliferi* J.H. Kirkbr. (1993) 70. — Type: *Cucumis metuliferus* E. Mey. ex Naudin.

- 38. *Cucumis metuliferus*** E. Mey. ex Naudin (1859) 10. — Type: *C. Naudin s.n.* (lecto P (Kirkbride, 1993)), France, Muséum Nationale d'Histoire Naturelle, 1857.

- 39. *Cucumis rostratus*** J.H. Kirkbr. (1993) 72. — Type: *J.P.M. Brenan* 8875 (holo K), Nigeria, Benin Distr., Benin Div., Okomu Forest Reserve, compartment 69, 22.01.1948.

- 40. *Cucumis saculeuxii*** Pailleux & Bois (1890) 371. — Type: *H.G. Faulkner* 2865 (neo BR, n.v. (Kirkbride, 1993)), Tanzania, Zanzibar, Massazine, 15.07.1961.

CUCUMIS section **CUCUMELLA** (Chiov.) H. Schaef., *stat. nov.* — Species 41–52

Basionym: *Cucumella* Chiov. (1929) 183. — Type: *Cucumella robecchii* Chiov.

- 41. *Cucumis aëtheocarpus*** (C. Jeffrey) H. Schaef., *comb. nov.*

Basionym: *Cucumella aëtheocarpa* C. Jeffrey (1965) 215. — Type: *M. Richards* 17751 (holo K), Tanzania, Tunduru Distr., Tunduru-Masasi Road, 05.03.1963.

- 42. *Cucumis asper*** Cogn. (1901) 882.

Synonym: *Cucumella aspera* (Cogn.) C. Jeffrey (1962) 349. — Type: *Dinter* 1447 (holo BR, n.v.), Namibia, Ababis, Hereroland, 16.02.1900.

- 43. *Cucumis bryoniifolius*** (Merxm.) H. Schaef., *comb. nov.*

Basionym: *Hymenosicyos bryoniifolia* Merxm. (1953) 205. — *Cucumella bryoniifolia* (Merxm.) C. Jeffrey (1962) 350. — Type: *R. Dehn* 25'52" (holo M), Zimbabwe, Rusape, Aug. 1952.

- 44. *Cucumis cinereus*** (Cogn.) H. Schaef., *comb. nov.*

Basionym: *Kedrostis cinerea* Cogn. (1901) 883. — *Cucumella cinerea* (Cogn.) C. Jeffrey (1962) 350. — Type: *Dinter* 1440 (holo Z, n.v.), Namibia, Giftkopje, Hereroland, 12.02.1900.

45. *Cucumis clavipetiolatus* (J.H. Kirkbr.) H. Schaefer, *comb. nov.*

Basionym: *Cucumella clavipetiolata* J.H. Kirkbr. (1994) 178. — Type: *B. Nordenstam 3657* (holo S, n.v.), Namibia, Distr. of Omaruru, Brandberg, Orabeswand, 2000 m, 03.04.1964.

46. *Cucumis engleri* (Gilg) H. Schaefer, *comb. nov.*

Basionym: *Kedrostis engleri* Gilg (1904) 359. — *Cucumella engleri* (Gilg) C. Jeffrey (1962) 350. — Type: *Engler 1992* (lecto BR, n.v. (Kirkbride, 1994)), Kenya, Lake Nakuru, 30.08.1902.

47. *Cucumis indicus* H. Schaefer, *nom. nov.*

Replaced synonym: *Melothria ritchiei* Chakrav. (1952) 898. — *Cucumella ritchiei* (Chakrav.) C. Jeffrey (1965) 215. — Type: *Ritchie 67* (holo E, n.v.), India, Bombay Presidency, Santavadi State, Ram Ghat.

Note — As both *Dicoelospermum ritchiei* C.B. Clarke and *Cucumella ritchiei* (Chakrav.) C. Jeffrey must be transferred to *Cucumis*, only one of them can keep its epithet. We decided to choose a new epithet for *Cucumella ritchiei* which was described in 1952, while *Dicoelospermum ritchiei* should keep the epithet because it was already described in 1879.

48. *Cucumis kelleri* (Cogn.) H. Schaefer, *comb. nov.*

Basionym: *Oreosyce kelleri* Cogn. (1896b) 822. — *Cucumella kelleri* (Cogn.) C. Jeffrey (1962) 350. — Type: *Keller 111* (holo Z, n.v.), Ethiopia, Harrar, Webi Abdallah, 1891.

49. *Cucumis kirkbrideana* H. Schaefer, *nom. nov.*

Replaced synonym: *Cucumella jeffreyana* J.H. Kirkbr. (1994) 168. — Type: *L.C.C. Liebenberg 954* (holo K), Uganda, on roadside in grass country, Oct. 1929.

Note — A new epithet is required as *jeffreyanus* is preempted by *C. jeffreyanus* Thulin. The replacement name honours the botanist Joseph H. Kirkbride, who did groundbreaking biosystematic work on *Cucumis*.

50. *Cucumis oreosyce* H. Schaefer, *nom. nov.*

Replaced synonym: *Oreosyce africana* Hook.f. (1871) 548. — Type: *Mann 1285* (lecto K (here designated)), Equatorial Guinea, Bioko (Fernando Po).

Note — A new name is required as the epithet *africanus* is occupied by *Cucumis africanus* L.f.

51. *Cucumis reticulatus* (R. Fern. & A. Fern.) H. Schaefer, *comb. nov.*

Basionym: *Cucumella reticulata* R. Fern. & A. Fern. (1969) 307. — Type: *Milne-Redhead 4012* (holo K), Angola, Moxico, between Mumbala River and Namavumba River, 09.01.1938.

52. *Cucumis silentvalleyi* (Manilal, T. Sabu & P. Mathew) H. Schaefer, *comb. nov.*

Basionym: *Cucumella silentvalleyi* Manilal, T. Sabu & P. Mathew (1985) 283 (as '*silentvalleyii*'). — Type: *Sabu SV 10662* (holo CAL, n.v.), India, Kerala, Palghat District, Silent Valley, Poochapura, 1370 m, 20.10.1982.

KEY TO THE SPECIES OF CUCUMIS
(modified after Kirkbride, 1993, 1994)

- 1a. Tendrils absent 2
 b. Tendrils present 5
 2a. Leaves deeply palmatisect, the lobes 1–2 mm wide **26. C. messorius**
 b. Leaves entire or 3–5-lobed 3
 3a. Subshrub with erect stems **33. C. rigidus**
 b. Herbaceous creeper 4
 4a. Petioles 4–8 mm long **51. C. reticulatus**
 b. Petioles 20–65 mm long **16. C. canoxyi**
 5a. Tendrils 5–8 per node. Fruit geocarpic, maturing below ground
 **2. C. humifructus**
 b. Tendrils solitary. Fruit maturing above ground 6
 6a. At least some tendrils bifid **22. C. insignis**
 b. All tendrils simple 7
 7a. Anther thecae straight or bent once at the apex into a short hook 8
 b. Anther thecae sigmoid 24
 8a. Ovary and fruit bristly-tuberculate. Ripe fruit greenish, expelling seeds explosively **50. C. oreosyce**
 b. Ovary and fruit smooth, ribbed, aculeate-bristly or finely hairy. Fruit indehiscent 9
 9a. Seeds globose, with faint central ridge, c. 3 per fruit. **9. C. ritchiei**
 b. Seeds distinctly flattened, > 3 per fruit 10
 10a. Seeds without distinct margin 11
 b. Seed margin distinct 19
 11a. Leaves obtuse at base, without a basal sinus **48. C. kelleri**
 b. Leaves cordate at base, with a basal sinus 12
 12a. Petioles with two different types of hairs 13
 b. Petioles with a single type of hairs 14
 13a. Leaves entire, apex obtuse. Tendrils 10–25 mm long **46. C. engleri**
 b. Leaves pentalobate, apex acute. Tendrils 35–55 mm long **49. C. kirkbrideana**
 14a. Fruit blunt at the apex 15
 b. Fruit rostrate at the apex 17
 15a. Petioles claviform. Leaf-blade margin entire **45. C. clavipetiolatus**
 b. Petioles cylindrical. Leaf-blade margin serrate 16
 16a. Plants herbaceous, hispidulous. Female flowers with six finger-like projections on the margin of the stigma **43. C. bryoniifolius**
 b. Plants subshrubs, scabrous. Female flowers with three finger-like projections on the margin of the stigma **42. C. asper**
 17a. Male flowers solitary **41. C. aëthecarpus**
 b. Male flowers in 3–19-flowered fascicles or racemes 18
 18a. Plants hispidulous or retrorse-strigose **44. C. cinereus**
 b. Plants hirsute, pilose, villous or glabrate **47. C. indicus**
 19a. Seeds pubescent **52. C. silentvalleyi**
 b. Seeds glabrous 20

- 20a. Leaves ovate-oblong, usually longer than broad **3. C. gracilis**
 b. Leaves about as long as broad 21
- 21a. Fruit ellipsoid, 20–35 mm long **10. C. rumphianus**
 b. Fruit globose or ellipsoid, < 15 mm long 22
- 22a. Fruit ellipsoid, pericarp translucent. Seed faces flat **5. C. javanicus**
 b. Fruit globose, pericarp not translucent. Seed faces convex 23
- 23a. Hairs of petiole spreading or recurved. Seed faces smooth or low-warted, the margin separated by a groove **6. C. leiospermus**
 b. Hairs of petiole spreading or upcurved. If seed faces smooth, then without a distinct margin **7. C. maderaspatanus**
- 24a. Fruit not aculeate 25
 b. Fruit aculeate 30
- 25a. Seeds < 2.5 mm wide **37. C. sagittatus**
 b. Seeds 2.5–13 mm wide 26
- 26a. Fruit rostrate at apex **39. C. rostratus**
 b. Fruit blunt at apex 27
- 27a. Plant monoecious 28
 b. Plant dioecious 29
- 28a. Leaf-blade lobe elliptic, oblong or ovate in outline. Corolla tube 0.8–2.8 mm long **8. C. melo**
 b. Leaf-blade lobe broadly triangular in outline. Corolla tube 3.4–6.5 mm long **11. C. sativus**
- 29a. Internodes 25–40 mm long. Leaves hirsute. Male flowers in groups of up to 11, pedunculate **1. C. hirsutus**
 b. Internodes 50–70 mm long. Leaves pilose. Male flowers solitary, sessile **15. C. baladensis**
- 30a. Stems and petioles aculeate 31
 b. Stems and petioles not aculeate 32
- 31a. Petioles glabrous. Fruit pedicel glabrate. Fruit 60–80 mm long **12. C. aculeatus**
 b. Petioles hispidulous. Fruit pedicel hispidulous. Fruit 25–40 mm long **19. C. ficifolius**
- 32a. Fruit rostrate at apex **4. C. hystrix**
 b. Fruit blunt at apex 33
- 33a. Pedicel of male flower glabrate **17. C. carolinus**
 b. Pedicel of male flower pubescent 34
- 34a. Fruit aculei 20–22 mm long **28. C. proliator**
 b. Fruit aculei 0.5–15 mm long 35
- 35a. Pedicel of female flower and fruit pedicel flaring upwards from a narrower base to a wider apex 36
 b. Pedicel of female flower and fruit pedicel cylindrical 38
- 36a. Annual, woody rootstock absent **14. C. anguria**
 b. Perennial with woody rootstock 37
- 37a. Leaves antrorse-strigose or scabrous. Pedicel of female flower 8–13 mm long **25. C. meeusei**
 b. Leaves hispidulous. Pedicel of female flower 15–45 mm long **31. C. pustulatus**

- 38a. Plant dioecious 39
 b. Plant monoecious 40
- 39a. Woody rootstock and tubers present. Nodes not geniculate. Leaf lobes 5–30 mm wide **24. C. kalahariensis**
 b. Woody rootstock and tubers absent. Nodes geniculate. Leaf lobes 1–5 mm wide **21. C. heptadactylus**
- 40a. Fruit glabrous 41
 b. Fruit pubescent 52
- 41a. Fruit aculei laterally compressed below 42
 b. Fruit aculei terete 43
- 42a. Stems and petioles scabrous. Petioles 20–85 mm long. Male flowers in 5–10-flowered racemes. Fruit ellipsoid or cylindrical **13. C. africanus**
 b. Stems and petioles retrorse-strigose. Petioles 5–15 mm long. Male flowers solitary. Fruit globose **36. C. globosus**
- 43a. Tendrils antrorse-strigose or retrorse-strigose 44
 b. Tendrils not strigose 47
- 44a. Female corolla puberulent inside. Petiole with 3 different types of hairs in different zones **27. C. myriocarpus**
 b. Female corolla glabrous inside. Petiole with 1 type of hairs 45
- 45a. Annual. Pedicel of female flower 55–65 mm long **32. C. quintanilhae**
 b. Perennial. Pedicel of female flower < 40 mm long 46
- 46a. Male corolla glabrous inside, the lobes 2.4–5.6 mm long. Leaves hispidulous **29. C. prophetarum**
 b. Male corolla puberulent inside, the lobes c. 10 mm long. Leaves antrorse-strigose **23. C. jeffreyanus**
- 47a. Seeds c. 8.5 mm long, c. 5.5 mm wide and c. 3.7 mm thick **36. C. globosus**
 b. Seeds < 8 mm long, 2–4 mm wide, 0.9–1.6 mm thick 48
- 48a. Woody rootstock absent. Female sepals 4.8–11 mm long. Female corolla glabrous inside 49
 b. Woody rootstock present. Female sepals 1.2–4.2 mm long. Female corolla pubescent inside 50
- 49a. Male and female corolla lobes obovate in outline, acute at apex. Female pedicel 5–15 mm long. Fruit aculei 4–6.4 mm long. Seeds 4–5 mm long, c. 2 mm wide **18. C. dipsaceus**
 b. Male and female corolla lobes elliptic in outline, obtuse at apex. Female pedicel 55–65 mm long. Fruit aculei 8.5–13 mm long. Seeds 6–6.5 mm long, 2.5–3 mm wide **32. C. quintanilhae**
- 50a. Corolla lobes 8–12 mm long, scabrous outside. Seeds < 4 mm long **30. C. pubituberculatus**
 b. Corolla lobes 2.4–5.6 mm long, hispidulous outside. Seeds 4.3–6 mm long 51
- 51a. Leaf base obtuse, truncate or cordate. Fruit green with paler longitudinal stripes **29. C. prophetarum**
 b. Leaf base sagittate. Fruit monocoloured, yellow **34. C. thulinianus**
- 52a. Seeds ovate, 3.3–4 mm wide. Female corolla lobes 5.1–12 mm wide **38. C. metuliferus**
 b. Seeds elliptic, 2–3.1 mm wide. Female corolla lobes 2–4 mm wide 53

- 53a. Stems and petioles antrorse-strigose or retrorse-strigose. Central leaf-blade lobe pinnatifid. Aculei on fruit 1.3–13 mm 54
 b. Stems and petioles hispidulous, pilose, or scabrous. Central leaf-blade lobe entire. Aculei on fruit < 1.3 mm 55
- 54a. Male and female corolla glabrous inside, male corolla lobes obtuse at apex **29. C. prophetarum**
 b. Male and female corolla puberulent inside, male corolla lobes acute at apex. **35. C. zeyheri**
- 55a. Annual. Stems, petioles, leaves, pedicels of female flowers and fruits with break-away hairs. Male corolla lobes 4.8–6 mm wide **40. C. sacleuxii**
 b. Perennial. Stems, petioles, leaf blades, and pedicels of female flowers and fruit with persistent hairs. Male corolla lobes 1.3–2 mm wide. 56
- 56a. Leaf-lobes elliptic in outline. Leaf-blades hispidulous . . . **29. C. prophetarum**
 b. Leaf-lobes ovate in outline. Leaf-blades scabrous. **20. C. hastatus**

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