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A REVISION OF CYSTOSTEMON BALF. f. (BORAGINACEAE)

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ABSTRACT. The previously monotypic *Cystostemon* Balf. f. is revised and its circumscription widened to include *Vaupelia* Brand. The affinities of this essentially African genus are discussed. Two subgenera are recognized: subgenus *Cystostemon* containing eight species and the new subgenus *Austrovaupelia* A. G. Miller & H. Riedl containing five species. Four new species, *C. somaliensis* A. G. Miller & H. Riedl, *C. intricatus* A. G. Miller & H. Riedl, *C. virescens* A. G. Miller & H. Riedl, and *C. ethiopicus* A. G. Miller & H. Riedl, and one new subspecies, *C. hispidissimus* (S. Moore) A. G. Miller & H. Riedl subsp. *zambiensis* A. G. Miller & H. Riedl, are recognized. There are five new combinations in *Vaupelia*.

The genus *Cystostemon* was originally described by I. Bayley Balfour in 1884, based on a single species, *C. socotranus*, confined to Socotra. He recognized the genus chiefly on account of the peculiar staminal structure (see fig. 1,C). The stamens much exceed the corolla tube and are attached to it by short filaments which have small basal, triangular, ciliate appendages. Above each anther is a conspicuous aristate sterile appendage, and those of contiguous anthers cohere along their margins. The genus derives its name, however, from the swollen, almost round, filaments which in the case of *C. socotranus* are broader than the anthers.

Similar staminal structures are also found in the genus *Vaupelia* which Brand separated from *Trichodesma* in 1914 mainly on account of the basal attachment of the nutlets to a flat gynobase. In his discussion he noted the similarities between *Vaupelia* and *Cystostemon*. I. M. Johnston (1954) also realised the great similarity between the two genera and suggested that they should probably be united. He did not go any further because of a lack of material at his disposal.

Whilst preparing the description of a new species, *Cystostemon somaliensis*, which we originally intended describing in *Vaupelia*, it was observed that the staminal structure was very similar to that of *C. socotranus* (see fig. 3). *C. somaliensis* has a particularly broad filament and well-developed basal appendage and it became obvious that it would be extremely difficult to keep the two genera apart.

Vaupelia, as Brand recognized it, contained two distinct elements: *V. hispida*

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and *V. heliocharis* from NE tropical Africa, Kenya and Tanzania, and *V. barbata*, *V. medusa*, *V. mechowii* and *V. macranthera* from Angola, Zaire and Zambia. Both elements have short corolla tubes and exserted stamens with the terminal sterile appendages cohering laterally. However, those from the southwest of Africa have linear filaments and the basal filament appendages are represented by thickened ciliate ridges. There are also differences in facies and nutlet characters: the former are tall herbaceous perennials with woody rootstocks and ± spherical round-backed, distinctly keeled nutlets, whilst the latter are low herbs or shrubs with ± triangular nutlets with oblique acute tips and humped backs (fig. 1). After studying a considerable amount of material and assessing all the available morphological characters we decided that these two elements should be recognized at the rank of subgenera. *C. socotranus* is in subgenus *Cystostemon* and the southern African species are in the new subgenus *Austrovaupelia*. Subgenus *Austrovaupelia* now contains five species (fig. 5), the four mentioned above and *C. hispidissimus* described by Moore in 1920. Subgenus *Cystostemon* now contains eight species from tropical NE Africa, Socotra and SW Arabia (fig. 2,4): *C. hispidus*, *C. heliocharis* and *C. socotranus* mentioned above; *C. kissenioides* which Brand transferred from *Trichodesma* to *Vaupelia* in 1921; and the four new species described in this paper, *C. ethiopicus*, *C. intricatus*, *C. somaliensis* and *C. virescens*. Within subgenus *Austrovaupelia* there is uniformity in staminal structure, but in subgenus *Cystostemon* the shape and development of the filament and basal filament appendages vary considerably (fig. 3). *C. socotranus* has a triangular basal filament appendage and round filament, whereas in *C. ethiopicus* the basal appendage is reduced to a ciliate tuft reminiscent of that in subgenus *Austrovaupelia*, and the filament is narrowly elliptic and considerably narrower than the width of the anther-thecae. Within the subgenus there are intermediate stages between these two extremes.

In his original description Balfour (1884) used the spelling *Cystostemon* for the genus; however, in his later more complete description (1888) he used the spelling *Cystistemon*. As Balfour originally used *Cystostemon*, the later *Cystistemon* should be regarded as an unnecessary amendment as there are no strong reasons for changing the name.

AFFINITIES OF THE GENUS*

The taxonomic position of *Cystostemon* and *Vaupelia*, then considered as separate genera, has been previously discussed (Riedl, 1961). There seems little doubt, as then suggested, that the closest relatives of *Cystostemon* are among such genera of Lithospermeae as *Chọriantha*, *Maharanga* and *Onosma*. *Choriantha* is characterized by minute scale-like protuberances at the base of the filaments which may or may not be homologous to those in some species of *Cystostemon*, likewise the groups of tiny hairs in *Maharanga* may represent the remains of a ciliate ridge found in *Cystostemon*. The deeply cleft corollas of *Cystostemon* are very similar to those of members of *Onosma* sect. *Podonosma*.

Despite the similarity in floral structure between *Cystostemon* and *Trichodesma* this must be regarded as an example of convergent evolution. Although *Trichodesma* is included by most authors in Cynoglosseae, it probably

*This section is entirely the work of H. Riedl.

should be placed in the separate tribe Trichodesmeae (Fedoseeva, 1963; Riedl, 1968).

Another possible case of convergent evolution involving *Cystostemon* is to be found in *Nonea* of the Borageae (formerly Anchuseae). Here small scale-like protuberances in the throat of an otherwise undifferentiated, subcylindrical corolla may be compared with similar scales found at the base of the anthers of *Cystostemon* subgenus *Cystostemon*.

The argument proposed in 1961 that *Cystostemon*, *Choriantha*, *Maharanga* and *Onosma* sections *Podonosma* and *Protonosma* are ancient groups now widely separated geographically and confined to tropical Africa, Arabia and small areas in the eastern Mediterranean on one side, and to southern China and the Himalayas on the other still seem valid. They possibly come close to the ancestral stock which has given rise to a new, successfully expanding genus, *Onosma* s.str., which is now represented by about 150 species throughout the whole Mediterranean area.

Taxonomic Revision

In the following account measurements of corolla are taken from the base of the corolla tube to the tip of the linear lobes; measurements of corolla lobes are taken from the base of the sinus between the lobes and the tips of the lobes. Stamen length is taken from the base of the anther-thecae to the tip of the terminal sterile appendage, and the terminal appendage is measured from the top of the thecae to the tip of the linear appendage. Care must be taken to observe the indumentum closely; a strong lens (× 20) is usually needed to ascertain the direction of the shorter hairs on the stem. All specimens have been seen except where otherwise indicated. We are grateful to the directors of the following institutes for the loan of material: BM, COI, E, ETH, FI, K, LISC, LUAI, P, UPS, W. We should like to thank Jenny Ryrie and Sally Mackay for the maps and illustrations, Rose King for suggesting improvements to the key, Ian Hedge and Dr R. Brummitt (Kew) for useful help and discussion, and Dr Mats Thulin (Uppsala) for providing extra material of *C. ethiopicus* and *C. virescens* and for his comments on these species.

Cystostemon Balf. f., in Proc. Roy. Soc. Edinburgh 12: 82 (1883).

Syn.: *Vaupelia* Brand in Feddes Rep. 13: 82 (1914) — nomen. conserv.; M. L. Green in Kew Bull. 1935: 528 (1935).

Herbs or shrubs. *Leaves* alternate, entire. *Inflorescence* simple, slightly branched, or a much-branched panicle. *Calyx* 5-lobed, divided almost to the base, sometimes accrescent in fruit. *Corolla-tube* short, cylindrical, without scales in throat; lobes 5, much longer than the tube, narrowing into a linear tip, spreading at anthesis. *Stamens* 5, inserted on the corolla-tube; filaments short, linear, narrowly elliptic to round, sometimes inflated, with a basal triangular or oblong appendage which is sometimes reduced or with a thickened ciliate ridge; anthers much longer than filaments, with elongate, sterile, aristate, terminal appendages, longer than the anther-thecae and coherent along their margins. *Style* gynobasic, elongated. *Stigma* capitate. *Fruit* of 1–4 triquetrous or pyramidal nutlets, straight and erect, or nearly so, from a flat gynobase.

Type: *C. socotranus* Balf. f.

13 species in tropical NE Africa, Kenya, Tanzania, Socotra and SW Arabia, and in Zaire, Zambia and Angola.

KEY TO THE SPECIES

1. Herbaceous perennial, 1.5–2 m tall; corolla 15–30 mm; style (2–) 3–6 × as long as fruiting calyx 9
+ Low shrubs or herbs to 50(–80) cm tall; corolla 6–12 mm; style up to 2 × as long as fruiting calyx 2
2. Hairs inside calyx at least half as long as lobes, densely tufted. [Somalia] 4. *C. somaliensis*
+ Hairs inside calyx less than a quarter as long as lobes 3
3. Stem indumentum of long bristles and shorter, ± adpressed, antrorse hairs 4
+ Stem indumentum of long bristles and shorter omnidirectional or mainly retrorse hairs [great care and a good hand lens (× 20) is needed to see the direction of the shorter hairs] 5
4. Calyx lobes to 5 mm long; leaves up to 15 mm; low intricately branched shrub. [Somalia] ..... 5. *C. intricatus*
+ Calyx lobes more than 5 mm long; leaves 20–120 mm; erect, woody based herb ..... 1. *C. socotranus*
5. Flowers bright blue; inflorescence lengthening markedly in fruit; annual, rarely perennating, herb; corolla lobes straight. [Kenya, Tanzania] ..... 7. *C. hispidus*
+ Flowers white, yellow, greenish, pink or mauve; inflorescence not lengthening markedly in fruit; shrubs or if herbs then corolla markedly curved 6
6. Annual or perennial herb, sometimes woody based; basal filament appendage obscure; bristles on stem spreading. [N Kenya, S Ethiopia] 8. *C. virescens*
+ Shrubs; basal filament appendage well-developed, triangular or oblong, or if obscure then bristles on stem antrorse, ± adpressed 7
7. Bristles below the region of the inflorescence adpressed; basal filament appendage obscure. [S Ethiopia] ..... 6. *C. ethiopicus*
+ At least some bristles below region of the inflorescence spreading; basal filament appendage triangular or oblong 8
8. Leaves elliptic, margin not or hardly revolute; nutlet echinate-muricate. [S Yemen] ..... 2. *C. kissenioides*
+ Leaves oblong or oblong-elliptic, margin distinctly revolute or thickened; nutlet slightly verrucate. [N Yemen, Somalia] ..... 3. *C. heliocharis*
9. Leaves linear to linear-lanceolate, margin strongly revolute; abaxial leaf surface glabrous or at most with scabrous protuberances; adaxial surface and veins coarsely hispid. [Zaire] ..... 11. *C. barbatus*
+ Leaves lanceolate or oblong-elliptic, margins flat or slightly revolute; leaves with similar indumentum on both surfaces 10
10. Pedicels with patent hairs 2–3 mm long; bracts cordate to truncate at base. [SW Angola, W Zambia] ..... 12. *C. hispidissimus*
+ Pedicels with patent or ascending hairs 0.5–1 mm long; bracts narrowed at base 11

11. Leaves with short patent hairs; corolla 25–30 mm long. [E Angola, W Zambia] ..... 13. *C. mechowii*
+ Leaves with adpressed hairs, corolla 15–20(–25)mm long 12
12. Abaxial surface of leaf with hairs 0.5 mm long. [W Zambia] ..... *C.* sp. A
+ Abaxial surface of leaf with hairs c. 1 mm long 13
13. Calyx lobes (6–) 7–14 mm, linear-lanceolate; stems often branched. [SW Angola] ..... 9. *C. medusa*
+ Calyx lobes 3–5(–6.5) mm, narrowly elliptic; stems unbranched. [SW Angola] ..... 10. *C. macranthera*

Subgenus **Cystostemon**

Low herbs or shrubs up to 80 cm tall. *Inflorescence* ± simple, rarely somewhat branched below. *Staminal filaments* narrowly elliptic to round, base of filament with a triangular or oblong ciliate appendage, sometimes poorly developed. *Style* up to 2 × as long as fruiting calyx. *Nutlets* ± triangular with an oblique, acute beak and humped back, normally 2–4 developing.
Distribution of subgenus: SW Arabia, Socotra, Somalia, Ethiopia, Kenya and Tanzania.

1. C. socotranus Balf. f. in Proc. Roy. Soc. Edinburgh 12: 82 (1883). Fig. 1A; 2; 3a, m. Ic.: Trans. Roy. Soc. Edinburgh 31: t.66 (1888).

Erect perennial herb. *Stems* 30–60 cm, simple or slightly branched, indumentum of spreading tuberculate-based bristles, 2–3 mm long, and shorter antrorsely adpressed hairs. *Leaves* narrowly obovate or narrowly elliptic, tip acute, base cuneate; lower and basal leaves 40–120 × 8–25 mm, decreasing considerably in size above; upper surface of leaf with spreading tuberculate-based bristles of varying lengths, lower surface with short spreading hairs and bristles only on the midrib. *Inflorescence* branched, many-flowered. *Calyx* linear-oblong, 5–6.5 mm, increasing to 9–10 mm in fruit; exterior indumentum like that of stem, interior of dense white hairs. *Corolla* blue (yellow when dry) c. 9 mm long; lobes 6–7.5 mm, ovate, narrowing gradually or ± abruptly above into a long attenuate tip, margin minutely denticulate below; tube 1.5–2 mm. *Stamens* 7.5–8.5 mm long; anther-thecae c. 2.5 mm; terminal appendage 4.5–5 mm; basal filament appendage triangular; expanded portion of filament round, as wide as or wider than anther. *Style* 1.5 × as long as fruiting calyx. *Nutlets* c. 3 × 1.5 mm, brown with whitish papillae.
Type: Socotra, *Balfour, Cockburn & Scott* 309 (K). *Schweinfurth* 593.
SOCOTRA. Homhill, 1898–9, *Forbes & Ogilvie-Grant* 157 & 184 (E); *Balf. f.* s.n. (E).

C. socotranus is endemic to Socotra. Balfour (1888) notes that it is not uncommon on the limestone cliffs at altitudes of over 1500′.

2. C. kissenioides (Deflers) A. G. Miller & H. Riedl, **comb. nov.** Fig. 2, 3e, l.
Syn.: *Trichodesma kissenioides* Deflers in Bull. Soc. Bot. France 43: 119 (1896).
Vaupelia kissenioides (Deflers) Brand in Engler, Pflanzenr. 78 (iv 252): 44 (1921).

Low shrub. *Stems* branched, 40–60 cm, indumentum with spreading, tuberculate-based bristles c. 2 mm, and shorter adpressed to spreading hairs. *Leaves* 10–30 × 3–10 mm, decreasing in size upwards, elliptic, base attenuate, apex

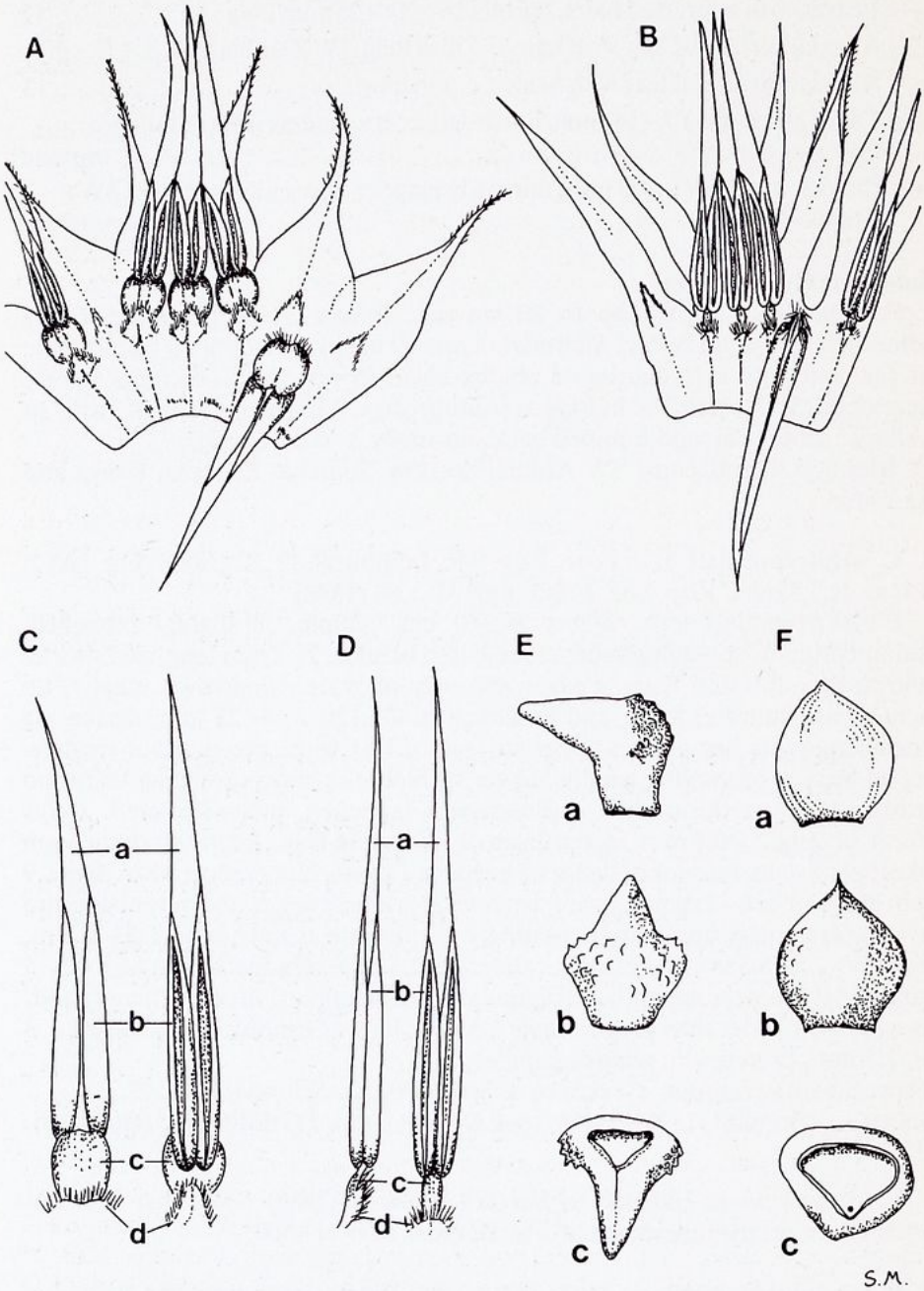

FIG. 1. A & B, opened corollas showing stamens: A, *Cystostemon socotranus*; B, *C. barbatus*. C & D, stamens showing outer and inner faces: C, subgenus *Cystostemon*; D, subgenus Austrovaupelia — a, terminal sterile appendage; b, anther-thecae; c, filament; d, basal sterile appendage. E & F, nutlets: E, subgenus *Cystostemon*; F, subgenus Austrovaupelia — a, side view; b, dorsal view; c, ventral view.

acute, margin not or hardly revolute, often with fascicles of smaller leaves in the axils of cauline leaves, indumentum ± same as stem except bristles adpressed. *Inflorescence* simple or slightly branched, c. 5-flowered, elongating slightly in fruit. *Calyx* linear-oblong, 6–8 mm elongating to 11–15 mm in fruit, indumentum like that of stem. *Corolla* yellow (when dry), 8–12 mm long; lobes 5–9 mm, ovate narrowing gradually above into long attenuate tip; tube 2–3.5 mm. *Stamens* c. 9 mm; terminal appendage c. 4 mm; basal filament appendage small ± triangular, hirsute; swollen part of filament elliptic, about half width of anther. *Style* ± equal to fruiting calyx. *Nutlets* 2–2.5 × 3.25–4 mm, whitish-brown, echinate-muricate.

Type: [PDRY, S Yemen] 'Hab. in convallibus regionis montanae inferioris. — Legi ad fauces australes montis el-'Areys (Bil. Fodhli), per altitud. 500–600 metr., mense Aprili desinente florens ac fructiferum', 1893, *Deflers* 1076. (holo. P).

C. kissenioides is known only from a single gathering from Jabal Areys in S Yemen. Deflers collected a number of new species on J. Areys, some of which are still only known from the type gatherings — for instance *Salvia areysiana* Defl., a very distinct species.

C. kissenioides is closely related to *C. heliocharis*. At first we thought that material from N Yemen also belonged to *C. kissenioides* but it is better placed under *C. heliocharis*. *C. kissenioides* differs from *C. heliocharis* mainly in the texture and shape of the leaves and in the surface patterning of the nutlet. More gatherings are needed from Jabal Areys before its relationship to *C. heliocharis* can be fully understood.

3. C. heliocharis (S. Moore) A. G. Miller & H. Riedl, **comb. nov.** Fig. 2; 3d, i.

Syn.: *Trichodesma heliocharis* S. Moore in J. Bot. 15: 68 (1877).
Vaupelia heliocharis (S. Moore) Brand in Feddes Rep. 13: 83 (1914).
T. stenosepalum Baker in Kew Bull. 1895: 221 (1895).

Woody-based perennial herb or low shrub. *Stems* branched 15–30 cm, indumentum with spreading or ± antrorse bristles and shorter adpressed or spreading hairs. *Leaves* 5–28 × 2–8 mm, ± decreasing in size upwards, oblong or oblong-elliptic, base cuneate, tip ± acute, margin thickened or revolute, often with fascicles of small leaves in the axils of the cauline leaves; indumentum ± same as stem except bristles adpressed, antrorse. *Inflorescence* simple or branched, 6–10-flowered, elongating slightly in fruit, ± secund. *Calyx* lobes linear-oblong, (5–)6.5–9 mm in flower, increasing to 9–12 mm in fruit; indumentum like that of stem but bristles ± antrorse, adpressed in flower; spreading in fruit. *Corolla* white, pink or mauve, (8.5–)9–11 mm long; lobes (6.5–)8–8.25 mm, ovate, narrowing gradually above into long attenutate tips; tube 3–3.5 mm. *Stamens* 7–8.5 mm; terminal appendage 4–4.5(–5) mm; basal filament appendage small, ± triangular or oblong, hirsute; swollen part of filament elliptic or oblong, one-quarter to two-thirds width of anther. *Style* 1.25–1.5 × as long as fruiting calyx. *Nutlets* 2.25–3 × 2 mm, whitish brown, slightly verrucose.

Type: [Somalia] Ad 'Serrusegebirge' ditione Somalensi, 1800 m, *Hildebrandt* 1417 (holo. BM; iso. K, W, FI).

N YEMEN. On stony hills S of Huth [16°15′N 43°59′E], 1900 m, 10 ix 1977, *J. R. I. Wood* 1606 (BM, K); Raydar, 60 km N of Sana'a, 2100 m, 31 x 1975, *Hepper*

6194 (K); Huth, 125 km N of Sana'a, 1900 m, 26 viii 1977, *Radcliffe-Smith & Henchie* 4783 (K,E); 5 km S of Huth on Sana'a road, 2100 m, 22 ix 1978, *Miller* 222 (E).

SOMALIA. Sugu, Al Hills, 10°58′N 48°53′E, 13 xi 1929, *C. N. Collenette* 268 (K); Gan Libah, 9°55′N 44°50′E, 1680 m, 15 xii 1958, *Mooney* 7630 (K); Mait escarpment, 1700 m, 28 x 1956, *Bally* 11248 (K); Hargeisa, 1400 m, 24 ix 1932, *Gillett* 4031 (K, FI); 18 miles E of Hargeisa, *Bally* 10833 (K); Hargeisa, 1200 m, 14 ix 1954, *Bally* 10374 (K); Golis range, 15 x 1906, *Drake-Brockman* 274 (K); Habrawal, Gan Libah, 1500 m, 1899, *Donaldson-Smith* s.n. (BM); Fodjor Escarpment, 1700 m, 13 ii 1954, *Bally* 9679 (K); Gan Libah, 1300 m, 2 vi 1949, *Bally* 7314 (K); Golis range, v 1895, *Cole* 291 (K) [type of *T. stenosepalum*]; Upper Sheik, *Lort-Philips* s.n. (BM); Upper Sheik, 1500 m, 2 vii 1919, *Godman* 74 (BM).

C. heliocharis in N Yemen is apparently restricted to a small area of limestone hills near Huth. It differs from the Somali plants in its white, not mauve or pink, corolla; there may also be differences in leaf shape and texture, although *Collenette* 268 is somewhat intermediate. More gatherings of *C. heliocharis* from Somalia may possibly prove it necessary to give the N Yemen population formal recognition.

The name *C. heliocharis* has previously been applied to all *Cystostemon* species collected in Somalia and Ethiopia. It is, however, geographically and ecologically distinct from the other species as it is found at higher altitudes on the escarpment in northern Somalia.

4. C. somaliensis A. G. Miller & H. Riedl, **sp. nov.** Fig. 2; 3b, j.

Differt a *C. heliocharidi* forma appendicis filamentorum, setis longioribus faciei interioris calycis et residuis persistentibus setosis petiolorum emortuorum in caulium basibus.

Suffrutex indumento argenteo-albo, hispidissimo. *Caules* 8–15 cm alti, ramosissimi, dense foliati, prostrati vel caespites densos formantes, in basi residuis persistentibus petiolorum emortuorum vestiti; setarum patentium 2–3 mm longarum ad basin interdum subbulbosarum et pilorum brevium pro maxima parte retrorsum. *Folia* oblanceolata, (5–)6–15 × 2–2.5 mm, margine revoluto, integro, sessilia, basi longe attenuata, apice acuta vel obtusa; indumentum setarum patentium usque ad 4 mm longarum et pilorum brevium. *Inflorescentia* pauciflora, cymae terminales ramis 1–2 lateralibus in parte inferiore. *Bracteae* foliis similes sed minores, 2 mm fere longae. *Pedicelli* patentes, 4–10 mm longi. *Calyx* (4–)5–6 mm in statu florifero, 7–8 mm sub fructu, lobis lineari-lanceolatis; indumentum eo foliorum simile sed pilis setisque antrorsis, intus usque ad 4 mm longis tenuioribus, dimidium longitudinis loborum ad minimum aequantibus. *Corolla* alba vel pallide flavescens, 7–10 mm longa, tubo 1.5–3(–4) mm inter stamina subglabra; lobi ovati, gradatim in apices longos attenuati, (4–)5–7 mm longi, extra pilosi. *Stamina* 5.5–6.5(–7) mm longa; antherae 2–2.5 mm, in dorso glabrae; appendix terminalis 3.5–4.5 mm; pars dilatata filamentorum latitudinem antherarum subaequens; appendices filamentorum manifestae, triangulares, decurrentes, breviter pubescentes, 0.75–1.5 mm supra basin coroliae affixae. *Ovarium* glabrum. *Stylus* filiformis, calycem aequans vel quarta parte superans. *Nuculae* dilute brunneae, triquetrae, rostro obliquo, acuto, dorso convexe gibboso, facie interiore concava, verrucosae, 2.5 × 1.5 mm.

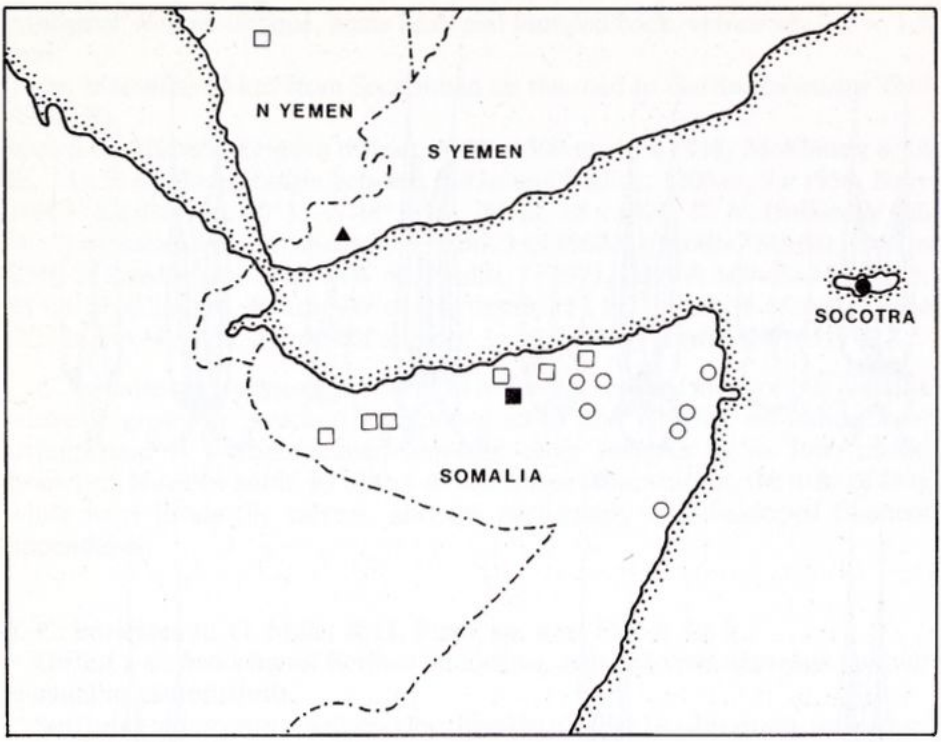

FIG. 2. Distribution of *C. socotranus* ●, *C. heliocharis* □, *C. kissenioides* ▲, *C. intricatus* ■, *C. somaliensis* ○.

Differing from *C. heliocharis* in the form of the filament appendage, the longer hairs inside the calyx, and the persistent, setose, petiolar remains on the stem.

Subshrub with a silvery-white, strongly hispid indumentum. *Stems* 8–15 cm high, much branched, densely leafy, prostrate or forming dense hummocks, clothed at base with persistent, setose, petiolar remains; indumentum of tuberculate, spreading setae, 2–3 mm long, and shorter, mainly retrorse, adpressed hairs. *Leaves* oblanceolate, (5–)6–15 × 2–2.5 mm, revolute, entire, sessile with long attenuate base, acute or obtuse; indumentum of patent setae up to 4 mm long and shorter antrorse hairs. *Inflorescences* few-flowered, terminal cymes with 1 or 2 lateral branches below. *Bracts* similar to leaves but smaller, c. 2 mm long. *Pedicels* 4–10 mm, erect-spreading. *Calyx* with linear-lanceolate lobes, (4–)5–6 mm, increasing to 7–8 mm in fruit; exterior indumentum as on stem but all hairs ascending, interior with long villous hairs c. 4 mm long, at least half as long as the calyx lobes. *Corolla* white or pale yellow, 7–10 mm, with tube 1.5–3(–4) mm, almost glabrous between stamens; lobes ovate, gradually narrowing into long attenuate tips, (4–)5–7 mm, tomentose outside. *Stamens* 5.5–6.5(–7) mm; anthers 2–2.5 mm, glabrous dorsally; terminal appendage 3.5–4.5 mm; expanded portion of filament almost equalling width of anthers; filament appendages well-developed, triangular, decurrent on corolla tube, shortly pubescent, attached 0.75–1.5 mm from base of corolla tube. *Ovary* glabrous. *Style* filiform, 1–1.25 × the length of the calyx. *Nutlets* light-brown,

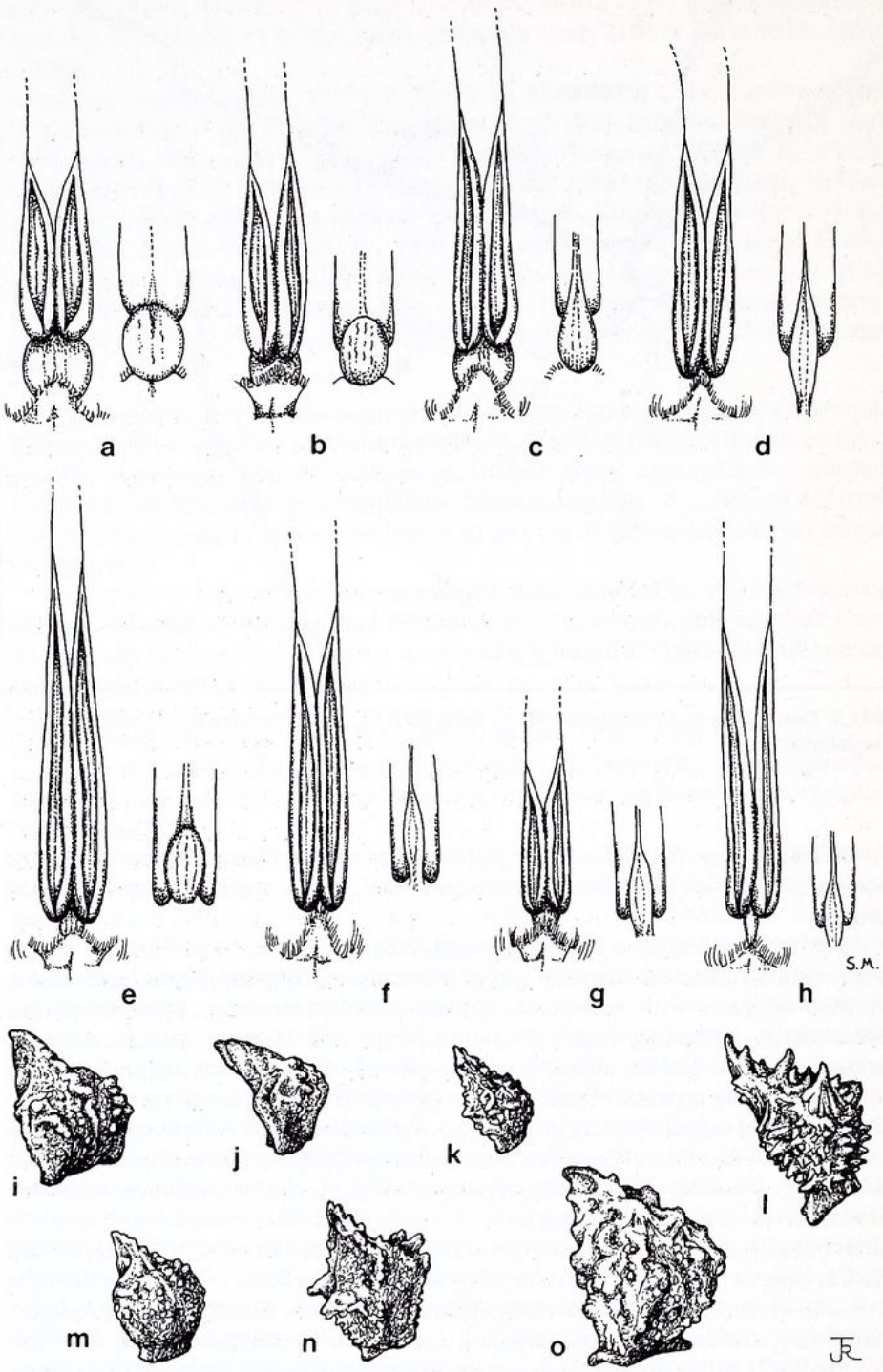

FIG. 3. Subgenus *Cystostemon*, anthers (insets show the outer faces of the filaments): a, *C. socotranus*; b, *C. somaliensis*; c, *C. hispidus*; d, *C. heliocharis*; e, *C. kissenioides*; f, *C. ethiopicus*; g, *C. intricatus*; h, *C. virescens* — all × 10. Nutlets: i, *C. heliocharis*; j, *C. somaliensis*; k, *C. intricatus*; l, *C. kissenioides*; m, *C. socotranus*; n, *C. ethiopicus*; o, *C. hispidus* — all × 6.

triangular with an oblique, acute beak and humped back, verrucose, 2.5 × 1.5 mm.

Type: [Somalia] 60 km from Scusciuban on the road to Gardo, *Lavranos* 7239 (holo. E).

SOMALIA. Hubera, Erigavo district, 1200–1500 m, 10 x 1938, *McKinnon* 8/12 (K, FI); E Al Madu Range, between Buran and Baditir, 1200 m, 9 x 1956, *Bally* 10963 (K); Hormo, 10°33′N 48°59′E, 760 m, 19 x 1929, *C. N. Collenette* 168 (K); S of Scusciuban on the road to Gardo, 3 xii 1969, *Lavranos* 7248 (E); 104 km ENE of Scusciuban, 14 km NW of Hordio, 7 i 1973, *Bally & Melville* 15640 (K); 95 km E of Sinugif, 40 km NW of Eil Airstrip, 1 i 1973, *Bally & Melville* 15464 (K); 16 km N of Eil, 2 km N of airstrip, 3 i 1973, *Bally & Melville* 15517 (K).

C. somaliensis is apparently restricted to the dry lowland areas of NE Somalia where it grows in *Acacia-Commiphora* scrub and is often an indicator of overgrazing. It is characterised amongst other features by its low, much-branched, shrubby habit, its silvery-white, setose indumentum, the tufts of long white hairs inside the calyces, and the particularly well-developed filament appendages.

5. C. intricatus A. G. Miller & H. Riedl, **sp. nov.** Fig. 2; 3g, k.

Differt a *C. heliocharidi* floribus minoribus, setis antrorsis appressis caulium et caulibus ramosissimis.

Suffrutex indumento argenteo-albo, hispido. *Caules* 10–25 cm alti, numerosi, ramosissimi, erecti vel ascendentes setis patentibus vel antrorse ascendentibus basi subbulbosis 1–1.5 mm longis et pilibus antrorsis appressis. *Folia* anguste oblonga, 6–14 × 1–1.5 mm, margine integro, revoluto, sessilia, acuta, setis appressis disco basali insidentibus et pilis appressis disco basali carentibus. *Inflorescentia* cyma terminalis simplex, 5–8-flora, post florendum paulo elongata. *Bracteae* foliis similes sed minores, c. 2 × 0.75 mm, pedicellis multo breviores. *Pedicelli* erecto-patentes, calycem aequantes vel eo breviores. *Calycis lobi* lineares, 3–4 mm longi, post florendum ad 4.5 mm accrescentes, setis longis patentibus et pilis antrorse adpressis brevibus strigosis vestiti, intus pilis longis villoso-sericeis. *Corolla* rosea, basin versus albescens, demum flavescens, tubo 1 mm longo inter filamenta breviter pubescens, lobis 4.5–5.5 mm longis, anguste lanceolatis apice longe attenuato, integris, extra apice pilosis. *Stamina* 5.5 mm longa; antherae 2 mm longae, in dorso glabrae; appendice terminali 2.5 mm longa, lineari; filamenta brevia, 0.5 mm supra basin corollae affixa, parte dilatata anthera paulo angustiore; appendice filamenti triangulari, breviter pubescenti. *Ovarium* glabrum. *Stylus* filiformis, calycis lobis quarta parte vel dimidio fere longior. *Nuculae* albescentes, rostro obliquo acuto, dorso convexe gibboso verrucosae, 2–2.5 × 1 mm.

It differs from *C. heliocharis* in the smaller flowers, antrorse, adpressed hairs on the stem and the much-branched stems.

Subshrub with a silvery-white, hispid indumentum. *Stems* 10–25 cm, numerous, much-branched, erect or ascending, with antrorse adpressed hairs and patent or ascending tuberculate-based setae 1–1.5 mm long. *Leaves* narrowly oblong, 6–14 × 1–1.5 mm, entire, revolute, sessile, acute; indumentum similar to stem but with antrorse adpressed setae. *Inflorescence* a simple terminal cyme, 5–8-flowered, elongating slightly in fruit. *Bracts* similar to leaves but smaller, c. 2 × 0.75 mm, much shorter than pedicels. *Pedicels* erect-

spreading, equalling to shorter than calyx. *Calyx* with linear lobes, 3–4 mm long increasing to 4.5 mm in fruit, with long patent setae and shorter antrorse, adpressed strigose hairs; inner surface with villous sericeous hairs. *Corolla* pink, shading to white then yellow at the base, tube 1 mm, shortly pubescent between filaments, lobes 4.5–5.5 mm, narrowly lanceolate with a long attenutate tip, entire, tip tomentose outside. *Stamens* 5.5 mm long; anthers 2 mm long, glabrous on back; terminal appendage 2.5 mm long, linear; filaments short, attached 0.5 mm from base of the tube; expanded part of filament slightly narrower than anther; filament appendage triangular, shortly pubescent. *Ovary* glabrous. *Style* filiform, 1.25–1.5 × as long as the calyx lobes. *Nutlets* whitish, triangular with an oblique acute beak and a humped back, verrucose, 2–2.5 × 1 mm.

Type: Somalia, Erigavo grazing reserve nr guest house, savannah scrub on gypsaceous plain in fairly dense bush, 18 i 1973, *Bally & Melville* 16024 (holo. K). SOMALIA. Erigavo, open gypsum plains, 1753 m, 29 v 1939, *McKinnon* 5/270 (K).

This distinctive species is apparently restricted to gypsaceous soils in the Erigavo district. H. B. Gilliland (in The vegetation of Eastern British Somaliland, *J. Ecol.* 40: 105, 1952) notes that 'Such gypsum-tolerant species are characteristic, and the vegetation of the gypsum areas is different from that on the small limestone, sandstone and volcanic rocks'. Another gypsum-tolerant species also recently described from the Erigavo district is the remarkable *Brassica somalensis* Hedge & Miller which occupies an extremely isolated position in its genus.

6. C. ethiopicus A. G. Miller & H. Riedl, **sp. nov.** Fig. 4; 3f, n.

A *C. heliocharidi* differt appendicibus filamentorum minoribus et imprimis setae omnino appresso infra regionem inflorescentiae.

Frutex (vel suffrutex) scabra, flavescenti-incana. *Caules* usque ad 80 cm alti, erecti vel ascendentes, paulo ramosi, indumento setis basi bulbosis pilisque brevioribus immixtis appressis vel subpatulis strigosis usque ad 1 mm longis composito. *Folia* anguste elliptica usque ad elliptica (vel subspathulata), 20–60 × (3–) 5–18 mm, margine integro, interdum revoluto, sessilia, apice acuta vel obtusa, setis tenuissimis et pilis brevioribus omnibus appressis vestita; rosulae steriles foliorum parvulorum in axillis foliorum caulinorum interdum evolutae. *Inflorescentia* cyma terminalis, vel axillaris, cymae (3–)6–9-florae, post florendum paulo elongatae. *Bracteae* foliis similes sed minores, lineares usque ovatae, c. 10 × 2 mm. *Pedicelli* (florendi tempore 2–3 mm) 7–9 mm, erecto-patentes. *Lobi calycis* lineari-oblongi, 6–7 mm longi, post florendum paulo accrescentes, indumento eo caulis simili, intus e pilis c. 1.5 mm longis villoso-sericeis. *Corolla* alba centro virescente, 12 mm longa, tubo 3.5 mm longo, inter filamenta pubescenti, lobis ovatis in apicem anguste linearem longe attenuatis apice extra pilosa. *Stamina* 9.5 mm longa, antheris 4.5 mm longis, in dorso tuberculatis, appendicibus terminalibus 5 mm longis, filamentis brevibus, 2 mm supra basin tubi affixis, parte dilatata angusta, dimidio latitudinis antherarum angustiore, appendicibus filamentorum parvulis, indistinctis, pilis villosis tectis. *Ovarium* glabrum. *Stylus* calyce fructifero sesqui ad duplo longior. *Nuculae* albidae, triquetrae, rostro obliquo, acuto, dorso convexe gibboso, minute verruculosae, 3 × 1.75 mm.

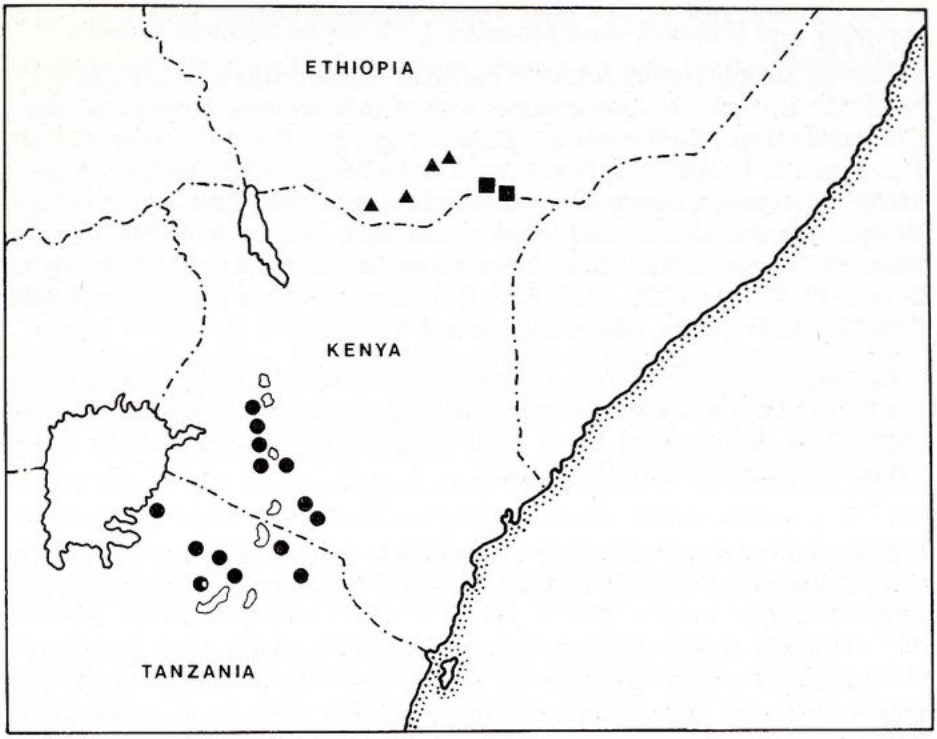

FIG. 4. Distribution of *C. virescens* ■, *C. ethiopicus* ▲, *C. hispidus* ●.

It differs from *C. heliocharis* in its smaller filament appendages and the totally adpressed setae below the inflorescence.

Shrub or subshrub; whole plant scabrous, yellowish grey. *Stems* c. 80 cm high, erect or ascending, sparsely branched; indumentum of antrorse, adpressed, tuberculate, strigose hairs, c. 1 mm long, and shorter spreading hairs. *Leaves* narrowly elliptic to elliptic or subspathulate, 20–60 × (3–)5–18 mm, entire, sometimes revolute, sessile, apex acute or obtuse, indumentum similar to the stem; fascicles of smaller leaves often present in the axils of the cauline leaves. *Inflorescence* terminal or of axillary cymes, c. (3–)6–9-flowered, elongating slightly in fruit. *Bracts* similar to leaves but smaller, linear to ovate, c. 10 × 2 mm. *Pedicels* (2–)7–9 mm, erect-spreading. *Calyx* lobes linear-oblong, 6–7 mm long, slightly enlarging in fruit, hairs similar to stem, inner surface villous-sericeous, hairs c. 1.5 mm long. *Corolla* white with greenish centre, 12 mm long, tube 3.5 mm, pubescent between filaments, lobes ovate narrowing into long attenuate, linear tip, tip pilose outside. *Stamens* 9.5 mm long; anther 4.5 mm long, tuberculate on back, terminal appendages 5 mm long; filaments short, attached 2 mm from base of corolla tube, expanded part of filament narrow, under half width of anther; filament appendages, small, poorly developed, with villous hairs. *Ovary* glabrous. *Style* 1.5–2 × as long as fruiting calyx. *Nutlets* whitish, triangular, with an oblique, acute tip and humped back, minutely verrucose, 3 × 1.75 mm.

Type: Ethiopia, Sidamo region, 11 km from the turning to Mega on the road from Negele, c. 5°12′ N 39°37′ E, limestone slope with scattered low trees of *Pistacia*, *Combretum* etc., shrub, 0.5 m, flowers white with green centre and

brown stamens, 1650 m, 11 v 1980, *Thulin, Hunde & Tadesse* 3572 (holo. UPS; iso. ETH, K).

ETHIOPIA. Sidamo region: About 35 km SE of Negele on the road to Filtu, 5°15′ N 39°55′ E, rocky limestone slopes with *Acacia nilotica, Barbeya oleoides, Commiphora* sp., *Terminalia* sp., *Balanites* sp., etc., 2 xi 1972, *Friis, Gilbert, Rasmussen & Vollesen* 908 (K); 38 km on the Negele–Filtu road, c. 5°13′ N 39°52′ E, *Acacia, Commiphora* woodland on limestone, shrublet, 0.5 m high, flowers with green centre and brownish stamens, 1500 m, 12 v 1980, *Thulin, Hunde & Tadesse* 3576 (UPS, K); Negele, 3 iv 1937, *Cufodontis* 233 (FI); Negele, 24 iv 1939, *Corradi* 6225, 6227, 6229 (FI); Mega, 8–24 ix 1939, *Corradi* 6400 (FI); Uacille [Wachille], 25 ix 1939, *Corradi* 6224 (FI).

C. ethiopicus is known from a number of gatherings from the Sidamo region of southern Ethiopia, and is geographically separated from its closest allies in the genus. It is distinguished by its small filament appendages and the totally antrorse setae below the inflorescence.

7. C. hispidus (Baker & Wright) A. G. Miller & H. Riedl, **comb. nov.** Fig. 4; 3c, o.

Syn.: *Trichodesma hispidum* Baker & Wright in Oliver, Fl. Trop. Africa 4(2): 45 (1905).

Vaupelia hispida (Baker & Wright) Brand in Feddes Rep. 13: 83 (1914).

Annual, sometimes perennating, hispid, green herb. *Stems* 30–60 cm, sparsely branched, indumentum with long, 1–2 mm, patent to ascending hispid setae and shorter, retrorse hairs. *Leaves* 40–150 × (2–)4–18 mm, lanceolate, base attenuate, tip acute, revolute or not; indumentum as stem but all hairs antrorse. *Inflorescence* elongating markedly in fruit to 10–20 cm. *Calyx* 4–5 mm increasing to 5–6(–8) mm in fruit, linear lanceolate. *Corolla* blue, 6.5–10 mm; tube 2.3 mm; lobes 4.5–7 mm, triangular narrowing to an attenuate tip. *Stamens* 6–7 mm, terminal appendage 3–4 mm, filament appendage hirsute. *Style* 1.25–1.5 × fruiting calyx. *Nutlet* (2.5–)3–3.5 × 1.5–2.25 mm, whitish brown, verrucate.

Type: [Kenya] nr Lake Elmeita, *Scott-Elliot* 6640 (lecto. K — selected here; isolecto. BM).

KENYA. Lake Naivasha distr., 1900 m, 8 i 1964, *Polhill* 46 (K); ibid., 1800 m, v 1932, *Napier* 2078 (K); ibid., West Rift, 1900 m, 20 ix 1966, *Polhill* 20A (K); Naivasha, 1900 m, 31 vii 1971, *Polhill* 135 (K); Kikuya on road to Eldama ravine, 1200–1800 m, v 1900, *Whyte* s.n. (K); Namanya to Kojiado, 91 miles from Nairobi, 1300 m, 16 xii 1961, *Polhill & Paulo* 1008 (K, FI); 88 miles from Namanya on Nairobi road, 1500 m, 26 vi 1961, *Morrison* 3085 (K); Bissel, 1700 m, viii 1950, *Bally* 7769 (K).

TANZANIA. Serengeti, 1500 m, 24 iv 1965, *Richards* 20269 (K); Musoma district, Naabi Hill, Serengeti, 22 viii 1962, *Adamson* 12672 (K); Lake Kakesio, 1700 m, *Newbould* 5085 (K); Embagai, W Arusha distr., 2150–2450 m, 5 ii 1932, *St Clair-Thompson & Dale* 1253 (K); E Ngorongoro crater, 1500 m, iv 1941, *Bally* 2411 (K); Masai distr., Ngorongoro conservation area, Laetolil–Olduvai road, 1700 m, 26 ix 1977, *Raynal* 19290 (P, E); ibid., Kitumbeine Mt, 1828 m, 3 iii 1969, *Richards* 24269 (E); Arusha distr., Engari Nanyuki-oshi road, 4 miles from Arusha to Nairobi road turn-off, 1450 m, 28 xii 1961, *Greenway* 10416 (K); En Doinyo Embalen, 1650 m, 9 ii 1962, *Newbould* 6008 (K); Lake Laggia, 24 i 1937, *Moore* 16 (K).

Apparently common on low dry grasslands (rarely ascending to c. 2000 m in subalpine grassland) with *Pennisetum meziancum* and *Commiphora-Acacia* scrub.

8. C. virescens A. G. Miller & H. Riedl, **sp. nov.** Fig. 4; 3h.

Differt a *C. hispido* corolla virescenti-cremea, sursum versa, lobis ovatis apicibus abrupte attenuatis; appendicibus basalibus filamentorum inconspicuis anguste oblongis, parte dilatata filamenti angustiore; bracteolis calycem superantibus vel partim obtegentibus.

Herba annua vel perennis, viridescenti-flavescens, sparse hispida. *Caulis* 10–40 cm altus, erectus, simplex vel parce ramosus; indumentum constat ex setis patentibus, basi bulbosis, 2–3.5 mm longis et pilis brevioribus; in basi residuis foliorum emortuorum tectus. *Folia* lanceolata, 25–80 × 3–13 mm, margine paulo revoluto vel incrassato, integro, basin versus longe attenuata, superiora sessilia, inferiora ± petiolata, apice acuta; indumentum eo caulis similis, sed sat sparsum. *Inflorescentia* racema simplex vel cymae pedunculatae, c. 2.5 cm longae, terminales et e foliis superioribus axillares. *Bracteae* foliis similes; bracteolae saepe calycem superantes vel partim obtegentes. *Pedicelli* erecto-patentes, calyce breviores. *Calyx* 7–10 mm longus; lobi lanceolati ad linearioblongi, ut folia virides; indumentum extra constat e setis sparsis et pilis brevioribus antrorsis, intus e setis densioribus longioribusque. *Corolla* viridescenti-cremea, 7–10 mm longa, sursum versa; tubus 2.5–3 mm longus, inter filamenta pubescens; lobi ovati, abrupte attenuati, 3.5–5.5 mm longi, apicibus extra pilosis. *Stamina* 8–10 mm longa, antherae 3.5–5 mm, extra paulo tuberculata; appendices terminales 5–6 mm longae; filamenta brevia, 1.5 mm supra basin corollae inserta, parte dilatata antheris dimidio angustiores; appendix filamentorum anguste oblonga, 0.5 mm longa, subsericea. *Ovarium* glabrum. *Stylus* filiformis, calycem fructiferum partem quartam longitudinis superans. *Nuculae* ignotae.

Differs from *C. hispidus* in its greenish cream upwardly curved corolla and filament appendages, by the shape of the inconspicuous basal filament appendages, by the narrower expanded filament, and by the bracteoles exceeding the calyx or partly covering it.

Annual or perennial herb, sometimes shrubby; whole plant greenish yellow, slightly hispid. *Stems* 10–40 cm, erect, simple or sparsely branched; indumentum of patent, tuberculate-based hispid hairs, 2–3.5 mm long, and shorter, dense, patent hairs; sometimes clothed at base with withered leaves. *Leaves* lanceolate, 25–80 × 3–13 mm, margin slightly revolute or thickened, entire, base long-attenuate, upper leaves sessile, lower ± petiolate, apex acute; indumentum similar to stem but relatively sparse. *Inflorescence* a simple raceme or pedunculate cymes, c. 2.5 cm long, terminal and from the axils of the upper leaves. *Bracts* leaf-like; bracteoles often exceeding and partly hiding calyces. *Pedicels* erect-spreading, shorter than calyx. *Calyx* 7–10 mm long; lobes lanceolate to linear-oblong, somewhat leaf-like, green, outer indumentum with a few scattered antrorse bristles amongst loosely arranged antrorse hairs; inner indumentum denser with longer bristles or hairs. *Corolla* greenish cream, lobes paler; tube 2.5–3 mm long, pubescent between filaments; lobes 7–10 mm long, upwardly curved, ovate, narrowing, sometimes abruptly, into linear lips, 3.5–5.5 mm long, outer surface of tips pilose. *Stamens* 8–10 mm long, purplish; anthers 3.5–5 mm, slightly tuberculate on outer surface; terminal appendage

5–6 mm long; filament short, attached 1.5 mm from base of corolla tube, expanded portion less than one-half the width of anther; basal filament appendage inconspicuous, narrowly oblong, up to 0.5 mm long, villous to almost sericeous. *Ovary* glabrous. *Style* filiform, 1.25 × fruiting calyx. *Nutlets* unknown.

Type: Kenya, Northern Province, 24–27 km E of Banessa on Ramu road, 3°52′ N 40°34′ E, limestone with thin pale brown soil, *Commiphora-Acacia* scrub, 810 m, 22 v 1952, *Gillett* 13267 (holo. K).

KENYA. Mandera, 30 km from Ramu on Malka Mari road, 4°04′ N 40°59′ E, limestone valley, *Commiphora* woodland with scattered *Sterculia*, *Terminalia*, etc., 400 m, 6 v 1978, *Gilbert & Thulin* 1523 (UPS, K).

ETHIOPIA. Sidamo region, nr boundary marker 55 at the Kenya border, 4°07′ N 40°24′ E, hillside with *Acacia-Commiphora* woodland on thin soil, 960 m, 5 v 1978, *Gilbert & Thulin* 1492 (UPS).

C. virescens superficially resembles *C. hispidus* but differs in several important characters: the most obvious being the greenish cream, not blue, corolla and the upwardly curved corolla lobes and terminal staminal appendages — the last a character not developed strongly elsewhere in the genus. The basal filament appendage and expanded portion of the filament are poorly developed and relatively inconspicuous compared with those of *C. hispidus*. Other differences in the form of the inflorescence and in the indumentum, together with its isolated geographical position, point to this being a distinctive new species.

Subgenus **Austrovaupelia** A. G. Miller & H. Riedl, **subgen. nov.**

Herbae 1.5–2 m altae caulibus simplicibus vel ramosis e rhizomate lignoso orientibus. *Inflorescentia* thyrsus ramosissimus. *Stamina* filamentis basi haud dilatatis elevatione transversali ciliata ad basin ornatis. *Stylus* (2–)3–6-plo calyce fructifero longior. *Nuculae* subsphaeroideae apice carinato, dorso rotundato.

Herbs, 1.5–2 m tall, with simple or branched stems from a woody rootstock. *Inflorescence* a much-branched thyrse. *Stamens* with linear unexpanded filaments; base of filament with a thickened, ciliate ridge. *Style* (2–)3–6 × as long as fruiting calyx. *Nutlets* ± spherical with a keeled tip and rounded back.

Type species: *C. barbatus* (Vaupel) A. G. Miller & H. Riedl

Distribution of subgenus: Angola, Zaire and Zambia.

9. C. medusa (Baker) A. G. Miller & H. Riedl, **comb. nov.** Fig. 5; 6c.

Syn.: *Trichodesma medusa* Baker in Kew Bull. 1894: 29 (1894).

Vaupelia medusa (Baker) Brand in Feddes Rep. 13: 82 (1914).

Perennial herb. *Stems* 80–180 cm, many from woody rootstock, branched above, indumentum with ± tuberculate-based antrorse or spreading bristles and shorter hairs. *Leaves* lanceolate, (5–) 6–8(–11) cm, apex acute, rounded at base, subsessile, with indumentum of adpressed strigose hairs. *Inflorescence* a dense terminal panicle. *Calyx* lobes linear-lanceolate, (6–)7–14 mm, outside with dense spreading to antrorse dirty white hairs, inside with ± tufted finer hairs, c. half as long as calyx. *Corolla* blue or violet, 17–25 mm long; tube (3–)5–6 mm; lobes (3–)5–20 mm, ovate or triangular below, narrowing into a

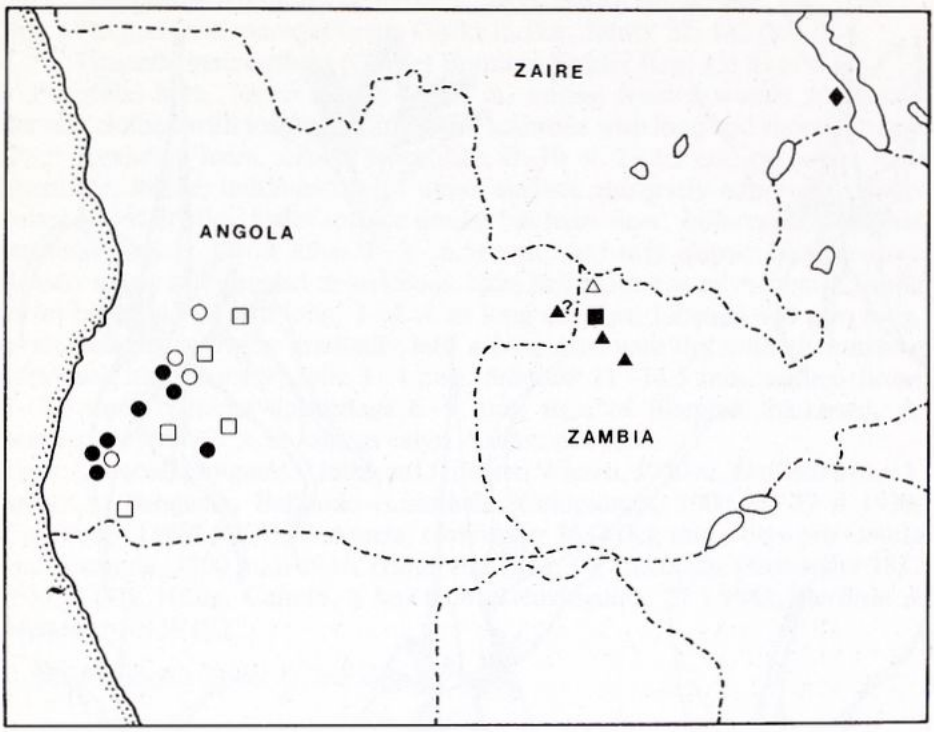

FIG. 5. Distribution of *C. barbatus* ◆, *C. macranthera* ○, *C. medusa* ●, *C. hispidissimus* subsp. *zambiensis* △, *C. hispidissimus* subsp. *hispidissimus* □, *C. mechowii* ▲, *C.* sp. *A* ■.

long attenuate tip, outside with short spreading hairs. *Stamens* (12–)15–20 mm long, anther-thecae 5–7 mm; terminal appendage 9–13 mm long; base of filament thickened, pubescent. *Style* 2–3 × as long as calyx. *Nutlets* c. 4 × 5 mm, rugose.

Type: Angola, Humpata plateau in Huila district, *Welwitsch* 5302 (lecto. K — selected here; isolecto. BM, COI, P).

ANGOLA. Benguela, *Gossweiler* s.n. (K); ibid., 4 v 1906, *Gossweiler* 3163 (K, BM); ibid., between Ganda and Caconda, 1700 m, 1932/3, *Hundt* 556 (BM, COI); ibid., Caconda, 1600 m, 22 vi 1937, *Exell & Mendonça* 3028 (COI); Huila, Quilengues, between Cacula and Negola, 13 viii 1965, *Azancot de Menezes* 1859 (LISC, LUAI); ibid., Sa de Bandeira, Hoque, 3 vi 1966, *Henriques* 1083 (LISC); ibid., road Sa de Bandeira to Nova Lisboa, 1 mile N of Caluquembe, 29 iv 1968, *Kers* 3415 (LISC); ibid., Sa de Bandeira, road to Cacula km 13, 10 v 1962, *Henriques & de Sousa* 23 (BM, LUAI, LISC, COI); ibid., *Newton* s.n. (COI); ibid., Humpata, Palanca, 2000 m, 4 vi 1937, *Exell & Mendonça* 2556 (BM, COI); Humpata, Chella mts, ix 1883, *Johnston* s.n. (K); Serra da Chella, nr Sa de Bandeira (Lubango), 1900 m, viii 1937, *Humbert* 16241 (BM, K); Kassinga to Chihanda, 1328 m, 19 v 1900, *Baum* 928 (E, BM, W).

C. medusa has often been confused with *C. macranthera*. Apart from the longer calyx lobes, *C. medusa* can also be separated by a difference in texture of the leaves which is difficult to describe but which perhaps reflects a slight fleshiness *in vivo*.

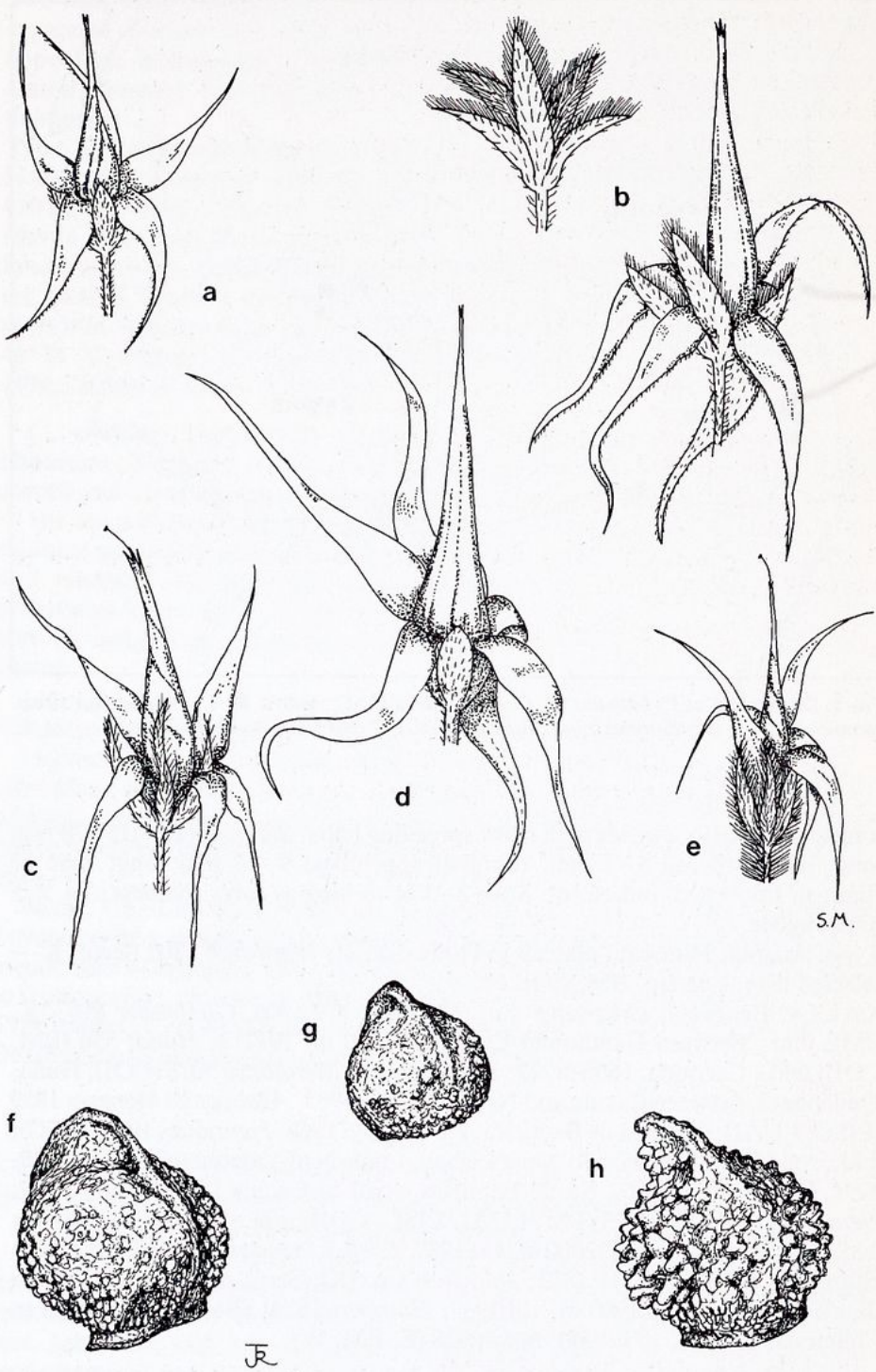

FIG. 6. Subgenus Austrovaupelia, flowers: a, *C. macranthera*; b, *C. barbatus*, with fruiting calyx; c, *C. medusa*; d, *C. mechowii*; e, *C. hispidissimus* — all × 2. Nutlets: f, *C. hispidissimus* subsp. *zambiensis*; g, *C.* sp. A; h, *C. mechowii* — all × 6.

10. C. macranthera (Gürke) A. G. Miller & H. Riedl, **comb. nov.** Fig. 5; 6a.
Syn.: *Trichodesma macrantherum* Gürke in Bot. Jahrb. 32: 142 (1902).
Vaupelia macranthera (Gürke) Brand in Feddes Rep. 13: 83 (1914).

Perennial herb. *Stems* simple 1.5–2 m, arising from a woody rootstock, densely clothed with leaves, indumentum scabrous with long and short antrorse or ± spreading hairs. *Leaves* lanceolate, 6–10 × 2–2.5 cm, tip acute, base attenuate, sessile; indumentum of upper surface antrorsely adpressed, tuberculate-based bristles; lower surface similar but hairs finer. *Inflorescence* a dense terminal panicle. *Calyx* lobes 3–5(–6.5) mm, narrowly elliptic; indumentum densely antrorse adpressed ± sericeous, hairs half as long as calyx lobes. *Corolla* violet-blue, 14–16 mm long, 3–4 × as long as calyx; lobes 11–13 mm long, ovate below narrowing gradually into a long attenuate tip, with ± antrorse adpressed hairs outside; tube 3–4 mm. *Stamens* 11–14.5 mm, anther-thecae 5–7.5 mm, terminal appendage 6–9 mm; base of filament thickened, ± bearded. *Style* 4–5 × as long as calyx. *Nutlets* not seen.
Type: [Angola] Benguela: Huila, auf feuchten Wiesen, 1720 m, *Dekindt* 8 (n.v.).
ANGOLA. Benguela, Bailundo–Luimbale, Colupiango, 1900 m, 27 ii 1938, *Gossweiler* 11973 (COI); Benguela, *Gossweiler* 3637 (K); ibid., between Ganda and Caconda, 1700 m, ii 1934, *Hundt* 831 (BM, P); Caconda, *Gossweiler* 3837 (BM, COI); Huila, Caholo, 8 km from Tchivinguiro, 27 i 1962, *Barbosa & Mendosa* 10139 (K).

See comments under *C. medusa*.

11. C. barbatus (Vaupel) A. G. Miller & H. Riedl, **comb. nov.** Fig. 1 B; 5; 6b.
Syn.: *Trichodesma barbatum* Vaupel in Bot. Jahrb. 48: 528–9 (1913).
Vaupelia barbata (Vaupel) Brand in Feddes Rep. 13: 82 (1913–15).
Ic.: Flore d'Afrique centrale (Zaire-Rwanda-Burundi), Boraginaceae, t. 6 (1971).

Woody based perennial herb. *Stems* simple, to 1.2 m, with a dense indumentum of short scabrid hairs with scattered longer bristles. *Leaves* densely clothing stem, linear to linear-lanceolate, 3.5–8 × 0.3–0.6 cm, sessile, base ± truncate, tip acute, margin strongly revolute, abaxial surface except for midrib ± glabrous, adaxial surface and midrib coarsely hispid with antrorse bristles. *Inflorescence* a dense terminal panicle. *Calyx* lobes 6–9 mm, linear-lanceolate; outside with antrorse, adpressed, short, dense hairs; inside with long ± tufted bristles. *Corolla* blue, 18–23 mm; tube 3–6 mm; lobes 17–20 mm, linear-lanceolate with a long acuminate tip; outside densely pubescent. *Stamens* 19 mm long; anther-sacs c. 7 mm long; terminal appendage c. 11 mm long; base of filament thickened, pubescent. *Style* 3–4 × as long as calyx. *Nutlets* 'subtriquetrous, outside rounded, ± rugose and wrinkled' [description of nutlet from *Fl. Zaire, Rwanda & Burundi*].
Type: [Zaire] Katanga, Mt Senga, 30 v 1908, *Kassner* 2925 (K, P, E).
ZAIRE. Tonipa, Marungu, *Dubois* 1373 (n.v.); Mont Mwanza, Marungu, *Van Den Brande* 29 (n.v.).

12. C. hispidissimus (S. Moore) A. G. Miller & H. Riedl, **comb. nov.** Fig. 5; 6e, f.
Syn.: *Vaupelia hispidissima* S. Moore in J. Bot. 58: 49 (1920).

Perennial herb. *Stems* many, simple, 1–2.5 m; indumentum of spreading bristles, 2–3 mm long, and shorter hairs. *Leaves* densely clothing stem, 6–12 ×

1–1.8 cm, narrowly lanceolate, tip acute, base truncate, with indumentum of antrorse tuberculate-based bristles. *Inflorescence* a dense terminal panicle with dense indumentum of patent yellowish bristles, c. 2–3 mm long. *Calyx* 6–14 mm increasing to 9–15 mm in fruit; lobes linear-lanceolate, with patent or ± ascending bristles outside, and dense ascending ± sericeous hairs inside. *Corolla* whitish blue outside, violet-blue inside, 12–27 mm; lobes 13–16 mm, narrowly triangular with attenuate tip, with short adpressed hairs outside. *Stamens* 12–17 mm long; anther-thecae 6–8 mm; terminal appendage (5–)6–9 mm; basal filament appendage hairy. *Style* 1.75–2 × as long as calyx. *Nutlet* c. 4 × 5 mm, minutely verrucose on back.

C. hispidissimus has a disjunct distribution (see fig. 5) between Angola and N Zambia. The plants from N Zambia differ from those in SW Angola in the points mentioned below.

1. Calyx 6–9 mm in flower increasing to 9–12 mm in fruit, corolla 12–19 mm long, stamens 12–15 mm.....subsp. *hispidissimus*
\+ Calyx 8–14 mm in flower increasing to 12–15 mm in fruit, corolla 26–27 mm, stamens 16–17 mm .....subsp. *zambiensis*

subsp. **hispidissimus.** Figs 2; 6e.

Type: Angola in thickets between old Munonque and Ujaio, *Gossweiler* 3132, (K, BM).

ANGOLA. Benguela, *Gossweiler* 1316 (K); ibid., Cuima, 1700 m, 19 & 20 vii 1940, *Gossweiler* 12193, 12262 (BM, LISC); nr Kutato, 7 vi 1906, *Gossweiler* 3958 (K, BM); Huila, Artur de Paiva on road to Chi-Pindo, 10 v 1969, *Santos & Barrosa* 2675 (COI); Mossamedes, Chinguari, *Mazzecchi-Alemanni* 216 (FI); ibid., Tunda, *Mazzecchi-Alemanni* 101 (FI).

subsp. **zambiensis** A. G. Miller & H. Riedl, **subsp. nov.** Fig. 5; 6f.

Habitu omnino subspeciei hispidissimis similis sed indumento laxiore mollioreque. *Calyx* 8–14 mm florendi tempore, ad 12–15 mm accrescens sub fructu, indumento exteriore sericeo adpresso usque ad apicem fere. *Corolla* 26–27 mm. *Stamina* 16–17 mm, antherae 8–10 mm, appendice terminali 8–9 mm, filamenta 6–7 mm supra basin corollae affixa.

Like subsp. *hispidissima* but with softer indumentum. *Calyx* 8–14 mm in flower, increasing to 12–15 mm in fruit, inner indumentum sericeous, adpressed almost to the tip. *Corolla* 26–27 mm. *Stamens* 16–17 mm, anthers 8–10 mm, terminal appendage 8–9 mm, filament attached 6–7 mm from base of corolla tube.

Type: [Zambia] Mwinilunga District, between R. Wanulolo and R. Lunga, 8 viii 1930, *Milne-Redhead* 560 (holo. K).

ZAMBIA. Mwinilunga, vi 1955, *Holmes* 1187 (K).

13. C. mechowii (Vaupel) A. G. Miller & H. Riedl, **comb. nov.** Fig. 5; 6d, h.

Syn.: *Trichodesma mechowii* Vaupel in Bot. Jahrb. 48: 528 (1913).
Vaupelia mechowii (Vaupel) Brand in Feddes Rep. 13: 83 (1914).

Perennial herb. *Stems* 1.5–2 m, simple, arising from a woody rootstock, indumentum scabrous with short patent and scattered longer, weak, bristles. *Leaves* lanceolate to oblong-elliptic (40–)50–100 × 5–11 mm, tip acute, base attenuate; abaxial surface with short, patent, tuberculate-based bristles; adaxial surface similar but bristles ± antrorse, adpressed. *Inflorescence* a terminal, relatively open, panicle. *Calyx* lobes elliptic, 6–8 mm long in flower increasing to

7–12 mm in fruit; indumentum of short, spreading or ± antrorse weak bristles. *Corolla* violet at tips, whitish at base, 24–30 mm; lobes ovate below, gradually attenuate above into long linear tips, 20–24 mm long, with a line of short ± antrorse hairs on back. *Stamens* 20–22 mm; anther-thecae 6–7 mm; terminal appendage 14–15 mm; basal filament appendage hairy. *Style* 5–6 × as long as calyx. *Nutlets* c. 4 × 5 mm, verrucose.

Type: Angola, Station Cissacala, *Mechow* 533a (n.v.).

ZAMBIA. 43 km W of Chizera on Kabompo road, 23 iii 1961, *Drummond & Rutherford-Smith* 7216 (P, K); Mwinilunga district, 60 km S of Mwinilunga on road to Kabompo, 25 i 1975, *Brummitt, Chisumpa & Polhill* 14110 (BR, C, E, K, LISC, NDO, P).

We have been unable to find the locality of the type gathering of *C. mechowii* — the only record of this very distinct species from Angola.

14. C. sp. A. Fig. 5; 6g.

Zambia, Mwinilunga District, Muwozi stream, 42 miles S of Mwinilunga on Kabompo road, 31 v 1963, *Loveridge* 705 (K, LISC).

Loveridge 705 closely resembles *C. mechowii* but the floral parts are all smaller, e.g. calyx 4–5 mm increasing to 5–6(–7) mm in fruit, corolla 19–20 mm. The indumentum on the leaves is adpressed, strigose, not patent, and the nutlets are smooth, not papillose.

Loveridge 705 was collected only about 20 miles away from *Brummitt et al.* 14110, which represents good *C. mechowii*, and it would be expected that they represent the same species. However, until further material of *C. mechowii* becomes available, so that the variability of the above characters can be assessed, we prefer to treat the Loveridge specimen separately.

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