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A taxonomic study of the Centella rupestris group

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Centella rupestris, *C. restioides* and a new species, *C. thesioides*, are grouped together on the basis of a woody habit, acicular or linear leaves and large bracts which cover, or partially cover the flower and fruit. The taxonomy, geographical distribution and species delimitation of this complex have been clarified through herbarium studies and in situ studies of the habit, leaves, inflorescences, bracts and fruit.

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Introduction

Centella rupestris (Eckl. & Zeyh.) Adamson and two related species are recognized as a distinct group for the first time. They are distinguished by their woody habit, acicular or linear leaves and large bracts, which cover or partially cover the flower and fruit. The taxonomy of this intricate species complex is clarified in this paper. Adamson (1951) placed *C. rupestris* in series Glabratae and *C. restioides* Adamson in series Virgatae. An undescribed species which has already been collected by Zeyher in the early nineteenth century (and several times since), was misunderstood by Adamson (1951), who included the functionally female plants in *C. restioides*, but cited the male material variously under *C. linifolia* (L.f.) Drude, *C. macrocarpa* (A. Rich.) Adamson, *C. restioides* and *C. virgata* (L.f.) Drude.

Results and discussion

The three species described in this paper are likely to be monophyletic because of the large bracts of the female inflorescence, which are longer than the mature fruit. Other species in the genus *Centella* that show this feature are *C. flexuosa* (Eckl. & Zeyh.) Drude and *C. macrodus* (Spreng.) Burtt (= *C. hederifolia* (Burch.) Drude]. These two species however have cordate leaves and a decumbent habit and are unrelated to the group under discussion. The three species of the *C. rupestris* group can be distinguished from each other by a combination of habit-, leaf-, inflorescence- and fruit characters.

Habit

All three species have an erect, virgate habit and are distinctly woody, at least towards the base. *C. restioides* (Fig. 1) is characterised by exceptionally long internodes and axillary congested inflorescences. The new species (Fig. 2) can clearly be distinguished by its sparse inflorescences, borne well above the vegetative part of the plant. *C. rupestris* (Fig. 3) is more woody and robust than the other two species and the inflorescences are terminal as in the new species but congested and borne amongst the leaves.

Leaves

The new species has acicular juvenile and mature leaves of varying length depending on their position on the plant. The basal leaves are longer than those on inflorescence-bearing branches. The leaves are always glabrous and the petioles cannot be distinguished from the lamina (Fig. 2). In contrast, *C. restioides* has acicular, linear or obovate leaves, which are often sparsely villous at the base. When the leaves are ovate, they have a distinct petiole, which may be villous (Fig. 1). *C. rup-*

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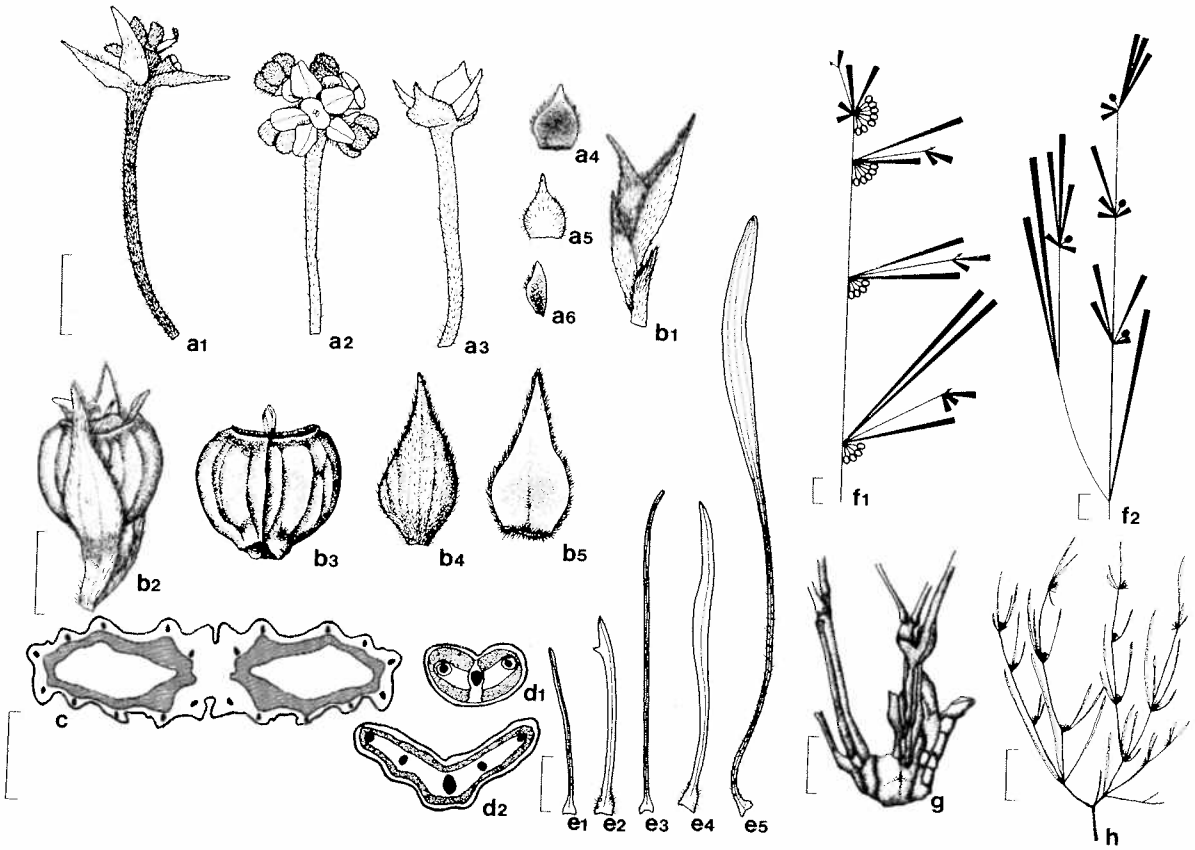

Fig. 1. *Centella restioides*. Male inflorescence (a): a1 & a2, umbellule of male inflorescence; a3, bracts of male um bellule; a4, outer bract in ventral view; a5, outer bract in dorsal view; a6, inner bract in ventral view (scale 2,5 mm). Female inflorescence (b): b1, bud stage; b2, almost mature stage; b3, mature fruit with bracts removed; b4, bract in dorsal view; b5 bract in ventral view (scale 10 mm). c, transverse section through mature fruit (scale 10 mm). Transverse sections through leaves (d): d1, acicular (terete) leaf; d2, oblong (flat) leaf (scale 10 mm). Leaves showing variation in shape and size (e): e1, leaf from short shoot; e2–5, leaves from long shoots (scale 10 mm). Inflorescences (f): f1, male inflorescence; f2, female inflorescence (scale 10 mm). g, woody base of plant (scale 10 mm). h, habit (scale 40 mm).

estris differs from the other two species by the invariably linear and laminate leaves (never acicular), which have a yellowish green colour (not dark green to brown as in the other two species) and a leathery texture. They are slightly broadened at the base, glabrous, and lack a distinct petiole (Fig. 3). Transverse sections of the leaves of all three species show that the midrib is sunken above and below in *C. rupestris*, which sets it apart from the other two species, where only the adaxial midrib is sunken.

Inflorescence and bracts

Of the three species, *C. rupestris* is the only one which may be monoecious or dioecious; the other two are invariably dioecious. The male and female umbels of *C. restioides* are axillary and are borne along the entire length of the long branches, while in the other two species the umbels are borne terminally on the plant (Figs 1–3). The male inflorescence of *C. restioides* provides further diagnostic characters: the male umbellules each bears two pairs of bracts below the five to seven villous subsessile male flowers (Fig. 1). This is different from the new species and *C. rupestris*, where the male umbellules bear only one pair of bracts and three almost glabrous male flowers (Figs 2 & 3). The functionally female inflorescences of all three species have a single umbellule with one bisexual flower, which at early stages of development is enclosed by four bracts. The pair of bracts closest to the flower eventually encloses the base of the fruit and are longer than the fruit. The outer (basal) bracts usually do not develop further and are persistent at the base of the ray or deciduous. In *C. restioides* however, these bracts occasionally develop to the same size as the inner bracts and remain attached to the base of the fruit, so that fruit with four bracts may be found amongst the more common bibracteate fruit.

Fruit morphology

The fruit of all three species are similar and varies only slightly in shape, size and surface sculpturing. They are isobilateral, with a lignified layer in the endocarp (Figs 1–3). Vascular bundles are associated with the ribs and the number of ribs is variable, even within the same species.

Geographical distribution

The three species are allopatric and all are localized in distribution (Fig. 4). *C. restioides* is limited to the mountains between Wellington and Frenchhoek (Slanghoek, Bainskloof, Du Toit's kloof and Drakenstein mountains) while the new species occurs only in the Riviersonderend mountains. *C. rupestris* appears to be restricted to the Kleinrivier- and Babilonstoring mountains.

Key to the species

1. Bracts small, much shorter than the fruit, or if large, then the leaves cordate ..... other *Centella* species
1. Bracts large, covering, or partially covering the fruit; leaves acicular or linear ..... *C. rupestris* group: 2
2. Male umbellule with 5–7 flowers and 4 bracts; leaf bases not persistent; stem somewhat woody at the base only ..... 1. *C.restioides*
2. Male umbellule with 3 flowers and 2 bracts; leaf bases persistent; stem distinctly woody 3
3. Inflorescence sparse, borne above the vegetative leaves; leaves acicular; bracts obtuse at maturity . 2. *C. thesioides*
3. Inflorescence congested, borne amongst the vegetative leaves; leaves flat, linear to narrowly oblong; bracts acuminate at maturity ..... 3. *C. rupestris*

1. Centella restioides Adamson

in Jl. S. Afr. Bot. 17: 40 (1951); B. L. Burtt in Edinb. J. Bot. 48: 198 (1991). – Type: South Africa, Cape Province, Paarl district, Witte Rivier (3319CA) Adamson 4239 (BOL!, male, lectotype, designated here); Adamson 4240 (BOL!, female, isolectotype).

Resprouting dioecious perennial herb with flowering branches developing from a woody base; older stems without prominent leaf bases. Leaves variable, usually acicular, but sometimes narrowly oblong (mainly in basal parts or coppice shoots), mostly sessile, sometimes petiolate; midrib depressed above and raised below; lamina mostly indistinguishable from the petiole, narrowly elliptic or narrowly oblong when present; (30–) 77–105 (–152) mm long, (0.5–) 1–2.5 (–5) mm wide, the base slightly widened, the margin entire, apex acute; surface brown, concolorous, mostly glabrous on dorsal and ventral side, sometimes sparsely pubescent towards the base of the petiole (Fig. 1). Inflorescences separated by long internodes, borne along the entire length of the long shoots, secund (all directed to the same side); male inflorescence with 4–6 umbellules; rays (3.5–) 5–8 (–11) mm long; bracts 4 (2 pairs), with bluntly obtuse apex, abaxially villous, outer bract pair larger and more regular in shape than inner bract pair; male flowers 5–7 on each umbellule, petals abaxially villous; female inflorescence with single umbellule; ray (3–) 6–14 (–20) mm long; bracts 4 (2 pairs), lower bract pair mostly undeveloped, usually persistent at base of ray, upper pair covering entire fruit at base, narrowly acuminate (4.5–) 5–5.5 (–8) mm long, 2–2.5 mm wide, always longer than the fruit (Fig. 1). Fruit broadly obovate in commissural view, (3.5–) 4–4.5 (–5) mm long, 3–5 mm wide, flattened; ribs relatively prominent, irregularly distributed (Fig. 1).

Habitat. C. restioides is found at medium to high altitudes in the mountains between Frenchhoek and Wellington (Fig. 4).

Material examined. 3319 (Ceres): Mitchell's Pass, Castle Rock (-AD), Stokoe 2060 (BOL). 3319 (Worcester): Ceres Peak (-AD), Esterhuysen 17531 (BOL); Bainskloof (-CA), Van der Merwe 1 (STE), Balkema s.n. (STE), White 5559a (PRE), White s.n. (GRA), Compton 18623 (NBG); Prospect Peak (-BC), Esterhuysen 5930 (K); Bainskloof, Baviaanskloof (-CA), Gillett 801 (STE), Leighton 2163 (BOL, NBG); Bainskloof, Limietberg (-CA), Thompson 242 (K, PRE, STE); Bainskloof, Happy Valley (-CA), Adamson 4394, 4386 (BOL), Gray 6 (BOL); Bainskloof, Witterivier Valley (-CA), Adamson 4239 (BOL), 4240, 4241 (BOL, K), 4384 (SAM), Esterhuysen 12471 (BOL, STE); Du Toits Kloof (-CA), Esterhuysen 12340 (BOL), 15640 (BOL, NBG, STE), 15667 (BOL), Adamson 4334, 4335 (BOL), Stokoe s.n. (SAM); Elgin, Boschemans Kloof (-CA), Stokoe s.n. (SAM, PRE); Slanghoek mountains (-CA), Esterhuysen 9461 (BOL), 16519 (BOL, NBG); Haalhoek, Spitzkop (-CB), Esterhuysen 13520 (BOL); Frenchhoek (-CC), Esterhuysen 2816 (BOL, K), 11414 (BOL), Compton 8157 (PRE); Theewater kloof, Palmiet valley (-CC) Hugo 2163 (PRE, STE).

2. Centella thesioides Schubert & Van Wyk sp. nov.

C. rupestri similis sed valde inflorescentiis sparsis perspicue supra folia vegetativa portatis (inflorescentia in *C. rupestri* congesta, inter folia portata) et foliis semper acicularibus in sicco brunnescentibus (in *C. rupestrifolia* semper plana, linearia, in sicco non brunnescentia) differt. Etiam similis est *C. restioidi* sed hec specie inflorescentiis terminalibus (in *C. restioide* inflorescentiae axillares), basibus foliorum persistentibus (in *C. restioide* bases foliorum caducae), atque umbellulis masculis *C. thesioidis* flores 3 mascules florentibus (in umbellulo masculo *C. restioidis* 5–7 flores), cum paro unico bractearum glabrarum (in *C. restioide* duo para bractearum villosarum), et bractearum fructuum apicibus obtusis (in *C. restioide* bracteae fructuum apice acuminatae) differt.

Type: South Africa, Cape Province, Worcester, Jonaskop, between second and third gates (3319DC), Schubert & Van Wyk 34 (PRE, holotype; BOL, E, GRA, JRAU, K, MO, NBG, S, WIND, isotypes).

Resprouting dioecious perennial herb with flowering

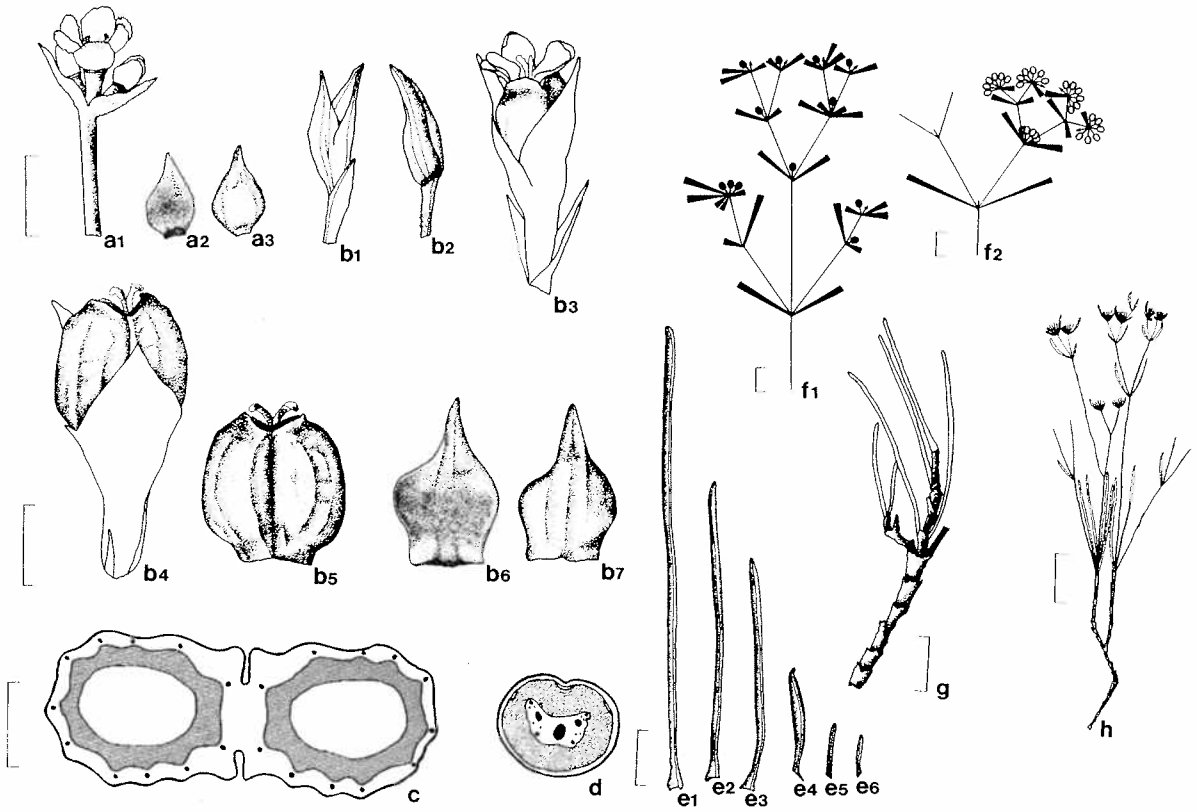

Fig. 2. *Centella thesioides*. Male inflorescence (a): a1, umbellule of male inflorescence; a2, bracts of male umbellule in ventral view; a3, in dorsal view (scale 2,5 mm). Female inflorescence (b): b1–2, bud stage; b3, young stage; b4, almost mature stage; b5, mature fruit with bracts removed; b6, bract in ventral view; b7, bract in dorsal view (scale 10 mm). c, transverse section through mature fruit (scale 10 cm). d, transverse section through leaf (scale 10 mm). Leaves showing variation in shape and size (e): e1–2, basal leaves; e3–4, leaves from inflorescence-bearing branch; e5–6, leaf-like bract from inflorescence (scale 10 mm). Inflorescences (f): f1, male inflorescence; f2, female inflorescence (scale 10 mm). g, woody base of plant with permanent leaf bases (scale 10 mm). h, habit (scale 40 mm).

branches developing from a woody base; stems with persistent, scale-like leaf bases. Leaves acicular; midrib depressed above; lamina indistinguishable from petiole; basal leaves 53–72 mm long, (1–) 1.2–1.5 (–1.7) mm wide, upper leaves (6.5–) 18–21 (–29) mm long; 0.5–1 mm wide; base slightly widened, margin entire, apex acute; dark green, concolorous, surface glabrous on dorsal and ventral side (Fig. 2). Inflorescences sparse, borne above vegetative leaves on long shoots; male inflorescence with 6 umbellules; rays 3–4 mm long; bracts 2, bluntly obtuse at apex, glabrous; male flowers 3 on each umbellule, petals almost glabrous; female inflorescence with single umbellule; ray 2.5–6.5 mm long; bracts 4 (2 pairs), lower pair undeveloped, remaining at base of ray, upper pair covering entire fruit at base, obtusely blunt at apex, (4.5–) 5–6 (–7) mm long, 2.5–4 wide, always longer than the fruit (Fig. 2). Fruit widely elliptic in commissural view, 3–5 mm long, 3.5–4.5 mm wide, flattened; ribs indistinct, irregularly distributed (Fig. 2).

Notes. C. thesioides is similar to *C. rupestris* but differs markedly in its sparse inflorescences, which are borne well above the vegetative leaves (inflorescences congested, borne amongst the leaves in *C. rupestris*) and by the invariably acicular leaves which turn brown on drying (leaves invariable flat and linear, not turning brown on drying in *C. rupestris*). It is also similar to *C. restioides* but differs from this species in the terminal inflorescences (axillary in *C. restioides*), the persistent leaf bases (not persistent in *C. restioides*) and in the male umbellules, which have 3 male flowers in *C. thesioides* (5 to 7 male flowers in *C. restioides*), with a single pair of glabrous bracts (bracts in two pairs and villous in *C. restioides*) and in the obtuse apices of the fruit bracts (fruit bracts acuminate in *C. restioides*). The new species is geographically isolated from *C. restioides* and *C. rupestris* and is known only from the Riviersonderend mountain range (Fig. 4).

Material examined. 3319 (Worcester): Boschjesveld mountains (-CD), Stokoe s.n. (SAM); Riviersonderend mountains, Boesmans Pass road (-DC), Bean & Trinder-Smith 2725b (BOL);

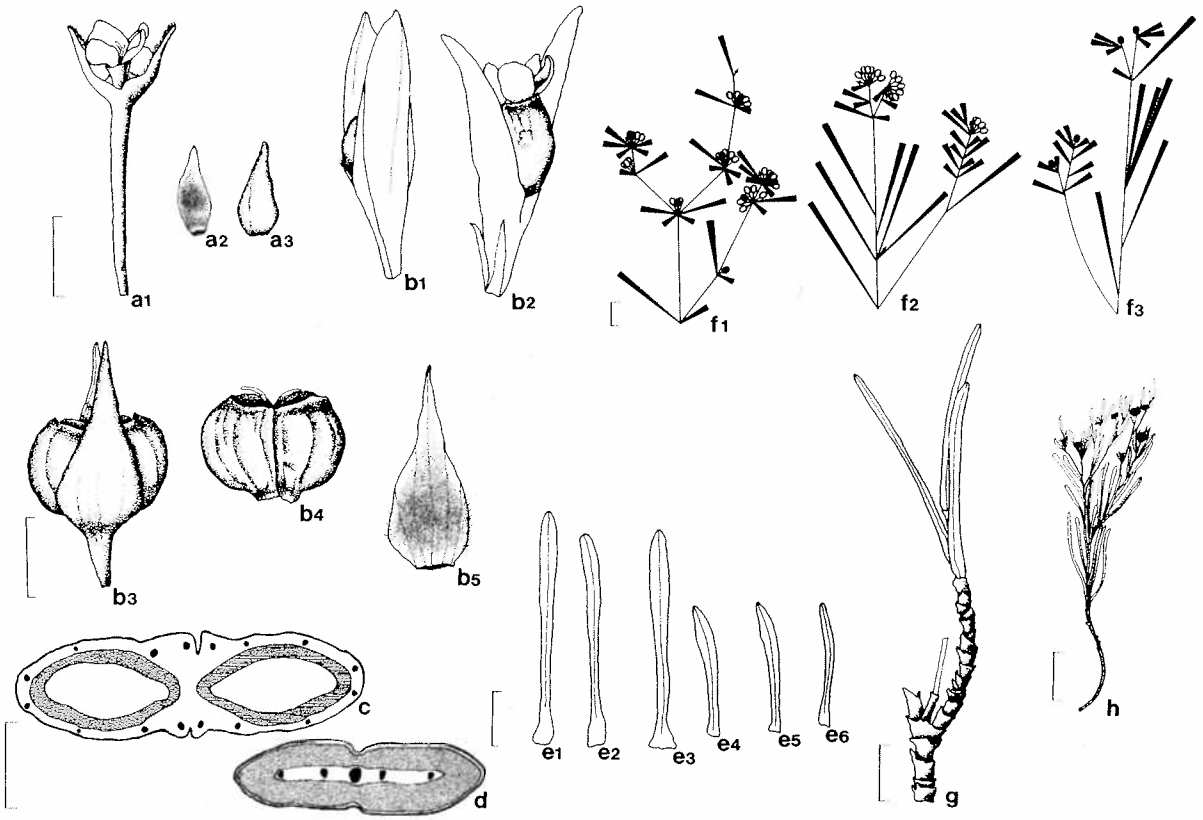

Fig. 3. *Centella rupestris*. Male inflorescence (a) a1, umbellule of male inflorescence; a2, bracts of male umbellule in ventral view; a3, in dorsal view (scale 2,5 mm). Female inflorescence (b): b1 & b2, bud stage; b3, almost mature stage; b4, mature fruit with bracts removed; b5, bract in ventral view (scale 10 mm). c, transverse section through mature fruit (scale 10 mm). d, transverse section through leaf (scale 10 mm). Leaves showing variation in shape and size (e): e1–3, basal leaves; e4–6, leaves from inflorescence-bearing branch (scale 10 mm). Inflorescences (f): f1, mixed male and female inflorescence; f2, male inflorescence; f3, female inflorescence (scale 10 mm). g, woody base of plant with permanent leaf bases (scale 10 mm). h, habit (scale 40 mm).

Riviersonderend mountains, Jonaskop (-DC), Andreae 327 (PRE, STE), Boucher 5017 (STE), Greuter 22015 (PRE), Hilliard & Burtt 13054 (NBG), Stokoe 20 (STE), 1168b (PRE); Poesjenels River (-DC), Levyns 10805 (BOL). 3419 (Caledon): Boesmanskloof (-BA), Adamson 4433 (BOL, PRE), 4435 (BOL, PRE), Barker 2398 (BOL), Brenan 14006A (NBG), Esterhuysen 4483 (BOL), Levyns 9202 (BOL); Galgeberg (-BA), Van Jaarsveld 6427 (NBG); mountains at Genadendal (-BA), Zeyher s.n. (SAM); Schilpadkop (-BA), Esterhuysen 21017A (BOL); Riviersonderend mountains, NE foothills (-BB), Theron et al. 3301 (GRA, PRE).

3. Centella rupestris (Eckl. & Zeyh.) Adamson

in Jl. S. Afr. Bot. 15: 95 (1949); Adamson in Jl. S. Afr. Bot. 17: 32 (1951); B. L. Burtt in Edinb. J. Bot. 48: 198 (1991). – Type: South Africa, Cape Province, Caledon, Kleinrivier mountains [3419AB], Ecklon & Zeyher 2170 (S!, lectotype, designated here; K!, SAM!, isolectotypes). Note. The lectotype is chosen from S because the most complete collection of Ecklon and Zeyher specimens are in Stockholm. Furthermore, the SAM isosyntype appears to be a mixture of this collection with Zeyher 2667, and the individual twigs of the two numbers can no longer be told apart with certainty.

≡ *Hydrocotyle rupestris* Eckl. & Zeyh., Enum.: 334 (1837). – Type as above.

= *Hydrocotyle arbuscula* Schltr. in Bot. Jahrb. 27: 127 (1890). – Type: South Africa, Cape Province, Caledon, Bot River (3419AC), Schlechter 9444 (B+?; BOL! lectotype, designated here; GRA!, K!, S! isolectotypes). Note. Since the original specimen is presumed to be destroyed, we choose the BOL isosyntype.

≡ *Centella arbuscula* (Schltr.) Domin in Bot. Jahrb. Syst. 41 (3): 168 (1908).- Type as above.

= *Hydrocotyle centella* var. *coriacea* Sond. in Fl. Cap. 2: 532 (1862) pro parte. – Type: South Africa, Cape Province, Caledon, Kleinrivier mountains (3419AB), Ecklon & Zeyher 2170 (S! lectotype, designated here, K!, SAM! isolectotypes). Note. Sonder (1862) cited both Ecklon & Zeyher 2169 and 2170 as syntype of his variety. By choosing Ecklon & Zeyher 2170 (S) as lectotype (which is a good choice anyway), we intentionally avoid the confusion surrounding the so-called "*C. montana*", which was originally based on the only other syntype specimen, Ecklon & Zeyher 2169.

Resprouting dioecious or monoecious perennial herb with distinctly woody flowering branches developing from a woody base; older stems with persistent, scale-like leaf bases. Leaves linear to narrowly oblong, lamina

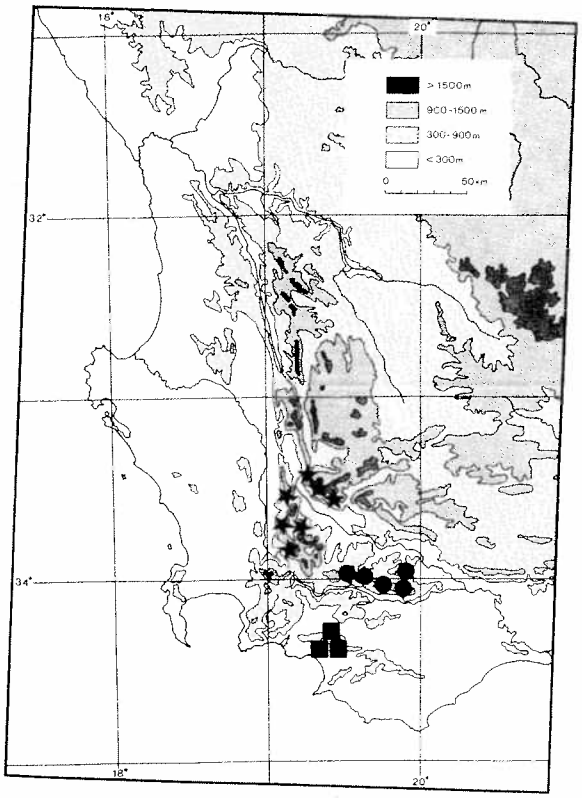

Fig. 4. The known geographical distribution of *Centella restioides* (★), *C. thesioides* (●) and *C. rupestris* (■).

indistinguishable from petiole; midrib depressed above and below; (11–) 49–60 (–78) mm long, (2.5–) 4–5 (–6) mm wide; base slightly widened, the margin entire, apex acute; surface yellowish green, concolorous, glabrous on dorsal and ventral side (Fig. 3). Inflorescences congested, borne amongst vegetative leaves; male inflorescence with 4–6 umbellules; rays (2.5–) 4–4.5 (–5) mm long; bracts 2, acuminate at apex, glabrous; male flowers 3 on each umbellule, petals almost glabrous; female inflorescence with single umbellule; ray 1–2.5 mm long; bracts 4 (2 pairs), lower pair undeveloped, remaining at base of ray, upper pair covering entire fruit at base, acuminate at apex, (4.5–) 4.5–6 (–7) mm long, 2.5–3 mm wide, always longer than the fruit (Fig. 3). Fruit widely depressed ovate in commissural view, 3–4 mm long, 3–4.5 mm wide, flattened; ribs indistinct, irregularly distributed (Fig. 3).

Habitat. C. rupestris is a localised species and appears to be endemic to the Kleinrivier- and Babilonstoring mountains (Fig. 4).

Material examined. 3419 (Caledon): in mountains above Bot River (-AC), Schlechter 9440, 9444 (BOL, K); in mountains at mouth of Kleinrivier (-AD), Zeyher 2667 (S, SAM), Ecklon & Zeyher 2170 (K, S, SAM); Vogelgat (-AD), Williams 2931, 2987 (NBG, PRE); Hermanus (-AD), Rogers 26549 (GRA); Hermanus, Fernkloof Nature Reserve, Droëkloof (-AD), Drewe 175 (HER, K), 179 (HER), Robertson 23 (HER, NBG), Schubert & Van Wyk 55b (JRAU); Hermanus, Maanskynkop (-AD), Taylor 8371 (STE); Hermanus, Rotary Road, 1 km from eastern end (-AD), Schubert & Van Wyk 55a (JRAU); Shaw's mountain (-AD), Esterhuysen 29624 (BOL, K), Schelpe 4718 (PRE).

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