

Studies in the liverwort genus *Riccia* (Marchantiales) from the south-west Cape

O. H. VOLK* and S. M. PEROLD**

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ABSTRACT

A new species of *Riccia*, *R. parvo-areolata* Volk & Perold, as well as sporophytes and spores of *R. villosa* Steph. ex Brunthaler, are described. Earlier descriptions of *R. villosa* were based on sterile plants. The unique structure of the dorsal epithelium consisting of loose cell pillars in these two species (and also present in allied species grouped together in the section *Pilifer*) is described and illustrated.

Riccia parvo-areolata Volk & Perold, sp. nov.

Dioica (?), perennis, singulares vel subgregaria. *Gametophytum* mediocra ad 10 mm longa, ad 5 mm lata, ad 1,3 mm crassa, oblonge-ovata, in sicco subalbido-viridis, fissurata-tomentosa, in tumido pallide-viridis, subnitida, velutina; furcis brevibus, divergentibus, lata rotundato-truncatis breviterque emarginatis, apice sulcatis, ceterum convexis marginibus deflexis, costa subplana, viridis vel rare purpureo-maculata, in sicco apicibus contractis, squamis obvelatis breviterque sulcatis ceterum lata concavis, marginibus elevatis, subtus lunatis. *Squamae* excedentes hyalinae, ad 600 µm magnae, semiorbicularae, basi plus minusve rare purpureae, confertae, integerrimae, cellulae longiusculae, ad 120 × 50 µm magnae, 5–7 angulosae, parietibus rectis. *Frondis* adultis sectio transversalis fere (2–) 3–4-plo latioribus quam altis, stratum piliferum (epithelium) ca 1/6, stratum aeriferum 3/6–4/6, stratum penarium 2/6 altitudine frondis; pili liberi, hyalini, conferti, (3–) 4 cellulae tumidae seriatim, ad 200 µm longi, 60–90 µm crassi, cellulae terminales obconici vel mamillati; columnae strati aeriferi ad 600 µm longae, 8–12 cellulae seriatae; canalabis aeriferibus 4–7 (–8) angulati, perpendicularibus vel gradatim extrorsis inclinatis et apice versus oblique adscendentes, canales aeriferos includentes. *Antheridia et archegonia* non visa. *Sporangia* matura libera, 400–900 spores continentia; illae fuscae, subtriangularo-globosae, 70–85–96 µm in diametro, alae angustae, minutissime crenulatae, poribus inconspicuae, distaliter parvo-areolata, inde nomen, 18–24 foveoli in diametro, anguli reticuli minute papillatae, proximaliter tres facetae parvo-areolatae subdistinctae limitatae. Chromosomata n=8 (Bornefeld) *Riccia albomarginatae* subsimilis, sed differet inter aliis ab colore pallido-viridis, cellulae pilorum crassiorae et ornatio sporarum parvo-areolata. Habitat in pascuis (?) temporaliter humidis, subarenosis, acidis, expositis radiatonis.

TYPE.— Cape, 3318 (Vanhynsdorp): near Doringbaai, W of Vredendal, Kliphoek farm, gravel on sandstone (–CD), J. M. Perold 23 (PRE, holo.).

Dioecious?, perennial, single or in loose patches. *Gametophyte* medium-sized, segments up to 10 mm long, 5 mm broad, 1,2 mm thick; shape broadly oblong-ovate; seldom branching, and then branches short, divergent; dorsal surface when wet pale green, slightly glistening, velvety, apex roundly truncate and shortly emarginate, grooved apically, otherwise convex with downward sloping margins (Fig. 1.2, 1.3); in dry state dorsal surface greenish-white, felt-like, apex inflexed and groove covered by scales, otherwise broadly concave with margins ascending, nearly acute (Fig. 1.1); ventral surface slightly convex, green, occasionally flecked with violet. *Scales* semi-circular (Fig. 1.10) projecting above margin, size up to 600 µm hyaline, base flecked with wine-red, imbricate, erect, margin smooth, with cells elongate, 5–7 sided, straight-walled, size up to 120 × 50 µm. *Thallus* in transverse section (2–) 3–4 times broader than high, epithelium about 1/6, assimilation tissue 3/6 to 4/6, storage tissue 2/6 the height of the thallus (Fig. 1.3); dorsal cell pillars (Fig. 2.2, 2.5, 2.7) free, hyaline, about 200 µm long with (3–) 4 inflated cells 60–90 µm wide, terminal cell mamillate or bluntly conical; assimilation tissue about 600 µm thick, columns 8–12 cells deep, enclosing 4–7 (–8)-sided air canals, rising vertically or frequently sloping towards the sides or the apex (Fig. 1.3); the canals in the centre of the thallus narrow (Fig. 1.8) and enclosed by four cell columns, while those nearer the margin are broader and enclosed by 5–8 cell columns (Fig. 1.9); storage tissue cells often with oil droplets.

Antheridia and *archegonia* not seen. *Sporangia* when ripe lie freely in the decaying thallus and contain about 400–900 spores. *Spores* (Fig. 3.1–3.6) rounded, triangular-globular, brown, size 70–80–90 µm with narrow crenulate wing and inconspicuous pores at marginal angles, distal face with ornamentation finely areolate (hence its name), 18–22 areolae across the diameter, the corners of the areolae with short papillae; proximal face with three finely areolate facets, not sharply demarcated (Fig. 3.1).

Chromosome number: n=8, (Fig. 1.11, Bornefeld). Their shapes are similar to those of *R. albomarginata* and *R. albovestita* (habil T. Bornefeld, pers. comm).

Riccia parvo-areolata colonizes exposed open

* Botanische Anstalten d. Univ., Würzburg D 8700, Germany.

** Botanical Research Institute, Department of Agriculture, Private Bag X101, Pretoria 0001.

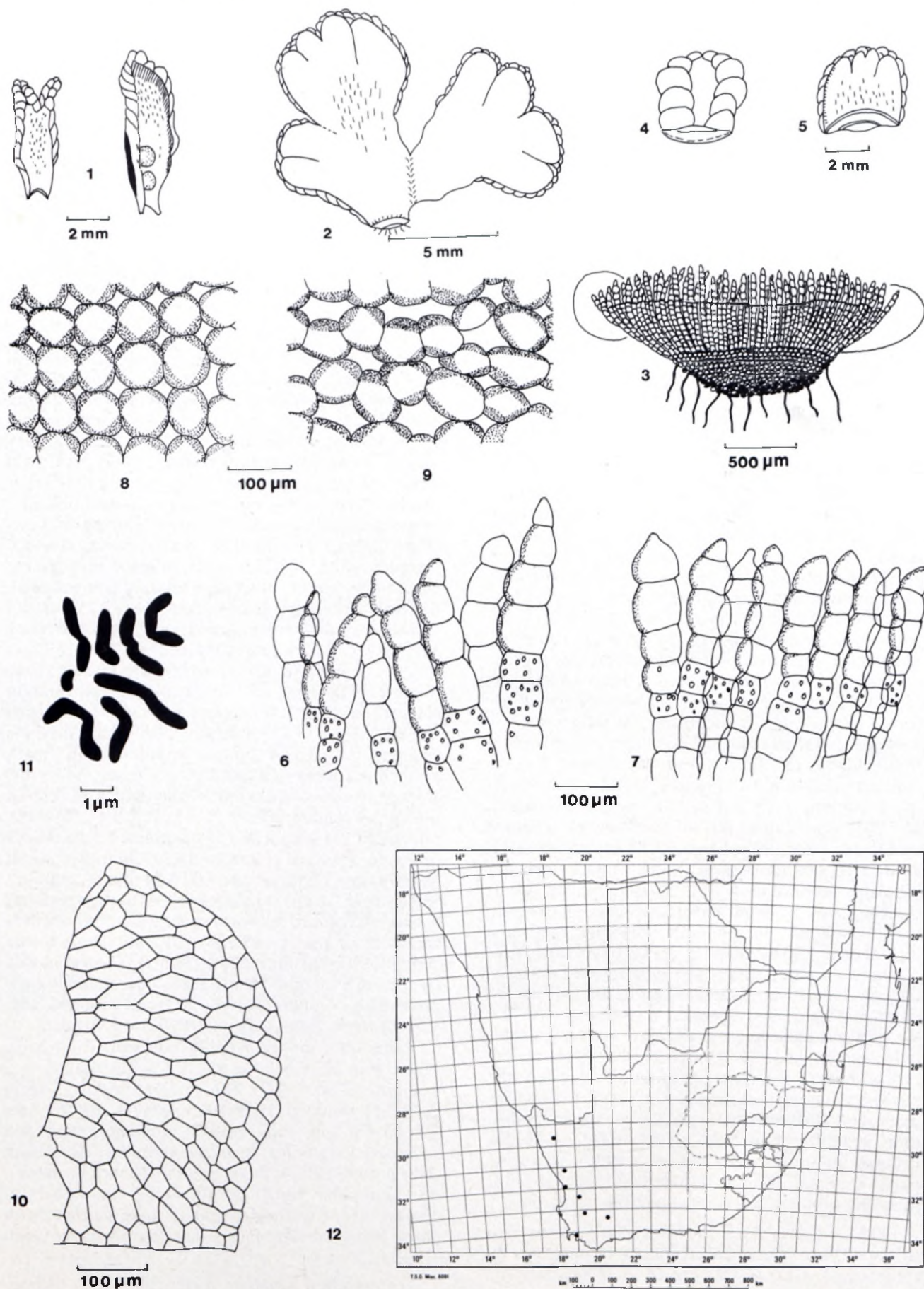


FIG. 1.—*Riccia parvo-areolata* (Perold 23, PRE). Structure of the thallus. 1, two dry thalli; 2, fresh thallus; 3, cross section of the thallus; 4, thallus apex from below; 5, thallus apex from above; 6, epithelium marginally; 7, epithelium centrally; 8, air canals at centre of thallus (chloroplasts adjacent to canal walls) seen from above; 9, air canals at margin of thallus; 10, ventral scale; 11, chromosomes; 12, distribution of *Riccia parvo-areolata*. (1, 2, 4, 5, 6–10 by O. H. Volk; 3 by R. Holcroft; 11 by habil T. Bornefeld.)

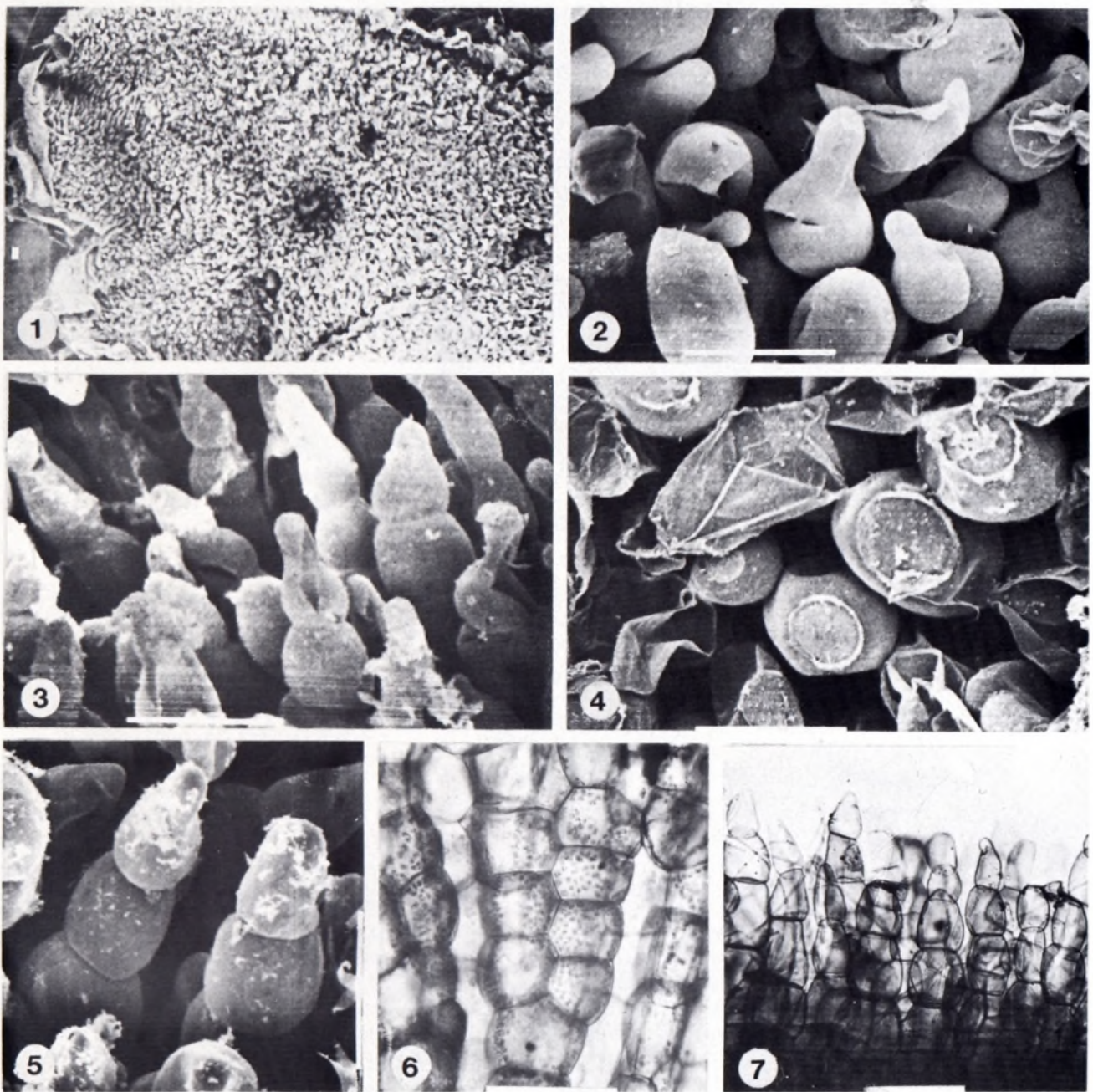


FIG. 2.—*Riccia parvo-areolata* (Perold 23, PRE). Epithelium and assimilation tissue. 1, thallus; 2–5, different shapes of the terminal cells of the epithelium; 6, air canals widening by the inclusion of new cell pillars; 7, epithelium on cross section. (1–5 SEM micrographs by O. H. Volk; 6–7 LM photographs by O. H. Volk.) Scale bar = 50 μ m.

stands in veld grazed by sheep, well-watered during infrequent rainfall, on weakly acid (pH 5.2–5.8) shallow sandy loam soil, together with moss species *Bryum argenteum* Hedw., *Bryum bicolor* Dicks, *Oedipodiellia australis* (Wager & Dix.) Dix.

Apparently the species is endemic to the western Cape. Together with *R. albovestita* Volk, *R. albomarginata* Bisch. emend. Sim, *R. villosa* Steph., *R. concava* Bisch. emend. S. Arnell and other as yet undescribed species (*R. sarcosa* ined., *R. duthieae* ined.) it belongs to a group of species which Volk (1983) has grouped together in the section *Pilifer*. They are characterized by a dorsal covering epithelium of free hyaline hair-like cell pillars (Figs 1.6, 1.7 & 2.7). This epithelium is mostly very fragile and can hardly be preserved. It is therefore rarely reconstituted in herbarium material and then only by

using chloral hydrate, lactophenol or KOH. Even when fresh material is transferred to dilute alcohol, these cell pillars collapse. The cell walls are also not easily wettable and the resistance to water remains even after fixation in a mixture of alcohol-acetic acid (Volk, 1984). The composition of the cell walls is unknown. The zinc chloride-iodine reaction for cellulose is negative.

These free dorsal pillars are lacking in species of the *Lichenoides*, where the dorsal epidermal cells are not free standing and almost always arranged in parallel lines — an arrangement which is revealed in species of the *Pilifer* group only on horizontal sections through the chlorenchyma (Fig. 1.8, 1.9). The structure of the epithelium was studied with the light microscope (LM) as well as with the scanning electron microscope (SEM) using living material

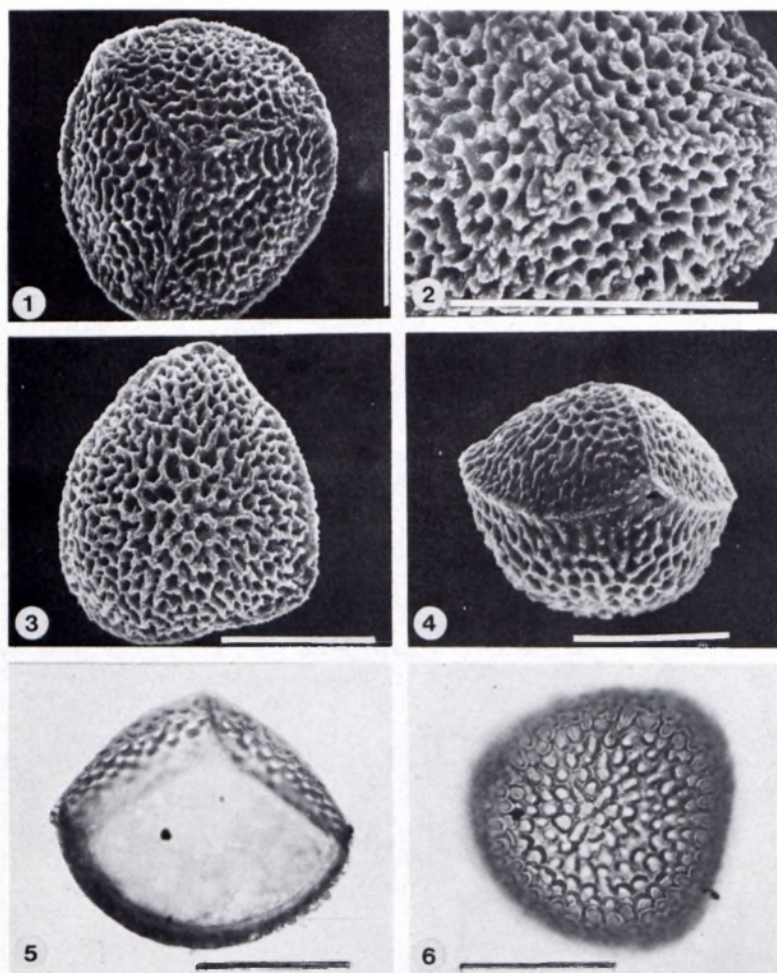


FIG. 3.—*Riccia parvo-areolata* (Perold 23, PRE). Spores. 1, proximal face; 2, apex; 3, distal face; 4, side. (SEM micrographs by S. M. Perold); 5, side; 6, distal face. (LM photographs by O. H. Volk.) Scale bar = 50 µm.

prepared by the usual procedure of critical point drying. At low magnification tangled, furry dorsal cell pillars are seen from above (Fig. 2.1). At high magnifications cells of the pillars of *R. parvo-areolata* are found to be extraordinarily variable in shape (Figs 1.6, 1.7 & 2.2–2.7). The terminal cells of the variably wide (25–90, but mostly 40–50 µm) pillars are mamillate (Fig. 2.2), vermiculate (Fig. 2.3) to conically inflated (Fig. 2.5). Measurements of a large number of terminal cells of the pillars from different thalli revealed a length : breadth ratio of 1.2 : 1, where the length varied between 25–49–75 µm, and the breadth between 24–40–77 µm (average value italicized). The rest of the cells of the epithelium have similar dimensions (Table 1).

Riccia parvo-areolata is somewhat similar to *R. albomarginata* but differs from it in the pale green colour, the size of the epithelial cells and the finely areolate ornamentation of the spores.

Older collections of a number of *R. parvo-areolata* specimens were incorrectly identified as *R. concava*. This is not surprising as in the dry state the thallus is pronouncedly concave (Fig. 1.1, 1.4) (Sim, 1926). *R. parvo-areolata* differs from *R. concava* in that it lacks radially arranged ridges in the ornamentation of the outer face of the spore, nor do the epithelial cells swell out again once they have collapsed.

CAPE.—2917 (Springbok): Hester Malan Res. nr Springbok (–DB), *Schelte* 7759, 7776 (BOL). 3118 (Vanrhynsdorp): Nortier Exp. Farm nr Doringbaai (–AB), *Perold* 14, 15 (PRE); Kliphoeck Farm, nr Doringbaai (–CD), *Perold* 19, 22–26 (PRE). 3219 (Wuppertal): Wuppertal Miss. Sta. (–AC), *Malherbe & Davies* 5375 (BOL). 3220 (Sutherland): nr Sutherland (–BC), *Duthie* 5407 (BOL). 3319 (Worcester): Op-die-Berg (–AB), *Stirton* 9169 (PRE). 3418 (Simonstown): Knorhoek (–BB), *Duthie* 5414 (BOL).

Riccia villosa Steph. ex *Brunnthaler* in Denkschr. Kais. Akad. Wiss. Math.–Nat. Kl. 88:

TABLE 1.—Measurements of the cells of the epithelium of *Riccia parvo-areolata* (in µm) (Perold 23)

	Average size		Length/Breadth	Variations in size	
	Length	Breadth		Length	Breadth
Terminal cell					
3	49	40	1.2 : 1	25–75	24–77
2	56	44	1.3 : 1	33–75	25–66
2	52	40	1.3 : 1	42–75	25–59
1	50	42	1.2 : 1	33–67	33–59

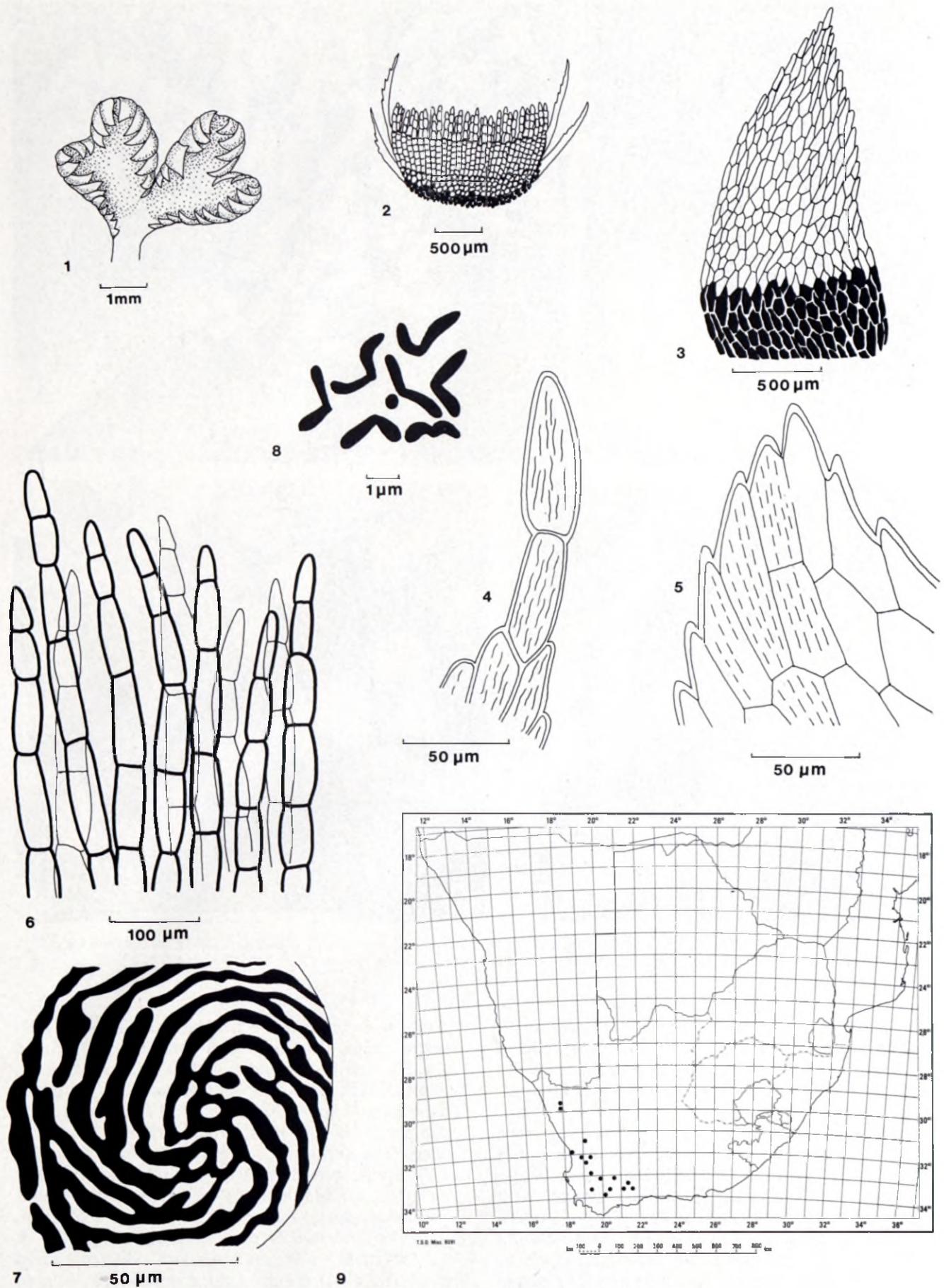


FIG. 4.—*Riccia villosa*. Structure of the thallus. 1, thallus; 2, cross section; 3, ventral scale; 4, apex of scale; 5, toothed margin of scale and striolate cuticle; 6, epithelial cells; 7, ornamentation of distal spore face (LM); 8, chromosomes; 9, distribution of *Riccia villosa*. (1, 2, 3 from Stephens 24726, BOL (by R. Holcroft); 4, 5 from leg. unknown 63, BOL (by O. H. Volk); 6, 7 from Perold 20, PRE (by O. H. Volk); 8, from Perold 20, PRE (by habil T. Bornefeld).

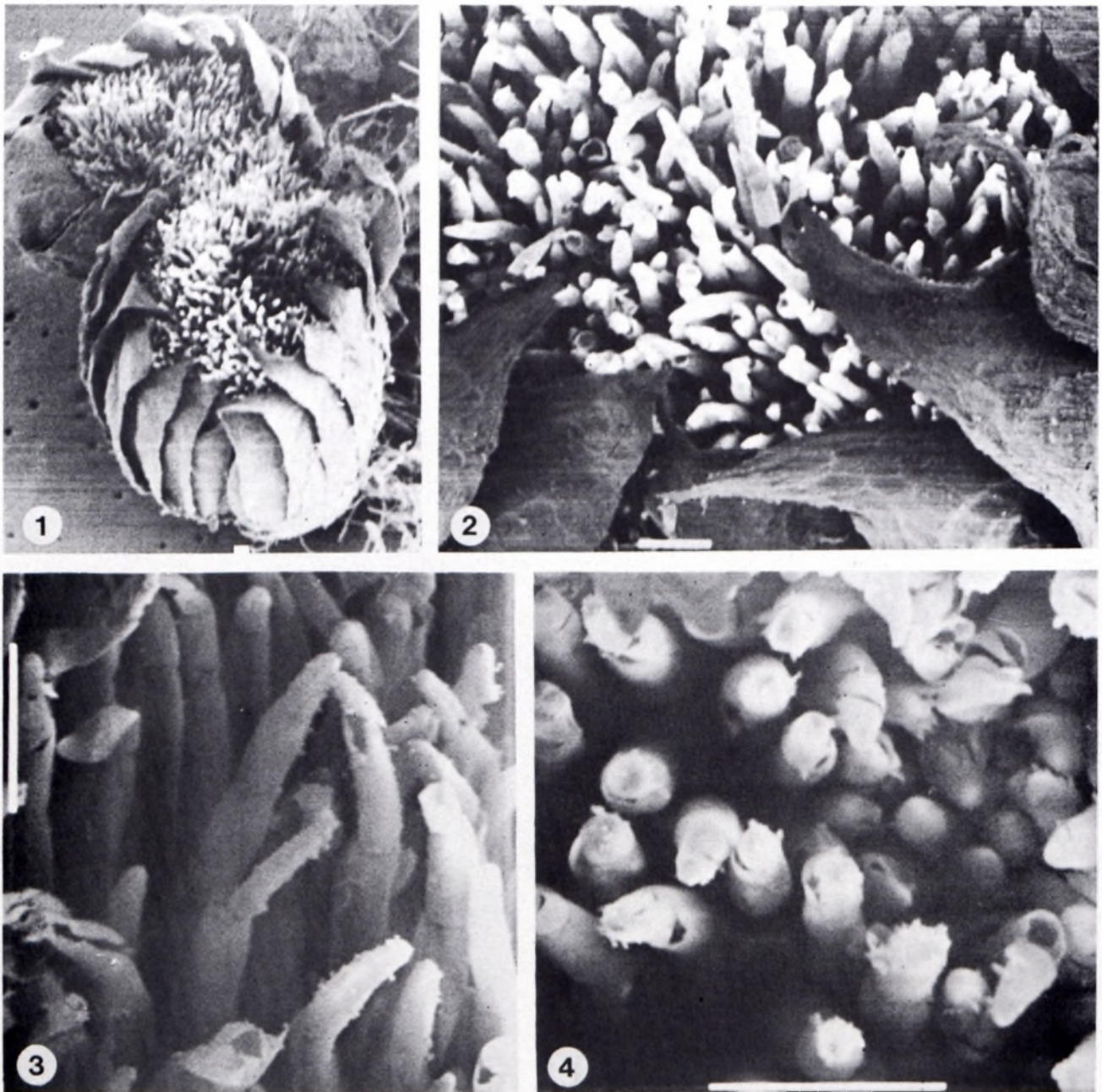


FIG. 5.—*Riccia villosa* (Perold 20, PRE). Epithelium and assimilation tissue. 1, end on view of thallus; 2, epithelial cells and scales; 3, side view of epithelial cell pillars; 4, the same from above. (SEM micrographs by O. H. Volk.) Scale bar = 50 μ m.

724 (1913); Arnell in *Hepaticae of South Africa*: 19, 20 (1963). Type: Kapland, 3320 (Montagu): Karoo bei Matjiesfontein, auf sandigem Boden, zirka 900 m (–BA), *Brunnthaler*, s.n. XI, 1909 (G) Iconogr. Hepat. (G).

Dioecious?, perennial, in crowded gregarious patches. *Gametophyte* small, segments up to 8 mm long, 2.5 mm broad and 1.5 mm thick; shape narrowly oblong-ovate; single or furcate with branches diverging at an acute angle (Fig. 4.1); when wet dorsal surface whitish-green, apex bluntly obtuse; in dry state upper surface white, plane to concave; margins obtuse, flanks steep, often purple to nearly black; ventral surface light brown to purplish black, flat to slightly convex. *Scales* very prominent, projecting beyond the margin, closely imbricate (Fig. 5.1), laterally in one row, hyaline; when dry, white to yellowish, up to 1.8 mm long and

1 mm wide at base which is purple (Fig. 4.3–4.5); shape triangular-acuminate, margins denticulate apically, frequently ending with a narrow caducous terminal cell; most cells oblong-hexagonal, larger at the base and up to 110 μ m long and 40 μ m wide, with straight thickened walls, cuticle striolate. *Thallus* in transverse section 1–2 times broader than high (Fig. 4.2), epithelium about $\frac{1}{5}$ to $\frac{2}{5}$, assimilation tissue $\frac{1}{5}$ to $\frac{2}{5}$, storage tissue $\frac{1}{5}$ the height of the thallus (Fig. 4.2); dorsal epithelium consists of colourless, nearly cylindrical free cell pillars (Figs 4.6 & 5.2–5.4) 300 – 700 μ m long, each pillar composed of (4–) 5 (–6) fragile, tender cells which collapse easily, (40–) 80–130 (–200) μ m long, (20–) 30–50 (–70) μ m wide, widening gradually towards base of pillars, 2–3 times longer than wide (Table 2); below epithelium a layer of chlorophyllose assimilation tissue about 250–400 (–600) μ m deep, consisting of

TABLE 2.—Measurements of the cells of the epithelium of *R. villosa* (in μm) (Perold 20)

	Average size		Length/Breadth	Variations in size	
	Length	Breadth		Length	Breadth
Terminal cell	76	26	2.9 : 1	40–110	20–40
4	92	33	2.9 : 1	46–100	32–34
3	88	40	2.2 : 1	56–100	30–68
2	120	43	2.3 : 1	55–120	30–60
Basal cell	122	45	2.7 : 1	45–200	36–80

rows of nearly isodiametric cells 25–60 μm in diameter, with narrow air spaces between rows; at the base a layer of parenchymatous tissue 300–400 μm thick, consisting of polygonous cells about 40 μm in diameter, sometimes filled with oil droplets; rhizoids colourless, both smooth and tuberculate, up to 40 μm thick. *Antheridia* not seen. *Archegonial ostioles* purple, about 60 μm long. *Sporangia* develop July to September singly or close together along median part of the thallus, causing slight bulging of dorsal surface, blotched with purple where it covers sporangia. *Spores* about 350 per capsule, released by disintegration of surrounding tissue, shape triangular-globular, polar, wingless,

(85–) 90–110 (–115) μm in diameter, colour brown to very dark brown or black (Fig. 6.1–6.6); distal face convex, ornamentation papillose to vermiculate, in a whorl which spirals from the centre outwards to the margin in 10–15 thick ridges (Figs 4.7 & 6.5); some spores, probably riper, have flattened ridges; proximal face with similar sculpturing, but ridges not in obvious spirals (Fig. 6.1 – 6.3); apex blunt, triradiate mark not prominent, each of the three suture lines of the mark terminate in a pore at the margin.

Most plants are sterile. Of eighteen specimens examined, only four were fertile, propagation

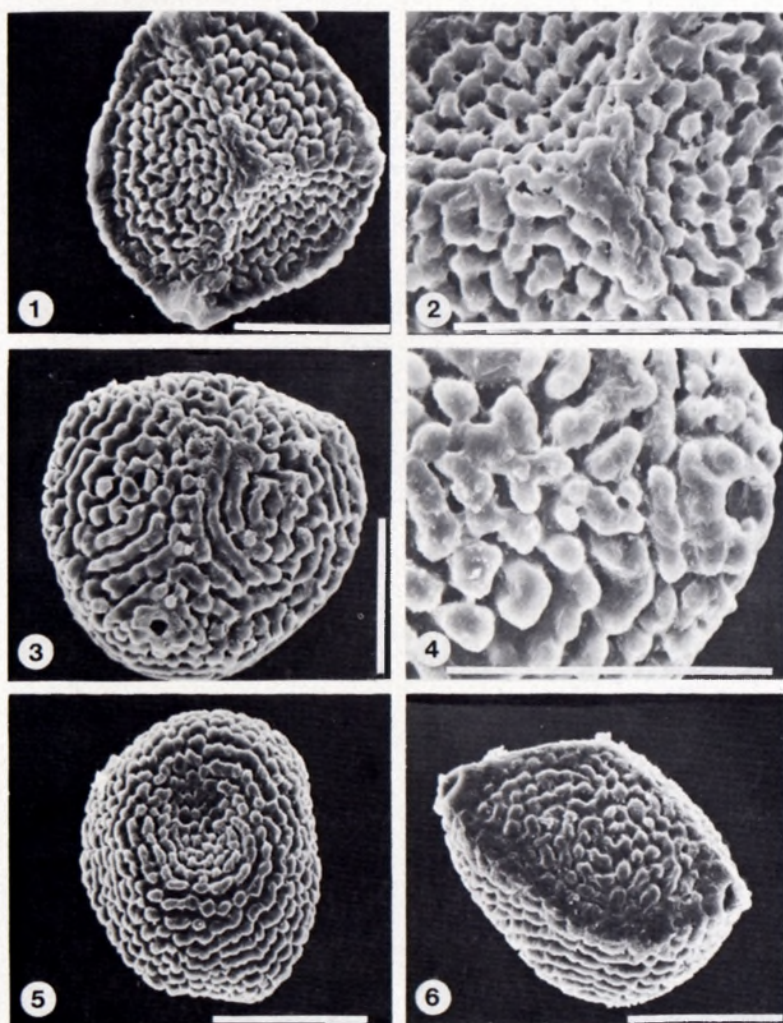


FIG. 6.—*Riccia villosa*. Spores. 1, proximal face; 2, apex; 3, 2 facets of proximal face; 4, pore at margin; 5, distal face; 6, side. (1, 2, 5, 6 from Levyns s.n. July 1954, BOL; 3, 4 from Compton 5428, BOL. (SEM micrographs by S. M. Perold.) Scale bar = 50 μm .

usually being adventitious. *R. villosa* produces globular gemmae originating from the thallus and later perforating the epithelium of the older parts.

This species is endemic to South Africa and known from several localities in the drier winter rainfall parts of the Cape like the Karoo, the Knersvlakte and Namaqualand. It grows at altitudes of 300–1 000 m in depressions, on sandy to gravelly non-calcareous soils, fully exposed to the sun and in association with small moss species, *Desmatodon convolutus* (Brid.) Grout, *Oedipodiella australis* (Wager & Dix.) Dix., with Mesembryanthemaceae *Ruschia* spp., *Dactyloopsis digitata* (Ait.) N.E.Br., *Argyroderma* spp., *Conophytum* spp., and with *Crassula* spp.

R. villosa, with its free epithelial cell pillars, is a member of the section *Pilifer*. It is recognized by the large hyaline triangular scales. In drying out, the thallus margins curve inwards and the large scales meet and project upwards along the midline. This, together with the collapse of the epithelial cells, protects the living tissue of the thallus. It is a distinctive plant. A drawing of *R. villosa* appears on the cover of S. Arnell's book on South African hepatics.

CAPE.—2917 (Springbok): Springbok (–DB), *Vogel C 791* (Mainz)*; Messelpad Pass, W Heights (–DD), *Schelte 7814a* (BOL). 3118 (Vanrhynsdorp): nr Doringbaai, Kliphoeck Farm (–CD), *Perold 20* (PRE). 3119 (Calvinia): S of Nieuwoudtville on plateau (–AC), *Leg. unknown 23885* (BOL). 3218 (Clanwilliam): N of Barrage Scheme (–BB), *Stephens 24726* (BOL); Pakhuis Pass (–BB), *Vogel C 5548* (Mainz)*. 3219 (Wuppertal): Bidouw Valley, on Mertenhof Farm (–AB), *Oliver 1467* (BOL); Cedarberg Range E side, Welbedacht (–AC), *Compton 5428* (BOL)*. 3319 (Worcester): Inverdoorn (–BB), *Vogel C 1351* (Mainz)*; Worcester (–CB), *Leg. unknown, 5430* (BOL). 3320 (Montagu): Matjiesfontein, 3 miles W (–BA), *Pillans 10036* (BOL); Dobbelaarskloof (–CB), *Levy's s.n.*

(BOL)*; Cogman's Kloof (–CC), *Arnell 803* (BOL); nr Montagu Baths, on veld (–CC), *Page s.n.* (BOL). 3321 (Ladismith): Seven Weeks Poort (–AD), *Levy's 25272* (BOL)*; Ladismith (–AD), *Vogel C 11* (Mainz)*; Ladismith Kloof (–CA), *Vogel C 1349* (Mainz)*; Olifants River (–DA), *Vogel C 5449* (Mainz)*; locality and collector unknown, 63 (BOL)*.

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UITTREKSEL

'n Nuwe spesie van *Riccia*, *R. parvo-areolata*, sowel as sporofiete en spore van *R. villosa* word beskryf. Vroeër beskrywings van *R. villosa* is gebaseer op steriele plante. Die unieke bou van die dorsale epidermis wat bestaan uit los kolomme selle in hierdie twee spesies (ook teenwoordig in verwante spesies wat saam gegroepeer is in die seksie *Pilifer*) word beskryf en geïllustreer.

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* Vogel's collection is housed at D–6500 Mainz, Herbarium Botanisches Institut der Universität.

* fertile specimen.