

## Studies in the liverwort family Aneuraceae (Metzgeriales) from southern Africa. 3. *Riccardia compacta*

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### ABSTRACT

*Riccardia compacta* (Steph.) S.W.Arnell is described and illustrated. Its presently known distribution in southern Africa is indicated on an accompanying map. Some differences between local plants of the species and those from Tanzania are discussed.

### INTRODUCTION

*Riccardia compacta* (Steph.) S.W.Arnell is the third species to be treated in the current revision of southern African taxa of this family. It was originally collected on Table Mountain by Jelinek, while on a Novara Expedition, and described as *Aneura compacta* by Stephani in 1893. Sim (1926) referred to it briefly, stating that it frequently occurred in forest districts throughout South Africa, which is doubtful, however, as it is apparently rare. Later on, two more specimens were collected on Table Mountain: one by Pillans, and the second by Arnell, who also collected it at Knysna. Arnell (1952) then transferred it to the genus *Riccardia*. During the 1950s Esterhuysen collected more specimens on high altitude peaks in Western Cape, but, regrettably, there have been no local collections since then. Arnell (1959) described an Esterhuysen specimen from Tanganyika (Tanzania) as *R. kilimandjarica* S.W.Arnell, which was placed in synonymy under *R. compacta* by Meenks & Pócs (1985). Pócs, either alone or with Ochyra, collected more material on Mt Kilimanjaro and Mt Meru during the 1980s. It was concluded by Meenks & Pócs that there were a few differences between Tanzanian plants of the species and the type specimen collected by Jelinek on Table Mountain. They also state that *R. compacta* is an Afro-alpine species which occurs at higher altitudes in East Africa than in South Africa.

***Riccardia compacta*** (Steph.) S.W.Arnell in Botaniska Notiser 1952: 141 (1952); S.W.Arnell: 88 (1963); Meenks & Pócs: 84 (1985). Type: Cap, Tafelberg, Jelinek, Novara Expedition, (19560G, holo.!; EGR).

*Aneura compacta* Steph.: 19 (1893); Steph.: 755 (1901–1905); Sim: 29 (1926).

Thalli prostrate, in compact cushions or patches, up to 3 or 4 mm thick, in several overlying layers of dense and intricately intertwined, slightly rounded, narrow bands, quite fleshy and firm, but rather brittle, bright green, with an ill-defined, somewhat darker, narrow strip occupying median  $\frac{1}{3}$  or more of branches; when dry, brown to dark brown. *Main axis* up to 15 mm long, not markedly dif-

ferentiated, though often retaining its dominance, branching generally crowded and irregular (Figure 1A), sometimes bifurcate (Figure 1B), branches narrowing somewhat toward tips or maintaining same width throughout, rarely slightly dilated distally, apically  $\pm$  truncate, shallowly notched, margins obtuse, not winged. *Primary branches/pinnae* arising laterally from axis, very close together or at intervals of 0.30–0.95 mm between successive ones, opposite or subopposite, obliquely spreading at angles up to 30° with axis, occasionally suberect, often relatively well developed, 2.0–3.5 mm long, up to 0.5 mm wide, usually linear, some bifurcate, rarely trifurcate, others poorly developed, almost rudimentary. *Secondary branches/pinnules* quite rare, if present, mostly remaining small. *Stolons* unbranched, generally arising on basal part of axis, occasionally developing more distally from apices of some primary branches. *Dorsal epidermal cells* in median part of apical segment of main axis (Figure 1C) from above 4–6-sided, thick-walled, 40–50  $\times$  27.5–37.5  $\mu$ m, subdorsal cells larger, 75–130  $\times$  30.0–42.5  $\mu$ m, subventral cells 50.0–87.5  $\times$  15–20  $\mu$ m, ventral epidermal cells 35–60  $\times$  30–40  $\mu$ m. *Oil bodies* not seen in material studied. *Margins* of apical segment of main axis (Figure 1D) entire, from above outer cells 25.0–37.5  $\times$  27.5–35.0  $\mu$ m, subquadrate to rectangular, intramarginal cells 5- or 6-sided, 32.5–50.0  $\times$  27.5–37.5  $\mu$ m, walls somewhat thickened. *Cross sections* of main axis at  $\pm$  middle of ultimate segment (Figure 1E) and toward base (Figure 1F) biconvex,  $\pm$  180  $\mu$ m, or 6/7 cell layers up to 240  $\mu$ m, or 8 cell layers thick medianly, and up to 460  $\mu$ m wide, margins tapering to obtuse, dorsal epidermal cells 27.5–30.0  $\mu$ m high, medullary cells ovoid to almost spherical, sizes variable, 25–45  $\times$  22.5–35.0  $\mu$ m, walls thickened, ventral epidermal cells 30–35  $\mu$ m high; cross section of primary branch at  $\pm$  its middle (Figure 1G) plano-convex,  $\pm$  200  $\mu$ m or 5/6 cell layers thick medianly, up to 475  $\mu$ m wide, medullary cell walls slightly thickened; cross section of stolon (Figure 1H) oval,  $\pm$  160  $\mu$ m or 6 cell layers thick medianly,  $\pm$  210  $\mu$ m wide, cell walls somewhat thickened. *Mucilage papillae* ventral, clustered at emarginate apex of pinnae and then in two, spaced, acropetal rows, one on either side of midline, reddish brown, club-shaped, 62.5–75.0  $\times$  20–25  $\mu$ m above, narrower below, rarely persistent. *Rhizoids* in widely scattered, irregular patches along ventral surface of pinnae, hyaline, up to 15  $\mu$ m wide. *Asexual reproduction* by gemmae not seen.

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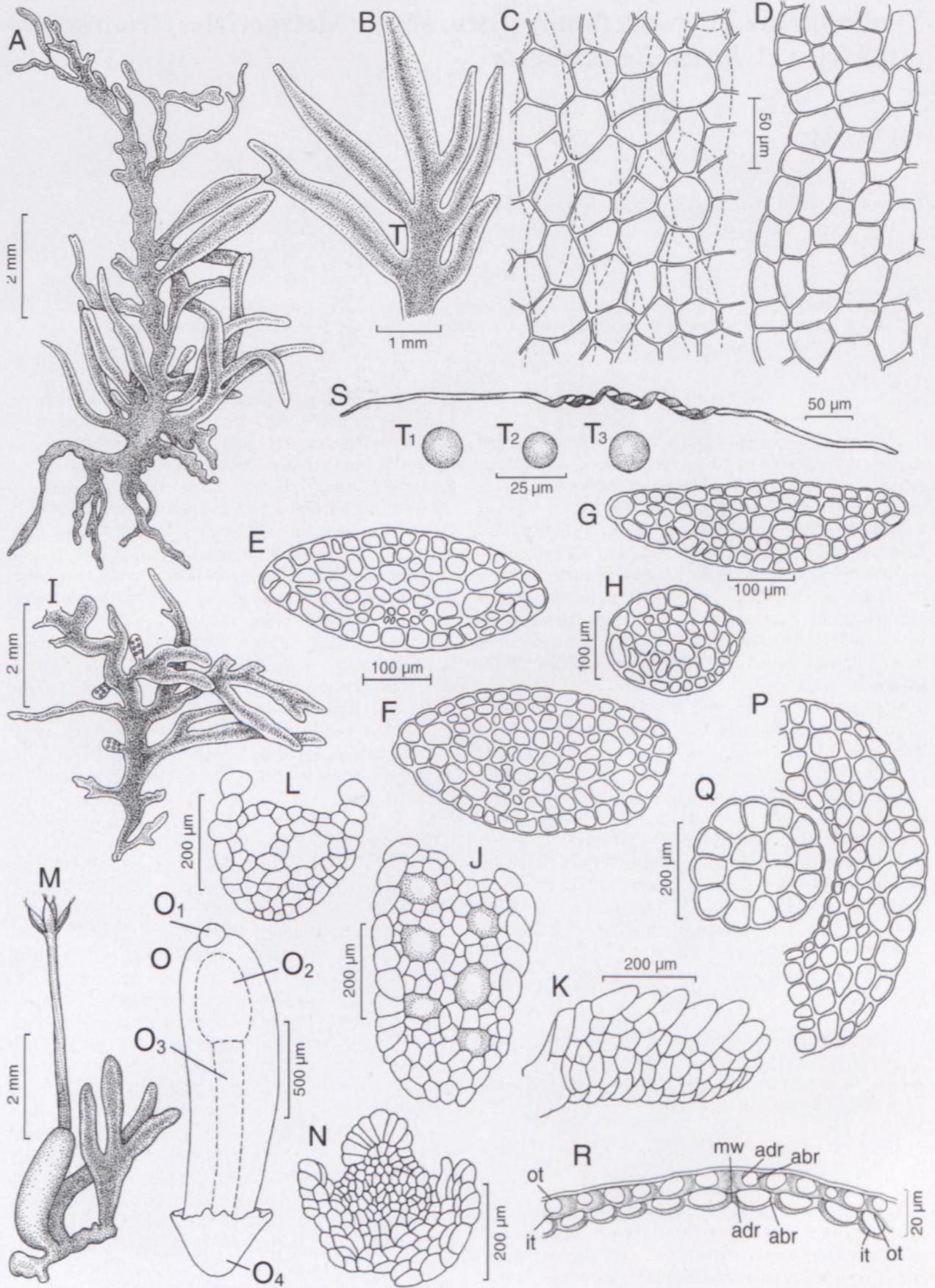


FIGURE 1.—*Riccardia compacta*. A, sterile thallus with axis and irregular lateral branches crowded below; B, axis with primary branches; C, median dorsal epidermal cells (solid lines) of ultimate segment of axis, and large subdorsal cells (stippled lines); D, margin of ultimate segment of axis; E, c/s axis at ± middle of ultimate segment; F, c/s axis below; G, c/s primary branch; H, c/s stolon; I, male thallus with 3 antheridial branches. J–L, antheridial branch: J, from above; K, from side; L, c/s. M, female thallus with calyptra, seta and dehiscent capsule valves; N, gynoecial branch with very young calyptra and paraphyses. O, calyptra: O<sub>1</sub>, corona; O<sub>2</sub>, capsule; O<sub>3</sub>, seta; O<sub>4</sub>, basal portion. P, c/s calyptra wall; Q, c/s seta; R, c/s part of bistratose wall of capsule valve showing different cell walls: abr, abaxial radial; adr, adaxial radial; it, inner tangential; mw, median; ot, outer tangential. S, elater; T<sub>1–3</sub>, spores. A–F, H–T, Arnell 963; G, Jelinek 19560G, holo.

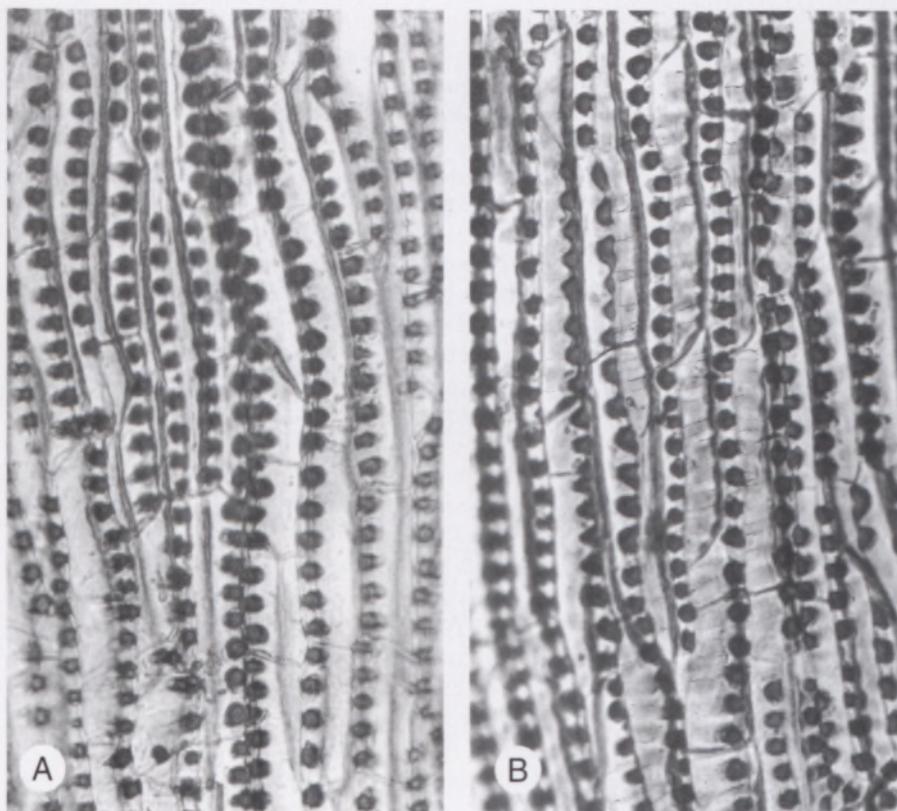


FIGURE 2.—A, cells of epidermal layer of wall of valve in external longitudinal view. B, cells of inner layer of wall of valve in internal longitudinal view. A, B, Arnell 963. A, B,  $\times 446$ .

Dioicous. *Antheridial branches* solitary or occasionally in sympodial pairs, lateral on main axis opposite or subopposite primary branch, otherwise on primary branch close to its base (Figure 1I), stipitate,  $\pm$  oblong (Figure 1J), up to 600  $\mu\text{m}$  long,  $\pm 320 \mu\text{m}$  wide, mostly bearing 3 or 4, rarely up to 8 pairs of antheridia, cavities 70–100  $\mu\text{m}$  diam., encircled by 2 or 3 rows of cells, 25–30  $\times$  30  $\mu\text{m}$ ; in cross section  $\pm 250 \mu\text{m}$  high (Figure 1L), margins winged (Figure 1K), with single, incurved row of large, obliquely orientated cells, 75.0–112.5  $\times$  40–45  $\mu\text{m}$ , apically rounded and free, otherwise adjoining; ventral papillae up to 30  $\mu\text{m}$  long, in lateral pairs, but rare. *Gynoecial branches* (Figure 1N) short and obliquely ventro-lateral on main axis, opposite or at base of primary branch,  $\pm$  sessile, not seen with archegonia, only with very young calyptra, up to 500  $\mu\text{m}$  long, including corona, the latter with apical row of radiating cells, width across widest part below 480–525  $\mu\text{m}$ , including surrounding paraphyses, which are scale-like and dentate, with cells 40.0–52.5  $\times$  27.5–30.0  $\mu\text{m}$ . *Calyptra* (Figure 1M, O) clavate, up to 2.4  $\times$  0.7 mm, cross section of wall  $\pm 180 \mu\text{m}$  or 5/6 cell layers thick (Figure 1P), some outermost ones with low protrusions, at apex corona smoothly rounded above, cells thick-walled, dislodged at maturity by emerging capsule. *Seta*  $\pm 6.5 \text{ mm}$  long,  $\pm 280 \mu\text{m}$  wide, with 4 central and an outer row of 12 cells, i.e. 4 cells diam. (Figure 1Q). *Capsule*  $\pm$  ellipsoidal, 790–850  $\mu\text{m}$  long, elaterophore internally attached to apex; valves 280–350  $\mu\text{m}$  or 21–24 cell rows wide, cells of epidermal layer in external longitudinal view (Figure 2A), 55–110  $\times$  10.0–12.5  $\mu\text{m}$ , with strong vertical (radial) thickenings, evident as nodular brown bulges; in cross section (Figure 1R) cells rectangular,  $\pm 7.5 \mu\text{m}$  thick, thickenings on adaxial radial and abaxial radial walls extending slightly onto outer and inner tangential walls, resulting in a crescentic ring of thickening, bands on one

side of median wall alternating with those on the other side in a mirror image; inner cells in internal longitudinal view (Figure 2B) 67.5–85.0  $\times$  12.5–17.5 ( $-20.0$ )  $\mu\text{m}$ , with nodular thickenings and with faint semiannular bands; in cross section (Figure 1R) cells  $\pm 10 \mu\text{m}$  thick, thickened on adaxial radial and abaxial radial walls, extending slightly onto outer tangential walls and further across inner tangential walls. *Spores* (Figure 1T<sub>1-3</sub>)  $\pm$  orbicular, 12.5–15.0  $\mu\text{m}$  diam., translucent, scabrate. *Elaters* (Figure 1S) 97.5–317.5  $\times$  7.5–10.0  $\mu\text{m}$ , with single spiral band, tapering to unspiralled apical portions. *Chromosome no.*:  $n =$  unknown. [It was suggested by Hewson (1970), that the 'normal' number of  $n = 10$  may be associated with the dioicous state and the monoicous state with double that number, i.e. 20].

#### DISCUSSION

The occurrence of *Riccardia compacta* in southern Africa appears to be restricted to Western Cape (Figure 3), generally at altitudes between 1 085 and 1 220 m, but it has also been collected close to sea level. It usually grows in wet, shady places, with low light intensity, on rotten wood, soil banks or on Table Mountain Sandstone.

The oil bodies were initially and briefly described by Arnell (1952) as 'rare, 3–8  $\times$  8–22  $\mu\text{m}$ , brownish' and he also illustrated a cell containing one (Arnell 1952: fig. 2h). In a much more detailed account, Meenks & Pócs (1985) observed that the oil bodies were 'rare or even absent in the epidermal cells and never in the cells of the wing'. They were, however, 'frequently present in the inner cells of the thallus', and were described by the above authors as 'light brown, 1 or 2 per cell', as well as 'globose to ellipsoid or bean-like, 8  $\times$  8–30  $\times$  12  $\mu\text{m}$ '.

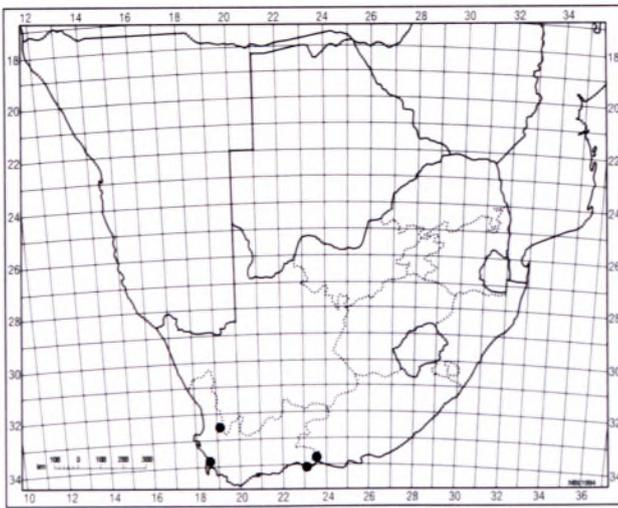


FIGURE 3.—Distribution of *Riccardia compacta* in southern Africa.

During a visit to Table Mountain (and other areas in Western Cape) in October 2000 by Perold & Koekemoer, we were unable to find fresh material in order to study the oil bodies. All the collections that I examined, had long ago lost their oil bodies. The colour of fresh plants could also not be observed, but Pillans had noted on the label of his collection from Table Mountain, that they were bright green and Meenks & Pócs (1985) stated that they were emerald green to dark brown.

In a comparison between plants from Tanzania and those from South Africa (with information reported by Arnell 1963), Meenks & Pócs (1985) found that the former specimens were generally longer at 20 mm versus 7 mm; in transverse section 6 or 7 cell layers thick, versus 4 or 5 cell layers; spore diameter 12–22  $\mu\text{m}$  versus 12–14  $\mu\text{m}$ ; wing of main axis 1 cell wide, cells elongated, up to 75  $\times$  40  $\mu\text{m}$ , versus wing absent.

In my findings the thalli of our plants are up to 15 mm long and in cross section the ultimate segment of the main axis is 6 or 7 cell layers thick, the spore diameter is 12.5–15.0  $\mu\text{m}$ , and the male branches are shorter at  $\pm$  600  $\mu\text{m}$  long, with 3 or 4, rarely up to 8 pairs of antheridia; the wing is formed by a row of elongated, apically rounded cells that are laterally adjoined, but apically free. Male branches in the Tanzanian specimen that I studied are mostly longer than ours, i.e. up to 1600  $\mu\text{m}$  long, with 4–14 pairs of antheridia, the wing consisting of a row of quadrate to rectangular cells, 42.5–45.0  $\mu\text{m}$  high, 37.5–42.5  $\mu\text{m}$  wide, their sides joined together right up to the edge; ventrally there are 2 rows of conspicuous red-brown mucilage papillae, up to 60  $\mu\text{m}$  long, rarely seen in South African specimens. As Meenks & Pócs observed, there are a few differences between Tanzanian and South African plants. The general facies of the plants from the two areas is, however, closely similar and there is no doubt that they belong to the same species.

Meenks & Pócs expressed the opinion that all continental African records of *R. caespitans* (Steph.) E.W.Jones (nom. inval.) probably belong to *R. compacta*. Apparently, Jones (1956) had identified Hedberg specimens from Mt Muhawara, Uganda, as 'possibly *Aneura*

*caespitans*', but had added that *R. caespitans* is 'known with certainty only from the Mascareignes' [Stephani (1892) Bourbon, leg. Rodriguez]. I have examined Dusén G010680 from Cameroon, incorrectly labelled as 'TYPUS' with a red sticker, and also figure no. 236 in Stephani's *Icones hepaticarum* (1985), which was probably drawn from the aforesaid Dusén specimen (according to a note with it). This plant is decidedly different from *R. compacta* specimens: in cross section the ultimate segments of the main axis are 4 cell layers thick and winged, with 3 unistratose cell rows at both margins. The lower axis in cross section is 6 cell layers thick medianly and not 9 cells as in Stephani's *Icones hepaticarum*. Whether Dusén's specimen belongs to the same species as Rodriguez's type collection from Réunion, is very doubtful, as the latter species was reported by Stephani to be 10 cell layers thick medianly.

For several reasons I also hesitate to accept *R. kilimandjarica* as a synonym of *R. compacta*, as was done by Meenks & Pócs. In *R. kilimandjarica* the thalli appear to be lighter-coloured, lacking the central dark line, and more delicate than in *R. compacta*. Cross sections of the ultimate segment of the main axis are  $\pm$  500  $\mu\text{m}$  wide and 5 or 6 cell layers rows (or 150–170  $\mu\text{m}$ ) thick, with the medullary cells clearly thin-walled, not thick-walled as in *R. compacta*.

Schuster (1963) suggested that a number of species, among them *R. compacta*, may be assigned to the subgenus *Phycaneura*, which is, however, characterized by relatively large, thin-walled dorsal epidermal cells. Although they had not studied specimens and illustrations of *R. compacta*, Brown & Braggins (1989) think that the species that Schuster (1963) grouped together, appear to be members of section *Alcicornia*, subgenus *Riccardia*, rather than of subgenus *Phycaneura*. Stephani (1899) had placed together some of these species, e.g. *A. alcicornis*, *A. compacta*, *A. diminuta*, *A. subsimplex*, *A. sumatrana* and others, as 'Plantae filiformes, subteretes'. *R. compacta* appears to bear some similarities to *R. subalpina* Furuki (1991) from Japan, as it also grows (mostly) at higher altitudes, and has small thalli and thick-walled cells.

*R. compacta* specimens are distinguished by the following characters: 1, the plants grow in dense, thick cushions of several layers of intricately intertwining branches, mostly at high altitudes; 2, the thalli are narrow and small, only up to  $\pm$  15 mm long, with irregularly branched, lateral branches, their margins generally parallel and unwinged; 3, from above the dorsal cells of the ultimate segment of the main axis are thick-walled, and in cross section, so are the medullary cells; 4, the antheridial branches in South African plants are usually short and have conspicuous marginal cells; and 5, the corona of the calyptra is smooth and the cells thick-walled.

#### SPECIMENS EXAMINED

##### *R. compacta*

Arnell 963, Table Mountain (S); 1623, near Park Station, Knysna (BOL).

*Esterhuysen 24253A, 24255*, N side of Tsitsikama Mts (BOL); 25497, Apollo Peak, Cederberg (BOL, PRE).

*Jelinek 19560G* (holotype), Table Mountain (G).

*Pillans 4247*, Table Mountain (BOL). *Pócs & Ochyra 88152/R*, Mt Meru, Tanzania (PRE).

Quite a few specimens (held at BOL, PRE & S) have been incorrectly referred to *R. compacta*, probably because of the small size of some of these plants. *Arnell 1689*, Gouna Forest, Knysna (PRE) is, in fact, *R. multifida* (Perold 2001).

### *R. kilimandjarica*

*Esterhuysen 27249* (holotype of *R. kilimandjarica*), Mt Kilimanjaro, Tanzania (S).

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