Studies in the liverwort family Aneuraceae (Metzgeriales) from southern Africa. 2. The genus *Riccardia* and its type species, *R. multifida*, with confirmation of its presence in the region

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Keywords: Aneuraceae, Riccardia Gray, Riccardiaceae, R. multifida (L.) Gray, R. saccatiflora (Steph.) S.W.Arnell, southern Africa, type species

ABSTRACT

A generic description of *Riccardia* Gray is presented, as well as confirmation of the local presence of its type species, *R. multifida* (L.) Gray, which is described and illustrated. Arnell (1952; 1963) incorrectly identified his collections of this species as *R. saccatiflora* (Steph.) S.W.Arnell; some notes on it are added.

INTRODUCTION

In my previous account of the Aneuraceae (Perold 2001), I distinguished between the two locally occurring genera, *Aneura* Dumort. and *Riccardia* Gray, and briefly traced the taxonomic history of the family in our region, as well as that of the areas to the north. Short descriptions of the family and the genus *Aneura* were presented, as well as a detailed description and an illustration of *A. pinguis* (L.) Dumort.

In the present publication a short account of the genus *Riccardia* is given, as well as a detailed description and illustration of *R. multifida* (L.) Gray. Lehmann (1829) had previously reported the presence of this species and two of its varieties on Table Mountain, and Gottsche *et al.* (1844–1847: 788) mentioned its occurrence at the Cape. Arnell (1952, 1963), however, did not allude to it at all, having misidentified his collections of it as *R. saccatiflora.* Reports of its local occurrence by Müller (1951–1958) and by Smith (1990), were probably based on Lehmann's work and the brief reference to it by Gottsche *et al.*

Riccardia *Gray*, A natural arrangement of British plants: 679, 683 (1821) as '*Riccardius'*, correction by Trevis.: 785 (1874) to '*Riccardia'*; Hewson: 75 (1970); Brown & Braggins: 25 (1989); Furuki: 323 (1991); R.M.Schust.: 579 (1992); Paton: 540 (1999); Bednarek-Ochyra et al.: 178 (2000). Lectotype: *Riccardia multifi-da* (L.) Gray (*Jungermannia multifida* L.).

Synonyms are given in Hewson (1970); Brown & Braggins (1989) and R.M. Schust. (1992).

Thalli prostrate to ascending, pale to dark green, cell walls sometimes turning brown, rather delicate, somewhat fleshy or not, short or long, length up to 40 mm, sometimes more, narrow, 0.5–2.0 mm wide, lingulate to linear, apices truncate, rounded or emarginate, margins obtuse to acute. *Branching* lateral, pinnate to quadripinnate, rarely multipinnate, stolons sometimes present. *Dorsal epidermal cells*

thin-walled, smaller than internal cells. *Oil bodies* 1–3 in each epidermal cell, sometimes more, rarely absent, ovoid, spherical or ellipsoid, $12.5-22.5 \times 10.0-12.5 \mu m$, also present, although larger, in internal cells, composed of numerous fine globules, opaque, black or brown. *Cross section* of branches plano-convex, biconvex or concavo-convex, rarely circular, 3–9 cells thick medianly, at margins acute to winged or not. *Mucilage papillae* ventral, in 2 acropetal rows, one on each side of midline and at branch apices. *Rhizoids* usually present, numerous on ventral surface, unicellular. *Asexual* reproduction by 2-celled gemmae, endogenously produced by epidermal cells, frequently present.

Monoicous, dioicous or synoicous. Male branches lateral on main axis or on pinnae/primary branches, linear to ligulate, sometimes in sympodial clusters, antheridia in 2 regular rows, in chambers usually separated by unistratose cell walls, dorso-lateral wing up to 8 cells wide. Female branches short, lateral on main axis or on pinnae. archegonia in 2 rows, protected by fringe of finger-like or lamellate paraphyses. Shoot-calvptra large and fleshy, up to ± 5 mm long, 0.7–1.1 mm wide, wall 5 or more cell layers thick, surface smooth to rough, apical cells, i.e. corona, poorly to well developed. Seta in cross section with 4 inner and 12 outer cell rows (4 cells diam.). Capsule ellipsoidal, 4-valved, wall bistratose, cells of external layer with thickenings on adaxial radial and inner tangential walls, cells of inner layer mostly without thickenings, although the adaxial radial wall is sometimes slightly thickened. Spores spherical, finely scabrate, small, 9-15 µm diam. Elaters 120-350 µm long, 8-10 µm wide, unispiral.

The genus *Riccardia*, was named in honour of Vincento Riccardi, a resident of Florence during the early years of the 18th century, and a donor to Micheli's (1729) *Nova plantarum genera*.

Riccardia multifida (*L.*) *Gray*, A natural arrangement of British plants 1: 684 (1821); A.Evans: 22, 23 (1937); Müll.Frib.: 499 (1954); R.M.Schust.: 316 (1987); R.M.Schust.: 618 (1992); Paton: 541 (1999). Type: Europe.

Aneura multifida Dumort.: 115 (1822); Müll.Frib.: 336 (1908); Macvicar: 54 (1926).

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FIGURE 1.—*Riccardia multifida*. A, thallus with axis and lateral branches, 2- or 3-pinnate; B, median dorsal epidermal cells (solid lines) of ultimate segment of axis without oil bodies, but present in large subdorsal cells (stippled lines); C, ultimate pinnule, some marginal cells with oil bodies, medianly opaque; D, margin of ultimate pinnule, oil bodies mostly absent in outer, but present in inner cell rows; E, F, c/s axis at ± middle of ultimate segment; G–J, c/s ultimate pinnules; K, ventral surface of part of pinnule, with mucilage papillae at apex. L, M, antheridial branch: L, from above; M, c/s. N, synoicous branch; O, gynoecial branch with paraphyses; P, Q, calyptra: Q, c/s wall. R, c/s seta; S, capsule with 4 dehisced valves. T–V, valve: T, cells of epidermal layer in external longitudinal view; U, cells of inner layer in internal longitudinal view; V, c/s part of bistratose wall (thickenings partly after Evans 1937). Wall: mw, median; ot, outer tangential; it, inner tangential; adr, adaxial radial; abr, abaxial radial. W1, W2, spores; X, elater. *Perold & Koekemoer* 4449–4452: A, C, F–M, P, W1, W2, X, 4449; B, 4452; D, R, 4450; E, N, O, Q, S–V, 4451.

Jungermannia multifida L.: 1136 (1753).

For a complete list of synonyms, Schuster (1992) may be consulted.

Thalli prostrate to suberect, in loosely or densely overlying and intricately intertwining mats, rather light green, sometimes at maturity cell walls brown, opaque, with narrow, translucent margins (Figure 1A); when dry, dark green; medium-sized to large, flat and flabellate above. Main axis dorsally plane to convex or slightly concave, often retaining its dominance, up to 27 mm long, 0.82-1.05 mm wide, apically rounded or slightly emarginate, eventually narrowing somewhat toward base, margins acute and unistratose for a width of 1 or 2 cells. Primary branches lateral, opposite or subopposite, 0.8-1.4 mm between successive ones, obliquely spreading, often overlapping, regularly pinnate with pinnae well developed, linear, distally with 2 or 3 paired pinnules, proximally with 4 or sometimes even 5 paired pinnules, older, primary branches/pinnae up to 4.7 mm long, 590-650 µm wide, secondary branches/pinnules 0.75-1.6 mm long, 475-530 µm wide; from base of main axis or from apices of secondary branches, flagelliform branches sometimes produced. Dorsal epidermal cells in median part of apical segment of main axis (Figure 1B), from above 5-7-sided, thin-walled, $62.5-105.0 \times 25.0-37.5(-55.0) \mu m$, subdorsal cells larger, 4–7-sided, $155.0-262.5 \times 62.5-87.5 \mu m$, subventral cells $170.0-237.5 \times 60-85 \,\mu\text{m}$, ventral epidermal cells 75-100 \times 30.0–47.5 µm. Oil bodies rare or absent in dorsal and ventral epidermal cells, absent in up to 70% of marginal cells, present in internal cells, 1 or occasionally 2 per cell, $15-25 \times 7.5-12.5 \ \mu m$, subspherical, ellipsoidal or ovoid, with rounded ends, light brown, opaque, composed of numerous small globules. Margins of ultimate pinnules crenulate (Figures 1C, D; 2A), outer cells smaller than intramarginal ones, from above $35-55 \times 35.0-47.5 \ \mu m, \pm$ subquadrate, with free walls bulging, intramarginal cells often obliquely orientated, polygonal, 72.5-100.0 × 47.5-52.5 µm, generally with 1 oil body each. Cross section of main axis at middle of ultimate segment (Figure 1E, F) plano-convex, or weakly concavo-convex, sometimes biconvex, 180 µm or 6(7) cell rows thick medianly, gradually tapering to unistratose margins, 1 or 2 cells wide, dorsal cells $\pm 27.5 \,\mu$ m thick, internal cells $37.5-50.0 \,\mu$ m thick; cross section of ultimate pinnule of primary branch (Figure 1G-J) 100 µm or 3 or 4 cells thick medianly, pellucid, unistratose margins 2 or 3 cells wide. Mucilage papillae ventral (Figure 1K), clustered at slightly emarginate apex of branch and in 2 spaced, acropetal rows, one on either side of midline, 300-360 µm between successive ones, reddish, club-shaped, 2-celled, above $45.0-62.5 \times 25.0-32.5 \mu m$, narrowing to inconspicuous basal cell, non-persistent. Rhizoids ventral on axes, sometimes also on pinnae, hyaline, 7.5–15.0 µm wide. Asexual reproduction by gemmae seemingly absent.

Heteroicous, with male, female and rarely synoicous branches. Antheridial branches lateral, near base of primary pinnae, on one or both sides, occasionally at tips of secondary pinnules, oblong-linear (Figure 1L), \pm 700 µm long, 350 µm wide, in cross section 240 µm high (Figure 1M), margins crenulate, with single, erect layer of swollen cells, 62.5–77.5 × 45–50 µm, bearing 5 or more pairs of antheridia, separated by unistratose cell layer; very rarely synoicous (Figure 1N), basally with paired antheridia and apically with a few archegonia and



FIGURE 2.—*Riccardia multifida*: A, pinnule (living), with outwardly bulging marginal cells along both margins; B, fully rehydrated pinnule, (collected 1951), with marginal cells not bulging outwardly. *R. saccatiflora*: C, fully rehydrated pinnule (collected late 1800s), with much smaller marginal cells not bulging outwardly, only one margin shown. A, *Perold & Koekemoer 4449*; B, *S.W. Arnell 1952* (S); C, *Rodriguez G10699* (G). A–C, × 114.

short, laciniate cilia at tip. *Gynoecial branches* short, arising opposite base of primary branch on main axis, or toward base of main axis, sometimes toward middle of primary branch, between pinnae of 1st and 2nd

orders, or between pinnae of 2nd and 3rd orders; paraphyses between and surrounding archegonia (Figure 10), up to 437.5 µm long, composed of single strands of 9 or more cells, joined end to end; sometimes up to 3 female branches in a sympodial cluster. Calyptra (Figure 1P) clavate, $3.2-5.3 \times 0.7-1.1$ mm, cross section of wall up to 225 µm or 4-6 cells thick (Figure 1Q), outermost row with scattered, thick-walled papillae, 65–90 \times 25–65 µm, extending upwards to apex, where they are grouped together, forming a corona. Seta ± 12 mm long, \pm 280 µm wide, with 4 inner and 12 outer cell rows, i.e. 4 cells diam. (Figure 1R). Capsule ± cylindrical, 1200-1450 µm long, with 4 dehisced valves (Figure 1S), 320–375 µm or 12–15 cells wide, bistratose; cells of epidermal layer in external longitudinal view (Figure 1T), 100.0–142.5 \times 25–35 µm, with straight or oblique end walls, and strong nodular thickenings; in cross section (Figure 1V) cells \pm rectangular in shape, thickenings on adaxial radial (adr) and inner tangential (it) walls sometimes extending slightly to outer tangential (ot) walls, mostly bands on one side of median wall (mw) alternating with those on the other side, i.e. forming a mirror image; inner cells in internal longitudinal view (Figure 1U), $112.5-132.5 \times 25-35 \mu m$, never with nodular thickenings; in cross section (Figure 1V) cells faintly thickened on adaxial radial (adr) and sometimes extending slightly on inner tangential (it) walls. Spores (Figure 1W1, W2) 15-20 µm diam., translucent, finely scabrate, pinkish, with inner, irregularly shaped, green areas. Elaters (Figure 1X) 245-390 µm long, 10-14 µm wide, with single spiral band, tapering to unspiralled tips. Elaterophores at valve apices (Figure 1S), in persistent tufts. Chromosome no.: n = 20.

Riccardia multifida is a widespread species or species complex which Schuster (1992) says, extends from the northern Spruce-Fir zone southwards. According to Schuster, two subspecies occur in North America, i.e. R. multifida subsp. multifida, with a more northerly range along the western states, and R. multifida subsp. synoica with a more southerly range along the eastern states. Apart from occupying a different geographical range, the latter subspecies is also distinguished from the former autoicous one, by most of its inflorescences being bisexual and by its preference for growing on rotting wood. R. multifida subsp. multifida is further known from Newfoundland, Greenland, Iceland, British Isles, Macaronesia, Europe, North Africa, Madagascar, Sikkim-Himalaya, West Java (Meijer 1959) and China (Yunnan). Another subspecies, R. multifida subsp. decrescens, is reported from Japan by Furuki (1991). Reports of *R. multifida* from the Falklands have been excluded according to Engel (1990). As far as is known, it also does not occur in Australia, New Zealand or in South America, although there is an unconfirmed report from the Andes (Gottsche 1864). Müller (1951–1958) remarked that, 'Die Angaben von der südlichen Hemisphäre gehören aber vielleicht nicht zu R. multifida." Wigginton & Grolle (1996) also do not include it in their Catalogue of the Hepaticae and Anthocerotae of sub-Saharan Africa. Jones (1956), however, observed that a specimen collected from the 'Foresta di Tusu, Mt Kenya' and described by Gola (1914), appeared to him to be identical with R. multifida. Schuster (1992), on the other hand, thinks that R. multifida may be the only Riccardia

species with a reasonably certain bipolar range, as a collection from Campbell Island, south of New Zealand, differs only slightly from holarctic plants, although he concedes that it needs more study.

Schuster (1992), with his extensive knowledge and customary astuteness, expressed the opinion that, of the species that Arnell (1952, 1963) reported from South Africa, *R. saccatiflora* 'seems virtually inseparable from *R. multifida*'. After thorough examination of Arnell's collections, I share this view, although it must be admitted that Arnell's drawings do not show the regular bi- and tripinnate branching generally exhibited by *R. multifida*. However, the narrow translucent margins of the ultimate pinnules of his specimens are conspicuous (Figure 2B), and may have misled him into thinking he was dealing with *R. saccatiflora*. Otherwise, it is surprising that Arnell made this mistake, as he should have been familiar with *R. multifida*, having treated it for the *Illustrated moss flora of Fennoscandia* (Arnell 1956).

Study of the type and five other Rodriguez collections of *R. saccatiflora* from Réunion (Bourbon), as well as Stephani's *Icones* (1985) nos. *000229* and *000230*, showed that the unistratose marginal cells of the ultimate pinnules form a distinct wing, but are small (Figure 2C); they measure $27.5-32.5(-45.0) \times 10-20(-35) \mu m$, whereas the intramarginal cells are only slightly larger, $37.5-42.5 \times 25-30 \mu m$. In cross section the ultimate pinnules are 4 or 5 cell layers or 100 μm thick medianly and the main axes 8 cell rows or 300 μm thick. Stephani (1890) referred to the marginal cells as 'multo-minores'.

Arnell (1963) reported the oil bodies of his '*R. saccatiflora*' collections to be 'dark, large, composed of very small droplets, one per cell'. In their examination of *R. saccatiflora* specimens, Meenks & Pócs (1985) found that their oil body data agreed well with Arnell's observations, but added that the oil bodies seem 'rather persistent, since they still occur in some older herbarium collections'. This is not the case in *R. multifida*, where the oil bodies are not persistent. Meenks & Pócs (1985) only cite the literature records from South Africa given by Arnell (1963: 92). Their reports of *R. saccatiflora* from East Africa are, however, accepted for the time being.

Paton (1999) states that, in British *R. multifida*, the occasional synoicous inflorescence occurs on the same thallus as unisexual and paroicous inflorescences, but that such populations are not referable to the American subspecies *synoica* R.M.Schust., in which nearly all the inflorescences are bisexual. The same criteria apply to the South African plants, where synoicous inflorescences are very rare.

The new Perold & Koekemoer collections of *R. multifida* are from Diepwalle Forest Station, near Knysna, in the southeastern part of Western Cape (Figure 3). This is the same vicinity as Gouna Forest, Bracken Hill, Buffels Nek and Garden of Eden, from where Arnell (1952) recorded several of his so-called *R. saccatiflora* gatherings, which have now been transferred to *R. multifida*.

R. multifida specimens are distinguished by the following characters: 1, the thalli are markedly feathery, with rather crowded and generally very regular, pinnate



FIGURE 3.—Distribution of R. multifida in southern Africa.

branching; 2, the ultimate and lateral pinnules are thin, linear and paralled-sided, with the outer 3 cell rows unistratose and translucent on either side of the thicker, opaque, median region; 3, the ultimate pinnules have crenulate distal margins, with the marginal cells bulging externally and smaller than the intramarginal cells; 4, the oil bodies are mostly absent from the marginal and epidermal cells of the median region, but present in the internal cells; 5, the epidermal cells of the median part are generally narrower than in allied species, i.e. $25.0-37.5(-55.0) \mu m$ wide; 6, the plants are rarely synoicous.

ECOLOGY

Riccardia multifida plants grow on soil, twigs, dead leaves or decaying wood in forested areas at streambanks or seepages, i.e. in constantly wet or damp sites in \pm diffused light.

ACKNOWLEDGEMENTS

The curators of BOL, G and S are thanked for the loan of specimens. I also express my sincere gratitude to Ms M. Koekemoer, curator of PRE, for all her help with fieldwork, and to the referees for their helpful suggestions and advice. The artist, Ms G. Condy, the photographer, Mrs A. Romanowski and the typist, Ms D. Maree are thanked for their valued contributions.

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SPECIMENS EXAMINED

Riccardia multifida

Arnell 1515 Buffels Nek, 1592•, 1731 Gouna For. (BOL), 1839 Diepwalle For. Res.(BOL), 1843*• (BOL, PRE), 1844*, 1845 (BOL), 1918 (PRE), 1929 (BOL), 1952 (S), 1974 Bracken Hill For. (BOL), 2079, 2133 Garden of Eden (BOL).

Perold & Koekemoer 4449, 4450, 4451, 4452, Diepwalle Forest Reserve, Knysna District, Western Cape.

Riccardia saccatiflora

Rodriguez G010697 (G) (type specimen), *G010698* (G), *G010699* (G), *G010700* (G), *G010702* (G), *G010703* (G) Bourbon (Réunion).

[•] on decaying wood.

^{* 1/2} mile south of Diepwalle Forest Reserve.