Studies in the genus *Riccia* (Marchantiales) from southern Africa. 8. *R. campbelliana* (subgenus *Riccia*), newly recorded for the region

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ABSTRACT

R. campbelliana Howe (1899), a rare species originally known from California and later from Georgia, Arkansas (Jacobs 1951; Wittlake 1954), Kansas and Nebraska (S. Jovet-Ast pers. comm.), as well as from Kazakhstan (Ladyzhenskaja 1967), has now also been found at a few localities in southern Africa. It is characterized by the distinctive yellow-brown or rusty colouration of the dorsal surface along the margins and over the proximal parts; enlarged cells, 'idioblasts', which differ in shape and contents from the adjacent cells, are generally found in all parts of the thallus.

UITTREKSEL

R. campbelliana Howe (1899), 'n seldsame spesie oorspronklik bekend van Kalifornië, en later van Georgia, Arkansas (Jacobs 1951; Wittlake 1954), Kansas en Nebraska (S. Jovet-Ast pers. kom.), sowel as Kazakhstan (Ladyzhenskaja 1967), kom ook by 'n paar lokaliteite in suidelike Afrika voor. Dit word gekenmerk deur die geel-bruin kleur van die dorsale oppervlak langs die rande van die tallus en oor die proksimale gedeeltes; vergrote selle, 'idioblaste', wat verskil in vorm en inhoud van die aangrensende selle, kom ook algemeen in alle dele van die tallus voor.

Riccia campbelliana *Howe* in Memoirs of Torrey Botanical Club 7: 26 (1899); Frye & Clark: 20 (1937); Hässel De Menéndez: 267 (1962); Ladyzhenskaja: 316 (1967).

TYPE.—California, near Stanford University, on hills above Mission Dolores, *D. H. Campbell s.n.* May 1, 1896 [NY, lecto.!, fide Grolle: 225 (1976)].

Thallus monoecious, perennial, in crowded gregarious patches or incomplete rosettes or scattered; simple or once to twice furcate, branches divergent or mostly parallel, oblong-linear, medium-sized, up to 8 mm long, 1,0-1,5(-2,0) mm broad, once to twice broader than thick (Figure 1A), segments up to 3,5 mm long; apex rounded and obtuse, emarginate, dorsal furrow deep, its sides raised and convex, becoming flatter in older parts (Figures 1B1-6; 2A, 2B); dorsally pale green, yellow or rusty brown along margins and more proximally over entire dorsal surface; margins acute, shortly winged, slightly undulating, flanks sloping upward and outward, bronze-brown; ventral surface rounded, green, occasionally flecked with red and brown; when dry, margins inflexed, forming brown lips, flanks with brown scales.

Anatomy of thallus: dorsal epithelium unistratose, hyaline, cells variously shaped, in younger parts and towards centre subglobose, $30-45 \times 35-50 \ \mu\text{m}$, laterally becoming somewhat flatter and up to 70 \mum m wide (Figures 1C, 2C), brown and collapsed at margins and in older parts, underlying layer of cells soon losing their chloroplasts (Figure 1D); air pores triangular, $\pm 7 \ \mu\text{m}$ wide, often rectangular and larger, $\pm 12 \ \mu\text{m}$ wide (Figure 1E); in section, assimilation tissue (chloren-

chyma) occupying about 1/2 the thickness of thallus and consisting of vertical columns of 6-10 cells, $50-60 \times$ $35-50 \ \mu m$ (Figure 1C), frequently some cells, referred to as 'idioblasts' (see p.39), differ from surrounding ones in the larger size, in the somewhat distended cell walls and in the contents (Figures 1D, 2F), air canals between assimilation cell columns up to 20 μ m wide; storage tissue occupying about ½ the thickness of thallus, cells rounded or angular, tightly packed, up to 55 μ m wide, containing chloroplasts and starch granules, usually with some scattered 'idioblasts' (Figure 2E). Rhizoids hyaline, some smooth, others tuberculate, $15-20 \ \mu m$ wide, arising from ventral epidermis of thallus and base of scales. Scales imbricate, fragile, inconspicuous, not projecting above thallus margin (Figure 2D), up to 750 \times 450 μ m; margin hyaline, rest of scale with groups of brown and different shades of violet cells, interspersed with single, or with groups of hyaline, 4-6-sided cells, walls straight or sometimes sigmoidal, cells elongated to nearly isodiametric, up to 65×40 μ m, some 'idioblasts' may be present, marginal cells smaller, $\pm 40 \times 40 \ \mu m$ (Figure 1F). Antheridia with short hyaline or white necks along dorsal groove. Archegonia with purple necks, also along groove. Sporangia infrequent, single or crowded, large, \pm 500 μ m wide, with about 200 spores each, in median part of thallus, causing bulging of overlying tissue which turns brown. Spores (85-)90-110(-120) µm in diameter, pale straw-coloured to brown, semitransparent, triangularglobular, polar, with wing up to 5 μ m wide (Figure 3B), pores at angles \pm 7,5 μ m or more wide, margin \pm smooth, ornamentation on both faces vermicular to irregularly and incompletely reticulate; distal face with 10-15 incomplete areolae across diameter, $\pm 5 \ \mu m$ wide (Figure 3C, F), ridges often sinuous and raised into blunt papillae at the nodes (Figure 3D), in transmitted light ridges often appear to have a midline; proximal face with triradiate mark generally clearly defined (Figure 3E) and with the ridges somewhat lower than those on

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FIGURE 1.—*Riccia campbelliana*. Structure of thallus, scales and chromosomes. A, fresh thalli; B1-6, transverse sections of thallus branch at different distances from apex to older parts; C, transverse section through dorsal epithelium, chlorenchyma and storage tissue; D, transverse section through collapsed dorsal cells and chlorenchyma, showing 'idioblasts' and air canals; E, epithelial cells and narrow air pores from above, dotted lines indicate contact with chlorenchyma cells below; F, scale; G, chromosomes, the letters A-E identify the chromosomes (see text): A-D, F, S. M. Perold 888; E, Van Rooy & Perold 634; G, Van Rooy & Perold 637; A-F, by Volk; G, by Bornefeld. Scale bar on A, B = 2 mm⁻ C-F = 100 μ m; G = 1 μ m.



FIGURE 2.—*Riccia campbelliana*. Structure of thallus and cells. A, dorsal surface view of thallus; B, apex and groove; C, dorsal cells; D, scales at margin; E, transverse section through thallus branch, showing 'idioblasts'; F, dorsal epithelial cells and 'idioblasts' in chlorenchyma. A–F, S. M. Perold 888. A–D, SEM micrographs by Perold; E & F, LM micrographs by Volk. Scale bar = 50 μm.

distal face (Figure 3A). Chromosome number n = 8[Figure 1G: the letters A-E identify the chromosomes, T. Bornefeld pers. comm.; Siler (1934)].

In adapting Tatuno's (1941) method, which in principle is also that used by Jovet-Ast (1969; 1986), this species with n = 8 chromosomes, has the following karyotype, according to Bornefeld (1984): A, BB, CC, DD, E. Capital letters of the alphabet are assigned to the different chromosome types, whereby the largest are denoted by the letter A and the smallest by the letter E. It presents the basic set of chromosomes in the genus *Riccia*, from which all other sets can be derived (Bornefeld 1984).

The 'idioblasts' in *R. campbelliana* are variable in size, colour and contents; in the assimilation tissue they are up to 100 μ m long × 45–60 μ m wide, single or arranged in groups and are free of chloroplasts (fluorescence assay by Volk); those occurring in the epithelium, the storage tissue and in the scales are also larger than the surrounding cells. In fresh or dry material, the 'idioblasts' can be brown, grey or hyaline, and appear to be clear and homogeneous or granular. They are readily stained with Heidenhain's iron haematoxylin (Howe 1899) or with diluted aqueous solutions of Thiacine

stains which are rapidly absorbed and produce metachromatic effects. Bienfait & Waterkeyn (1976) reported that metachromatic effects demonstrate the presence of acid muco-polysaccharides when Toluidine blue is used as a stain in histochemical assays. The 'idioblasts' in R. campbelliana are stained blue with Toluidine blue, whereas other cell walls are violet. It may therefore be assumed that pectines (derivatives of uronic acid) in the cell walls, are responsible. With iodine-potassium iodide, the cells turn brownish. In his original description of R. campbelliana Howe (1899) and R. dictyospora Howe (1901), both from North America, Howe regarded these 'idioblasts' as 'oil cells'. Ladyzhenskaja (1967) confirmed the presence of 'oil cells' in these two species and also reported their occurrence in the European species, R. breidleri Steph. and R. oelandica Jensen. Examination of four specimens of R. breidleri from Austria (B!; W!) and four from Switzerland (G!) failed however, to show the presence of 'idioblasts', but instead demonstrated numerous droplets of 'fatty oil' in the storage tissue. 'Idioblasts' were not found in R. oelandica (G!) either, and only rarely could globules of fatty oils be demonstrated, which also occur in R. campbelliana, but only after boiling, when they can be stained with Tincture of Alkanna, Sudan III-glycerine or with other stains for fats. 'Idioblasts' similar to those in R. campbelliana,





were found in *R. dictyospora* (G!; PRE!) and in *R. macrocarpa* Levier (B!; W!) — described in the latter by Jovet-Ast (1986) as 'cellules à contenu orangé éparses', and in specimens of *R. nigrella* from many parts of the world. In southern African *Ricciae*, the presence of 'idioblasts' is a unique feature and only known in these two species, *R. campbelliana* and *R. nigrella* [*R. capensis* auct. non Steph.: S. Arnell (1952)], see Perold & Volk (1988).

According to Howe (1899) the epithelial cells of *R. campbelliana* are usually longer than wide, but the South African specimens have \pm globose, to depressed globose cells. He also reported the antheridial necks to be 100–170 μ m long, i.e. more prominent than in our plants. The SEM micrographs of the spores published by Steinkamp & Doyle (1979), bear a close resemblance to those in the present study.

R. campbelliana is new to southern Africa. It is known from only three localities in central Transvaal, ranging from Derby, eastwards to Middelburg, and from a single locality in the eastern Orange Free State, near Fouriesburg (Figure 4). It grows in summer rainfall areas with an annual precipitation of 600-800 mm and at altitudes of 1 500–1 800 m above sea level. It prefers

shallow, acid soils overlying granitic, quartzitic or sandstone rock outcrops (pH \pm 4,6), fully exposed to the sun, and is often associated with other *Riccia* species, such as *R. nigrella* DC. and *R. okahandjana* S. Arnell, with small moss species, e.g. *Pleuridium nervosum* (Hook.) Mitt. and with crustaceous lichens.



FIGURE 4.—Map showing distribution of *R. campbelliana* in southern Africa.

Localities of *R. campbelliana* outside southern Africa are the following: USA, California, where it was found by Campbell, in whose honour Howe named it; Georgia (Jacobs 1951), Arkansas (Jacobs 1951; Wittlake 1954), Kansas and Nebraska (S. Jovet-Ast pers. comm); USSR, Kazakhstan, Western Siberia (Ladyzhenskaja 1967) and Argentina, Tucumán, [*Sleumer 1755 (LIL 19853*!)]. The latter specimen was referred to *R. campbelliana* by Hässel de Menéndez (1963) but it is doubtful whether it has been correctly identified as it lacks 'idioblasts' and the scales are deep red and large, definitely not inconspicuous; only the ornamentation of the spores shows some resemblance.

R. campbelliana is a very rare species with a strikingly disjunct distribution, viz. North America, (?) South America, South Africa and central Asia. These 'relictual areas' (Wulff 1950), may have resulted from intermediate localities becoming extinct, as the transport of spores over such immense distances in modern times by for example, migratory birds, can hardly be accepted. Consequently, R. campbelliana is regarded as a very ancient species, similar to the almost equally rare \vec{R} . crustata Trabut with remnant populations likewise spread over several continents, namely Central Asia (Kazakhstan), Europe, North Africa (Jovet-Ast 1973) and, if it were agreed that R. crustata and R. albida Sullivant ex Austin constitute a single species (Jovet-Ast 1986; Scott & Bradshaw 1986), also occurring in North America and Australia.

R. campbelliana can be recognized by the yellowbrown colour along the thallus margins, by the inconspicuous scales, partly hyaline and partly flecked with brown and violet, and by the sinuous vermicular ridges on the proximal and distal spore faces. Although small forms of R. campbelliana bear some resemblance to R. *nigrella*, they can be distinguished by the usually wider and longer branches, by the thinner, slightly attenuate margins and by the epithelial cells that are not persistent. *R. nigrella* is generally a smaller plant and it often grows in rosettes or partial rosettes; the thallus is dorsally deep brown except toward the apex, the scales are closely appressed and shiny black; when it sporulates, it is seen with overlying masses of dark brown spores; the spores are smaller and have vermicular ridges on the distal face and generally on the proximal face too.

SPECIMENS EXAMINED

Riccia campbelliana

Besides the lectotype specimen (NY), the following specimens were examined:

South Africa

TRANSVAAL.—2527 (Rustenburg): 2 km to Derby on road from Rustenburg (-CC) S. M. Perold 888 (PRE). 2528 (Pretoria): 19 km N of Bronkhorstspruit, overlying granite (-DC), Volk 81/024 (M, PRE). 2529 (Witbank): N of Middelburg, on road R35, at plateau near Klein Olifants River (-CB), S. M. Perold 69, 80, 81 (PRE); Van Rooy & S. M. Perold 634, 637, 642 (PRE); Volk 81/010 (M, PRE).

O.F.S.—2828 (Bethlehem): 11 km E of Fouriesburg on road from Clarens, around weathered sandstone outcrops on slope (-CB), S. M. Perold & Germishuizen 1307 (PRE).

North America

NEBRASKA.-Lancaster Co., Lincoln, Walter Kiener 9961 (US).

KANSAS.—Woodson Co., Baker's Bluff, R. R. Ireland Jr. 83 (US).

CALIFORNIA.—Balboa Park, San Diego, C. C. Haynes 2823 (US).

South America

ARGENTINA.—Tucumán, *Sleumer 1755 (LIL 19853)* (doubtfully referred to *R. campbelliana*).

Other species examined

R. breidleri from Austria (B; W), Switzerland (G); *R. dictyospora* from North America (G; PRE) and *R. macrocarpa* from Turkey, Italy and France (B; W).

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