

***Riccardia sphagnicola* sp. nov. (Marchantiophyta, Aneuraceae) a filamentous penalpine bog species of the New Zealand mountains with a comparison to six similar New Zealand species**

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Abstract

Riccardia sphagnicola is described from seven penalpine locations and one coastal location in both North and South islands, New Zealand. It is similar to six filamentous *Riccardia* species in New Zealand that have a main axis less than 0.6 mm wide (*R. breviala*, *R. lobulata*, *R. papulosa*, *R. aequicellularis*, *R. multicorpora*, and *R. asperulata*), five of which also have an unornamented epidermis. In all seven species, epidermal cells are approximately equal in size to internal thallus cells, a marginal wing no more than one unistratose cell wide, and endomycorrhizae absent or difficult to see. *Riccardia sphagnicola* is more robust than the others, as measured by main axis width and depth. It is most similar to *R. breviala* but differs in a number of respects, including habitat differences. *Riccardia sphagnicola* is brown in older parts of thallus versus uniformly yellow-green in *R. breviala*; it is loosely prostrate versus prostrate with erect branches; it has branch apices rounded versus slightly retuse; mucilage papillae at shoot apices are always present versus usually absent. Stolons in *Riccardia sphagnicola* are rare but common in *R. breviala*. *Riccardia sphagnicola* is mainly known from bogs in the penalpine zone whereas *R. breviala* is a forest species on a mineral soil substrate and does not reach the penalpine zone. *Riccardia asperulata* is reported new for Tasmania and Australia as a result of this study.

Introduction

The genus *Riccardia* S.F.Gray in New Zealand and Australia was revised by Hewson (1970) for Australia, and Brown and Braggins (1989) for New Zealand. Brown and Braggins (1989) commented that they knew of up to four alpine *Riccardia* species but had insufficient material to publish them and limited their study almost completely to freshly collected specimens. *Riccardia sphagnicola* Glenny, described here, was found in the course of examining existing collections at CHR. The earliest specimen was collected by Berggren in 1874 at Arthur's Pass. It is similar to six filamentous New Zealand species that have a main thallus axis less than 0.6 mm wide. For this reason, comparisons are made with those six species and the differentiating features of each is illustrated.

Secondary sexual dimorphism was noticed in plants of the new species described here. Glenny (2024) discussed the occurrence of this in *Riccardia* and found a significant difference between male and female plants of *R. dimorpha* Glenny in plant length, main axis width and number of meristematic tips, with male plants being longer, narrower in the main axis and with fewer branches per plant. The six dioicous species considered here were assessed for the same three characters.

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Methods

Dried plants were soaked briefly in warm water then soaked in pure domestic bleach for a few minutes until the thallus was clear, rinsed in water and then stained with 0.2% methylene blue for a few seconds and rinsed again in water. This “bleach and blue” method of Rico (2011), cited in Reeb and Bardat 2014), re-inflates and rigidifies collapsed thalli allowing stem sectioning and highlighting surface features such as surface texturing, mucilage papillae, and rhizoids. Ruthenium red stain was also used to highlight surface features in a few cases. Light microscope photographs were taken with a Leica DMLB 2500 compound microscope with a Flexacam camera and differential interference contrast. Bleached plants were viewed with crossed polaroid filters below and above the specimen slide to detect an core of cells in the main and pinna axes that alters the orientation of polarised light, as illustrated in Figure 14A.

Table 1. *Riccardia* species and voucher specimens used for morphological character assessment.

Species	Herbarium vouchers
<i>R. aequicellularis</i>	CHR 668238, CHR 425900, CHR 409761, CHR 620074
<i>R. asperulata</i>	CHR 527318, CHR 678269, CHR 689639, CHR 409820, CHR 409820
<i>R. breviala</i>	CHR 668216, CHR 668208
<i>R. lobulata</i>	CHR 627663, CHR 527318, AK 320010, CHR 627663, CHR 627665, CHR 691417, AK 320234
<i>R. multicorpora</i>	CHR 691416, CHR 691415, CHR 507034, CHR 536340
<i>R. sphagnicola</i>	CHR 691238, CHR 691413

For each species, a MANOVA analysis using R Statistical Software v. 4.4.2 2024 (R Core Team, 2021) was done for the three characters to test the null hypothesis that male and female plants do not differ in non-sexual morphology.

Characters and terminology

Terminology follows Brown and Braggins (1989) for parts such as stolons and mucilage papillae. Main axis width was measured for the narrowest point of the widest internode on the main axis between pinnae. Mucilage papillae tend to increase in size as they persist on older parts of the thallus. In species with persistent mucilage papillae, they were measured as far from the shoot apex as possible to get the largest dimension.

The term innovation is used here for new, non-terminal branches that develop from latent vegetative points, following Evans (1921) and Hässel (1972). Evans (1921, p. 121) referred to innovations in his description of the large erect species *R. prehensilis*: “In rare instances a branch is formed which represents a new axis. It takes its origin between two photosynthetic systems [Evans’ term for pinnae], diverging but slightly in direction from the main axis, and eventually gives rise to a separate individual.” Hässel (1972, p. 3) also described such branches in *R. prehensilis* as innovations, stating that they develop from latent vegetative points: “The latent vegetative points ... interspersed between maximally developed branches, ... are made up of cells similar to apical meristematic cells, located in a small depression, surrounded by papillae and they represent branch primordia ... Their latency is apparently controlled by the following distal branches. From these vegetative points, innovations originate

Secondary sexual dimorphism in thallus morphology of dioicous species *R. sphagnicola*, *R. breviala* E.A.Br., *R. lobulata* (Colenso) E.A.Hodg., *R. asperulata* R.M.Schust., *R. aequicellularis* (Steph.) Hewson, and *R. multicorpora* E.A.Br. was assessed by measuring 10 plants of each sex. A plant, as defined for the purposes of this study, comprises a single shoot system wherein all branches are linked by living tissue. Three characters were assessed: plant length, main axis width, and number of meristematic tips per plant. These were the three characters that were visibly different in male and female plants of some species examined and were found to differ between male and female plants in *R. dimorpha* (Glenny 2024).

Specimens used to test this are listed in the Specimens Examined section below. Plants measured are detailed in Table 1.

with a tendency to produce thallus with characteristics similar to the axis ... Specifically, they are found in these conditions in *R. prehensilis*, *R. duriuscula*, *R. thaxteri*, etc.” Hässel (1972) recorded innovations in 11 of 45 species treated and while most were large erect species such as *R. prehensilis*, she also recorded them in small filamentous prostrate species such as *Riccardia engelii* Hässel. Innovations were not recorded by Schuster (1992), or Furuki (1991) and were rarely mentioned by Brown and Braggins (1989), e.g., for *Riccardia marginata*: “New branches may arise from any of the latent vegetative apices along the length of the thallus, particularly if the growing tip is damaged.”

Apices of shoots are described here as either rounded or retuse. In retuse shoots the apical meristem is at the base of a sinus and the lobes each side of the sinus become new branches. In rounded shoots the apical meristem is slightly ventral of the apex and when shoot division takes place the shoot apex widens to become truncate before the two branches become distinct. The distinction was made by Brown and Braggins (1989) describing the apex as rounded versus cleft or dissected.

Results

Table 2 shows the results of testing for secondary sexual dimorphism in the six dioicous species considered here. Three of the six species assessed showed significant dimorphism.

Table 2. Results of MANOVA tests for *Riccardia aequicellularis*, *R. asperulata*, *R. breviala*, *R. lobulata*, *R. multicorpora* and *R. sphagnicola* to test for secondary sexual dimorphism in three characters: plant length, main axis width, and number of meristematic tips per plant.

Null hypothesis of no difference between sexes	
<i>R. aequicellularis</i>	Not rejected (p<0.51)
<i>R. asperulata</i>	Not rejected (p<0.95)
<i>R. breviala</i>	Rejected (p=0.072)
<i>R. lobulata</i>	Rejected (p<0.0016)
<i>R. multicorpora</i>	Not rejected (p=0.0.27)
<i>R. sphagnicola</i>	Rejected (p<0.0001)

All three characters measured were significantly different between the sexes in t-tests for *Riccardia sphagnicola* with plant length being the most dimorphic feature, female plants being at least 1.5 times longer, wider in the main axis and with 1.7 times the number of meristematic tips (Table 3). In *Riccardia breviala* only male and female main axis width differed significantly at the

5% level, to a degree that would not be noticeable in specimens (Table 3). *Riccardia lobulata* also differed in main axis width at the 5% level, and mean number of tips per plant differed significantly at the 1% level to a degree similar to that of *R. sphagnicola* (Table 3). In *Riccardia asperulata*, *R. aequicellularis*, and *R. multicorpora* the sexes did not differ.

Table 3. Secondary sexual dimorphism in three characters assessed for *Riccardia sphagnicola*, *R. breviala*, *R. lobulata*, *R. asperulata*, *R. aequicellularis* and *R. multicorpora*. Each range gives the minimum, mean, and maximum of 10 plants measured. Significance levels: *** = p > 0.001, ** = p > 0.05, n.s. = not significant and result from ANOVA tests of each variable.

	male	female	signif.	ratio of female to male
<i>Riccardia sphagnicola</i>				
Plant length, mm	14–15.8–20	20–24.9–30	***	1.5
Main axis width, µm	250–529–650	530–834–1080	***	1.6
Number of meristematic tips	10–16.5–23	18–28.8–49	**	1.7
<i>Riccardia breviala</i>				
Plant length, mm	5–27.6–11	6–33.5–12	n.s.	
Main axis width, µm	220–271–320	250–337–480	*	1.2
Number of meristematic tips	9–27.6–58	13–33.6–76	n.s.	
<i>Riccardia lobulata</i>				
Plant length, mm	3.5–4.6–5.5	2.0–4.6–6.0	n.s.	
Main axis width, µm	150–195–290	240–271–340	***	1.4
Number of meristematic tips	13–22.7–43	15–41.2–73	**	1.8
<i>Riccardia asperulata</i>				
Plant length, mm	3–6.8–10	4–6.8–11	n.s.	
Main axis width, µm	110–244–580	200–262–310	n.s.	
Number of meristematic tips	5–14.1–32	12–15.2–22	n.s.	
<i>Riccardia aequicellularis</i>				
Plant length, mm	4–5.7–7	4–5.7–9	n.s.	
Main axis width, µm	10–173–260	100–218–400	n.s.	
Number of meristematic tips	8–14.7–22	9–16.8–22	n.s.	
<i>Riccardia multicorpora</i>				
Plant length, mm	10–13.5–18	6–10.2–12	n.s.	
Main axis width, µm	240–348–430	240–338–430	n.s.	
Number of meristematic tips	34–41.6–55	14–41.5–102	n.s.	

Male plants of *Riccardia sphagnicola* and *R. breviala* were compared for mean plant length, main axis width, and meristematic tip number. They differed significantly in the first two characters but not tip number. Female plants of the two species were likewise compared and also differed in mean plant length and mean main axis width.

Innovations of the type described by Evans (1921) and Hässel (1972) were observed. They are not stolons, which are cylindrical,

positively geotropic, and often develop rhizoids. They appear to be normal terminally-forming branches except at the base where there is a different arrangement of epidermal cells at the junction (compare Fig. 1C–E and Fig. 1A–B). The innovation is narrowly joined to the shoot it originates from, easily breaks off and may function as a regenerant. Male branches can also be of this type (Fig. 1F).

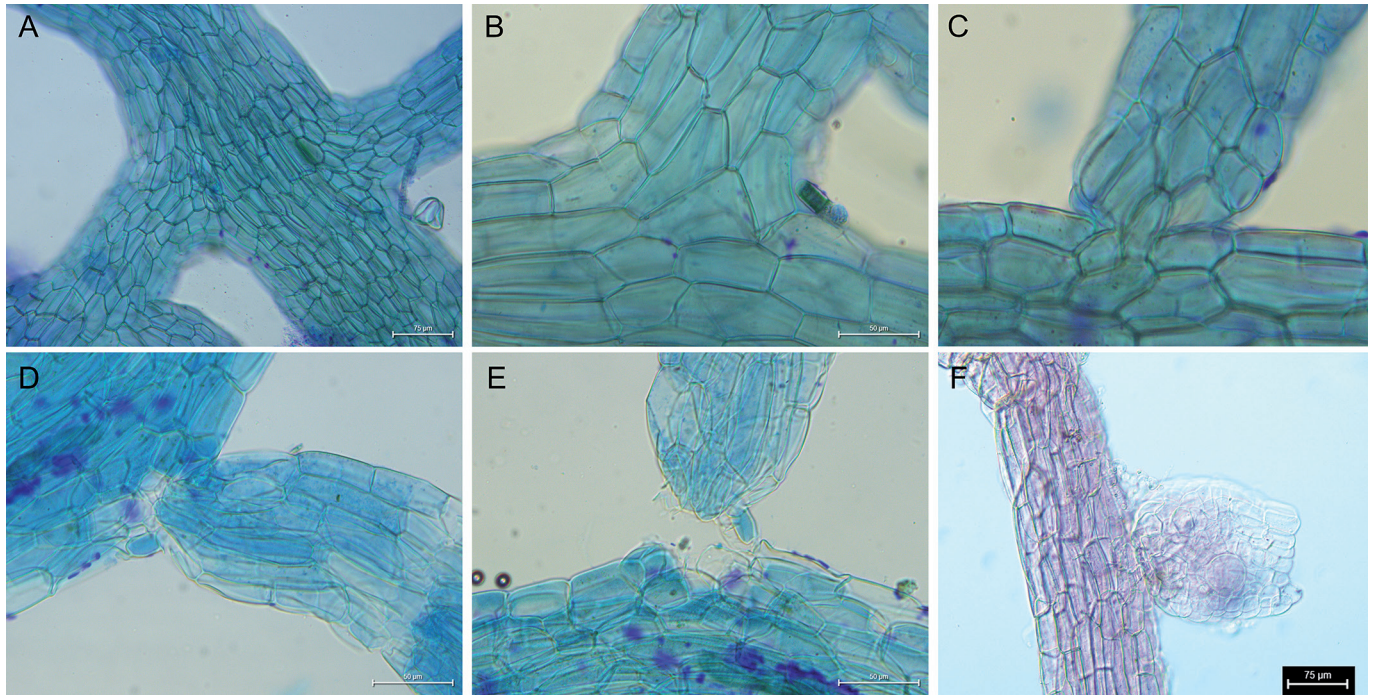


Fig. 1. Branching types in *Riccardia*. A–B. Normal terminal branches. C–E. Innovation progressively detached to show the narrow, weak attachment. F. Male branch from innovation. A–E from *R. aequicellularis*, CHR 639987, bleached and stained with methylene blue. F from *R. asperulata*, CHR 678269, bleached and stained with ruthenium red.

Taxonomy

Riccardia sphagnicola Glenny, sp. nov.

Type: New Zealand: Westland, Newton Range, Mt Brown, 1122 m, 171.201°E 42.869°S, growing through *Sphagnum cristatum*, in sloping bog of *Chionochloa rubra* + *Juncus effusus* / *Oreobolus pectinatus* + *Sphagnum cristatum* + *S. falcatum*, with *Lichenomphalia umbellifera*, *Celmisia glandulosa*, *Pleurophascum ovalifolium*, and *Drosera arcturi*, 10 Jan 2024, D. Glenny 15670. Plants male. Holotype: CHR 691238; isotypes: AK, F, HO.

Diagnosis: Plants most similar to *Riccardia breviala* but differing in being loosely prostrate with pinnae unbranched or sparingly branched and in the same plane as the main axis; shoot apices rounded rather than slightly notched; mucilage papillae at shoot apices always present and obvious at ventral apex rather than mostly absent; stolons rare; gemmae sometimes present; found in penialpine sphagnum bogs, usually growing on sphagnum.

Description: Plants loosely prostrate and interwoven with other bryophytes, green at apices, orange-brown in older parts of thallus due to pigments in the ventral cell walls. Male plants 14–20 mm long, female plants 20–30 mm long. Plants sexually dimorphic in plant length, main axis width, and number of meristematic tips, female plants being longer, the main axis wider, and with more tips per plant than males. Male and female plants distinctly monopodial with the main axis always obvious. Male plants 2–5 mm wide including branches, pinnate. Branches alternate with simple pinnae up to 1.3 mm long, or pinnae sparsely branching. A pinna occasionally becoming the leading shoot after main axis is broken. Latent branches present, more common in male plants than female. Meristematic tips per plant (i.e. branch tips) in male plants 10–23 per plant. Main axis of male plants up to 250–693 µm wide, 104–210 µm and 5–8 cells deep, plano-convex, concavo-convex, or biconcave in transverse section, width to depth ratio 2.0–3.3:1,

unwinged. Dorsal and ventral epidermal cells smaller in cross-sectional view to internal cells (epidermal cells 20–28 µm deep, versus 27–46 µm deep for internal cells) (Fig. 3A). Epidermal surfaces smooth. Female plants 5–10 mm wide including branches, monopodial and usually bipinnate with distinct main axis and pinnae of indeterminate length that almost invariably branch; pinnae up to 7 mm long and with 6–7 pinnules. A pinna sometimes becoming the leading shoot after main axis is broken off (Fig. 2A). Meristematic tips per female plant 18–49 per plant. Main axis of female plants 350–530 µm wide, 100–250 µm and 7–11 cells deep, slightly biconvex in transverse section, width to depth ratio 4.6:1, unwinged but with a single cell row forming the margin. Dorsal and ventral epidermal cells approximately equal in transverse sectional view as the largest internal cells (dorsal epidermal cells 23–30 µm deep, ventral 23–25 µm; versus 20–28 µm deep for internal cells). Both male and female plants main axis and branch apices rounded, without an apical sinus (Fig. 6C). Mucilage papillae 4–15 per shoot apex, or absent, in a transverse row slightly ventral to the apex and projecting apically, persisting very sparsely on ventral surface but never in 2 longitudinal rows, absent from the dorsal surface (Fig. 6A and B); 27–51 µm long, 16–24 µm diameter at widest, clavate and narrowed to a 10–16 µm diameter base attachment, cell wall smooth and walls thin. Rhizoids frequent, in clusters from ventral side of main axis, conspicuous, simple to highly branched, 95–150 µm long, composed of a single cell (Fig. 4). Stolons infrequent, 170 µm diameter, from main axis margin. Innovations infrequent, lateral, forming normal branches from main axis and pinnae, the base narrow and breaking off as regenerants. Dorsal epidermal cells (of both sexes) elongated-rhomboid (1.8–3.1:1), 46–96 µm long, 25–35 µm wide, 24–36 µm deep, thin-walled. In transverse section view, dorsal epidermal cells wider than tall. Ventral epidermal cells elongate-rhomboid (length to width ratio 1.3–3.4:1), 55–85 µm long, 22–44 µm wide, 25–35 µm deep, thin-walled (1.0 µm). In transverse section, internal rows of cells larger than epidermal cells, 29–46 µm deep. Dorsal subepidermal

cells (of both sexes) 118–160 μm long (Fig. 3B), 41–67 μm wide, 27–43 μm deep. Cell walls in transverse sectional view all c. 2 μm thick, evenly thickened. *Oil-bodies* absent from dorsal and ventral epidermal cells. In dorsal subepidermal cells one per cell, present in every apical cell but very sparse in older parts of the thallus, brown, broadly ellipsoidal, moderately granular, 10.8–18.4 \times 10.3–14.5 μm . In ventral epidermal cells oil-bodies one per cell, in every apical cell but very infrequent in older parts of the thallus, brown, broadly ellipsoidal, moderately granular, 9.7–16.8 \times 6.2–13.2 μm . *Gemmae* 2-celled, 48–57 \times 37–38 μm , each gemma cell gibbous, forming from dorsal and ventral epidermal cells in older parts of the thallus, the subepidermis exposed where gemmae have formed and peeled off (Fig. 6C). *Endophytic mycorrhizae* absent. *Dioicous*, male and female plants usually in separate colonies, rarely mixed. *Male branches* 1–6(11) branches per plant, solitary, rarely a pair side-by-side and rarely

two on one branch, originating from main axis and pinnae, facing dorsally, shortly stalked, 450–1300 μm long, the fertile part 300–1100 μm long, 250–300 μm wide, a marginal wing of one row of enlarged cells (80–84 μm long) present, sometimes forming a pair of “ears” each side of the apex (Fig. 7A). *Antheridia* 2–6(10) per male branch in pairs. Antheridia 105 μm diameter, antheridial stalk not seen. *Female branches* solitary, 1–3 per plant on main axis or on a very short branch and facing dorsally, sessile, 550–1000 μm long, with 3–7 pairs of archegonia, the gynoecium surrounded on its dorsal surface with two broad scales 8–10 cells long, 10–20 cells wide, bicelled gemmae developing on the inner surface of the gynoecial scales (Fig. 7B). *Calyptra* 900 μm long, 220 μm diameter, clavate, 80–100 μm and three cells thick plus an incomplete outer layer of pachydermal cells that detach (Fig. 5B). Umbo a cone of smooth, thick-walled quadrate cells, 12 cell rows forming the umbo base. Sporophyte not seen.

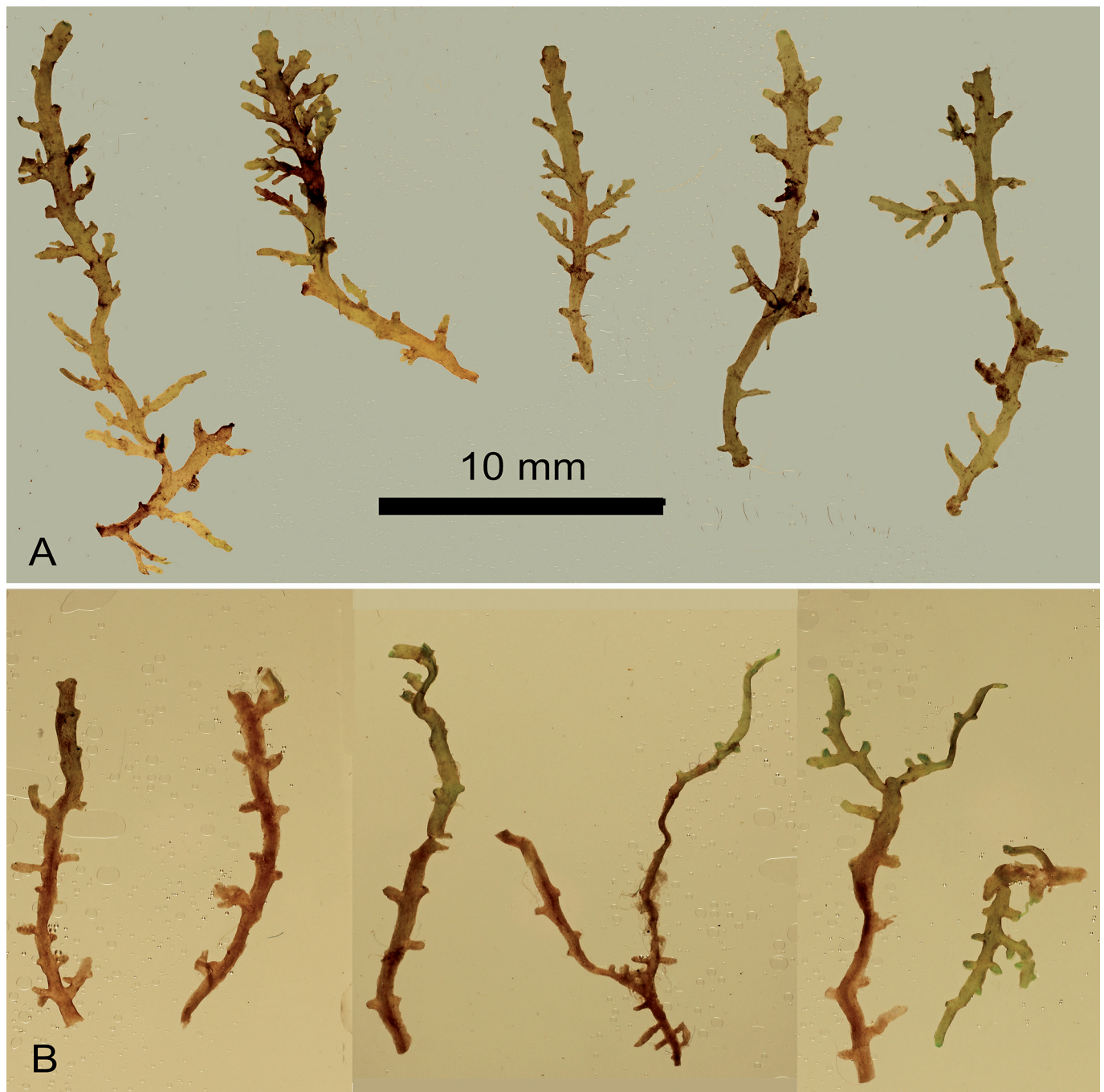


Fig. 2. *Riccardia sphagnicola*, whole plants. A. Five female plants. B. Six male plants. A from CHR 691238, B from CHR 691413.

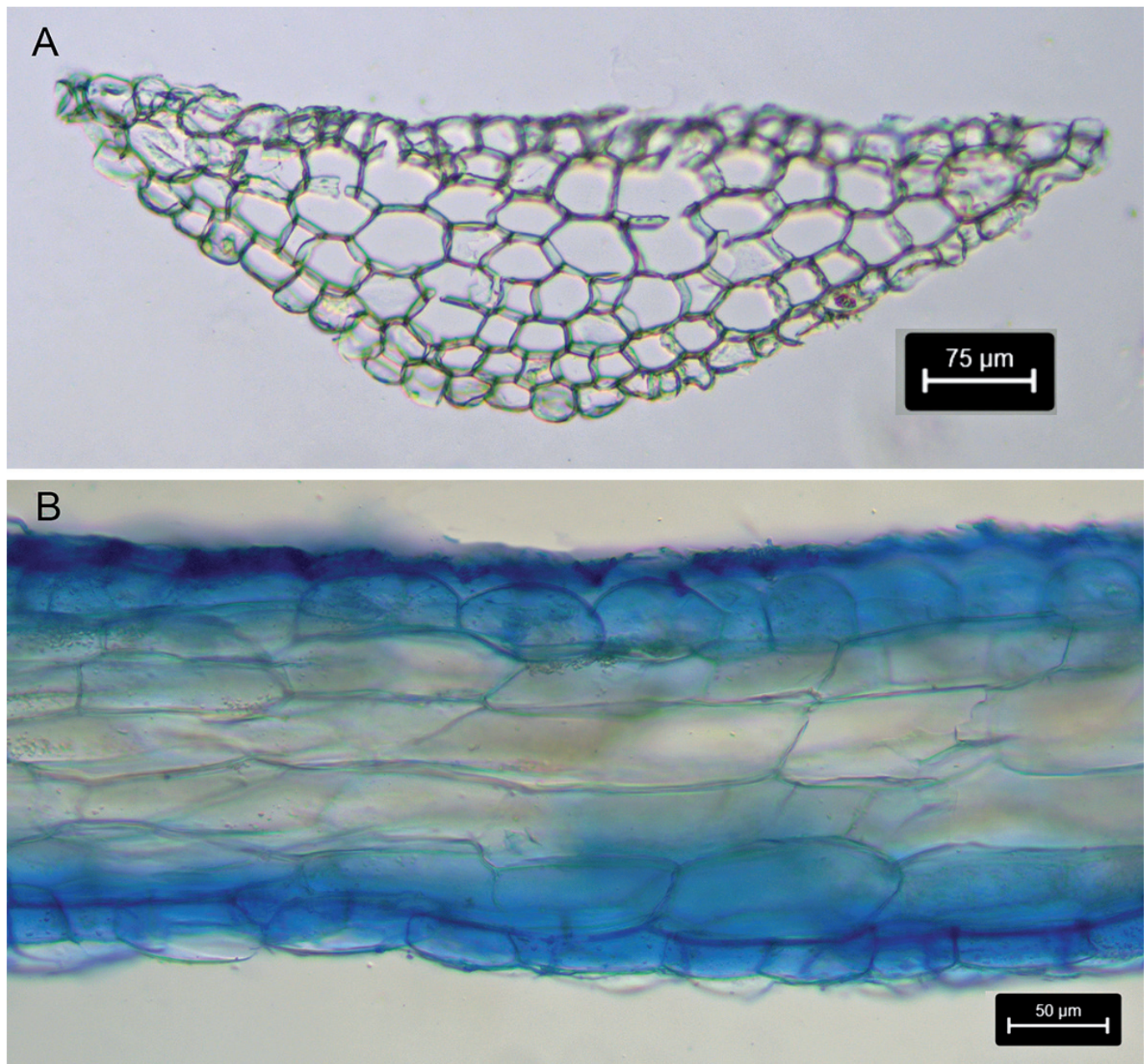


Fig. 3. *Riccardia sphagnicola* main axis sections of male plant. A transverse section. B. longitudinal section, dorsal epidermis uppermost in both. Both from CHR 691238. Both bleached and B stained with methylene blue.

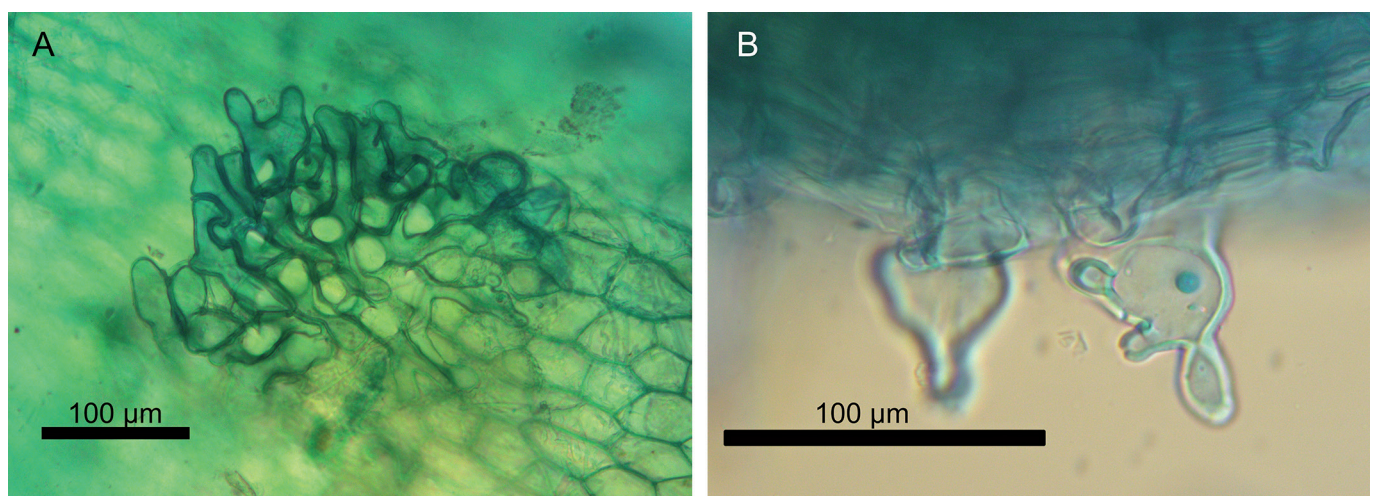


Fig. 4. *Riccardia sphagnicola* rhizoids. A. Rhizoid field on ventral surface of main axis. B. Side view of two branched rhizoids on ventral surface of main axis. A from CHR 671897, B from CHR 507093. Both bleached and stained with methylene blue.

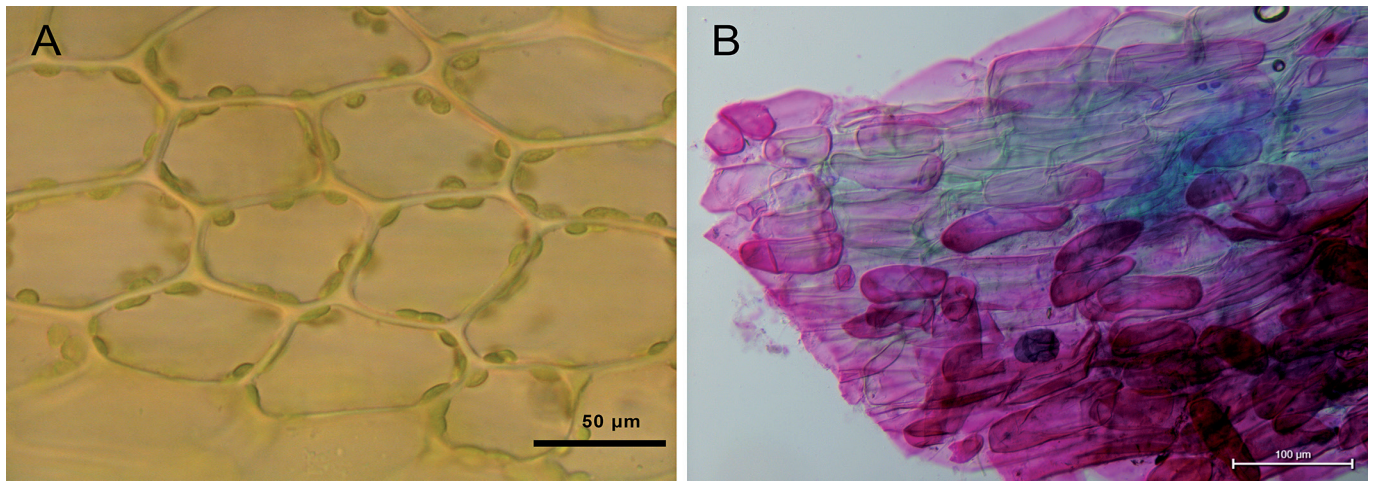


Fig. 5. *Riccardia sphagnicola*. A. Ventral epidermis. B. Outer surface of calyptra showing an outer layer of cells that detaches. In B tissue bleached then stained with ruthenium red. A from CHR 671890, B from CHR 503856.

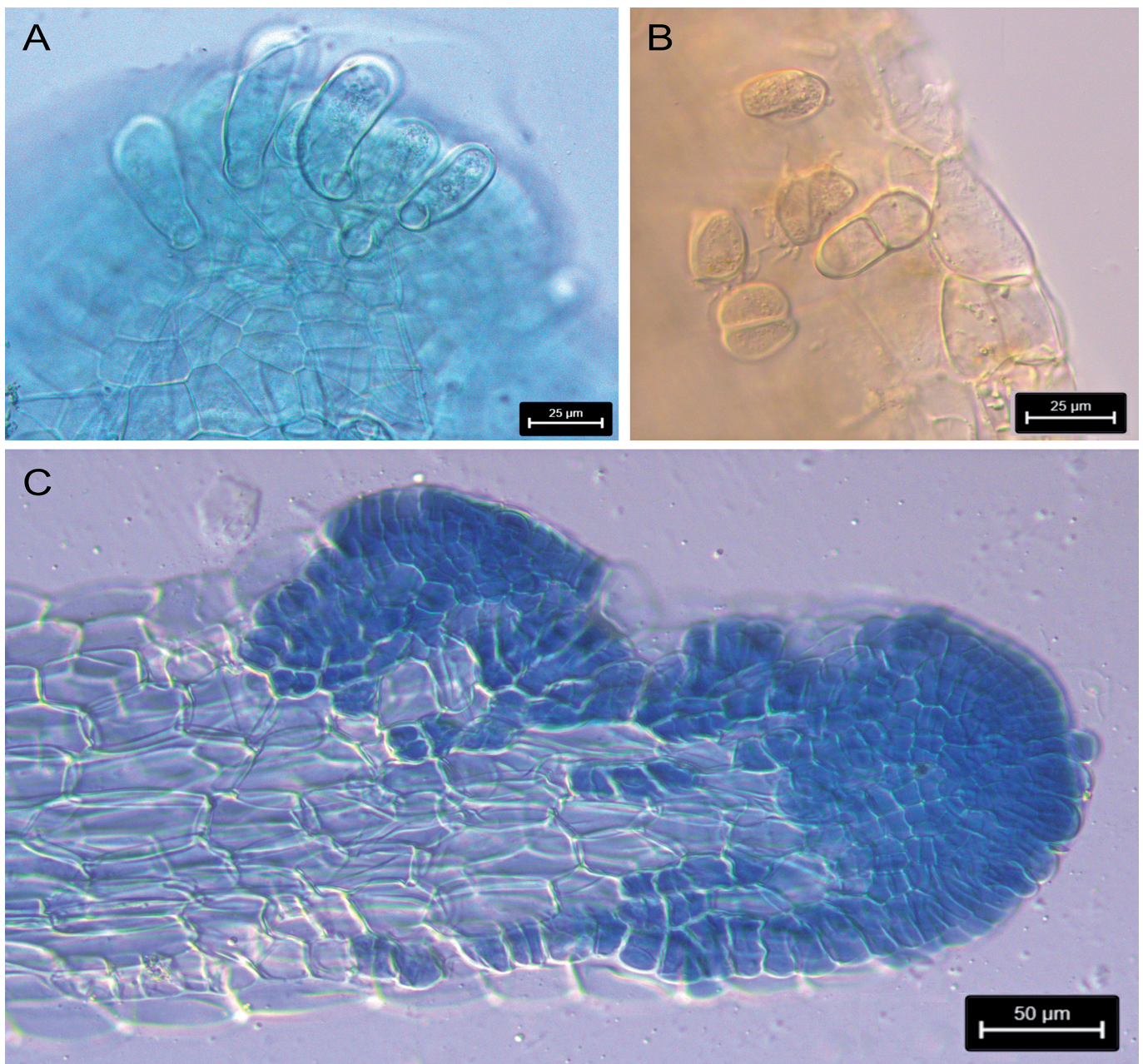


Fig. 6. *Riccardia sphagnicola*. A. Ventral shoot apex showing mucilage papillae. B. Bicellular detached gemmae. C. Apex of shoot, ventral view, showing epidermal cells (stained blue) becoming gemmae and peeling off to expose the sub-epidermis (unstained cells). A from CHR 691238. B from CHR 503856, C from WELT H10586. A–C bleached, A and C stained with methylene blue.

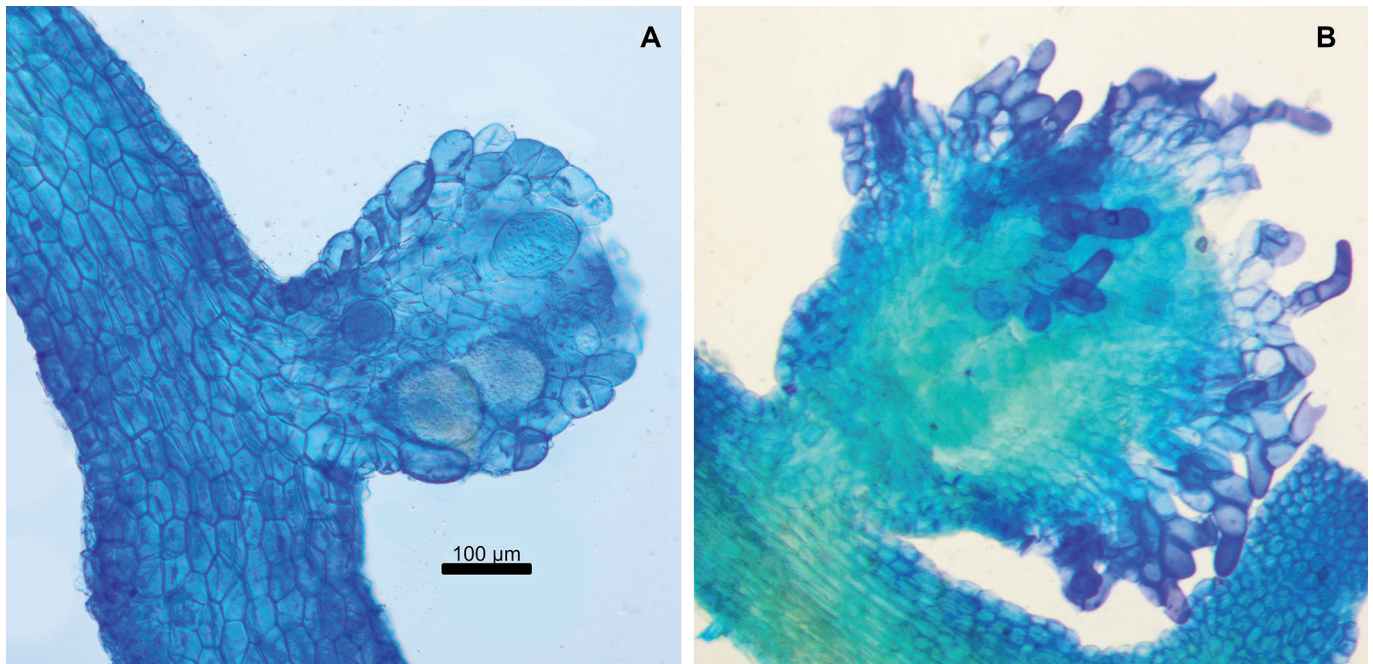


Fig. 7. *Riccardia sphagnicola*. A. Dorsal view of male branch. B. Dorsal view of female branch. A from CHR 691238. B from MPN 20083. 100 µm scale bar applies to both. Both bleached and stained with methylene blue.

Distribution: Endemic to New Zealand; North Island (1310 m) and South Island ([2]1100–1370 m). Known from southern North Island (Taranaki Range), Western Nelson (Paparoa Range, Brunner Range), Westland (Mt O'Shannesy, Mt Brian O'Lyn, Newton Range), Westland-Canterbury border (Arthur's Pass), and Southland (Awarua Bog).

Ecology: Usually found growing through *Sphagnum cristatum* cushions in penialpine bogs but also found growing on peat in such bogs. With *Oreobolus pectinatus*, *Caltha obtusa*, *Celmisia glandulosa*, *Cheilolejeunea campbelliensis*, *Forstera purpurata*, *Gackstroemia alpina*, *Kurzia helophila*, *Isotachis montana*, *Lepidozia ulothrix*, *Pachyglossa tenacifolia*, *Pleurophascum ovalifolium*, *Riccardia crassa*, *R. pennata*, and *Tetracymbaliella cymbalifera* (Fig. 8).

Recognition: Plants are brown-pigmented in older parts of the thallus and filamentous (up to 0.5 mm wide) but are compressed, not terete. Rhizoids are frequent on the ventral surface in dense

clusters and are mostly branched. Two-celled gemmae may be common on the ventral surface. Stolons are rare. Plants are dioicous and show secondary sexual dimorphism (female plants are longer, the main axis wider, and there are more branches per plant). Epidermal cells are thin-walled and unornamented and are slightly smaller than internal cells. There is no unistratose marginal wing except on the male branch. Mucilage papillae are invariably present at branch apices, clavate, 25–28 µm long and persist sparsely on the ventral surface but never in two longitudinal rows. The main axis in male plants is 220–550 µm wide, 104–198 µm and 5–7 cells thick. The main axis in female plants is 350–530 µm wide, 165–250 µm and 5–7 cells deep. Oil-bodies are absent from the epidermis and one per cell in the subepidermis in young parts of the plant and do not persist in older parts of the plant. Male branches are short, solitary, and often have 2–4 (but up to 10) pairs of antheridia. Female branches have marginal scales. The calyptra surface has pachydermal cells that detach from the surface and the umbo is a smooth-celled cone.



Fig. 8. *Riccardia sphagnicola*, habitat. A. The type locality, showing sparse *Chionochloa rubra* tussocks, a shallow pool with *Sphagnum falciculatum*, and raised cushions of *Donatia novae-zelandiae* and *S. cristatum*. B. The type of *R. sphagnicola* growing among *S. cristatum* mixed with *Kurzia helophila*.

Conservation status: Despite being only known from eight localities, the species is probably not threatened as its penalpine habitat is quite common.

Etymology: *Sphagnum*-loving, as the species has most often been found growing through *Sphagnum cristatum*.

Specimens examined: **NEW ZEALAND: North Island:** Southern North Island, Tararua Range, Mt Hector north face, 4300 ft [1310 m], watercourse, V.D. Zotov, 31 Dec 1933 (CHR 7402, female). **South Island:** Western Nelson, Giles Creek pakihi, 170 m, 171.823°E, 42.042°S, on soil in *Leptospermum scoparium* / *Gleichenia* shrub fernland, D. Glenny, 20 Nov 1985 (WELT H10586, male); Western Nelson, Brunner Range, 1240 m, 172.010°E, 42.006°S, on edges of *Oreobolus pectinatus* cushions and *Blindia* mossfield in wet peat, with *Kurzia helophila* and *Hygroblebium acrocladum*, D. Glenny 9399a, 24 Feb 2005 (CHR 574607, male); Westland, Haupiri River, track to Brian O'Lyn, 1200 m, 171.711°E, 42.626°S, on *Sphagnum cristatum* cushion at tarn margin, tarn set in *Dracophyllum longifolium* – *Chionochloa pallens* shrubland, D. Glenny 14737, 23 Feb 2020 (CHR 671897, F, male); Westland, Haupiri River, Mt O'Shannesy, 1134 m, 171.711°E, 42.661°S, on peat soil in *Chionochloa pallens* tussockland on hillslope, with *Tetracymbaliella cymbalifera*, D. Glenny 14742b, 24 Feb 2020 (CHR 671890, sterile); Westland–Canterbury border, Arthur's Pass, on *Sphagnum cristatum*, S. Berggren 4120, 1874 (MPN 20083 ex herb. Hodgson 8484, male and female mixed); Westland, Newton Range, Mt Brown, 1100 m, 171.200°E, 42.869°S, growing over *Sphagnum cristatum* in bog, D. Glenny 6172, 27 Nov 1995 (CHR 507093, female); Westland, Newton Range, Mt Brown, 1100 m, 171.202°E, 42.869°S, growing on peat in *Sphagnum cristatum* bog, D. Glenny 15671a, 10 Jan 2024 (CHR 691413, female and male mixed); Southland, Awarua Plain 400 m from Bluff Harbour, 2 m, 168.334°E, 46.542°S, growing on *Sphagnum cristatum* in shrubland of *Ulex europaeus*, *Coprosma*, *Phormium tenax*, *Carex*, *Juncus*, *Blechnum*, mosses, K Ladley, 12 Apr 2005 (CHR 503856, female with calyptra).

Specimens examined for comparative species

Riccardia aequicellularis (Steph.) Hewson

NEW ZEALAND: North Island: Volcanic Plateau, Waihaha River, 500 m, 175.670°E, 38.697°S, dripping wet ignimbrite cliff with *Breutelia pendula* and *Riccardia crassa*, D. Glenny 14257a, 11 Nov 2018 (CHR 639987, male). **South Island:** Western Nelson, Flora Track, 3000 ft, bank beside waterfall, with *Triandrophyllum subtrifidum* and *Chiloscyphus triacanthus*, J. Child H4780, 21 May 1983 (CHR 409761, male); Western Nelson, Tiropahi River, 150 m, 171.467°E, 41.983°S, *Leptospermum scoparium* / *Mascherina teretifolia* – *Gleichenia dicarpa* rush fernland, on peat soil, with *Campylopus clavatus*, D. Glenny 14807, 29 May 2020 (CHR 668238, female); Canterbury, Woolshed Hill, *Nothofagus cliffortioides* forest, L. Visch H1733, Nov 1960 (CHR 642074, male); Canterbury, Arthur's Pass, Scotts Track, soil on rock under *Nothofagus cliffortioides* forest, 2800 ft [850 m], G. Brownlie 747, 12 Nov 1976 (CHR 425900, female); Canterbury, Craigieburn skifield, 1166 m, 171.708°E, 43.115°S, on soil beside stream in *Schoenus pauciflorus* sedgeland, D. Glenny 15637b, 9 Nov 2023 (CHR 691418, sterile); Canterbury, Craigieburn skifield, 1335 m, 171.709°E, 43.109°S, *Podocarpus nivalis* scrub, D. Glenny 15643, 9 Nov 2023 (CHR 692719, male); Southland, Dipton, Dipton, Spirit Burn Road, 260 m, 168.427°E, 45.877°S, on

vertical wet sandstone bedrock under *Dacrycarpus dacrydioides* – *Prumnopitys spicata* forest, D. Glenny 14677, 17 Nov 2019 (CHR 678210). **Campbell Island:** on humus, J.H. Sorensen, 2 Apr 1946 (CHR 496181, female).

Riccardia asperulata R.M.Schust.

AUSTRALIA: Tasmania: Mt Field National Park, Lake Dobson, O. Selling, 16 Jan 1949 (MPN 20145 ex herb. Hodgson 10418, male). A new record for this species for Australia. **NEW ZEALAND: North Island:** Tararua Range, watercourse north of Field Hut, 2600 ft, V.D. Zotov, 1 Jan 1934 (CHR 7474, male and female); Taranaki, Mt Taranaki, 4000–4350 ft, on mineral soil, E.A. Hodgson, Jan 1955 (MPN 20085 ex herb. Hodgson 10193); Taranaki, Mt Taranaki, 660 m, 174.149°E, 39.316°S, *Leptospermum scoparium* / *Astelia grandis* / *Machaerina rubiginosa* shrub rushland, on *Sphagnum cristatum*, D. Glenny 7972, 12 Dec 1999 (CHR 527318, male). **South Island:** Westland, Aicken Range, Mt Pfeifer, 1286 m, 171.657°E, 42.806°S, soil on side of rill, stream in flush zone of *Oreobolus pectinatus* – *Carpha alpina* sedgeland, plants shaded by *Chionochloa flavescentes*, D. Glenny 12783, 1 Jan 2015 (CHR 689639, STU, female); Westland, Otira R, 3500 ft, on earth under subalpine scrub, J. Child H5347, 4 Feb 1984 (CHR 409820, female); Western Nelson, Stockton Plateau, St Patrick Stream Saddle with Cypress Stream, 700 m, soil under *Empodisma minus* – *Gleichenia* fern rushland, D. Glenny 7561, 27 Nov 1998 (CHR 675310, male); Canterbury, Arthur's Pass, McGrath Creek, 860 m, 171.425°E, 42.905°S, *Nothofagus cliffortioides* forest, on rock wall above stream, D. Glenny 14916, 3 Dec 2020 (CHR 678269, male).

Riccardia breviala E.A.Br.

NEW ZEALAND: North Island: Gisborne, Lake Waikaremoana, on mineral sandy soil, Jeffreys (MPN20087 ex herb. Hodgson 13670 as *Riccardia minuta*, male); Volcanic Plateau, Erua Forest, 720 m, 175.380°E, 39.227°S, volcanic sand in road ditch near pakihi, with *Paracromastigum drucei*, D. Glenny 12399, 25 Nov 2013 (CHR 689354); Taranaki, Whangamomona Saddle, 332 m, 174.699°E, 39.155°S, *Nothofagus solandri* – *Knightia excelsa* – *Beilschmiedia tawa* – *Quintinia serrata* – *Metrosideros robusta* forest on ridge, soil cave, D. Glenny 12079, 19 Nov 2013 (CHR 633081, male). **South Island:** Western Nelson, Oparara River, 220 m, 172.180°E, 41.147°S, soil on tree root plate in *Nothofagus fusca* – *N. menziesii* forest, D. Glenny 14766 & K. Frogley, 11 Mar 2020 (CHR 668208, female); Western Nelson, Oparara River, 220 m, 172.187°E, 41.147°S, soil on tree root plate in *Nothofagus fusca* – *N. menziesii* – *Pterophylla racemosa* forest, D. Glenny 14759 & K. Frogley, 11 Mar 2020 (CHR 668177, female); Western Nelson, Oparara River, 220 m, 172.199°E, 41.147°S, soil on tree root plate in *Nothofagus fusca* – *N. menziesii* forest, D. Glenny 14773 & K. Frogley, 11 Mar 2020 (CHR 668216, male); Western Nelson, Taipo River, 615 m, 172.347°E, 41.393°S, soil on tree root plate in *Nothofagus fusca* – *N. menziesii* forest, D. Glenny 14782 & K. Frogley, 15 Mar 2020 (CHR 668184, female).

Riccardia lobulata (Colenso) E.A.Hodg.

NEW ZEALAND: North Island: Auckland, Rodney County, Matakana, 129 m, 174.680°E, 36.331°S, on felled *Eucalyptus* trunk on trackside, *M. Ford* 2616, 23 Apr 2024 (CHR 691417, female); Volcanic Plateau, Pukerimu Bush, ca 2500 ft, on rotten log in bush, *K.W. Allison* H1782, Oct 1934 (CHR 627664). Cited as *R. lobulata* in Hodgson (1965); Volcanic Plateau, Kaingaroa Forest, bark of dead pine under pine forest, *K.W. Allison* H1746, 30 Nov 1935 (CHR 627663, male and female). Cited as *R. lobulata* in Hodgson (1965); Volcanic Plateau, near Taupo, under *Leptospermum scoparium* on steep shady bank, on leaf litter, *K.W. Allison* H1784, May 1934 (CHR 627665, female); Volcanic Plateau, east of Lake Taupo, 670 m, amongst moss on shady bank, *K.W. Allison* H1750 (MPN 20086, male and female); Volcanic Plateau, Kaingaroa Forest, damp ground under pines, *K.W. Allison* H1792, 6 Dec 1935 (CHR, MPN 20084, male and female); Volcanic Plateau, Hauhangatahi, *J. Braggins* 84/100d (AKU 71080, AK 320258, female); Volcanic Plateau, Blythe Track c. 1200 m, on *Breutelia*, *J. Braggins*, May 1987 (AKU 71083, AK 322822, female); Volcanic Plateau, Kaimanawa, upper Hinemaiaia Stream, 784 m, 176.160°E, 38.992°S, small patch amongst *Hypnum chrysogaster* mats on fallen log in beech forest, *M. Ford* 2576, 4 Mar 2024 (CHR 693552); Taranaki, Mt Taranaki, 660 m, 174.149°E, 39.316°S, *Leptospermum scoparium* / *Astelia grandis* / *Machaerina rubiginosa* shrub rushland, on *Sphagnum cristatum*, with *Riccardia asperulata*, *D. Glenny* 7972, 12 Dec 1999 (CHR 527318, male); Southern North Island, Ruahine Ra., Yeomans Track, 1200 m, on rotting wood in damp watercourse under sapling *Carpodetus*-beech forest, *E.A. Brown* 86/13b, Jan 1986 (AKU 71088, AK 320234, male and female). **South Island:** Sounds-Nelson, Left Branch Motueka River, Hunters Hut, 800 m, rotten wood beside small stream in *Nothofagus cliffortioides* forest, *E.A. Brown* 85/3a, 17 Jan 1985 (AKU 71087, AK 320266, female); Western Nelson, Bulmer Creek, 900 m, 172.524°E, 41.572°S, *Nothofagus menziesii* forest, on rotting log with *Cryptolophocolea mitteniana* and *C. trialata*, *D. Glenny* 14039b, 9 Jan 2017 (CHR 639867, male); Western Nelson, Glasgow Range 1000 m, rotten log in *Nothofagus menziesii* forest, *E.A. Brown* 86/41b, 16 Feb 1986 (AKU 71089, AK 320010, male and female); Canterbury, Broad Stream, 700 m, on rotting log with *R. papulosa*, *E.A. Brown* 86/72d, 2 Feb 1986 (AKU 71082, AK 320198, female); Westland, Pegleg Creek, 750 m, on dead *Olearia arborescens*,

E.A. Brown 86/55, 1 Feb 1986 (AKU 71081, AK 320195, female); Fiordland, Homer Huts, Gertrude Valley, 800 m, log at edge of *Nothofagus* forest, *E.A. Brown* 84/50b and *H.J. Hewson*, 11 May 1984 (AKU 71084, AK 324985, female); Fiordland, Stuart Mtns, Lake Thomson, 300 m, *Leptospermum scoparium* – *Nothofagus cliffortioides* forest, on rotting wood, *A.J. Fife* 7783, 24 May 1986 (CHR 406920); Southland, Blue Mountains, 1500 ft, *Pinus radiata* forest, on rotting *P. radiata* log, *J. Child*, 29 Dec 1984 (CHR 427541); Southland, Pourakino Valley, 80 m, *Nothofagus menziesii* forest, on rotting wood, *E.A. Brown* 84/92b, May 1984 (AKU 71085, AK320006, female).

Riccardia multicorpora E.A.Br.

NEW ZEALAND: South Island: Western Nelson, Tiropahi River, *D. Glenny* 6114, 171.426°E 41.941°S, 24 Nov 1995 (CHR 507034, male); Western Nelson, Te Kuha Ridge, 630 m, 171.740°E 41.816°S, *Leptospermum scoparium* shrubland, growing on *Sphagnum novozelandicum* with *Kurzia calcarata*, *D. Glenny* 8436, 19 Mar 2001 (CHR 526340, female); Western Nelson, Denniston, Whareatea River, 659 m, 171.785°E 41.763°S, *Leptospermum scoparium* – *Empodisma minus* – *Gleichenia* shrubland, on soil, *S. Fish* 183, 10 Feb 2024 (CHR 691416, female); Canterbury-Westland boundary, Arthur’s Pass, bog on summit of pass, 920 m, 171.558 E -42.908 S, *D. Glenny* 15696, 27 Apr 2024 (CHR 691415, male).

Riccardia papulosa (Steph.) Steph.

NEW ZEALAND: South Island: Western Nelson, Fenian River, on logs, *J.M. Blackburn* L159, 3 Mar 2004 (CHR 556631); Canterbury, Woolshed Hill, *Nothofagus cliffortioides* forest, on rotting wood, *L. Visch* H1738, Oct 1960 (CHR 642072); Canterbury, Woolshed Hill, *Nothofagus cliffortioides* forest, on decaying log, *L. Visch* H1730, Feb 1961 (CHR 642073); Canterbury, Mt Richardson, 650 m, 172.258°E 43.185°S, *Nothofagus cliffortioides* forest, on rotting *N. cliffortioides* log, *D. Glenny* 5973, 23 Sep 1995 (CHR 502529); Southland, Eyre Mtns, Big Jungle Creek, 820 m, 168.365°E 45.356°S, *Nothofagus menziesii* forest on terrace, rotten log of *N. menziesii*, *D. Glenny* 6259, 26 Dec 1995 (CHR 509777); Southland, Mararoa River, 620 m, *Nothofagus cliffortioides* forest, on rotting wood, *M.A.M. Renner*, 24 Apr 2002 (CHR 565302).

Table 4. Comparison of *Riccardia sphagnicola* with six similar filamentous New Zealand species, scored from Brown and Braggins (1989) and from specimens examined.

	<i>R. sphagnicola</i>	<i>R. breviala</i>	<i>R. lobulata</i>	<i>R. papulosa</i>	<i>R. asperulata</i>	<i>R. aequicellularis</i>	<i>R. multicorpora</i>
Plant length, mm	14–30	5–12	3.5–5.5	15–20(30)	5–10(20)	5–10(20)	10–30
Plant habit	loosely prostrate	prostrate with side branches erect	prostrate with side branches erect	prostrate with side branches erect	loosely prostrate	loosely prostrate	loosely prostrate
Plant form	both sexes monopodial	both sexes sympodial	female sympodial, male monopodial	sympodial	monopodial	sympodial	monopodial
Plant colour	green in younger, brown in older parts	uniformly green	uniformly green	brown in all parts	pale to dark green	uniformly green	green in younger, brown in older parts
Polarising central strand	absent	absent	present	absent	absent	absent	weakly present
Sexual dimorphism	present	present	present	(monoicous)	absent	absent	present

	<i>R. sphagnicola</i>	<i>R. breviala</i>	<i>R. lobulata</i>	<i>R. papulosa</i>	<i>R. asperulata</i>	<i>R. aequicellularis</i>	<i>R. multicorpora</i>
Innovations	uncommon	uncommon	absent	absent	common	frequent	absent
Stolons	absent or sparse	frequent	rare	absent	absent	absent	absent
Shoot apex shape	rounded	shallowly retuse	retuse	rounded or retuse	rounded	rounded	rounded
Mucilage papillae	present	sparse or absent	present	present	present	present	present
Mucilage papilla persistence	sparsely persistent	not persistent	persistent	sparsely persistent	not persistent	sparsely persistent	very persistent
Mucilage papilla length, μm	27–51	7–15(22)	30–56	30–80	20–30	20–30	48–60
Male main axis width, μm	220–693	220–320	150–180	170–650	(44)80–129 (147)	(46)176–412(670)	255–466
Female main axis width, μm	530–1150	250–480	150–250				300–420
Male main axis depth, μm	162–210	(66)76–136(160)	86–100	118–366	44–147	75–129(147)	177–215
Female main axis depth, μm	100–280	110–130	100–125				300–320
Main axis depth in cells, both sexes	5–8	4–7	4–6(8)	(6)8–12(14)	(3)4–6(7)	(3)4–6(7)	9–11
Dorsal epidermal cells size relative to internal cells	smaller	smaller	larger	larger	equal to larger	larger	equal
Epidermal cell ornamentation	smooth	smooth	smooth	smooth	asperulate	smooth	smooth
Gemmae	sometimes present on dorsal and ventral apical surfaces	sometimes present on dorsal apex	occasional	sometimes present	occasional	occasional	absent
Cells per gemma	2	2	2	1 or 2	2	2	–
Ventral epidermal cell walls thickness, μm	c. 1.0	2.5–5.0	1.8–3.2	c. 1.0	2.8–3.5	c. 1.0	2.8–3.8
Unistratose wing, cells wide	0.5–1	0–2	0.5–1	0–1	0–1	0–1	0–1
Oil-bodies in epidermal cells	absent	absent	usually one per cell	0–1(3)	0–2	0–2	(0)1–3(6)
Endomycorrhiza	absent	present in older parts, not persisting	absent	present in older parts, not persisting	absent	absent	present in lower 3 layers
Sexuality	dioicous	dioicous	dioicous	monoicous	dioicous	dioicous	dioicous
Male branch margin	erect wing	erect wing	incurved wing	erect wing	unwinged	unwinged	unwinged
Antheridia per male branch	2–6	(2)6–20	6–26	(6)10–12(22)	1–3	(1)6–8(14)	(4)6–8(10)
Gynoeceal branch margin before fertilisation	scales	scales and cilia	scales	scales	cilia	cilia	scales
Calyptra surface	scurfy	smooth	slightly scurfy	smooth	smooth	smooth	smooth
Umbo	smooth, thick-walled	smooth, thick-walled	smooth, thick-walled	unornamented bulging cells	ciliate	ciliate	smooth, thick-walled
Substrate	peat and Sphagnum	mineral soil	rotting wood	rotting wood	rock, peat soil, rarely on sphagnum	peat, sphagnum	peat
Elevational range, m	1100–1370	220–720 (1000)	660–1200	300–820	215–1380	150–1520	600–900

Discussion

Of 31 *Riccardia* species recognised in New Zealand by Brown and Braggins (1989) and. Glenny (2024), 20 are endemic (63%). Non-endemic species are mostly shared with Australia (10 species), one (*R. crassa*, as currently circumscribed) is also widespread in Asia and South America. *Riccardia alcornis* is shared by South America, Australia, and New Zealand. *Riccardia alba* is shared with Fiji and Australia. Comparison of *R. sphagnicola* with similarly filamentous New Zealand, Australian, and Patagonian species is presented below to show that *R. sphagnicola* is a distinct species and is endemic to New Zealand.

In Australia, three species are similar to *Riccardia sphagnicola*: *R. hypipamensis* Hewson, *R. macdonaldiana* Hewson (both of forest habitats in North Queensland) and *R. lobulata* (*R. minima* Carrington & Pearson in Hewson 1970, syn. *R. lobulata* fide Brown and Braggins 1989). The thallus in *R. hypipamensis* is 500–1000 µm wide, in *R. macdonaldiana* (300)500–800(1000) µm wide, but only 250–693 µm wide in *R. sphagnicola*. *Riccardia hypipamensis* and *R. macdonaldiana* both have oil-bodies present in the epidermal cells, absent from the epidermis of *R. sphagnicola*. Antheridia are up to 10 pairs per male branch in *R. hypipamensis* and up to 25 pairs in *R. macdonaldiana* but only 1–3(5) pairs per male branch in *R. sphagnicola*. These differences from *R. sphagnicola* make it very unlikely that the New Zealand plants belong to *R. macdonaldiana* or *R. hypipamensis*.

In Patagonia two species are similar to *R. sphagnicola* in most respects: *R. fuscobrunnea* (Steph.) A.Evans and *R. conimitra* (Steph.) A.Evans, both in section *Alcornia* (Hässel, 1972). *Riccardia sphagnicola* differs from *R. fuscobrunnea* in having abundant rhizoids (absent from *R. fuscobrunnea*), no fungal endophyte (present in *R. fuscobrunnea*), and plants are larger, 14–30 mm long (6–10 mm long in *R. fuscobrunnea*). *Riccardia sphagnicola* differs from *R. conimitra* in lacking oil-bodies in the epidermis (one per cell in *R. conimitra*) and the main axis is 5–11 cells thick (11–13 cells thick in *R. conimitra*).

Riccardia sphagnicola differs from *R. alcornis* in being dioicous (*R. alcornis* is monoicous), it has secondary sexual dimorphism (absent from *R. alcornis*, fide Glenny 2024), and the thallus is dorsiventrally compressed throughout (terete in the older part of the main axis of *R. alcornis*). *Riccardia sphagnicola* may belong

in *Riccardia* sect. *Alcornia* Hässel, as it fits Hässel's (1972) description of the section: the main axis is filamentous, biconvex, semi-terete, and there is no marginal wing.

In New Zealand, *Riccardia sphagnicola* most resembles four filamentous *Riccardia* species *R. breviala*, *R. lobulata*, *R. papulosa*, *R. aequicellularis* and *R. multicorpora* (Table 4 that share an unornamented epidermis. In addition, Table 4 presents data for *R. asperulata*, which has an asperulate thallus surface but is otherwise very similar to the other four species.

Of the six other species in Table 4, *Riccardia sphagnicola* is most similar to *R. breviala*, and the two species share many distinctive characteristics. Oil-bodies are absent from the epidermis in both species (Fig. 5A and Fig. 10A). The epidermal cells are slightly smaller than internal cells (Fig. 3A and Fig. 11A). Both species are dioicous and their female branches are very similar (Fig. 7B and Fig. 12B). There is an erect marginal wing of enlarged cells on the male branch of both species. Innovations are uncommon in both species.

The differences are that *Riccardia sphagnicola* is brown in older parts of thallus versus uniformly yellow-green in *R. breviala*. *Riccardia sphagnicola* is loosely prostrate and monopodial (Fig. 2) versus sympodial in *R. breviala* (Fig. 9) with branches erect and fan-like from a prostrate axis, presenting a turf-like surface. *Riccardia sphagnicola* has branch apices rounded versus slightly notched in *R. breviala* and mucilage papillae are always present at shoot apices versus usually absent in *R. breviala*. *Riccardia breviala* has ventral epidermal cells that are thick-walled, c. 5 µm thick (Fig. 10A–B), whereas in *R. sphagnicola* they are c. 1 µm thick (Fig. 5A). Stolons in *Riccardia sphagnicola* are rare but common in *R. breviala*. Male branches in *R. sphagnicola* have few pairs of antheridia (Fig. 7A) whereas in *R. breviala* the branches commonly have many pairs of antheridia and are much longer (Fig. 12A). The habitats occupied also differ: *Riccardia sphagnicola* occurs in penialpine bogs while *R. breviala* is an inhabitant of forests where it grows on mineral soils. The only known instance of overlap in elevational range of the two species is the *R. sphagnicola* specimen from Awarua Bog, at sea level. This suggests that the nearly total restriction of *R. sphagnicola* to penialpine bogs may be an artefact of the widespread conversion of wetland habitats, including bogs, in lowland areas to agricultural land use.

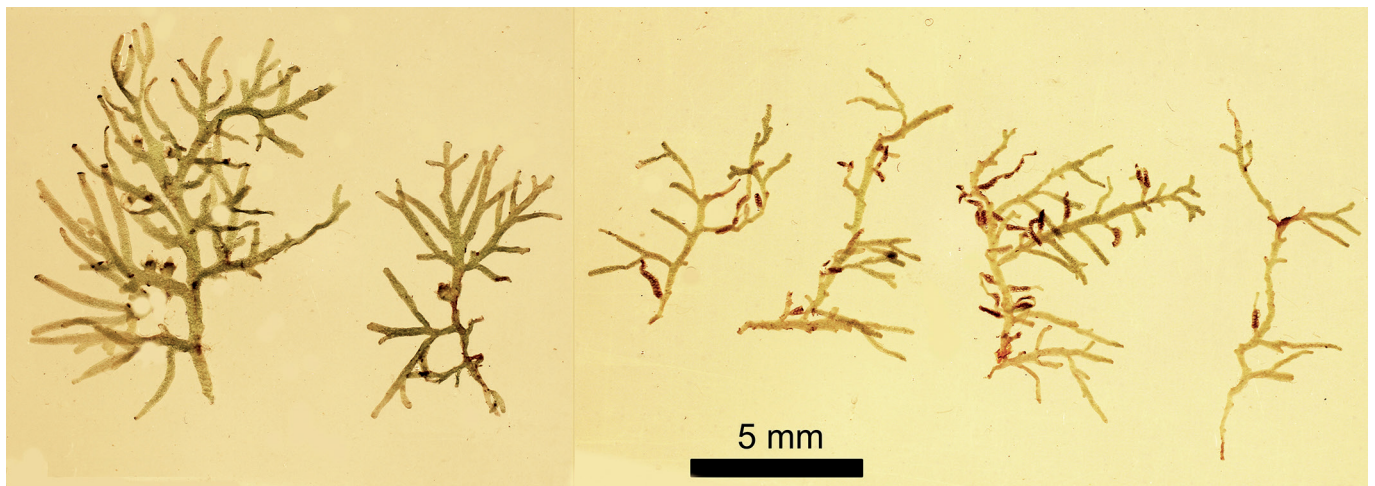


Fig. 9. *Riccardia breviala*, two female plants on the left, four male plants on the right. Female plants: CHR 668216, male plants: CHR 668208. All plants at the same scale.

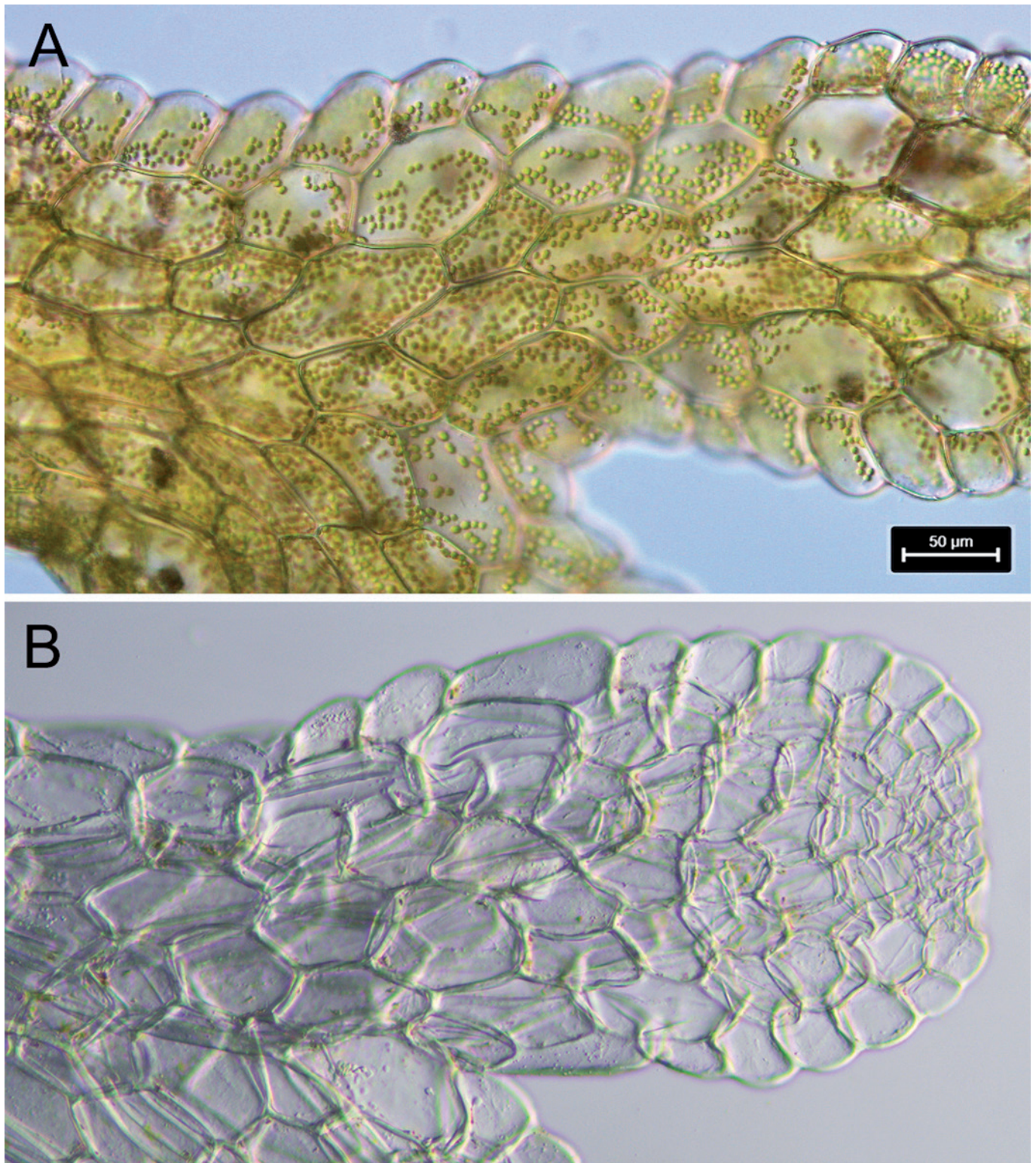


Fig. 10. *Riccardia breviala*, A. Ventral view of thallus branch showing absence of oil-bodies from the epidermal cells; brown oil-bodies are visible in the sub-epidermis. B. Ventral view of thallus branch showing absence of mucilage papillae at the apex or elsewhere on the ventral surface. Both from CHR 668208. 50 µm scale bar applies to both. B treated with bleach.

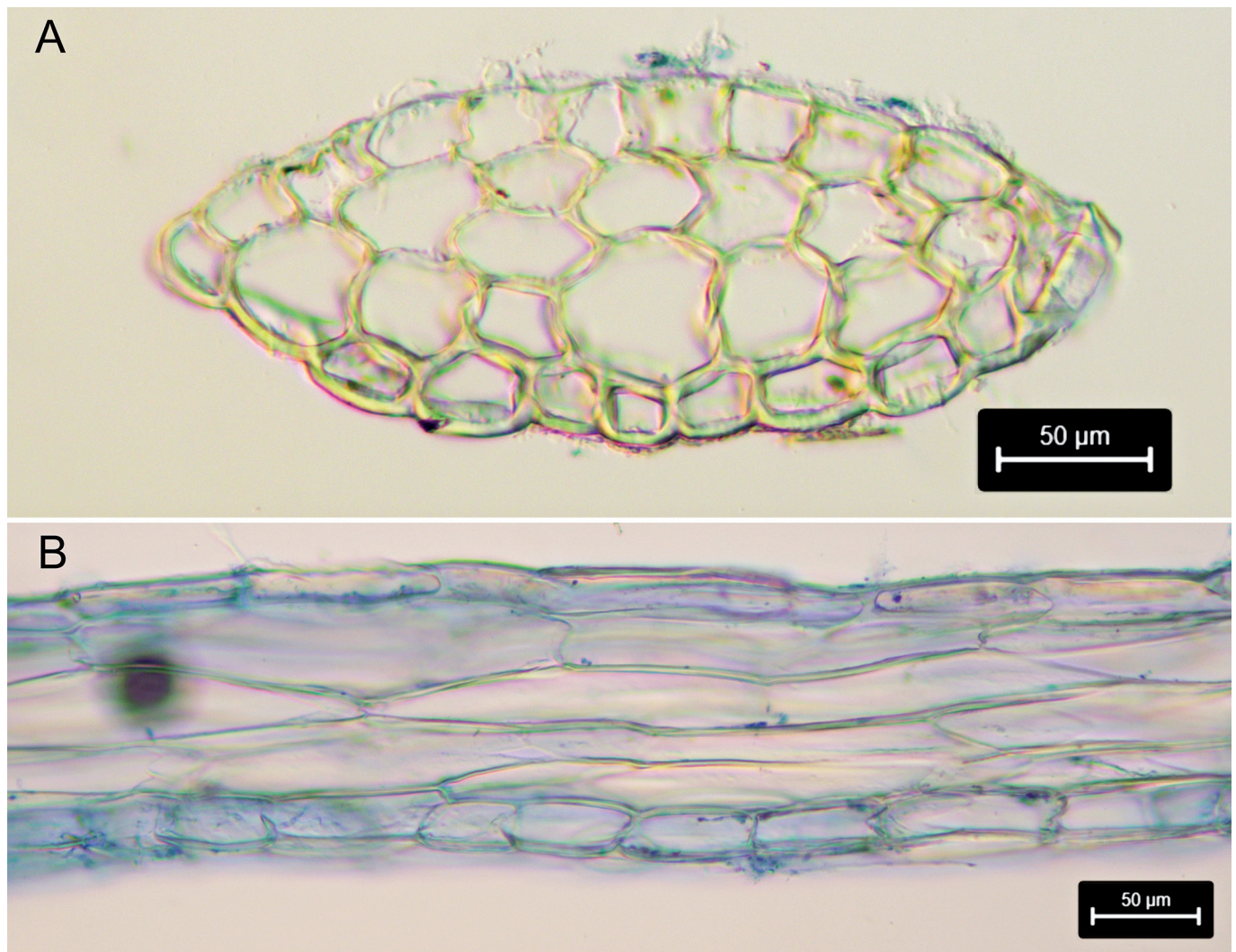


Fig. 11. *Riccardia breviala*, main axis sections. A. Transverse section showing thick-walled ventral epidermal cells. B. Longitudinal section showing internal cells up to 300 µm long, and thick-walled ventral epidermal cells that are 50–60 µm long. Both from CHR 668208, both bleached.

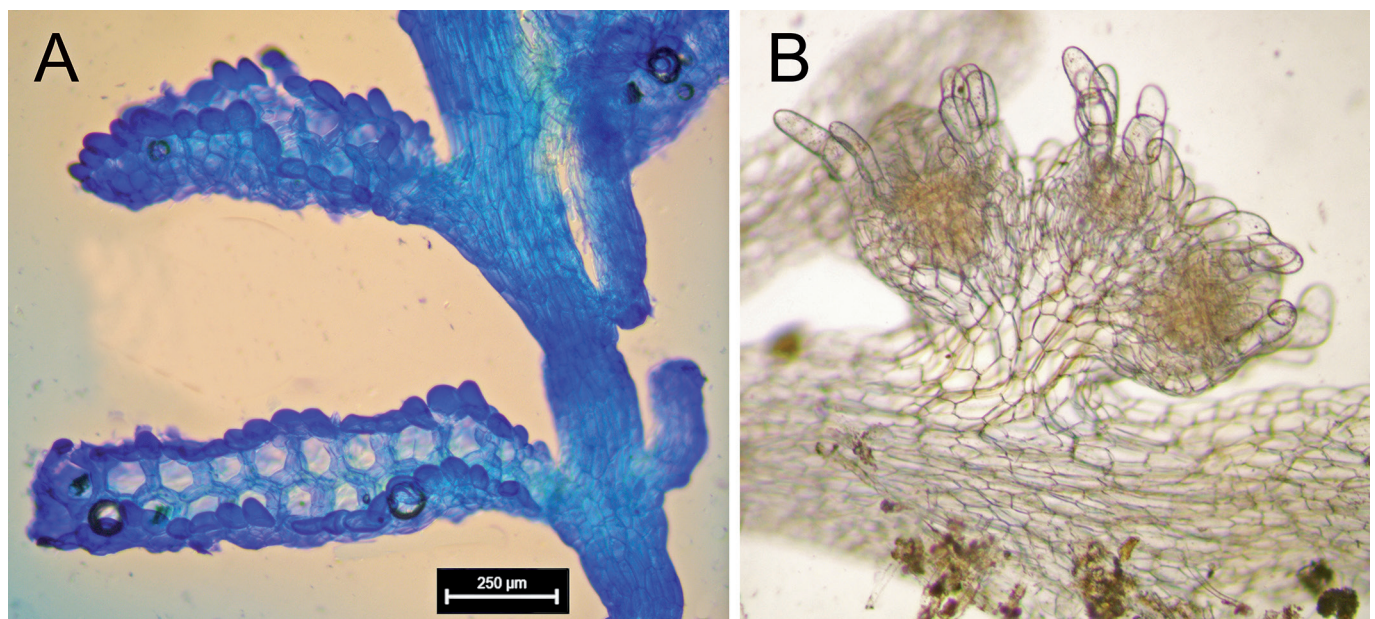


Fig. 12. *Riccardia breviala*. A. Dorsal view of thallus main axis with male branches. The lower branch has 10 pairs of antheridia. B. Dorsal view of a pair of female branches. A from CHR 668208, B from CHR 668184. 250 µm scale bar applies to A and B. Both bleached and A stained with methylene blue.

Riccardia lobulata is very similar to *R. sphagnicola* in size and monopodial form (Fig. 13) with the whole plant being loosely prostrate in both species. Both species have a unistratose thallus margin only 0.5–1 cell wide and the cells of that margin are large and translucent.

Riccardia lobulata has densely finger-like terminal branches that are narrower than the main axis, 120–160 μm at their widest, versus 220–250 μm wide in the main axis, i.e. pinnae are 0.54–0.64 \times the width of the main axis, while *R. sphagnicola* has distant pinnae that are 160–245 μm wide versus 210–307 μm in the main

axis, i.e. 0.70–0.83 \times the main axis width. *Riccardia lobulata* has internal thallus cells that change the polarisation of transmitted light (Fig. 13), a feature not shared by *R. sphagnicola*. *Riccardia lobulata* has oil-bodies in the epidermis, often more than one per cell but they are completely absent from *R. sphagnicola*. *Riccardia lobulata* has male branches with incurved elongated marginal cells (Fig. 16A) whereas *R. sphagnicola* has an erect wing with cells not elongated on the male branch margin (Fig. 7A). *Riccardia lobulata* grows on rotting wood in montane forests (Fig. 15A) whereas *R. sphagnicola* grows in penialpine bogs (but also in a bog at sea level at Awarua).

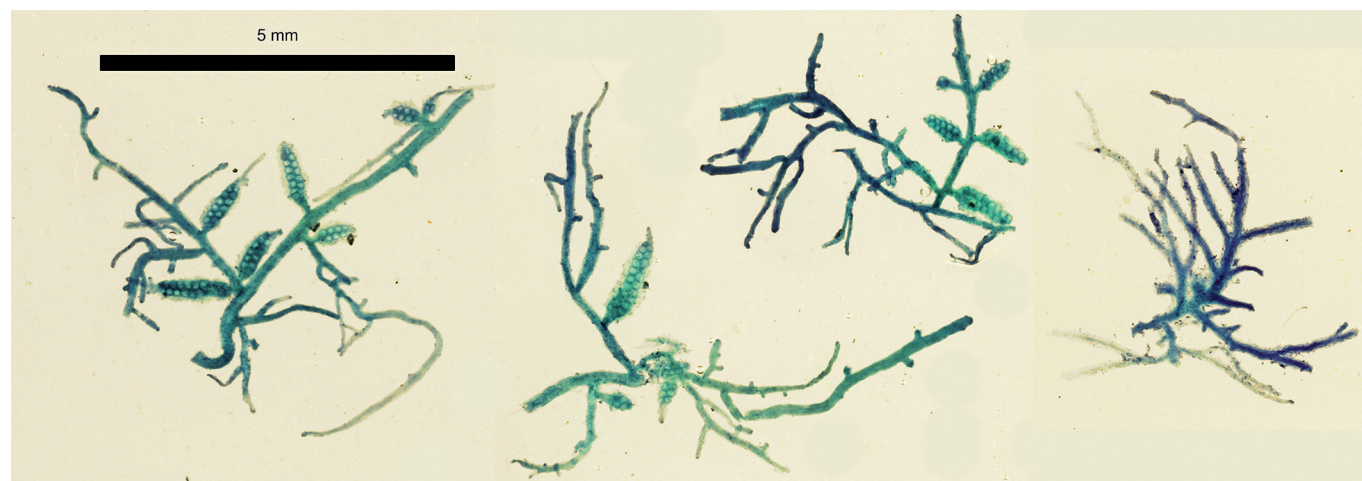


Fig. 13 *Riccardia lobulata*, whole male and female plants. Three male plants on left: CHR 627663, female plant on right: MPN 20086. All stained with methylene blue.

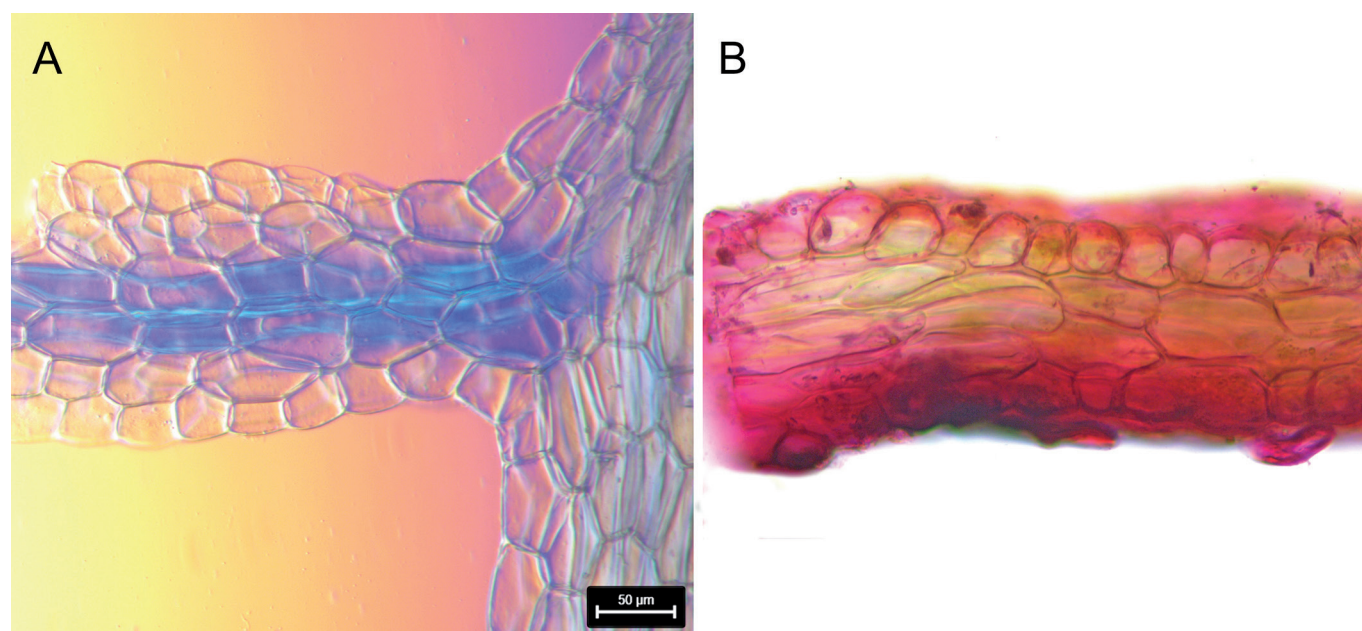


Fig. 14 *Riccardia lobulata*. A. Primary pinna showing inner strand of elongated cells two rows wide that rotate polarised light differently to the rest of the thallus cells. B. Longitudinal section through primary thallus showing elongated inner strand cells sandwiched by epidermal cells. A from CHR 627663, B from CHR 691417. Both bleached, B stained with ruthenium red. 50 μm scale bar applies to both.

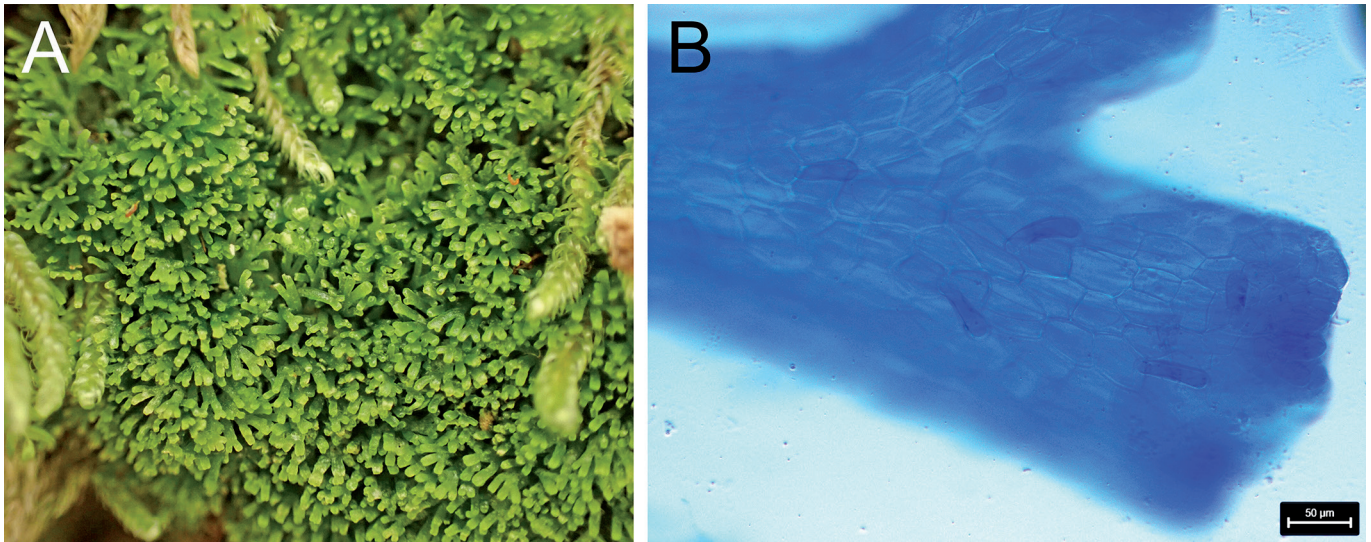


Fig. 15 *Riccardia lobulata*. A. Habit, branches erect, growing on rotting log. B. Mucilage papillae persisting in two rows on ventral thallus. A from CHR 693552. B from CHR 627663.

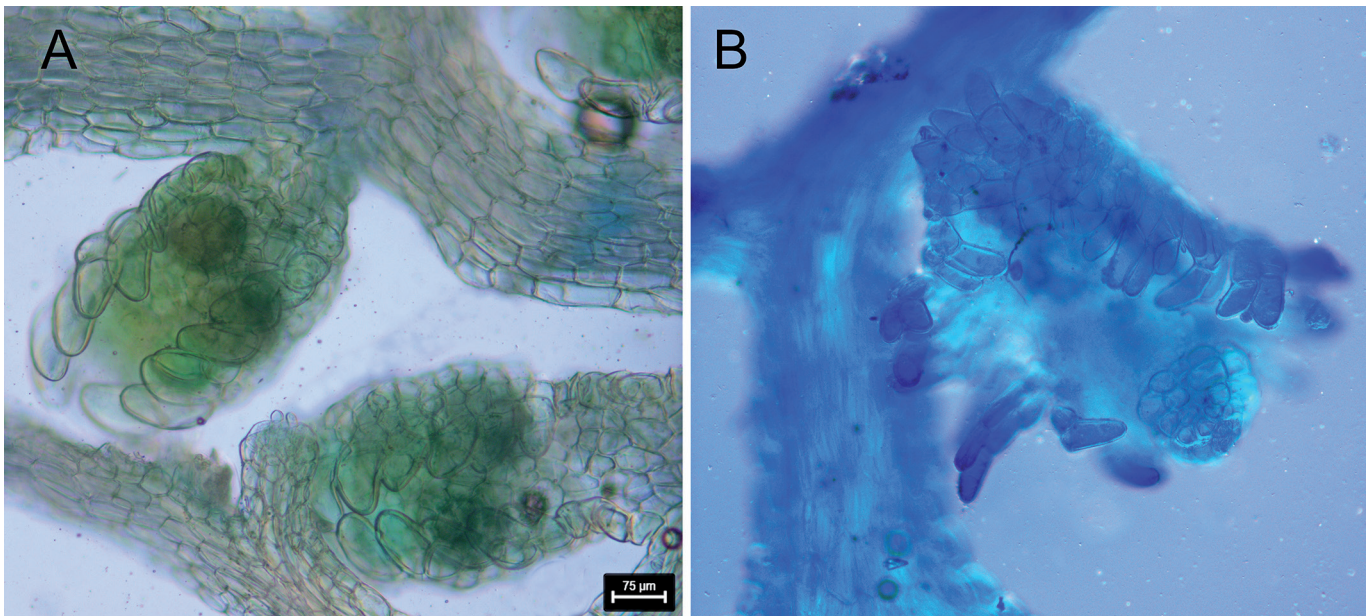


Fig. 16 *Riccardia lobulata*. A. Male branch showing the incurved wing cells. B. Female branch also showing incurved wing cells and small helmet-like umbo. A from CHR 627664. B from CHR 627663. Both bleached and stained with methylene blue. 75 µm scale bar applies to both.

Brown and Braggins (1989, p. 48) had doubts about the distinctness of *Riccardia lobulata* and *R. breviala*, dried specimens being very difficult to tell apart, and stated that their recognition of two species was based primarily on differences in oil-bodies observed in fresh material. They mentioned that alpine forms of *R. lobulata* tended to occur as sparse populations of thalli that crept among other bryophytes and lacked an erect habit, features suggestive of *R. sphagnicola*. None of the 10 specimens they cited was alpine, all were collected on rotting wood and are indeed *R. lobulata*.

Riccardia papulosa is also similar to *R. sphagnicola*. The two share thin-walled epidermal cells but *R. papulosa* has obviously enlarged cells on the thallus margins, particularly in the pinnae and these form a distinct wing (Fig. 17A) that makes the thallus channelled (concavo-convex). The cells forming the male branch

wing are erect and enlarged in both species. Oil-bodies are present in the epidermis of *R. papulosa* but not *R. sphagnicola*. Most importantly, *Riccardia papulosa* is monoicous whereas *R. sphagnicola* is dioicous. *Riccardia papulosa* has the main axis tightly attached to the rotting wood substrate with erect, free pinnae, whereas *R. sphagnicola* is loosely prostrate and the main axis and branches in one plane. In *R. papulosa*, bicellular gemmae are sometimes present on the ventral surface near the pinna apices (Fig. 18A) versus in older parts of the thallus in *R. sphagnicola* (Fig. 6B and C). In *R. papulosa* they can also be unicellular and originate from thallus margin cells that break off (Fig. 18B). Brown and Braggins (1989, p. 49) did not observe gemmae in *R. papulosa*.

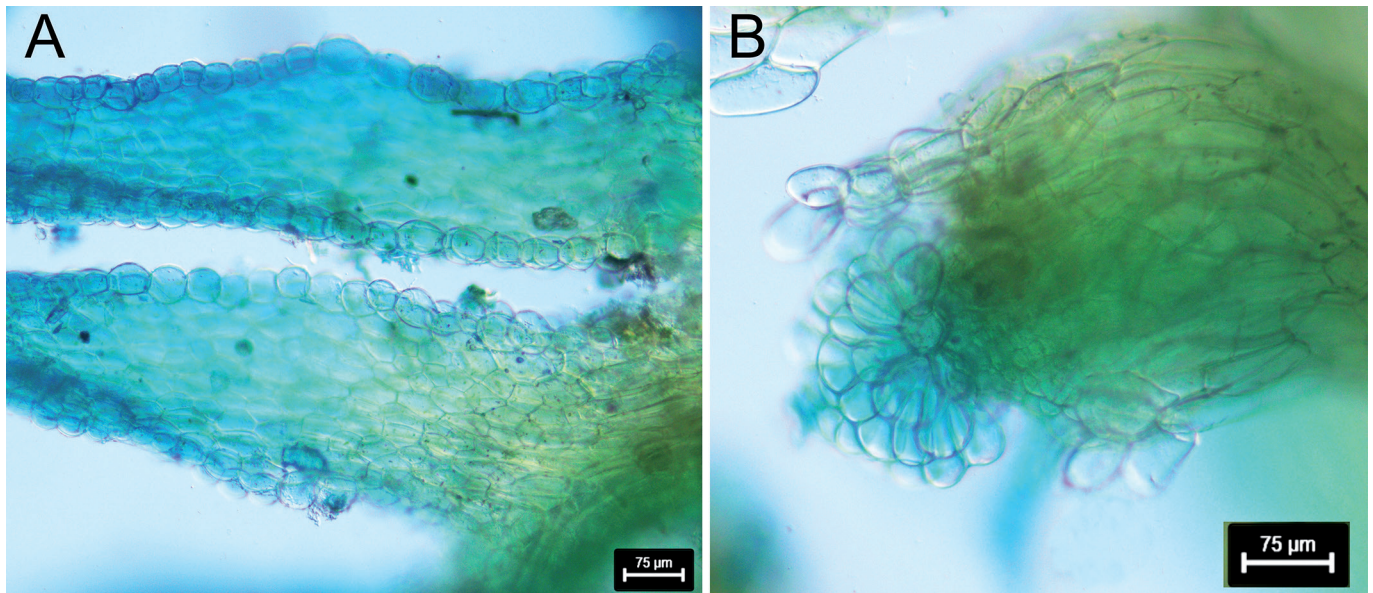


Fig. 17. *Riccardia papulosa*. A. Pinnae showing channelling with raised sides of channels formed by the enlarged marginal cells. B. Umbo with projecting cells. Both from CHR 509777. Both bleached and stained with methylene blue.

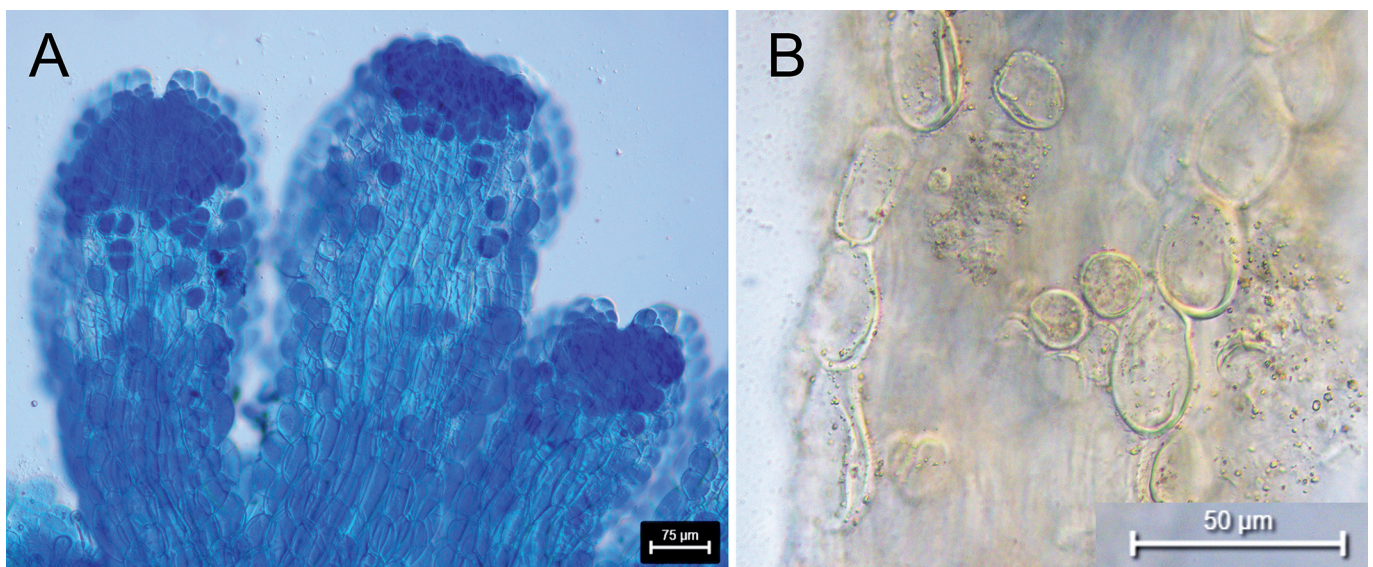


Fig. 18. *Riccardia papulosa*. A. Ventral view of branch apices showing bicellular gemmae developing from ventral epidermal layer (dark blue staining). B. Unicellular gemmae formed from thallus margin cells. A from CHR 502529, B from CHR 642073. Both bleached, A stained with methylene blue.

Riccardia asperulata is similar to *R. sphagnicola* in having thin-walled rectangular epidermal cells forming the thallus margin, and both are found in non-forested habitats. Male branches of both have few antheridia per branch (2–6 in *R. sphagnicola*, 1–3 in *R. asperulata* (Fig. 19C). However, *R. asperulata* has an asperulate epidermis, particularly visible at the thallus margin (Fig. 19A). Female branches of *R. asperulata* have a ciliate margin (Fig. 19B) but in *R. sphagnicola* the female branch margin has

scales, not cilia. *Riccardia asperulata* is marked by commonly having new branches developing on mature parts of the thallus, of two kinds. One kind develops from latent branch points and is broad-based and well attached. The other kind does not develop from latent branch points and is pinched at the base and easily broken off. Male branches may originate as this second type (Fig. 1F). New branches of these two types are uncommon in *R. sphagnicola*.

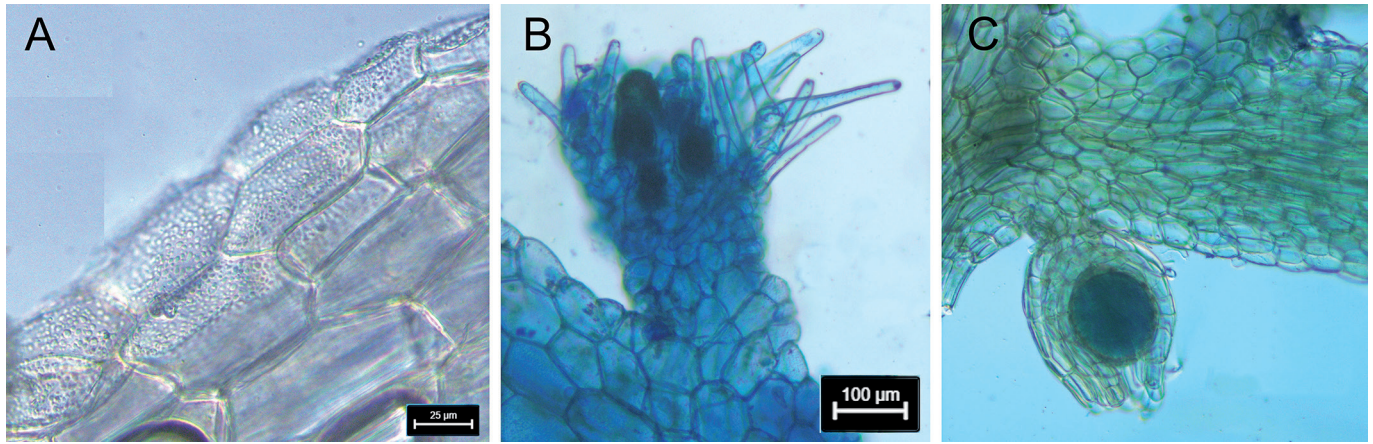


Fig. 19. *Riccardia asperulata*. A. Asperulate epidermal surface at thallus margin. B. Female branch with cilia. C. Male innovation with a single antheridium. A from CHR 7474, B from CHR 526338, C from CHR 675310. 100 µm scale bar in B applies also to C. A bleached, B and C bleached and stained with methylene blue.

Riccardia aequicellularis plants are of a similar size and loosely prostrate as are plants of *R. sphagnicola*. Male branches have few antheridia in both (Fig. 21A, cf. Fig. 7A). Both species have mucilage papillae that sparsely persist ventrally (Fig. 20A, cf. Fig. 6A). Both species can be penialpine and on *Sphagnum cristatum*. *Riccardia aequicellularis* differs from *R. sphagnicola* in the following respects. The dorsal epidermal cells are larger than ventral epidermal and internal cells (Fig. 20B) rather than smaller than internal cells (Fig. 2A). Oil-bodies are 1–2 per epidermal cell in *R. aequicellularis* but absent from the dorsal and ventral epidermis of *R. sphagnicola*. The female branch is ciliate in *R. aequicellularis* (Fig. 21B) but is never ciliate in *R. sphagnicola*.

The calyptra of *Riccardia aequicellularis* has an umbo with long-projecting thin-walled cells (Fig. 22A) whereas the umbo of *R. sphagnicola* is composed of thick-walled quadrate cells. In *R. aequicellularis* the male branch is unwinged (Fig. 21A, cf. Fig. 7A). *Riccardia aequicellularis* can be found in forest on a variety of terrestrial substrates whereas *R. sphagnicola* is never found in forest and is always in open bogs. In *Riccardia aequicellularis* innovations may be mixed with normal terminal branches (Fig. 1A–E). Marginal cells are thin-walled and elongated in the direction of the axis (Fig. 21A). Ventrally, the epidermis is thin-walled (< 2 µm).

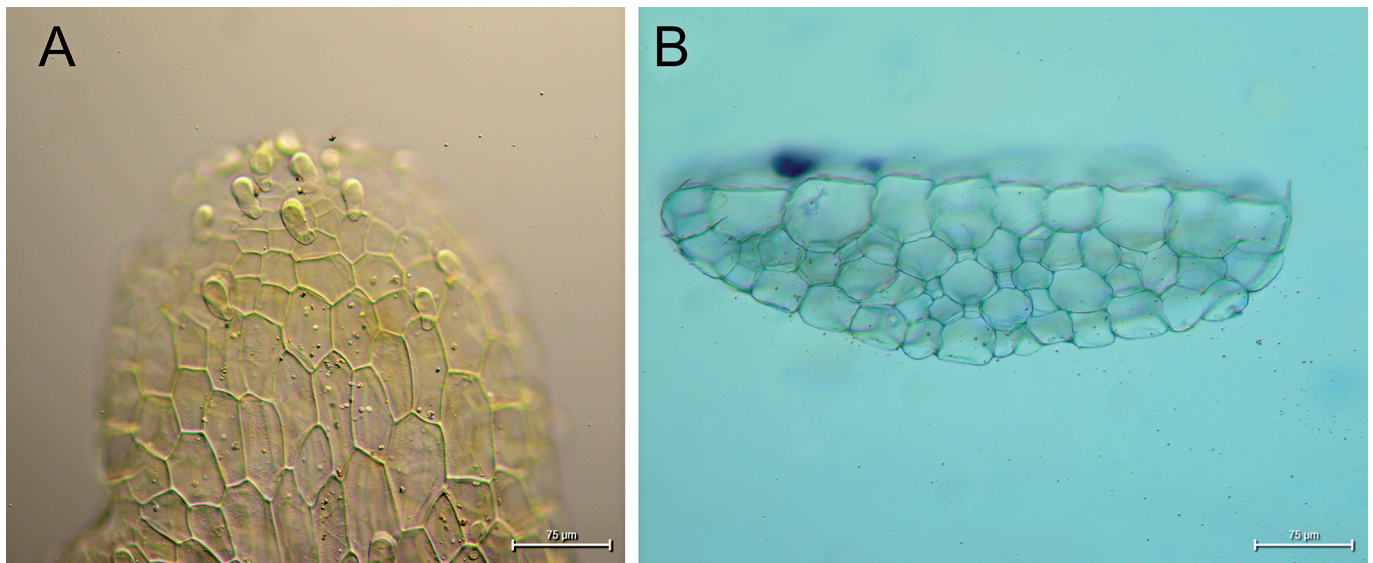


Fig. 20. *Riccardia aequicellularis*. A. Ventral mucilage papillae. B. Transverse section of main axis. Both from CHR 668238. Both bleached and B stained with methylene blue.

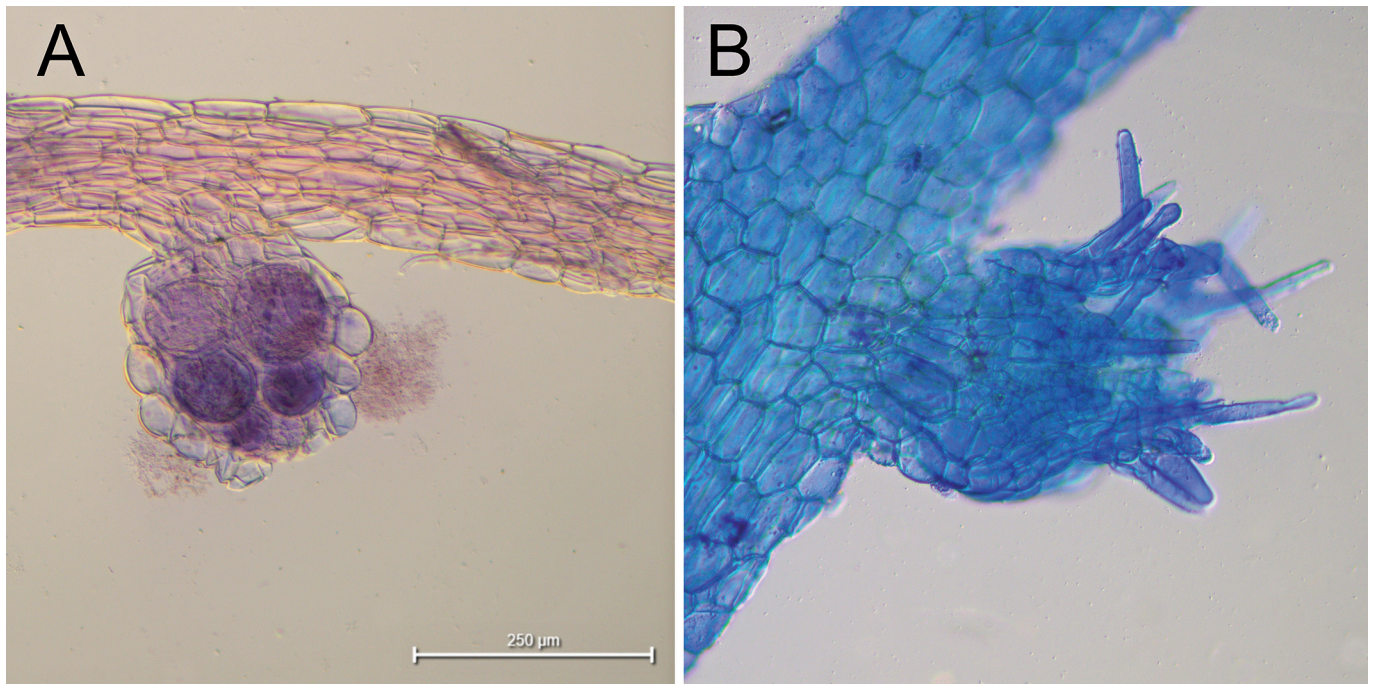


Fig. 21. *Riccardia aequicellularis*. A. Male branch, B. Female branch. A from CHR 642074; B from CHR 668238. 250 µm scale bar applies to A and B. Both bleached, A stained with ruthenium red, B stained with methylene blue.

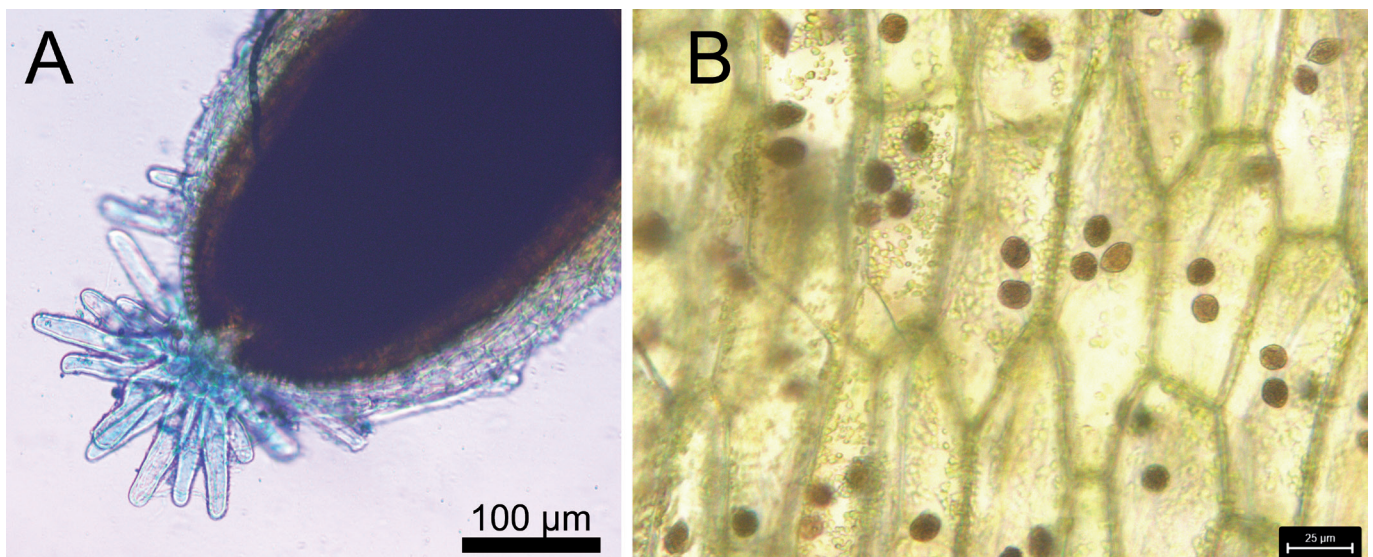


Fig. 22. *Riccardia aequicellularis*. A. Umbo with long-projecting thin-walled cells. B. Oil-bodies in epidermis. A from CHR 425900, B from CHR 691418. A bleached and stained with methylene blue.

Riccardia multicorpora has a similar size, growth form, and is found in similar open bog habitat as *R. sphagnicola*, where it sometimes grows on *Sphagnum*. Older parts of each plant are similarly pigmented brown (Fig. 23A). The epidermis of *R. multicorpora* usually has 2–5 oil-bodies per cell rather than none (Fig. 23C cf. Fig. 5A). Mucilage papillae are persistent on

the ventral surface of the thallus, (Fig. 23B) and are brown. The epidermal cells of *R. multicorpora* are no smaller than the internal cells (Fig. 23D) but in *R. sphagnicola* they are distinctly smaller (Fig. 3A). The main axis of *R. multicorpora* is 9–11 cells deep whereas in *R. sphagnicola* it is only 5–8 cells deep (Fig. 3A cf. Fig. 23D).

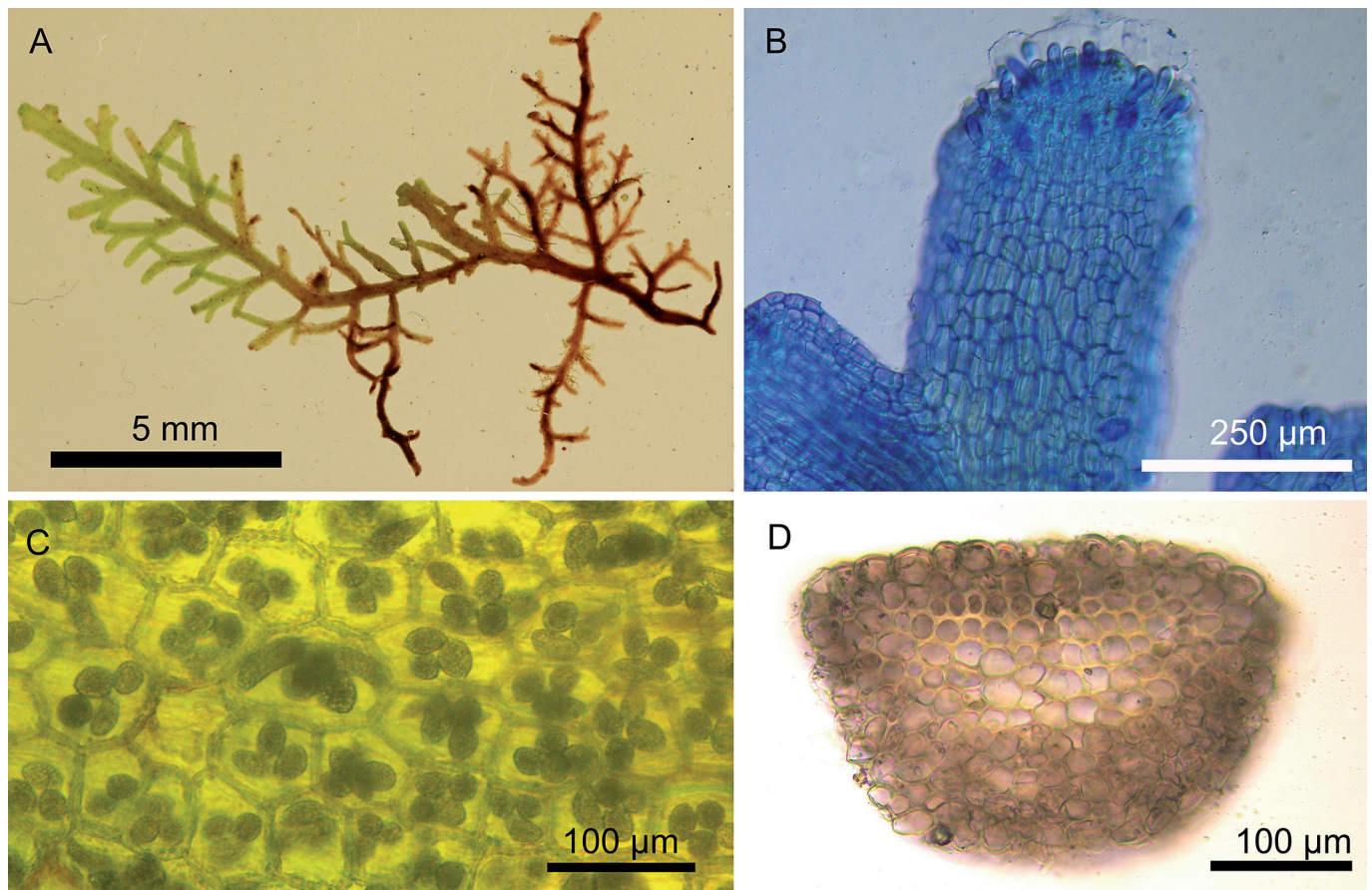


Fig. 23. *Riccardia multicorpora*. A. Whole female plant showing brown older parts. B. Persistent mucilage papillae on ventral thallus surface. C. Oil-bodies in ventral epidermis. D. Transverse section of main axis. A–C from CHR 691416, D from CHR 691415. B and D bleached, B stained with methylene blue.

Key to distinguish *Riccardia sphagnicola*

Riccardia sphagnicola can be inserted into the key to *Riccardia* species of Brown and Braggins (1989) after couplet 20 and paired with *R. breviala*:

- 20a Dorsal epidermal cells with oil-bodies present in some or all cells; ventral papillae persistent; stolons absent; male branches with 3–13 pairs of antheridia, wing cells elongated and incurved; female branches also with elongated incurved cells; nearly always found on rotting wood.....*R. lobulata*
- 20b Dorsal epidermal cells without oil-bodies; ventral papillae not persistent; stolons rare to common; male branches with 2–4 pairs of antheridia, wing erect of swollen cells; female branches with scales, lacking elongated cells; never found on rotting wood.....20'
- 20' Plants prostrate with pinnae erect and fan-like from a prostrate axis; shoot apices slightly notched; mucilage papillae rarely seen at shoot apices, when present only 7–15(22) µm long; stolons common; gemmae absent; found in lowland to montane forests on mineral soil.....*R. breviala*
- 20' Plants loosely prostrate with pinnae sparingly branched and in the same plane as the main axis; shoot apices rounded; mucilage papillae at shoot apices always present and obvious at ventral apex, 27–51 µm long; stolons rare; gemmae uncommon; found nearly always in penialpine *Sphagnum* bogs on *Sphagnum* or peat.....*R. sphagnicola*

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References

- Brown EA, Braggins JE (1989) A revision of the genus *Riccardia* S.F.Gray in New Zealand with notes on the genus *Aneura* Dum. *Journal of the Hattori Botanical Laboratory* 66: 1–132. [DOI](#)
- Evans AW (1921) The genus *Riccardia* in Chile. *Transactions of the Connecticut Academy of Arts and Sciences* 25: 93–209. [URL](#)
- Furuki T (1991) A taxonomical revision of the Aneuraceae (Hepaticae) of Japan. *Journal of the Hattori Botanical Laboratory* 70: 293–397. [DOI](#)
- Glenny D (2024) *Riccardia dimorpha* sp. nov. (Hepaticophyta, Aneuraceae) from Western Nelson, New Zealand, exhibiting sexually determined morphological dimorphism, an overlooked feature of some liverworts. *Teloepa* 27: 73–83. [DOI](#)
- Hässel de Menendez, GC (1972) Revision taxonomic del genero *Riccardia* (Hepaticae). Especies Andinopatigonicas y Subantarcticas incluyendo las islas Juan Fernandez, Malvinas, Georgias del Sur, etc. *Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", Botánica* 4: 1–242.

- Hewson HJ (1970) The family Aneuraceae in Australia and New Guinea. II. The genus *Riccardia*. *Proceedings of the Linnean Society of New South Wales* 95: 60–121. [URL](#)
- Hodgson EA (1965) New Zealand Hepaticae (Liverworts) –XVI. A miscellany of new genera, new species and notes, part I. *Transactions of the Royal Society of New Zealand, Botany* 3: 67–97.
- R Core Team (2024). R: A language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria)
- Reeb C, Bardat J (2014) Studies on African *Riccardia* types and related material. *Cryptogamie, Bryologie* 35: 47–75. [DOI](#)
- Rico G (2011) Methods for cell clearing and rehydration in thalloid liverworts. *Tropical bryology* 33: 12–18. [DOI](#)
- Schuster RM (1992) The Hepaticae and Anthocerotae of North America volume VI. (Field Museum: Chicago)

