

A new minute *Riccardia* species from penalpine tussockland in New Zealand's Southern Alps

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Abstract

Riccardia prorata Glenny is described from penalpine tussocklands of the Craigieburn Range, the Southern Alps Main Divide, and Fiordland. This new species is characterised by its small plants, only 4–7 mm long that are sympodial, have a narrow main axis (160–240 µm wide), and obliquely projecting (prorate) epidermal cells on dorsal and ventral surfaces and margins. It resembles *R. aequicellularis* (Steph.) Hewson in size, branching, and the position of gynoecia which are mostly on the main axis. The two grow together at the type locality and share habitat preferences, but *R. aequicellularis* does not have projecting epidermal cells.

Introduction

The genus *Riccardia* Gray in New Zealand and Australia was revised by Hewson (1970) for Australia, Hässel de Menendez (1972) for Patagonia, and Brown and Braggins (1989) for New Zealand. Of 31 species recognised in New Zealand by Brown and Braggins (1989), 20 are endemic (65%). Of the 11 non-endemic species, 10 are shared with Australia and three are more widespread, *Riccardia crassa* (Schwägr.) C.Massal., widespread in Asia, *R. alcornis* (Hook.f. & Taylor) Trevis. shared by South America, Australia, and New Zealand, and *R. alba* (Colenso) E.A.Br. is present in Fiji, Australia, and New Zealand.

Riccardia prorata Glenny was noticed in the field in 2025, distinct from the more abundant *R. aequicellularis* despite their small sizes. No plants were found in a day's searching on a second visit to the same site reflecting how little there is at this site but it was found 30 km to the northwest at a similar elevation two weeks later. There are no specimens of *R. prorata* among collections of *R. aequicellularis* (Steph.) Hewson at CHR but a newly accessioned specimen at WELT collected in Fiordland in 2009 had a small amount of *R. prorata* threaded through *Heteroscyphus coalitus* (Hook.) Schiffn. and *Temnoma quadripartitum* (Hook.) Mitt. The species is likely to be widespread in the penalpine tussocklands of the Southern Alps but is so small that it will be found only by careful searching in the field or by finding it in rehydrated specimens from penalpine habitats, as in the case of the Fiordland specimen.

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 (the "bleach and blue" method of Rico 2011, cited in Reeb and Bardat 2014). This method makes surface features such as the surface texturing, hyaline papillae, and rhizoids more readily discernible. Reeb and Bardat (2014: 52) note that 'bleach has the property of reinflating the old collapsed thalli, and the methylene blue rigidifies them, making possible nice cross sections'. Light microscope photography was done with a Leica DLB2500, with or without differential interference contrast. Scanning Electron Microscopy (SEM) photography was done with air dried material using a desktop Hitachi TM3050Plus microscope after coating the specimens with gold.

Glenny D (2025) A new minute *Riccardia* species from penalpine tussockland in New Zealand's Southern Alps.

Telopea 29: 299–306.

[doi:10.7751/telopea21437](https://doi.org/10.7751/telopea21437)

Received: 21 August 2025

Accepted: 30 October 2025

Published: 20 November 2025

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Terminology follows Brown and Braggins (1989) for naming of parts such as stolons and mucilage papillae. Following Glenny (2025b) the surface of the male branch that has antheridial pits is referred to as the clathrate surface as the male branch can face dorsally or ventrally in *Riccardia*. The surface usually faces dorsally but faces ventrally in some species.

Taxonomic Treatment

Riccardia prorata Glenny, *sp. nov.*

Type: New Zealand, Canterbury, Craigieburn Range, Craigieburn skifield, Alan's Basin, 800 m east of Craigieburn Valley Ski Club skifield, 43.109°S 171.709°E, 1335 m, *Chionochloa pallens* / *Celmisia walkeri* tussockland on hillslope, on A-horizon soil and damp decomposed *C. pallens* leaf litter in damp hollows underneath tussocks, 8 Mar 2025, D. Glenny 15813, Male and female (holo: CHR 699119).

Diagnosis: Shoots 4–7 mm long, loosely prostrate with brown pigments in older parts, young parts green, without stolons or innovations, main axis 160–240 µm wide, 150–176 µm and 6–8 cells deep, epidermal cells smooth-surfaced but strongly and obliquely projecting, more so on the dorsal surface and margins, unistratose marginal wing absent, mucilage papillae brown, persisting in two rows, clavate. Oil-bodies one per cell in a small proportion of epidermal cells. Fungal endophyte absent. Rhizoids absent. Gemmae present. Dioicous, gynoecea on main axis or pinnae. Gynoecea with branched marginal scales.

Description: Shoots loosely prostrate, on soil and growing through other bryophytes, 4–7 mm long, 2.5–6 mm wide (Fig. 1A). Main axis and older pinnae with brown pigments in the cell walls, green in young parts of pinnae. Epidermal cells with chloroplasts in green parts of the thallus, hyaline in older brown-pigmented parts of the thallus.

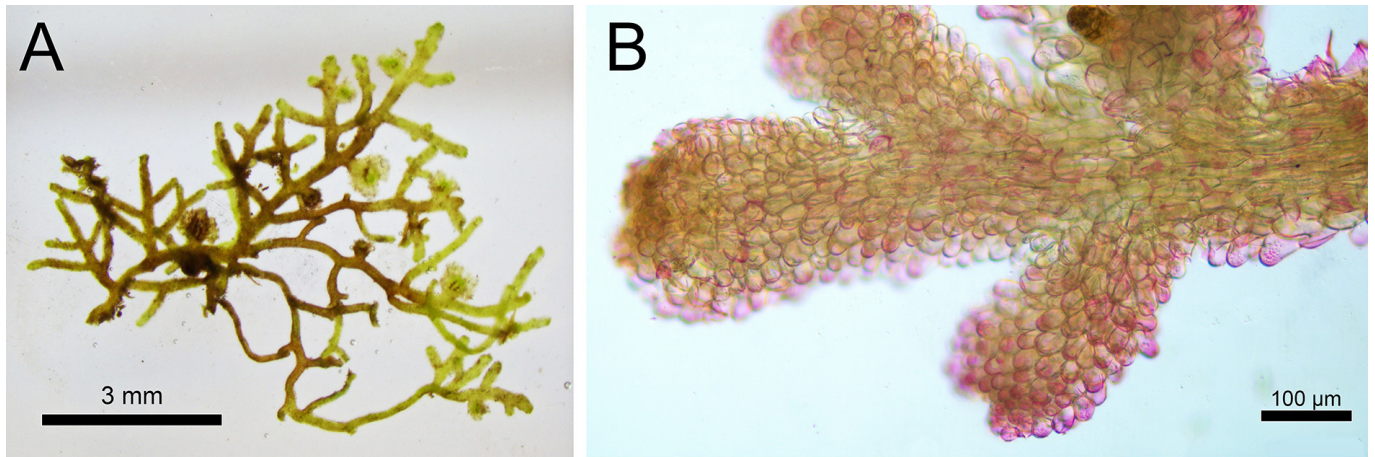


Figure 1. *Riccardia prorata*, A, shoot system of female plant. B, dorsal view of main shoot and branches near apex. Both from the type, D. Glenny 15813, Canterbury, Craigieburn Range (CHR 699119).

Secondary sexual dimorphism present: main axis 160–240 µm wide in females, 80–185 µm wide in males. Meristematic tips per shoot system 22–50 in female plants, 11–14 in male plants. Shoots 3-pinnate, sympodial, pinnae sometimes equal to the main axis in size and branch production with pinnae oblique to the main axis and up to 1100 µm long, alternate; main axis and side branches not differentiated in width. Pinnae sometimes with 1–3 pinnules. Stolons absent. Latent points absent. Innovations absent. Rhizoids not seen. Mucilage papillae ventral, not projecting at the shoot apex, persisting the length of the pinnae in two regular rows (Fig. 2A), the rows 0.4× the distance between the margin and the thallus mid-line; papillae mid-brown, clavate, 48–61 µm long, 16–25 µm diameter at the widest point, 8–11 µm diameter at the base, thin-walled, equal in length and diameter to the hyaline epidermal cells but narrowing to the base (8 µm diameter while epidermal cells are on a base of 40 µm) (Fig 2B).

Main axis planar or slightly convex dorsally, convex ventrally, 160–240 µm wide, 150–176 µm and 6–8 cells deep medially, 1.6–1.8× wider than deep, the lateral margins obtuse, wing absent, the margin formed by projecting epidermal cells 33–40 µm long (Fig. 1B, 3A, 4C). Shoot apices truncate, not retuse or notched (Fig. 1B).

Main axis in transverse section: epidermal projecting cells 20–50 × 20–30 µm, outer walls 2 µm thick. Medullary cells c. 18,

16–40 × 12–29 µm, quadrate, walls unevenly thick, 2–4 µm thick with concave trigones. Epidermal cells larger than internal cells and clavately-rounded at their apices. Epidermal cells in 23–30 cell rows. Dorsal epidermal cells and marginal epidermal cells in surface view broadly ellipsoidal, 43–88 µm long, 30–38 µm wide, the walls evenly 2 µm thick, the interior walls overlapping the next distal cell by up to ½, the distal end of the cell projecting more than the proximal end of each cell (prorate). Epidermal cells at margin projecting at 45° to shoot margin. Dorsal subepidermal cells hexagonal, 30 µm in diameter, 1.5 µm thick. Ventral epidermal cells in surface view broadly ellipsoidal, 60–80 µm long, 27–32 µm wide, the walls evenly 2 µm thick, the interior walls joined to neighbouring epidermal cells and the apex projecting from the surface less than the dorsal epidermal cells. Ventral subepidermal cells 34–52 µm long, 21–24 µm wide, walls evenly 3.0–3.2 µm thick. A strand of elongated central cells absent. External epidermal cell walls unornamented by surface thickenings. Oil-body one per epidermal cell in a small proportion of cells, in a greater proportion of cells near the shoot apex, broadly ellipsoidal, 10–13 µm long, 8–10 µm wide, finely granular, pale brown at 400× (Fig. 2C). Dorsal sub-epidermis oil-bodies 1–3 per cell in most cells, 10–15 µm long, 8–10 µm wide, mid-brown at 400×, finely granular, ellipsoidal to spherical (Fig 2D). Endophytic mycorrhizae not observed. Gemmae 2-celled, very sparse, developing from ventral subapical epidermal cells, 18 µm diameter (Fig. 4D).

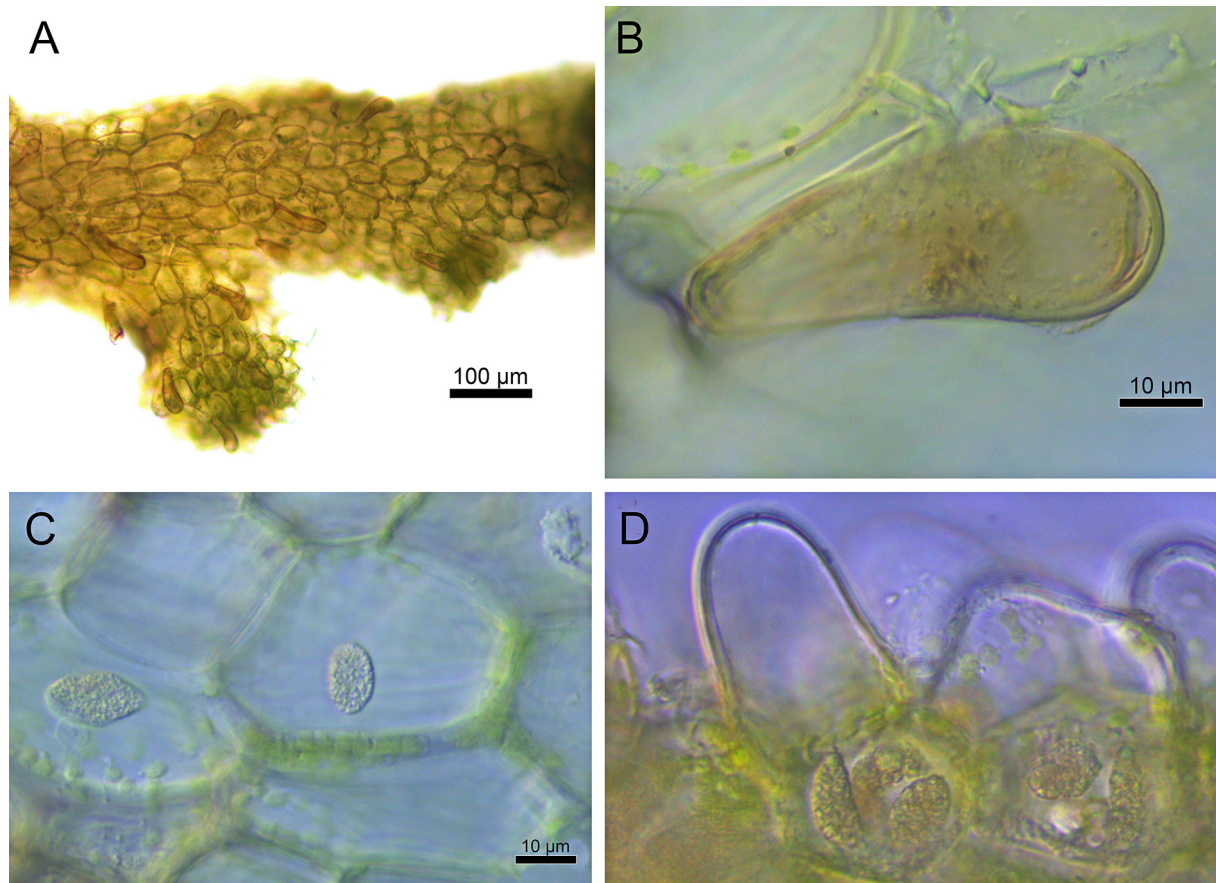


Figure 2. *Riccardia prorata*. A, slime papillae persisting on ventral thallus surface. B, papilla on thallus margin. C, oil-bodies in ventral epidermis. D, oil-bodies in marginal sub-epidermis. All from the type, Canterbury, Craigieburn Range, D. Glenn 15813 (CHR 699119).

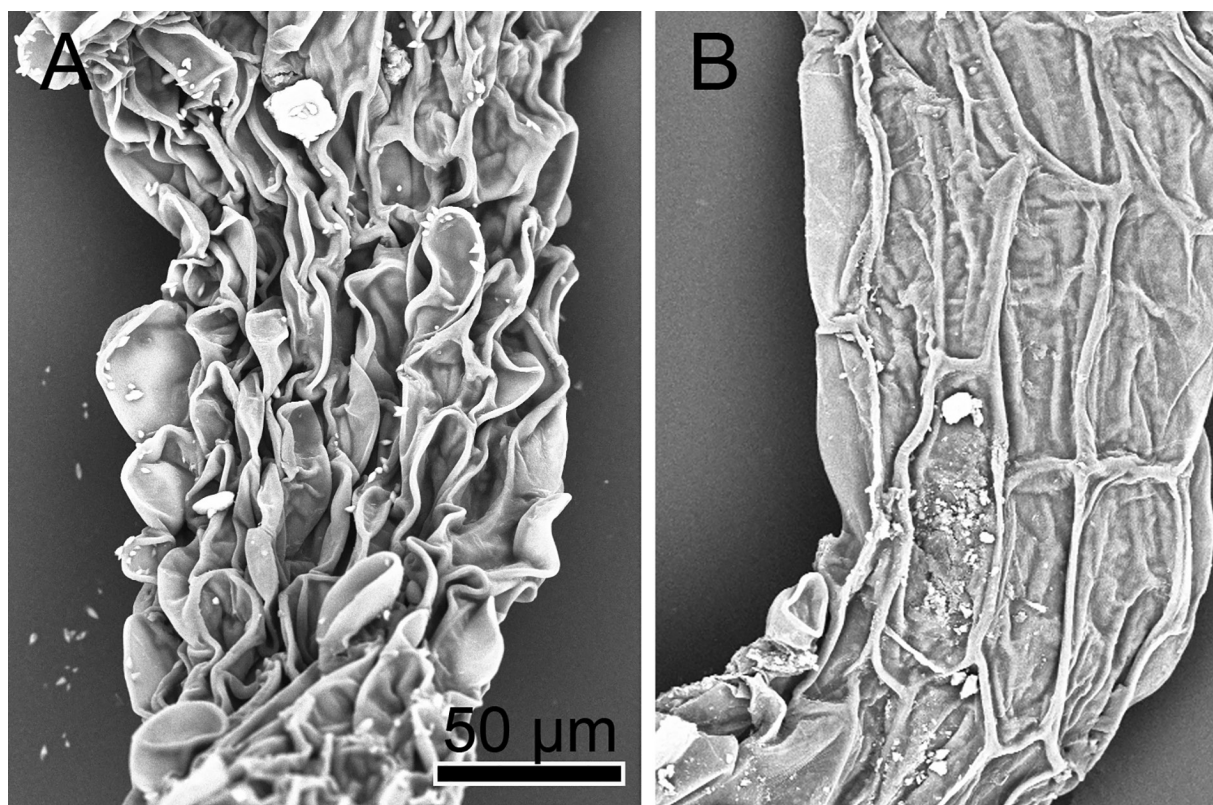


Figure 3. *Riccardia prorata* and *R. aequicellularis* main axes. A, *R. prorata*, SEM ventral view of main shoot showing a mixture of slime papillae and projecting epidermal cells. B, *R. aequicellularis*, dorsal view of main shoot showing epidermis without projecting cells. A from D. Glenn 15813, Canterbury, Craigieburn Range (CHR 699119). B from D. Glenn 15815, Canterbury, Craigieburn Range (CHR 699143). 50 µm scale bar applies to both.

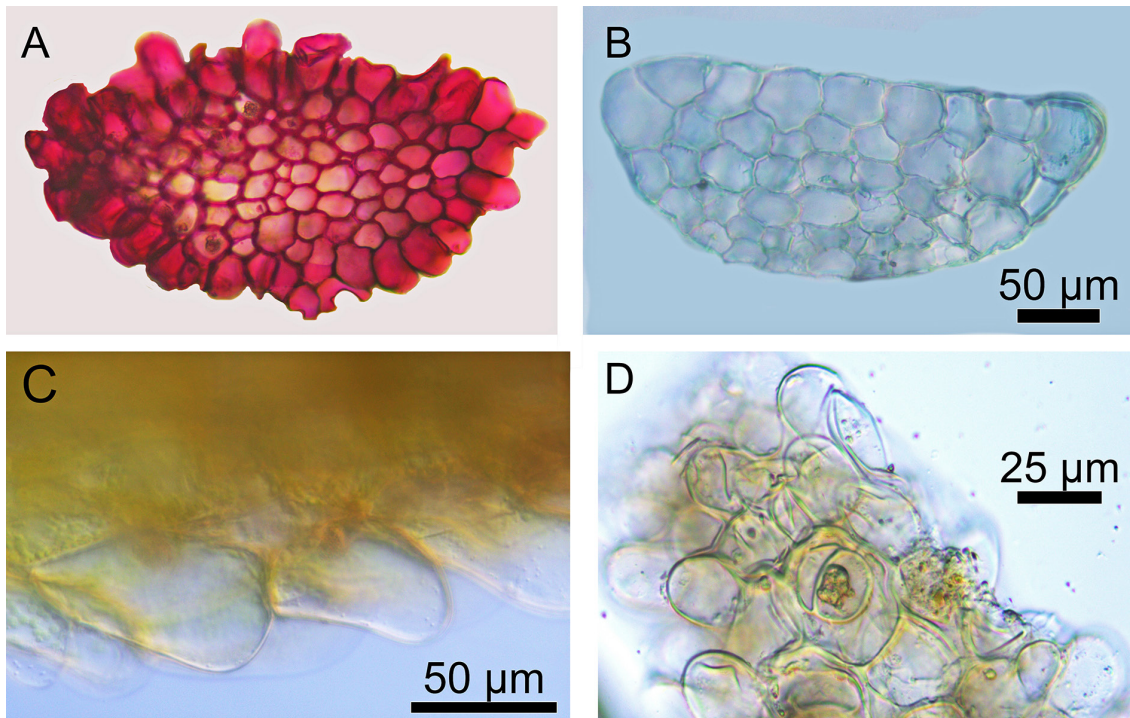


Figure 4. *Riccardia prorate* and *R. aequicellularis*. A–B, Transverse sections of main axis of A. *Riccardia prorate*, B. *R. aequicellularis*. C, *Riccardia prorate* dorsal view of thallus margin showing prorate epidermal cell. D, *Riccardia prorate*, ventral view of shoot apex showing two-celled gemma at the site of its production. A, C, D from the type, Canterbury, Craigieburn Range, D. Glenny 15813 (CHR 699119). B from Taranaki, North Egmont Chalet road, B.G. Hamlin 1624 (WELT H1059). A, B, and C bleached, A stained with ruthenium red, B with methylene blue. Scale bar of B also applies to A.

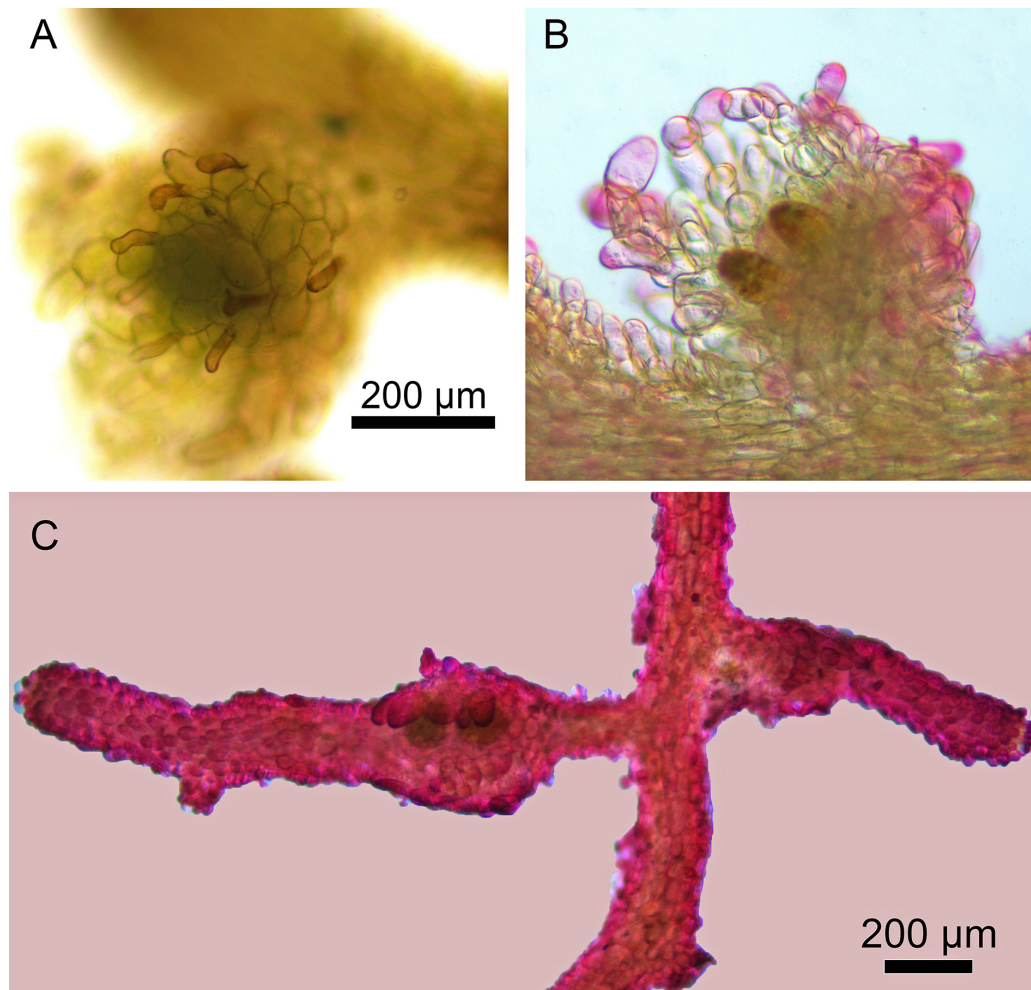


Figure 5. *Riccardia prorate* male and female branches. A, ventral view of gynoecium showing slime papillae. B, dorsal view showing two archegonia and marginal scales. C male branch in ventral view showing continuation of pinna beyond the androecium. B and C bleached and stained with ruthenium red. 200 μ m scale bar of A also applies to B.

Dioicous. Male branches solitary and 1–2 per plant, arising as pinnae from the main axis, sessile or on stalk up 30–300 µm long, the fertile part ellipsoidal to narrowly ellipsoidal, 330–480 µm long, 260–350 µm wide, facing dorsally, ventral surface with prorately projecting cells and two rows of persistent mucilage papillae, clathrate surface with two cells between each adjacent antheridal cavity and four cells between the pairs, a margin of prorately projecting cells, with 2–3 pairs of antheridia, antheridia 110–113 µm in diameter, the androecium becoming intercalary by continuation of the pinna for up to 1000 µm, the continuation giving rise to pinnules (Fig. 5C).

Female branches solitary, 1–2(–13) per plant, sessile, usually lateral on main axis but sometimes lateral on side branches, facing dorsally, 300–600 µm long, 400–880 µm wide, with 1–7 pairs of archegonia (Fig. 5A). Ventral surface with persistent mucilage papillae and epidermal cells projecting (Fig. 5BA), the margin dense with projecting single cells and branches of 3 cells that arch over and hide the archegonia, the margin without a raised wing or cells elongating into cilia. Calyptra and sporophyte unknown.



Figure 6. Habitat of *Riccardia prorata* at the type locality. In A the type locality is at image centre. B, *Chionochloa pallens* tussockland, the usual habitat of *Riccardia prorata*. C, *Podocarpus nivalis* scrub where plants were also found.

Recognition

Plants are small, equal in size to *Riccardia aequicellularis* and several other microthalline *Riccardia* species. At the type locality *R. prorata* was intimately mixed with *R. aequicellularis*. The two most obvious differences are that *R. prorata* has projecting epidermal cells that are visible in the field (compare Fig. 2A and 2B, and 4A and 4B), and thalli are yellow-brown to brown (Fig. 1A), while *R. aequicellularis* is transparently green in all parts.

Other microthalline species in New Zealand with a main axis of this width are *R. asperulata* R.M.Schust., *R. breviala* E.A.Br., and *R. furtiva* E.A.Br. & Braggins. None of these species has projecting epidermal cells.

Other species in New Zealand with projecting epidermal cells are *R. colensoi* (Steph.) W.Martin, *R. eriocaula* (Hook.) C.Massal., *R. papulosa* (Steph.) E.A.Br., and *R. umida* E.A.Br. None resembles *R. prorata*. *Riccardia colensoi* has upright projecting cells, not prorate, and the tip of the projection has a thickened cell wall. *Riccardia dendroides* Glenny has epidermal cells that partially detach and lie parallel to the thallus surface (Glenny 2025b). In *R. eriocaula* the epidermal cells are prorate as in *R. prorata*, but the plants are large, dendroid, erect or pendent, have a dark-pigmented stele in the main axis and pinnae, and is a forest

Distribution and ecology

Riccardia prorata is currently known from two localities. The type locality at the northern end of the Craigieburn Range in the South Island of New Zealand has a mean annual rainfall of 1544 mm (Bentley 2024). The vegetation is a mosaic of *Podocarpus nivalis*–*Coprosma fowerakeri* scrub and rather sparse *Chionochloa pallens* tussockland on a south-west-facing hillslope (Fig. 6), the substrate humus or A-horizon soil. Accompanying bryophyte species are *Acrocladium chlamytophyllum*, *Austrohondaella limbata*, *Canalohypopterygium tamarisci*, *Dicranoloma billardieri*, *Distichophyllum pulchellum* var. *pulchellum*, *Kurzia hippuroides*, *Leptoscyphus incomptus*, *Riccardia aequicellularis*, *R. bipinnatifida*, *Pseudocephalozia paludicola*, *Sauloma tenella*, and *Temnoma quadripartitum*.

The Temple Basin site, just east of the Main Divide, has a mean annual rainfall of 5000 mm (Anon., 2007). The vegetation there is rather sparse *Chionochloa pallens* tussockland on a south-facing hillslope, on soil in a rock crevice with alpine herbs *Kelleria dieffenbachii*, *Forstera purpurata*, *Gentianella bellidifolia*, *Raoulia grandiflora*, and *Hymenophyllum armstrongii*.

species that does not occur above 860 m elevation. *Riccardia papulosa* has bulging enlarged cells on the thallus margin that can be prorate but are not consistently so and cells of the dorsal and ventral surfaces do not project (see Brown and Braggins, 1989, fig. 10: 11). *Riccardia umida* does not have projecting epidermal cells but has dense and persistent, long, mucilage papillae (as in *R. eriocaula*) which could be mistaken for projecting cells but are not epidermal cells as they are attached by a narrow circular base to epidermal cells.

Of the Patagonian species of *Riccardia*, *R. hyalotricha* Hässel is most similar to *R. prorata* but has very long, crescent-shaped projecting cells at the margin. *Riccardia hyalotricha* is a much larger plant with a main thallus axis 400–500 µm wide.

Other specimens examined

Riccardia prorata

New Zealand: Canterbury, Temple Basin, 171.579°E, 42.909°S, 1391 m, soil in rock hollow on bedrock bluff in *Chionochloa pallens* tussockland, with *Kelleria dieffenbachii*, *Forstera purpurata*, *Gentianella bellidifolia*, *Raoulia grandiflora*, *Hymenophyllum armstrongii*, 22 Mar 2025, D. Glenny 15841, Female (CHR 699120).

New Zealand: Fiordland, Doubtful, Camelot River, Cozette Burn, 45.2717° S, 167.3134° E, 1095 m, subalpine scrub of *Brachyglottis* sp., *Coprosma pseudocuneata*, *C. serrulata*, and *Coprosma* sp., *Veronica subalpina*, with *Polystichum vestitum* beneath, seepage present, on humus of leaves and fine woody debris, with *Heteroscyphus coalitus* and *Temnoma quadripartitum*, 5 Mar. 2009, S. Kilduff (WELT H013747, pro parte).

Riccardia aequicellularis

New Zealand: Canterbury, Craigieburn Range, Craigieburn skifield, Alan's Basin, 800 m east of Craigieburn Valley Ski Club skifield, 171.709°E, 43.109°S, 1338 m, *Chionochoa pallens* / *Celmisia walkeri* tussockland on hillslope, on A-horizon soil and damp decomposed *C. pallens* leaf litter in damp hollows underneath tussocks, 8 Mar 2025, D. Glenny 15815 (CHR 699143).

Taranaki, Mt Taranaki, near road to North Egmont Chalet, 750 m, on streambank in dark wet forest, 16 June 1969, B.G. Hamlin 1624 (WELT H1059).

Conservation status

The species was unknown at the most recent threatened plant listing (de Lange et al. 2022) and should be classified as Data Deficient in the threat classification system of Townsend et al. (2008) as three localities are known. However, the penalpine habitat is very common and it is likely the species is more widespread throughout the Southern Alps, and perhaps the mountains of the southern North Island.

Etymology

The epithet *prorata* refers to the obliquely projecting cells of the epidermis, a feature not shared with any other *Riccardia* species in New Zealand or Australia. *Prora* means prow in Greek.

Discussion

The plants of *Riccardia prorata* have prorately projecting epidermal cells, a rare feature in the genus, seen in *R. dendroides* (New Zealand), *R. prehensilis* (Patagonia), (Glenny 2025b), *R. meagheri* (Myanmar), *R. hymenophylloides* Schiffner and *R. lachungensis* Singh & Singh (Sikkim) (Glenny 2025b, Muller 2013, Singh & Singh 2017). This makes recognition of this new species relatively straight forward. *Riccardia dendroides*, *R. prehensilis*, *R. meagheri*, *R. hymenophylloides* and *R. lachungensis* have much larger plants (30–46[70] mm long, not 4–7 mm long) and they all have an internal cylinder of thick-walled cells (a stele) at least in the main axis. As the type of *R. prorata* is fertile, it can be ruled out that it is the juvenile of those five species.

Similarities are strong with *R. aequicellularis* and a sister relationship with that species is a possibility which, if confirmed, may raise interesting questions about the processes promoting their divergence (Table 1).

Schuster (1963) made subgenus *Phycaneura* R.M.Schust. for two Australasian species, *R. aequicellularis* (as *R. reducta* R.M.Schust., syn. fide Hewson, 1970) and *R. asperulata*. He defined *Riccardia* subg. *Phycaneura* as follows: (1) plants small, (2) branching sparse, irregular with branches indeterminate in length, (3) thallus only 115–260 µm in diameter, 4–5(6) cells deep, (4) thallus biconvex, not flattened, (5) dorsal epidermal cells slightly larger to much larger than internal cells, (6) rhizoids absent or rare, (7) slime papillae ventral, marginal, dorsal, clavate, (8) oil-bodies absent, (9) gemmae absent, and (10) dioicous.

Hewson (1970) discussed subgenus *Phycaneura* and attempted to test the subgenus with a phenetic analysis but with inconclusive results. Subgenus *Phycaneura* was only distinguished from subgenus *Alcicornia* by a single character, female branches lateral versus latero-ventral, and Hewson points out that only one character out of nine (thallus width) that defined the five groups in her phenetic tree was one chosen by Schuster for his subgeneric classification. Hässel (1972) did not find that any Patagonian species belonged in the subgenus. Brown and Braggins (1989) described the subgenus as “distinctive” and corrected Schuster’s claim that the species lacked oil-bodies but noted similarities with subgenus *Riccardia* section *Pallidevirida* Hässel. None of these four authors placed any of their new species in subgenus *Phycaneura* and so it has remained a subgenus solely for *R. aequicellularis* and *R. asperulata*. A lack of gemmae listed by Schuster (1963) as characterising the subgenus is incorrect for the type species, *R. aequicellularis*, they occur uncommonly but can be abundant when present.

Riccardia prorata has the features of subg. *Phycaneura* including the presence of oil-bodies and gemmae. The feature least consistent with subg. *Phycaneura* is the brown pigmentation of much of the thallus of *R. prorata*. This is a feature of *R. alcicornis*, *R. multicorpora* E.A.Br., and *R. dimorpha* Glenny, all placed in subg. *Riccardia* sect. *Alcicornia* Hässel (1972). Section *Alcicornia* has most of the defining features of subg. *Phycaneura* and it is possible that *R. prorata* belongs in section *Alcicornia*. Alternatively, subg. *Phycaneura* and sect. *Alcicornia* may not be two distinct clades. A decision is not made here pending a phylogenetic study of New Zealand species.

Table 1. Comparison of *Riccardia prorata* with *R. aequicellularis*. Important differences between the two are in bold for *R. prorata*. Some differences are likely to be due to the limited amount of material studied of *R. prorata*. *Riccardia aequicellularis* scored from Brown and Braggins (1989) with minor changes.

	<i>Riccardia prorata</i>	<i>Riccardia aequicellularis</i>
shoot length, mm	4–7	5–10(20)
plant colour	brown except at shoot tips	green throughout
main axis width, µm	160–240	(46)83–412(670)
main axis depth, µm	150–176	(45)50–129(145)
main axis depth, cells	6–8	(3)4–6(7)
branching density and degree of division	dense, 3-pinnate	dense, 2–3-pinnate
stolons, innovations	both absent	both absent
fungal endophyte	absent	absent
gemmae	absent or present	absent or present
epidermal cells	prorate	mamillose
dorsal epidermal cells, size	larger than internal cells	larger than internal cells
ventral epidermal cells, size	larger than internal cells	equal to internal cells
epidermal cell chloroplasts	present in young shoots, absent from older parts	few or absent, especially from older parts of plant
wall thickness of internal cells	unevenly thick-walled, 2–4 µm	evenly thick-walled, 2.5 µm
sexuality	dioicous	dioicous
male branch origin	main axis and pinnae	main axis and pinnae
androecium stalk	stalked or sessile	stalked or sessile
androecium intercalary	sometimes	never
pairs of antheridia	2–4	1–3
gynoecium origin	sessile on main axis or pinnae	sessile on main axis or pinnae
mucilage papilla position	ventral, persistent in 2 rows	ventral, persistent in 2 rows
mucilage papilla length, µm	48–61	c. 20–30
gynoecial scales	branched	branched, becoming ciliate
archegonia, pairs per gynoecium	1–7	1–2
oil bodies in epidermis	0 or 1	0 or 1
oil bodies in subepidermis	1–4	1–4
oil-body length, µm	10–13	5–21
oil body texture, colour	finely granular, grey to brown	finely granular, grey to brown
habitat	penalpine humus and soil	lowland to penalpine humus and soil

Acknowledgements

This work was supported by the Ministry of Business, Innovation and Employment’s Strategic Science Investment Fund.

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