BOTANIC GARDENS OF SYDNEY

Telopea

Journal of Plant Systematics

ISSN 2200-4025 (Online)

Riccardia dendroides (Marchantiophyta, Aneuraceae), a new alpine species in subgenus *Arceoneura* from Western Nelson, New Zealand

David Glenny

Manaaki Whenua, P.O. Box 69-040, Lincoln 7640, New Zealand,

glennyd@landcareresearch.co.nz

Abstract

A new *Riccardia* species sharing distinctive morphological characteristics of subgenus *Arceoneura* is described from a single New Zealand alpine locality. *Riccardia dendroides* Glenny has a large, robust habit with the pinnae evenly spaced on erect axes and dense on prostrate axes, characters shared with *R. prehensilis* (Hook.f. & Taylor) C.Massal. of Patagonia and the South Atlantic Islands, and *R. eriocaula* (Hook.) Besch. & C.Massal of New Zealand and Australia. *Riccardia dendroides* differs in having predominantly 2-pinnate (not 3–4-pinnate) branching; epidermal cells partly detached and collapsed (not prorate or projecting); cells inside the cylindrical stele thick-walled as in *R. prehensilis*, not thin-walled as in *R. eriocaula*; male branches face dorsally (not ventrally); and it is found in a penalpine habitat.

Introduction

The genus *Riccardia* S.F.Gray was revised for the Southern Hemisphere by Hewson (1972) for Australia, Brown and Braggins (1989) for New Zealand, and Hässel (1972) for Patagonia. Two distinctive species, *R. prehensilis* (Hook.f. & Taylor) C.Massal. of Patagonia and the South Atlantic Islands, and *R. eriocaula* (Hook.) Besch. & C.Massal of New Zealand and Australia were recognised as forming subgenus *Arceoneura* Hässel. A new *Riccardia* species from a single New Zealand alpine locality shares many distinctive features with these two species and it is here described as *Riccardia dendroides* Glenny.

The three species share an erect form that is large for a *Riccardia*, typically 40–60 mm tall, and the branches are 2–4-pinnate with the pinnae evenly spaced on erect axes, dense on prostrate axes. When prostrate, species in subgenus *Arceoneura* have geotropically positive innovations or terete pinnules and few rhizoids. All three species have a brown-pigmented, thick-walled, cylindrical stele in the main axis that gives structural strength to the erect plants; the epidermal layer of cells is mostly hyaline and some or all of the epidermal cells project to varying degrees; they lack a fungal endophyte; and are dioicous. *Riccardia dendroides* is predominantly 2-pinnate, not 3–4-pinnate as in the other two species. In *R. dendroides,* epidermal cells are partly detached and collapsed rather than prorate or projecting. The cells inside the cylindrical stele of *R. dendroides* are thick-walled as in *R. prehensilis*, not thin-walled as in *R. eriocaula*. Male branches in *R. dendroides* face dorsally, not ventrally as in the other two, and are not coiled as in *R. eriocaula*. *Riccardia dendroides* is penalpine in its habitat while the other two are not found above 900 m.

Riccardia dendroides was first recognised among specimens of *R. eriocaula* at CHR because two collections were from 1330 m while all other collections were from no higher than 860 m. Examination of these two collections confirmed morphological differences from *R. eriocaula* as the epidermis lacked elongated hair-like projections. All *R. eriocaula* specimens at CHR were checked and no further specimens of *R. dendroides* were found. Auckland Museum (AK) has no records of *R. eriocaula* in New Zealand

Glenny D (2025) *Riccardia dendroides* (Marchantiophyta, Aneuraceae), a new alpine species in subgenus *Arceoneura* from Western Nelson, New Zealand.
Telopea 29: 263–277.
doi:10.7751/telopea21021

Received: 12 May 2025
Accepted: 29 August 2025
Published: 16 October 2025

from above 860 m and all specimens in both herbaria were collected from rotting wood in forest. The absence of specimens in AK suggests that no other New Zealand collections of *R. dendroides* have been made. Similarly, *R. eriocaula* in Tasmania has only been collected on wood under forest, often near to or overhanging streams.

Riccardia prehensilis is known from sea level to 800 m in Patagonia (Hässel, 1972). In the mid-South-Atlantic islands of Tristan, Gough, Inaccessible and Nightingale islands *R. prehensilis* also has an upper elevational limit of 800 m (Váňa and Engel, 2013). *Riccardia prehensilis* is recorded from living tree trunks and rotting wood in forest, but also occurs among bryophytes in heathland, and on wet peat soil in depressions.

Terminology

Terminology mostly follows Brown and Braggins (1989). Main axis width and depth, wing size, etc was measured for the widest internode on a plant, an internode being the main axis between adjacent pinnae on the same side of the axis.

Hässel (1972) used the term ***stele*** for the brown-pigmented and thick-walled, cylindrical, sub-epidermis layer that is present in the main axis and pinnae of all three species of subgenus *Arceoneura*. The term is used here in the same way.

Hässel (1972) is followed here in use of the terms '***latent vegetative point***' for a branch that is suppressed by more apical branches, and '***innovation***' for a branch that is negatively geotropic (i.e. growing upwards) from a latent point if that suppression stops.

The terms ***pinna*** and ***pinnule*** are used here for primary and secondary branches. Branches in subgenus *Arceoneura* correspond to the structure of a pinnatiform fern frond and these terms are universally used in this way in pteridology, but not in bryology. Hässel (1972) used the term "branch" for a pinna and "pinna" for what is called a pinnule here. Brown and Braggins (1989) used the terms "side-branches" and sometimes "primary pinnae" for what are called pinnae here, and "secondary pinnae" for what are called pinnules here. As with fern fronds, the degree of pinnateness (bipinnate, tripinnate, etc) expresses the maximum level of division.

The ***wing*** was defined by Hässel (1972) as the multi-stratose tapering tissue that extends on two sides of the cylindrical part of the main axis, and in the pinnae and pinnules projects beyond the thick-walled hyaline internal cells. Hässel (1972) put the word "wing" in quotes as normally a wing in *Riccardia* is a uni-stratose margin 1–3 cells wide when present. The term wing is used here with the same meaning, but without quotes.

The term ***stolon*** was used by Evans (1921), Hewson (1970), Hässel (1972), and Brown and Braggins (1989) but is inappropriate as stolons are horizontal stems that lie on the substrate. In *Riccardia*, what have been called stolons are ***geotropically positive branches***, which serve to anchor the plant in the way microphyllous ventral branches do in Lepidoziaceae, and are described as such here. They can form from innovations or by modification of branches.

Hässel (1972) differentiated ***mucilage papillae*** from projecting epidermal cells in *R. prehensilis* and noted, "Papillae distributed irregularly on the axes between the cells projecting from the epidermis". She illustrated apical mucilage papillae and a cap of mucilage on a shoot apex. Brown and Braggins (1989) were unclear on the distinction between mucilage papillae and projecting epidermis cells in *R. eriocaula* as they are very similar. Fig. 15A shows dense, persistent, scattered mucilage papillae at the pinnule apex. They are marked by having a very narrow circular attachment to the epidermal cells. Fig. 15B shows projecting epidermal cells that are prorate in a similar way to those of *R. prehensilis* (Fig. 19C).

Two new terms are introduced here. '***Platelet***' for the compressed dead epidermal cells found on the thallus and calyptra of *Riccardia dendroides*. They appear to be free on all their margins and attached at their centre but are not caducous. They are normal epidermal cells at the shoot apex but quickly attain their compressed and partially free form. '***Clathrate***' is the term adopted here for the surface of the male branch that is pierced with holes that allow antherozoids to escape from the antheridial pits. Brown and Braggins (1989) and Hässel (1972) described this as the dorsal surface but in *R. eriocaula* and *R. prehensilis* this surface faces ventrally and needs a term independent of orientation of the male branch.

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) to show surface features such as projecting cells, mucilage papillae, and rhizoids. Ruthenium red was used after bleaching in the same way to highlight surface features. Light microscope photographs were taken with a Leica DMLB 2500 compound microscope with Flexacam camera and differential interference contrast. SEM photos were taken with a Hitachi desktop SEM microscope. Plants for the SEM were cleaned in an ultrasonic bath before drying and mounting on a stub and coating with gold in a sputter coater. Critical point drying using an ethanol series and finishing with silizane (DMHS) was used to get clearer SEM images of projecting epidermal cells but with very limited success. Whole plants were photographed with a DSLR camera on a light box to provide diffuse transmitted light and plants were stained with safronin red to increase contrast.

Taxonomic Treatment

Riccardia dendroides Glenny, *sp. nov.*

Type: New Zealand: Western Nelson Province, Lead Hills Range, Amphitheatre Creek below Lake Clara, 1310 m, 40.895°S, 172.56°E, seepage on granite bedrock, under cover of *Empodisma minus* sedgeland, with *Schoenus pauciflorus*, 24 Jan 2008, *D. Glenny 10145* (holotype: CHR 595044).

Plants erect or prostrate, when fresh mostly brown but green in the young shoots (Fig. 1B).

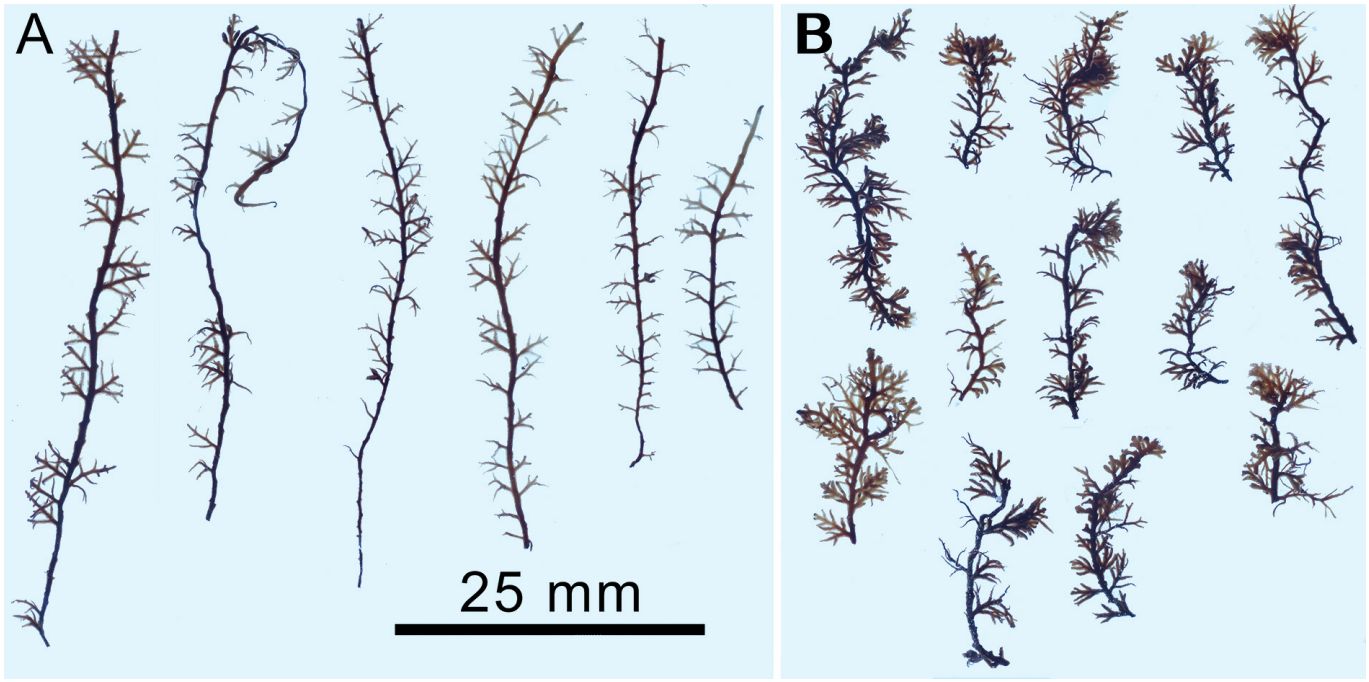

Fig. 1. *Riccardia dendroides*, whole shoots. A. Erect shoots. B. Loosely prostrate shoots. A from the type (CHR 595044), B from CHR 527434. Plants stained with safronin red. 25 mm scale bar applies to A and B.

Dried plants mostly dark brown, greyish-olive in the pinnules near the apex and wing tissue. Erect shoots 10–46 mm tall, regularly bipinnate, on well-developed pinnae some pinnules present (i.e. tripinnate). Prostrate shoots 10–35 mm long, 3-pinnate. Main axis, pinnae and pinnules all in one plane, the pinnae and pinnules not or only very slightly curled ventrally when moist, curling when dry. *Latent tips* sometimes present on the main axis but not producing innovations. When absent pinnae densely spaced on the main axis, only 1 mm apart. On loss of the leading shoot, a new main axis developing from either a pinna or pinnule. (Fig. 1A). Positively geotropic branches from innovations absent but pinnules throughout the plants often become terete and geotropically positive. Rhizoids absent.

Main axis 300–700 µm wide at the base, ellipsoidal in transverse section, 2.3–3.7 times wider than deep, with a wing 150–200 µm wide on each side, the wing at its thickest 130–170 µm thick and 5–6 cells thick tapering to 1 to several rows of cells only one cell thick at the margin (Fig. 3B); widening to 800–900 µm in the upper half of the plant and 220–330 µm and 12–15 cells deep. The wing is often absent from old parts of the main axis. (Fig. 2B) *Main axis in transverse section* differentiated into an epidermis of 2 cell layers, a stele of 3 cell layers, and a hyaline core 6 cells thick. The two epidermal rows of cells large and thin-walled, 13–27 µm diameter, 23–43 µm long the outer layer commonly collapsed and the cells partly detached. Cells of the stele cylinder 3 rows thick, cells 18–40 × 19–28 µm, walls yellow-brown and 8–15 µm thick, the wall thickenings bulging-trigonous, the cells thicker-walled and more brown-pigmented on the ventral side (Fig. 3B).

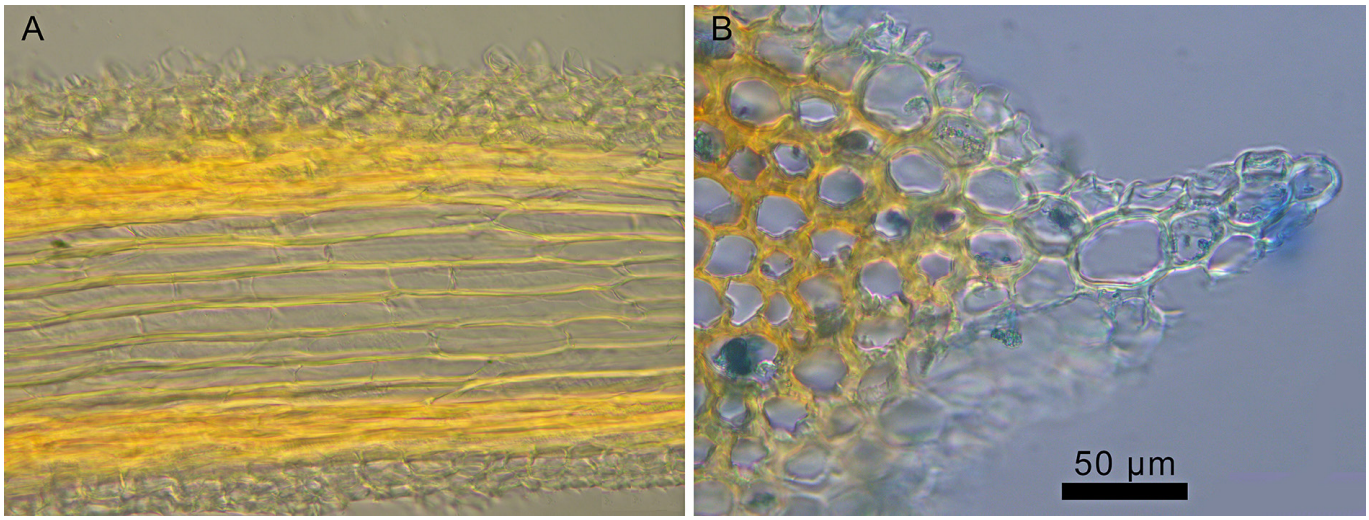

Fig. 2. *Riccardia dendroides*, sections of main axis of erect shoot. A. Longitudinal section showing elongated cells in the stele and internal core of thick-walled elongated cells. B. Multi-stratose wing. Both from the type (CHR 595044). 50 µm scale bar applies to both.

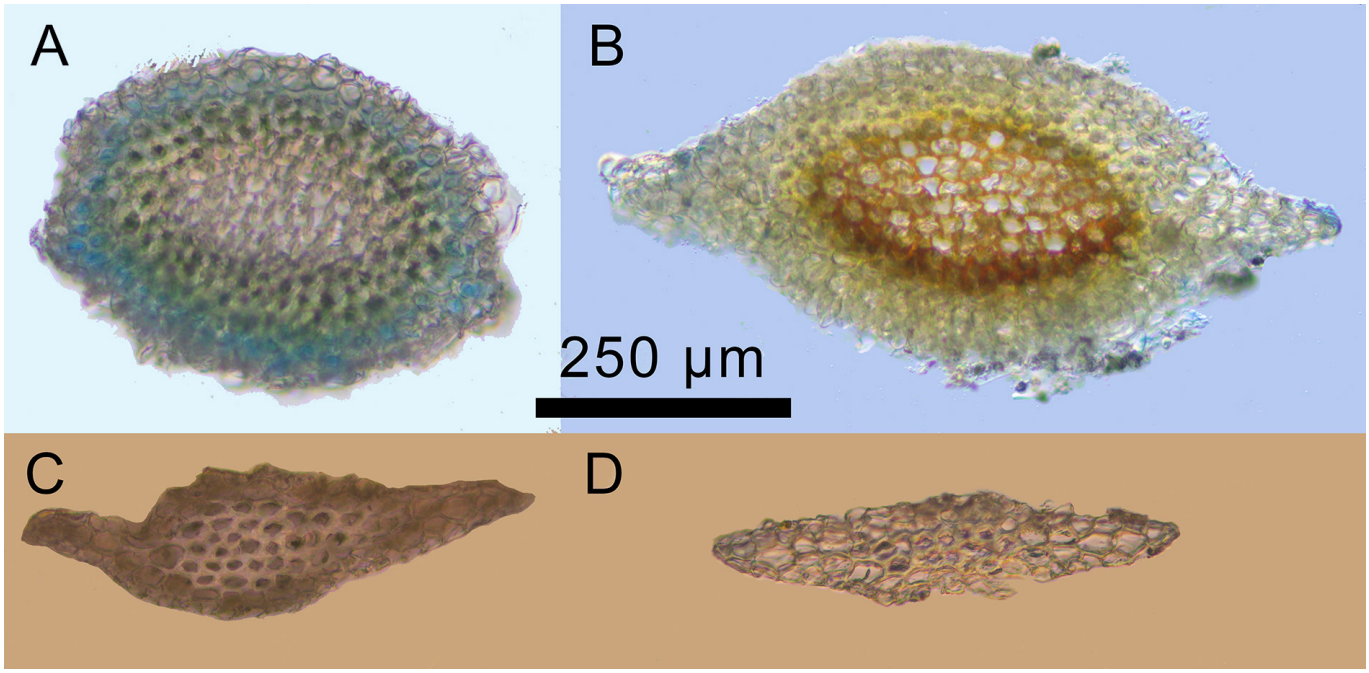

Fig. 3. *Riccardia dendroides*, stem transverse sections. A. Main axis of prostrate shoot with eroded wing. B. Main axis of erect shoot with intact wing. C. Pinna of erect shoot. D. Pinnule of erect shoot. A from CHR 527434, B–D from the type (CHR 595044). 250 µm scale bar applies to all.

Cells of core inside the stele 21–32 × 16–32 µm in section, elongated in the direction of the thallus longitudinal axis 100–170 µm long (Fig. 2A), walls hyaline, 2.0–3.5 µm thick, with trigonous thickenings at wall junctions that sometimes extend into intermediate thickenings. *Pinnae* 12–33 per shoot, spaced 1–5 mm apart on each side of the main axis; well-developed pinnae at mid-shoot determinate in length, the largest 2–3 mm long with 6–11 pinnules, angle of pinna to main axis 25–45°, angle of pinnules to pinna 20–35°. Pinna wings continuous with the main axis wing (adnate on both sides), and pinnule wings adnate on both sides to pinna wing. Pinnae at base 420–500 µm wide, 180–240 µm thick, wing 150–200 µm wide. Epidermis 1–2 cells thick over the stele. Stele 200–290 µm wide, 150–180 µm deep, not brown pigmented. Wing tapering evenly from 6 cells deep to a single marginal cell row. Cells walls in transverse-section throughout c. 4 µm thick, only the lumina varying in size in the layers, smallest in the stele. Light polarized by central strand in pinnae and pinnules. *Pinnules* longest at the base of pinnae and up to 2.0 mm long; sometimes with a single side branch (the plant then tripinnate), 300–500 µm wide at the base and adnate to pinna wing, tapering evenly to apices that are 200–340 µm wide and 100–170 µm thick, apices rounded-truncate, less often retuse. In transverse section, the pinnules with a single epidermal cell layer covering the midvein dorsally and ventrally and extending beyond the midvein to form two wings 4 cells thick, 70–110 µm and 3–6 cells wide (from midvein to margin) with a stele of thick-walled cells that are not brown-pigmented and an epidermis of thin-walled cells. *Epidermal surfaces* with smooth-surfaced cells, the ventral epidermis of the main axis with sparse platelets, i.e., collapsed, hyaline, rounded-rectangular cells that are attached at their centre but free on their margins, these platelets not caducous (Fig. 4A, 5).

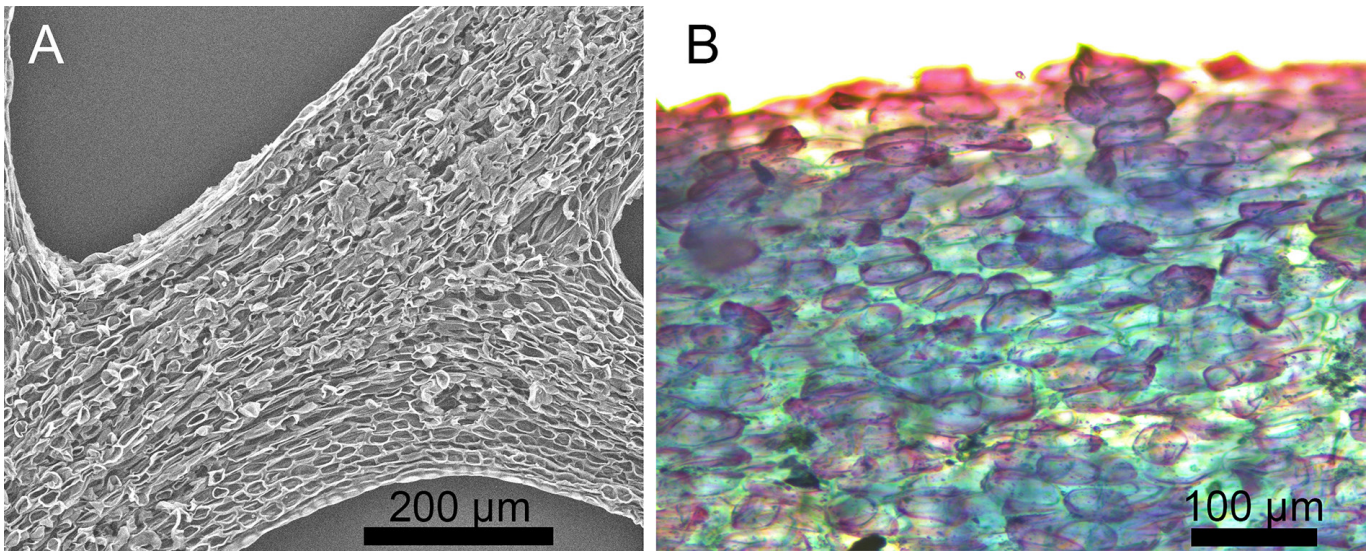

Fig. 4. *Riccardia dendroides*. A. Dorsal view of pinna and pinnules showing partially detached epidermal cells. B. Calyptra surface showing partially detached pachydermal cells. B bleached and stained with methylene blue then ruthenium red. Both from the type (CHR 595044).

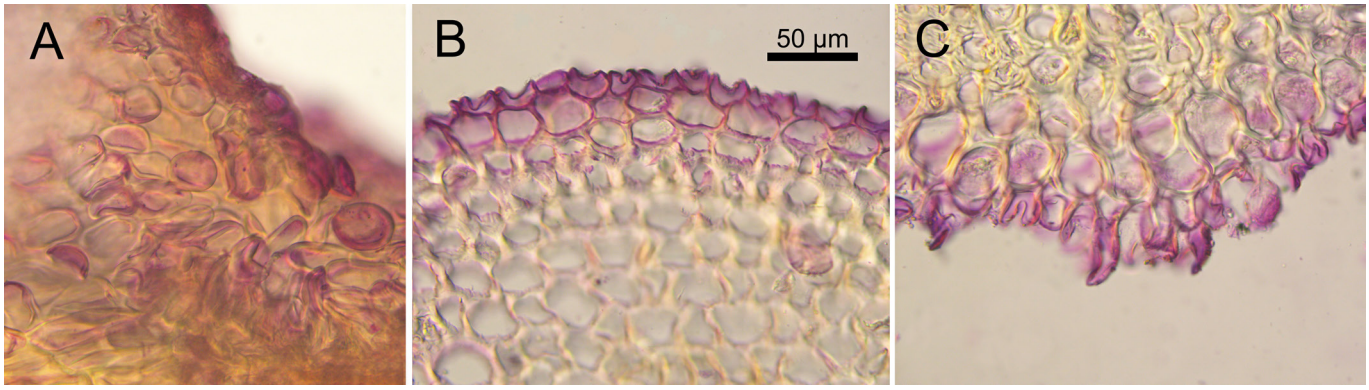

Fig. 5. *Riccardia dendroides*, epidermal cells of main axis. A. Collapsed epidermal cells at a latent vegetative point. B. Dorsal surface in transverse section showing collapsed epidermal cells. C. Ventral surface in transverse section showing projecting epidermal cells mixed with collapsed cells. B and C show thick-walled cells inside the stele. All photographed from the type (CHR 595044). All bleached and stained with ruthenium red. 50 µm scale bar applies to all.

Pinnae with a few platelets. Pinnules without such platelets. Male and female branches with platelets on the ventral surface at a similar density to the main axis. *Mucilage papillae* rarely present at ventral pinna and pinnule apices, when present not persisting, scattered on the ventral and surfaces, not in rows, 22–36 µm long, 14–20 µm in diameter, on a circular base 7–11 µm diameter, strongly clavate, hyaline (Fig. 6).

Papillae absent from dorsal thallus surface and from fertile branches. *Dorsal epidermal cells* in surface view over the main axis stele shortly rectangular, 22–44 µm long, 20–30 µm wide, ratio 1.1–1.6, walls 2 µm thick. *Dorsal subepidermal cells* over the main axis stele 57–96 µm long, 27–31 µm wide, only visible where epidermal cells have peeled off. *Ventral epidermal cells* over the main axis stele 24–60 µm long, 13–28 µm wide, rectangular, length to width ratio 1.4–2.4, cell walls 2 µm and evenly thick. Ventral epidermal cells near the margins quadrate and 24–36 µm long, 18–27 µm wide, walls 2–4 µm and evenly thick. *Ventral subepidermal cells* equal in size to ventral epidermal cells, difficult to see. *Marginal row of cells* slightly smaller, 12–25 µm long, 9–18 µm wide, and usually hyaline. Near-marginal cells 20–39 µm long 16–38 µm wide, square to shortly rectangular, length to width ratio 1.0–1.6(1.8), walls evenly 2–4 µm thick. *Oil-bodies* in dorsal and ventral epidermis in a small proportion of cells, one per cell, ellipsoidal with obtuse tips, finely granular, colourless, 11–14 × 5–8 µm (Fig. 7A). Oil-bodies in dorsal and ventral sub-epidermis 1–2 in most cells, 4–13 × 6–9 µm, also ellipsoidal, finely granular and colourless (Fig. 7B).

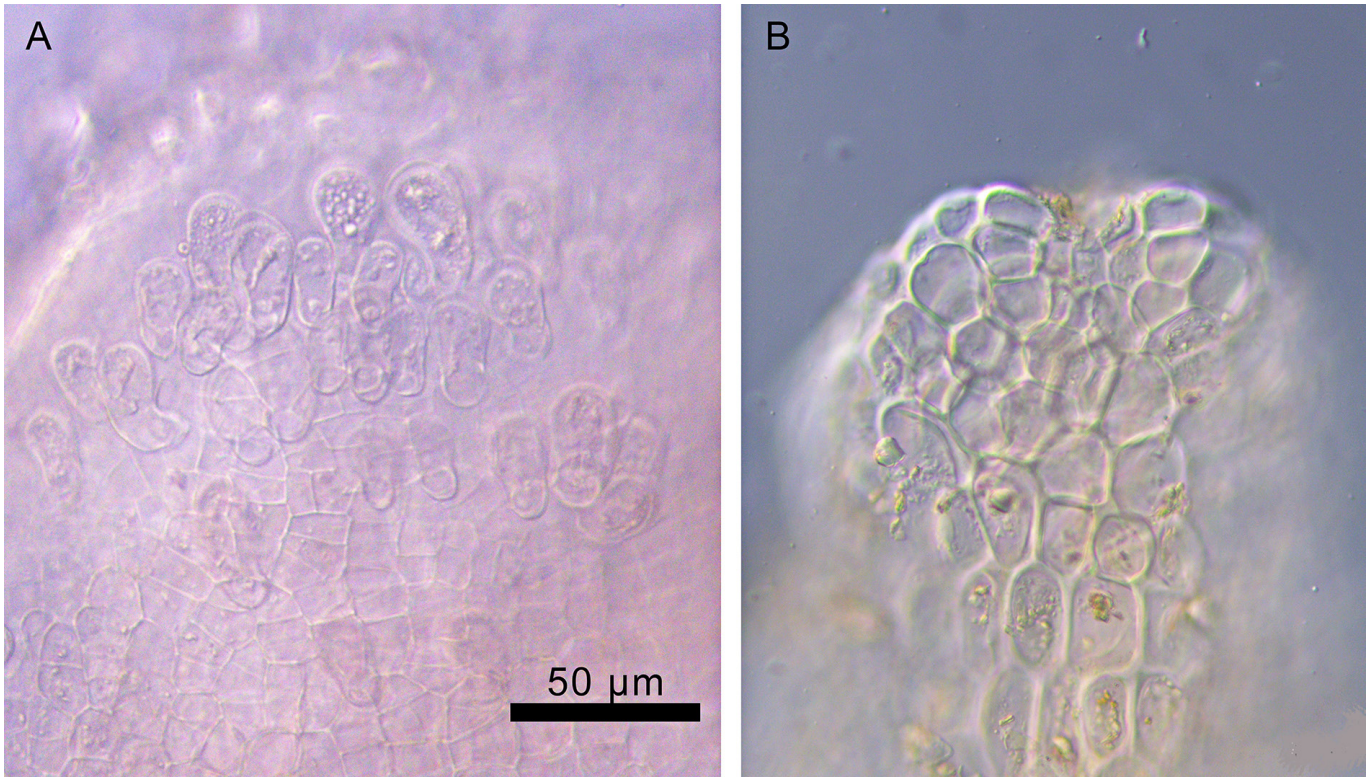

Fig. 6. *Riccardia dendroides*, ventral view of pinnule apex (bleached). A. Showing dense mucilage papillae. B. Showing a typical lack of apical papillae. Both from the type (CHR 595044). 50 µm scale bar applies to both.

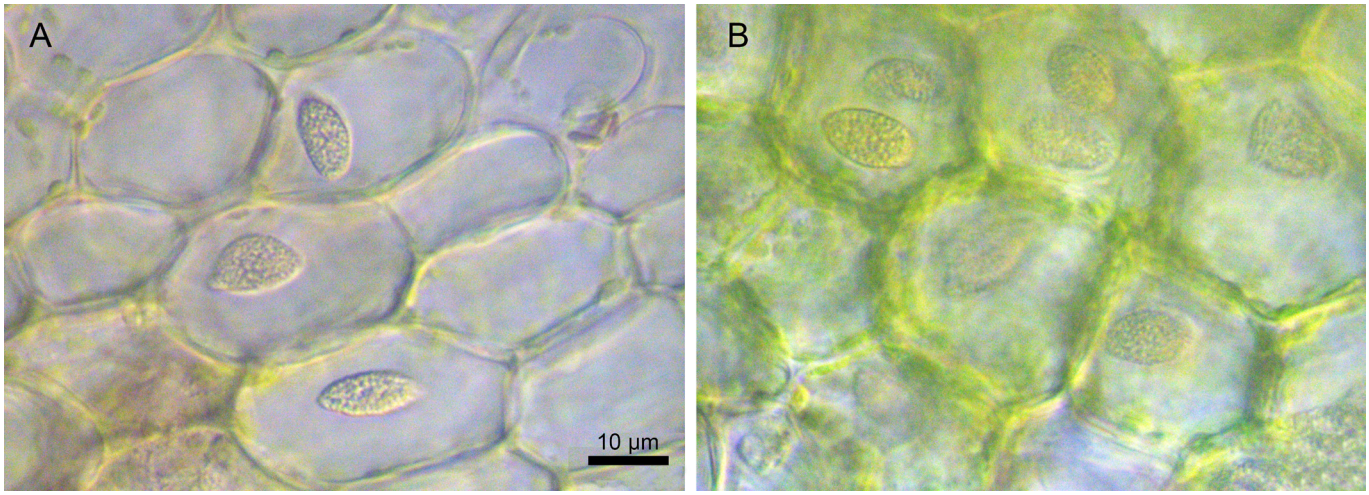

Fig. 7. *Riccardia dendroides*, oil-bodies. A. Ventral epidermal cells. B. Ventral subepidermal cells. Both photographed from CHR 698202. 10 µm scale bar applies to both.

Gemmae not seen but the dorsal and ventral epidermis of the main axis often with small patches of 2–4 epidermal cells missing. Endophytic mycorrhizae absent.

Dioicous. *Male branches* 400–1400 um long, 300–350 µm wide, 2–6 per pinna, usually formed from the first pair of pinnules at base of well-developed pinnae from near plant base to near plant apex, solitary and opposite on the pinna, straight and in the plane of the pinna, facing dorsally, or pinnules dividing dichotomously in two opposite pairs of male branches and tilted c. 45° toward each other. Antheridia in 2–6 pairs. Base of the male branch winged as for a normal pinnule to the first pair of antheridial pits, then narrowing to an insignificant, erect, crenate, marginal wing, cells not elongated and the wing hardly projecting above the antheridial pit surface. Male branch reverting to normal tissue beyond the male section that is up to 600 µm long. Clathrate surface of the male branch facing dorsally (Fig. 8B).

Ventral (back) surface of male branch with single-celled projecting teeth that lie almost against the surface. *Female branches* also at base of well-developed pinnae, solitary and opposite on the pinna, facing dorsally, angled slightly dorsally from the plane of the rest of the plant. Ventral surface with uniseriate hairs 200–316 um and 4–6 cells long and platelets (Fig. 9A); marginal wing laciniate, laciniae 220 µm and 5 cells long ending in 3 uniseriate cells (Fig. 9B), occasional club-shaped hairs that are biseriate throughout.

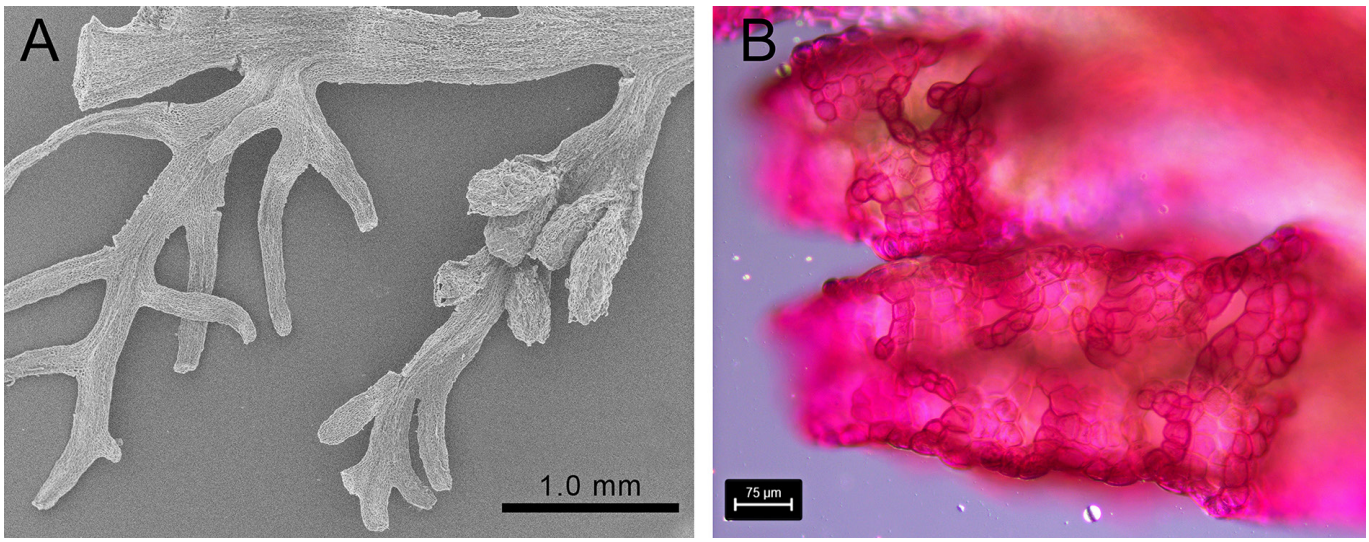

Fig. 8. *Riccardia dendroides*, male branches. A. Ventral view showing six branches on a pinna, the basal four in pairs on the same pinnule, the backs of the male branches visible. B. Dorsal view of male branches showing clathrate surface. Both photographed from the type (CHR 595044). B is bleached, then stained with ruthenium red.

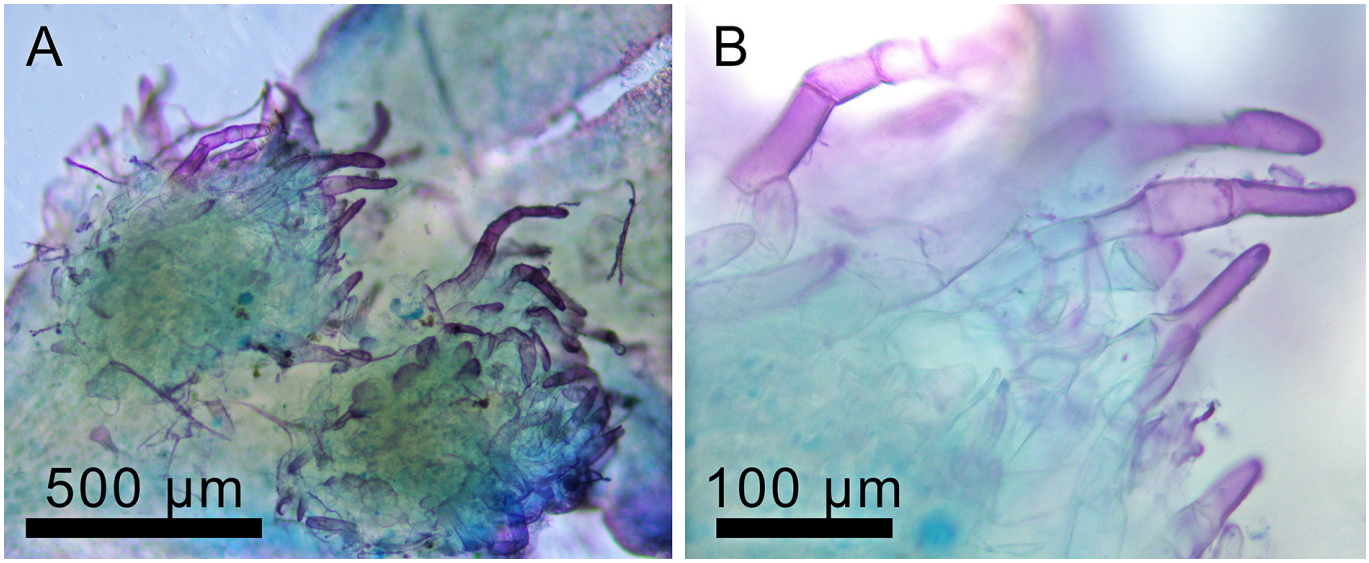

Fig. 9. *Riccardia dendroides*, gynoecium. A. Ventral view of gynoecium showing laciniate scales. B. Marginal scales. Both photographed from CHR 527434. Both bleached, then stained with methylene blue.

Calyptra when fully extended c. 2.5 mm long, a slightly dorsiventrally compressed cylinder, 675 × 526 µm in section, narrowed at the base to 380 µm diameter; in transverse section calyptra wall 88–128 µm and 4–6 cells thick, the cells all thin-walled, 20–25 µm wide, 25–40 µm long (Fig. 10A).

Pachydermal cells dense in bands on the surface and partially detached but not seen caducous (Fig. 4B, 10A). Umbo cap-shaped, 400 µm diameter and 16 cell rows circumference at base (Fig. 10B), 5 cells high, surface smooth and without projecting cells, cells thick-walled (up to 12 µm thick). Sporophyte unknown.

Distribution and ecology. Endemic to New Zealand and currently known from a single location, Amphitheatre Creek in Western Nelson, at 1300–1330 m, in an infertile seepage on a low-angled hillslope on granite bedrock with tussock shrubland of *Chionochloa rubra, Veronica odora, Leptospermum scoparium*, with *Empodisma minus, Gleichenia alpina, Oreobolus pectinatus, Donatia novae-zelandiae*, *Drosera spathulata, Centrolepis ciliata* and *Celmisia parva*. Plants grew on peat soil through cushion-forming plants *Oreobolus* and *Centrolepis* mixed with other bryophytes including *Riccardia crassa, R. pusilla, Isotachis montana*, and *Rhacocarpus purpurascens* (Fig. 11).

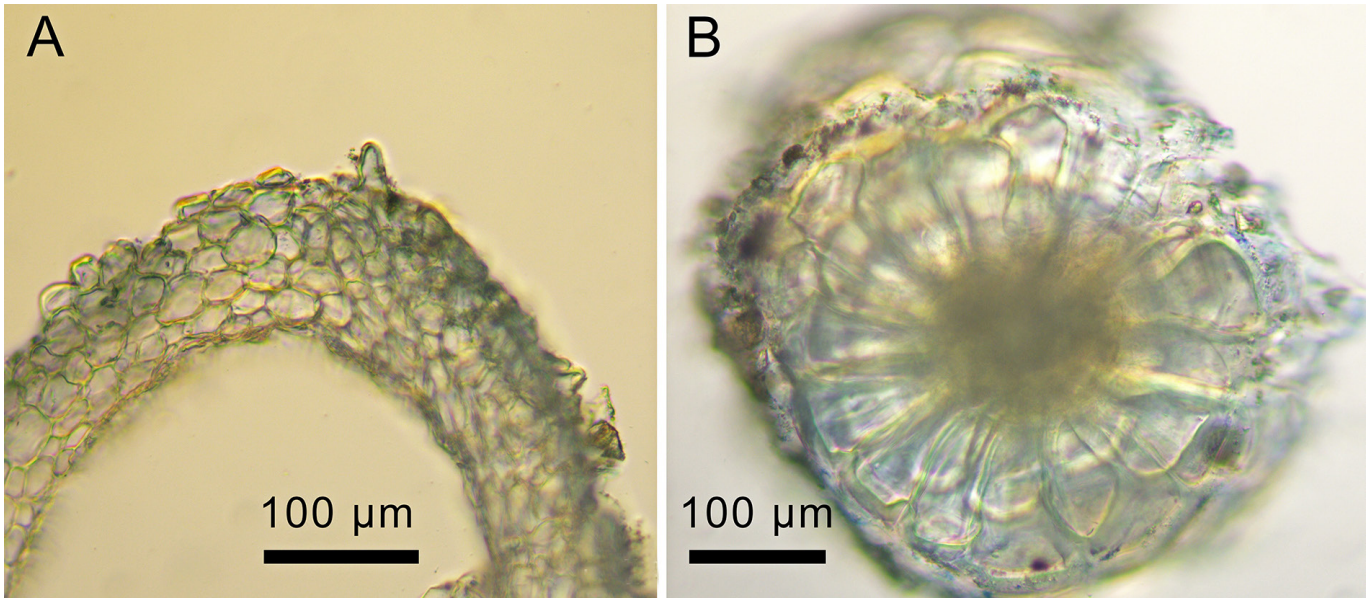

Fig. 10. *Riccardia dendroides*, calyptra and umbo (bleached). A. Calyptra transverse section. B. Umbo in apical view. Both photographed from the type (CHR 595044).

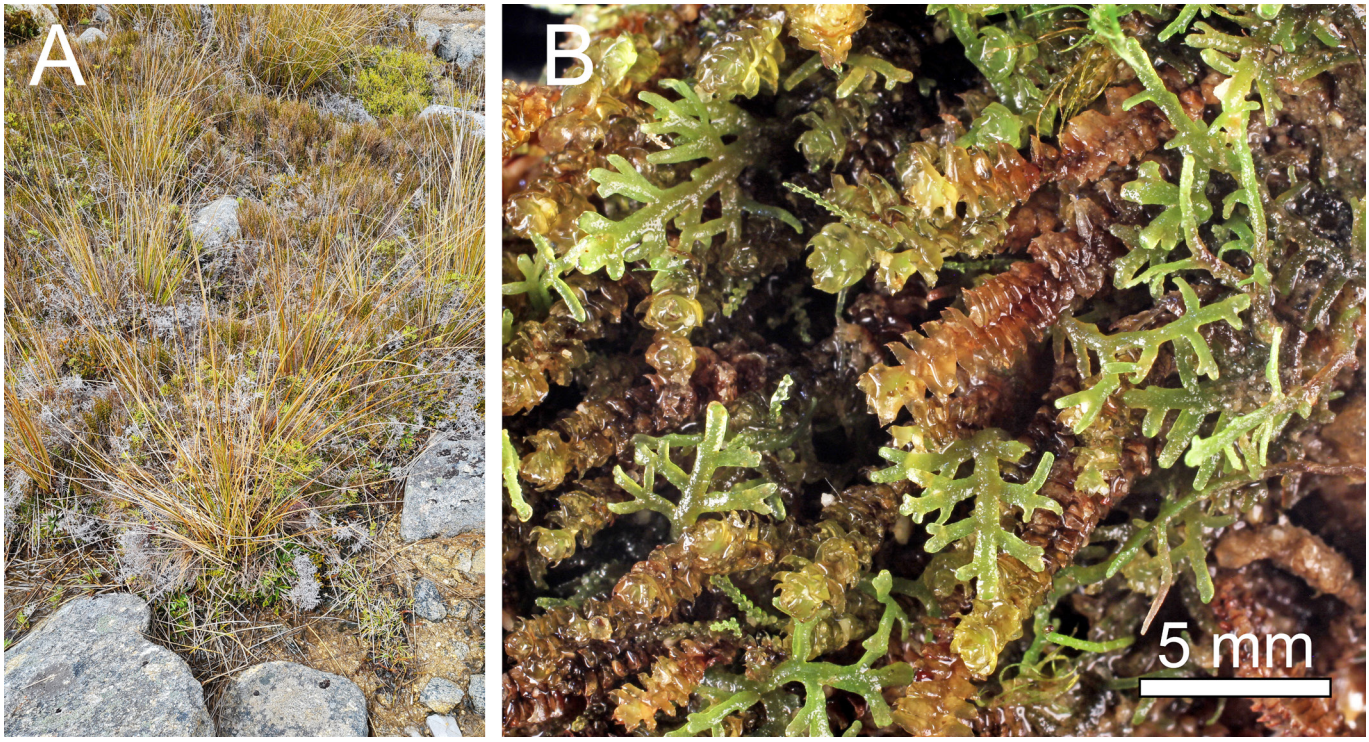

Fig. 11. *Riccardia dendroides*. A. Habitat, sparse *Chionochloa rubra* and *Gleichenia alpina*. B. Loosely prostrate plants growing among *Isotachis montana*. B from CHR 698202.

Recognition. *Riccardia dendroides* can be recognised by the large size of its erect shoots, which are c. 40 mm tall, and the evenly and distantly pinnatiform branching of the plants. *Riccardia eriocaula* is the other species in New Zealand that has this erect bipinnate form with a cylindrical and winged main axis. Both species share a stele of dark brown subepidermal cells which gives all axes except the pinnule apices a dark brown appearance. Both species have a multi-stratose wing that is most noticeable on the distal parts of the main axis and pinnae. While *R. eriocaula* commonly has several parallel, erect, main axes on a single shoot (Fig. 12), *R. dendroides* does not (Fig. 1).

Riccardia dendroides has a scurfy appearance due to collapsed, partially-detached hyaline epidermal cells and on the ventral surface sparse, spiked, cells, mostly over the stele (Fig. 6). *Riccardia eriocaula* has what appears to the eye as hyaline hairs and these are mainly mucilage papillae and are visible in the field on the main axis, pinnae and pinnules giving the whole plant a bristly appearance (Fig. 15A).

Riccardia dendroides is evidently a species of alpine habitats above tree line, whereas *Riccardia eriocaula* is a species of lowland to upper montane forest, up to around 900 m elevation. Microsite also differentiates the two, all collections of *R. eriocaula* at CHR are from rotting wood, whereas the habitat of *R. dendroides* is wet peat soils.

Plants of *R. dendroides* resemble those of *R. filicina* (Colenso) E.A.Hodgs., particularly when loosely prostrate (Fig. 11B). *Riccardia filicina* can be prostrate or erect, 25–35(70) mm tall when erect and 10–25 mm long when prostrate, 2–3 pinnate, sometimes regularly so (Brown and Braggins, 1989, Fig 28). The main axis of *R. filicina* is never a cylinder with a tapering wing on each side and lacks the dark brown pigmented stele of *R. dendroides* that gives the main axis and pinnae an opaque appearance.

Etymology. *Dendroides*, meaning tree-like, refers to the monopodial form of the plants that have a strongly differentiated main axis and a regularly bipinnate branching form.

Conservation. The species qualifies for listing as Data Deficient in the threat classification system of Townsend et al. (2008) as six collections are known from a single locality and it has not been searched for elsewhere.

Specimens examined

Riccardia dendroides: New Zealand: South Island: Western Nelson Province, Lead Hills Range, Amphitheatre Creek below Lake Clara, 1300 m, 40.894°S, 172.562°E, on a 15 cm high vertical bank, damp from seepage coming from a bog above, a small pool of water in granite sand at base of bank, low *Leptospermum scoparium* shrubs overhanging the bank and growing with *Empodisma minus, Aciphylla polita, Astelia linearis,* and with *Isotachis montana*, 14 Feb 2025, *G. Napp RD10* (CHR 698201); *loc. cit.*, on 45° bank with seepage, with *Oreobolus pectinatus, Empodisma minus* and *Donatia novae-zelandiae* above, mixed with *Rhacocarpus purpurascens* and *Riccardia crassa*, 14 Feb 2025, *G. Napp RD11* (CHR 698202); *loc. cit.*, on boggy seepage bank beneath *Chionochloa rubra* tussock with *Gleichenia alpina, Celmisia parva,* and *Empodisma minus,* plants at the base of *Oreobolus pectinatus* with *Riccardia crassa*, 14 Feb 2025, *G. Napp RD12* (CHR 698203); *loc. cit*., on an overhung bank wet from seepage from above, with *Celmisia parva, Drosera stenopetala*, *Isotachis montana,* and *Riccardia crassa*, 14 Feb 2025, *G. Napp RD14* (CHR 698204); *loc. cit*., 1330 m, 40.895°S 172.561°E, on soil in *Veronica odora / Empodisma minus + Celmisia petriei* shrubland, with *Centrolepis ciliata, Drosera spathulata, Isotachis montana, Riccardia crassa,* and *R. pusilla*, 10 Jan 2002, *D. Glenny 8104* (CHR 527434).

***Riccardia eriocaula*: New Zealand:** Southern North Island: Tararua Range, watercourse north of Field Hut, 2600 m, 1 Jan 1934, *V.D. Zotov*, male prostrate form (CHR 7473). Western Nelson: Fyfe River, 800 m, 41.543°S, 172.496°E, log over stream bed, under *Nothofagus fusca – N. menziesii* forest, 26 May 2013, *D Glenny 11804* (CHR 630582). Westland: Buller River gorge, Carter Creek, 160 m, 41.769°S, 172.153°E, 26 Feb 1999, *D. Glenny 7763*, female erect form (CHR 525257); Rotomanu, 130 m, 42.650°S, 171.533°E, rotten log under forest, 1 Jan 2015, *D. Glenny 12748*, female erect form (CHR 689605). Fiordland: Martins Bay, on *Blechnum colensoi* in forest near stream, 25 Jan 1955, *R.E. Hatcher 837*, prostrate form, juvenile (CHR 687953).

***Riccardia prehensilis*: Chile:** Petrohue, Feb 1945, *P. Moreau*, male, erect form (BA 10462, *n.v.*, CHR); Sierra Pelada, camino de Union a Haeicolla, tubera con *Dacrydium,* 5 May 1965, *G.H. de Menendez 2027*, male prostrate form (BA 13123, *n.v.*, CHR). **Argentina:** Neuquen, Brazo Blest, Arroyo Bravo, 8 Feb 1938, *Kuhnemann,* male erect form (BA 2161, *n.v.*, CHR).

Discussion

Membership of subgenus Arceoneura

Riccardia subgenus *Arceoneura* was circumscribed by Hässel (1972) for plants that were "dendroid, differentiated into axis and branches that are pinnate to 3-pinnate. In the mature state the epidermal cells are dead (lacking chloroplasts and oil-bodies). Internal cells with chloroplasts and oil-bodies. Capsule covered in grape-like cells. Seta with a central strand of 4 cells and a cortex of 12 cell rows. Gemmae present".

The type species of subgenus *Arceoneura* is *Riccardia prehensilis* and Brown and Braggins (1989) also assigned *R. eriocaula* to the subgenus. *Riccardia dendroides* is likely related to these two species. The three species share (1) prostrate, erect, or slightly pendant shoots; (2) erect shoots that are large for a *Riccardia*, typically 40–60 mm tall; (3) fertile branches never on the main axis, usually produced on the first pinnules of some pinnae; (4) shoots regularly 2–4-pinnate with the pinnae spaced on the main axis; (5) prostrate shoots often have geotropically positive branches and a paucity of rhizoids; (6) a brown-pigmented, thick-walled, cylindrical stele in the main axis and pinnae; (7) the main axis, pinnae, and pinnules have a wing that is several cells thick at the base tapering to a single marginal row of cells; (8) the epidermal layer of cells tend to be hyaline and some or all of the cells project to varying degrees; (9) fungal endophyte lacking; (10) mucilage papillae scattered, not in rows; and (11) dioicy. This set of eleven shared characters constitutes a revised circumscription of subgenus *Arceoneura*.

The three species of subgenus *Arceoneura* are compared in Table 1. There are pairs of similarities and differences among the three species as detailed below.

Erect shoots of *Riccardia dendroides* are predominantly 2-pinnate, while in *R. prehensilis* these are predominantly 4-pinnate (Fig. 12) and in *R. eriocaula* predominantly 3-pinnate (Fig. 13).

Table 1. Comparison of *Riccardia dendroides, R. eriocaula,* and *R. prehensilis.* Data from specimens examined with some ranges extended using data in Brown and Braggins (1989) for *R. eriocaula* and Hässel (1972) for *R. prehensilis*. Diagnostic differences are in bold.

	R. dendroides	*R. eriocaula*	*R. prehensilis*
Erect form arising from prostrate form	no	yes	unknown
Height of erect plants, mm	30–46	30–70	45–60(120)
Division of erect plants	**2(3) pinnate**	3(4) pinnate	3–4 pinnate
Spacing of pinnae in erect plants	distant	**contiguous**	distant
Length of prostrate plants, mm	10–35	15–24	10–30
Division of prostrate plants	3-pinnate	4-pinnate	2-pinnate
Positively geotropical branches on prostrate plants	forming from pinnules, not innovations	**absent**	abundant from innovations
Innovations from latent tips	**absent, new leading shoots develop from pinnules**	present	present
Pinnae per plant	18–33	15–19*	8–25
Pinnules per pinna	**up to 6**	6–15	9–17
Main axis width, µm	800–900	252–1005	480–600
Main axis depth	220–330 µm 12–15 cells	140–430 µm 15–17 cells	380–400 µm 18–19 cells
Main axis stele thickness, cell rows	3	3	3
Main axis, core cell wall thickness, µm	2–4	1–2	4–6
Main axis wing, cells wide	**4–6**	1	0–3
Pinna width, µm	420–500	360–380	400–420
Pinnae depth	180–240 µm 8–10 cells	100–340 µm 5–9 cells	180–250 µm 10–13 cells
Pinnule width at base, µm	270–400	150–200	370–430
Pinnule width at apex, µm	200–250	120–150	160–230

	R. dendroides	*R. eriocaula*	*R. prehensilis*
Pinnule depth, µm	100–170	90–100	103–120
cells	6–7 cells	4–6 cells	7–8 cells
Pinnule wing width	70–110 µm	30–50 µm	100–300 µm
	3–6 cells wide	2–3 cells wide	6–10 cells wide
Pinnule uni-stratose border, cells wide	0.5–1.0	1–1.5	1–2
Epidermal cells projecting	platelets over central strand on both surfaces	slime papillae and prorate cells on all epidermal surfaces	prorate cells on all epidermal surfaces, projecting cells over the stele
Mucilage papillae	**rare**	very abundant	present
Papilla persistence	**not persistent**	extremely persistent	persistent
Oil-bodies in epidermis	0–1	0–1(4)	absent
Oil-bodies in sub-epidermis	1–2	0–1(4)	1–3 per cell
Endophytic mycorrhizae	absent	absent	absent
Sexuality	dioicous	dioicous	dioicous
Position of sexual branches	**mid-plant**	developing near plant apex	mid- to upper plant
Grouping of male branches	solitary or pairs at base of pinna to middle of pinna	solitary or in opposed pairs throughout pinna	solitary or opposed pairs at base to mid-pinna
Pairs of antheridia per androecium	**2–6**	3–12	8–16
Male branch length, µm	500–1400	400–900	1100–1400
Orientation of male branch clathrate surface	**facing dorsally**	facing ventrally	facing ventrally
Male branch marginal wing	**insignificant, crenate**	serrate from projecting cells	ciliate, up to 6 uniseriate cells
Substrate	wet peat soil	rotting wood	rotting wood, tree trunks, clumps of moss on forest floor, heathland, peat in mires
Elevation (m)	**1310–1330**	1–860	1–800
Distribution	New Zealand	New Zealand, Australia	Patagonia; Gough, Tristan group, Marion and Crozet islands.

*an estimate because erect plants shoots have several leading apices.

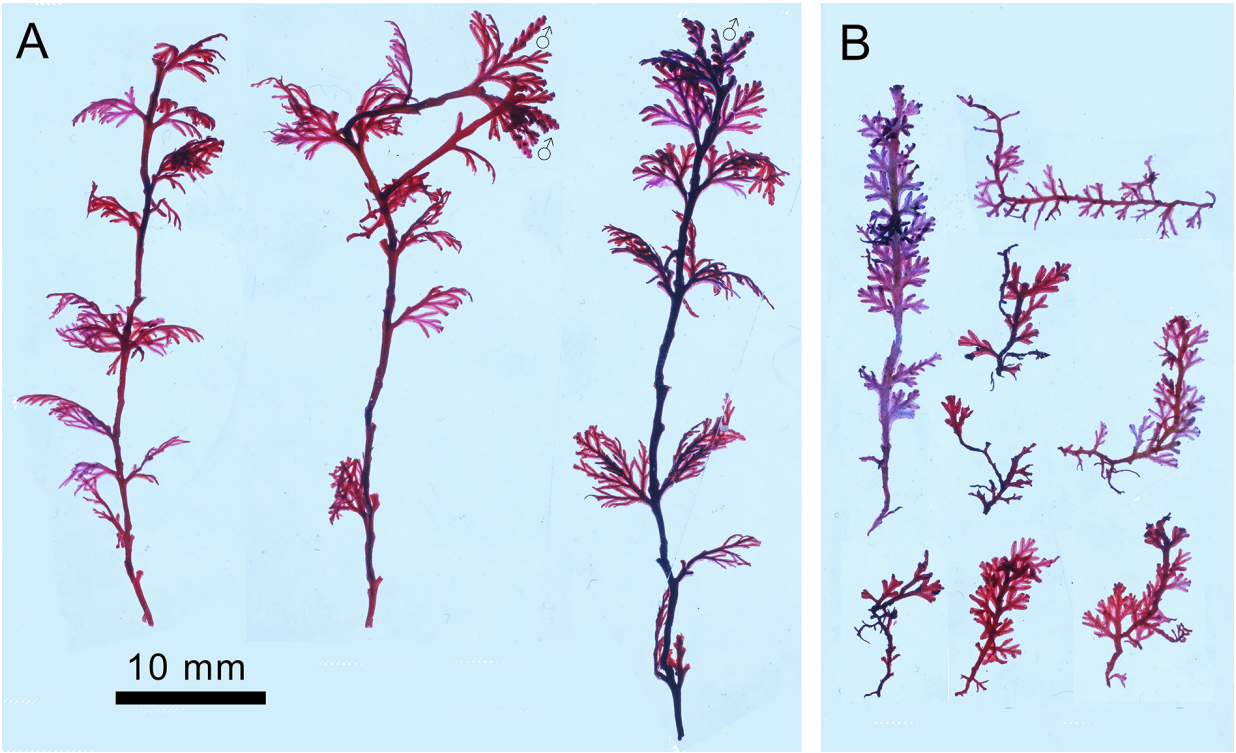

Fig. 12. *Riccardia prehensilis*, whole plants. A. Erect shoots. B. Prostrate shoots. In A, male symbol indicates male branches. 10 mm scale bar applies to A and B. Plants stained with safronin red. A from BA 10462 duplicate at CHR, B from BA 13123 duplicate at CHR.

The pinnules of *R. dendroides* and *R. prehensilis* are similar in width (270–430 µm wide) while those of *R. eriocaula* are narrower (150–200 µm wide) and often erode at the margins (Fig. 14B). The pinnules of *R. dendroides* can become narrowly terete and act as soil anchors for the whole plant.

Epidermal cells are merely prorate in *R. eriocaula* (Fig 14B) and *R. prehensilis* (Fig. 16A–C) but in *R. dendroides* they form partly detached platelets (Fig. 4A).

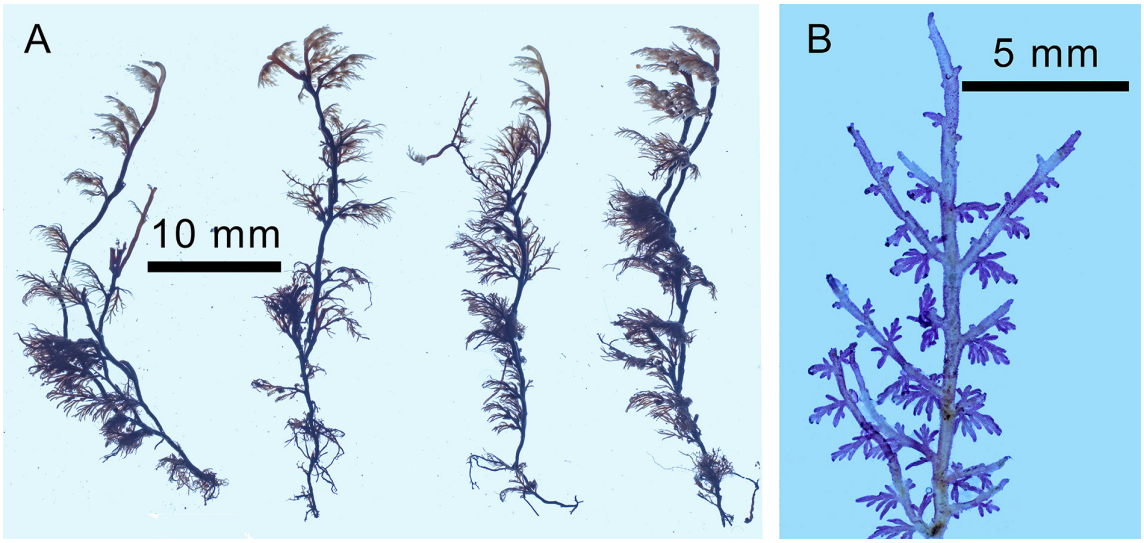

Fig. 13. *Riccardia eriocaula*, whole shoots. A. Erect shoots. B. Prostrate shoots. A from CHR 525257, B from CHR 687953. Plants in A stained with safronin red, B with ruthenium red.

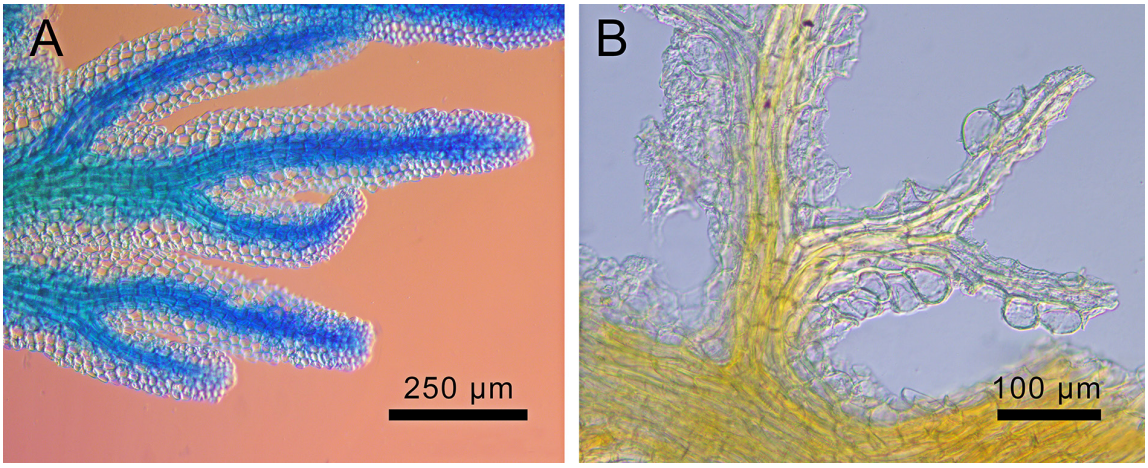

Fig. 14. *Riccardia eriocaula*, ventral view of pinnae and pinnules. A. Pinna showing 3-pinnate division and intact wings. B. Pinna showing pinnules with eroded uni-stratose wings. Both from CHR 689605. A stained with methylene blue.

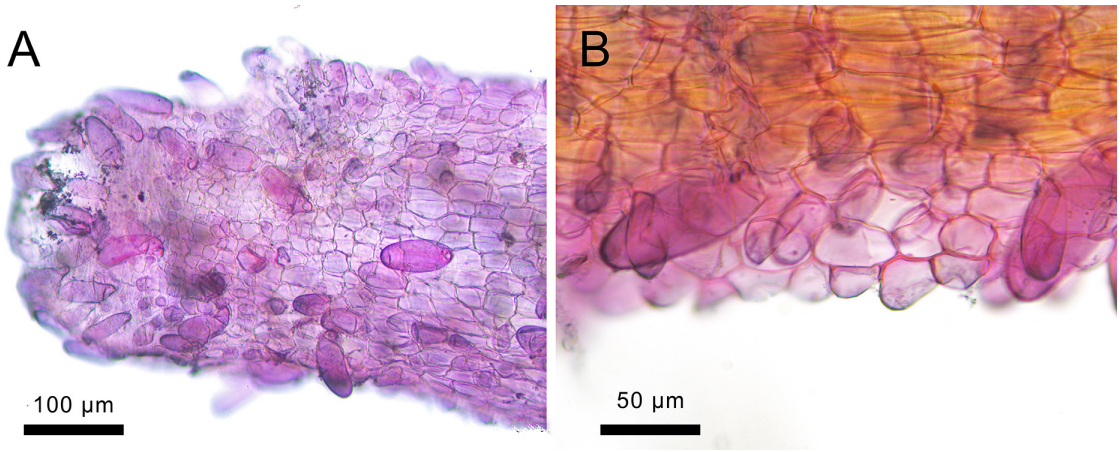

Fig. 15. *Riccardia eriocaula*, ventral view of pinnule showing persistent mucilage papillae. A. Apex of pinnule showing scattered and persistent ellipsoidal mucilage papillae that are attached by a very narrow base. B. Margin showing both mucilage papillae and projecting normal cells. Both from CHR 687953. Both bleached and stained with ruthenium red.

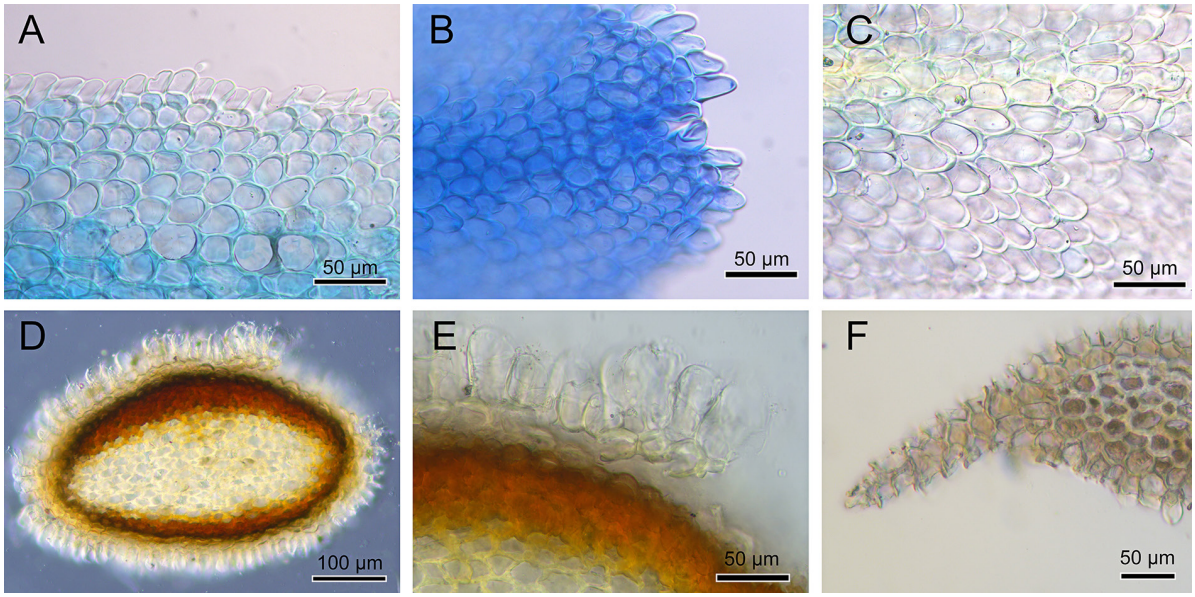

Fig. 16. *Riccardia prehensilis*. A. Epidermis at margin showing marginal row of hyaline cells and wing one cell thick. B. Pinnule apex showing marginal row of hyaline cells projecting beyond the apex. C. Epidermis over the stele showing prorate cells. D. Transverse section of main axis showing the pigmented stele. E. Transverse section of main axis showing epidermal layers peeling from the stele. F. Transverse section of pinna showing wing. All from BA 10462 duplicate at CHR. A and B bleached and stained with methylene blue, C–F bleached.

Hässel (1972) notes that in *R. prehensilis* the epidermal cells are "provided with an asymmetrical projection in the form of a papilla up to 40 µm long, directed obliquely toward the edge and forward; in adult plants they are dead, hyaline, and partially destroyed" [translated from Spanish]. In *R. eriocaula*, they are also forward-projecting but not collapsed (Fig. 16), while in *R. dendroides* the platelet cells are collapsed to varying degrees (Fig. 5, 6).

In *Riccardia dendroides* and *R. prehensilis* the innermost cells of the main axis are thick-walled 2–6 µm (Fig. 2, 3, 7B) while in *R. eriocaula* the walls are only 1–2 µm thick (Fig. 16A and B).

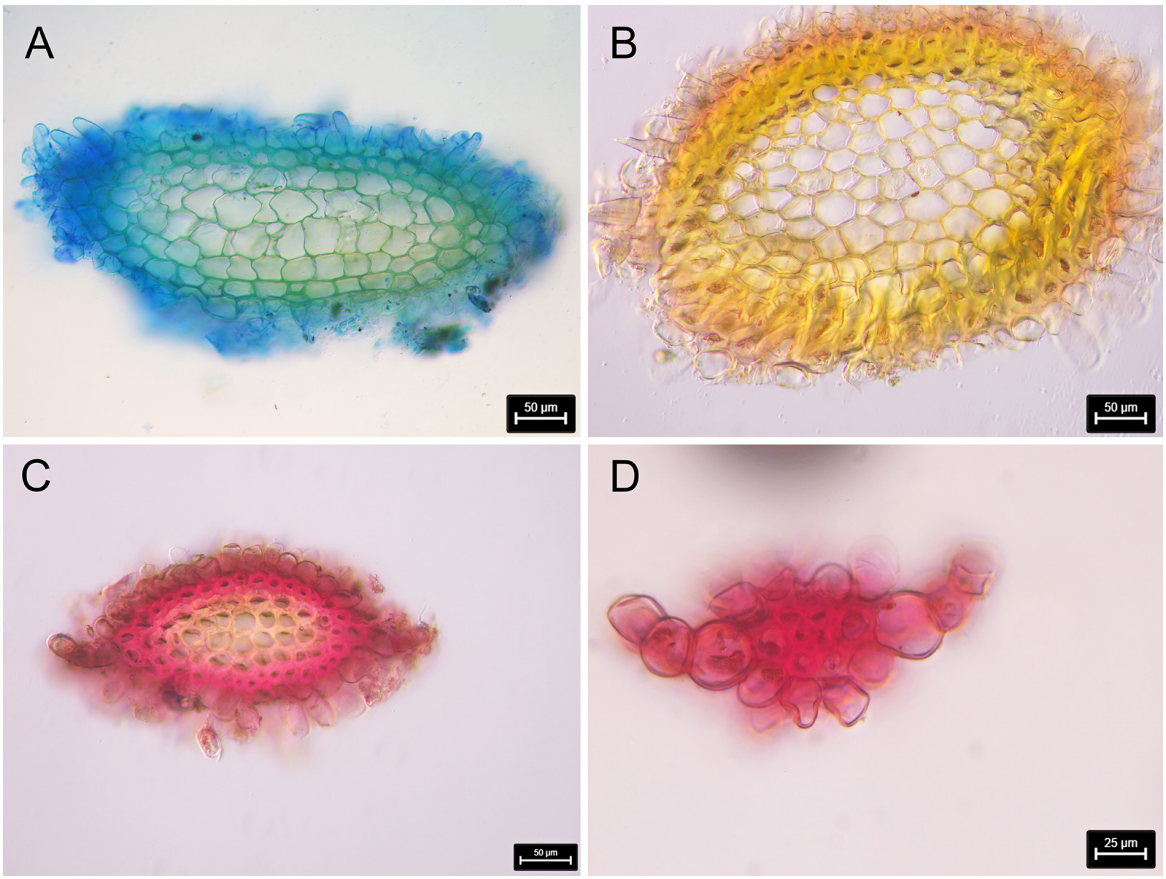

Fig. 17. *Riccardia eriocaula,* transverse sections of thallus. A. Main axis of prostrate shoot. B. Main axis of erect shoot. C. Pinna. D. Pinnule. A–C at the same scale but D at twice the scale of the others. A bleached and stained with methylene blue, B partly bleached but unstained, C and D bleached and stained with ruthenium red. A from CHR 7473, B–D from CHR 525257.

In all three species, sexual branches are at the position of the first pinnules of a pinna (Fig. 8A). In *Riccardia prehensilis* they tend to be on the distal-most pinnae whereas in *R. dendroides* and *R. eriocaula* they are usually on the largest pinnae at mid-plant. The male branch is coiled in *R. eriocaula* (Fig. 18) and angled in *R. prehensilis* (Fig. 19) so that the antheridial pits face ventrally, but in *R. dendroides* the branch faces dorsally (Fig. 8).

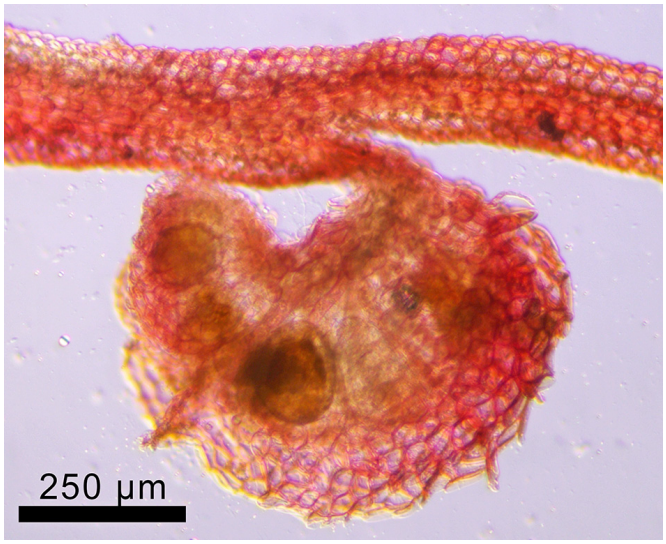

Fig. 18. *Riccardia eriocaula*, male branch in side view strongly curling ventrally from the pinna axis with a wing that has a toothed margin. Bleach and stained with ruthenium red. From CHR 525257.

Fig. 19. *Riccardia prehensilis*, two male branches in side view curling ventrally. From BA 10462 duplicate at CHR. Bleached and stained with ruthenium red.

A key to the three species of *Riccardia* subgenus *Arceoneura* is provided here.

Key to species of *Riccardia* subgenus *Arceoneura*

1. Plants predominantly bipinnate; epidermal cells on main axis collapsed and partly detached (forming "platelets"); male branches with clathrate surface facing dorsally; found on wet peat soils in open penalpine seepages above 1300 m ..... *Riccardia dendroides*

1: Plants 3–4 pinnate; epidermal cells projecting from the thallus surface, sometimes prorately, not forming platelets; male branches with clathrate surface facing ventrally 2

2. Mucilage papillae abundant and persistent on all surfaces and mixed with projecting cells; pinnule margins often eroded; main axis stele with thin-walled internal cells; found mainly on rotting wood in lowland to montane forests (to 860 m) in New Zealand and Australia ..... *Riccardia eriocaula*

2: Mucilage papillae present but less abundant; pinnule margins entire; main axis stele with thick-walled internal cells; found in forests, heathland, and wet soils up to 800 m in Patagonia and South Atlantic Islands ..... *Riccardia prehensilis*

Similar species

There are three other candidate species for membership of *Riccardia* subgenus *Arceoneura*. Hewson (1970) described *Riccardia demkarmana* Hewson from New Guinea on rotten logs at 2100–2800 m, which Müller (2023) believed to be a synonym of *R. hymenophylloides* Schiffn. of Sumatra and Java, on rotting logs at 2020–2500 m (Schiffner, 1898). Singh and Singh (2017) described *R. lachungensis* D.Singh & D.K.Singh from Sikkim at 3118 m. Most recently, Müller (2023) described *Riccardia meagheri* Frank Müll. from Myanmar at 2807–2839 m.

The shared features of these three species (*R. demkarmana, R. lachungensis*, and *R. meagheri*) that suggest they belong in subgenus *Arceoneura* are: (1) they are dioicous, (2) they are monopodial with an obvious main axis, (3) the main axis is stout, 500–1000 µm wide and 8–20 cells thick, (4) they are 2–4-pinnate with pinnae evenly spaced on the main axis, (5) they lack rhizoids, (6) they have a brown-pigmented stele of thick walled cells, (7) they have hyaline thin-walled epidermal and subepidermal cells, (8) the dorsal epidermal cells are mamillose or prorate (*R. meagheri*), (9) they have a multi-stratose wing, best developed in the upper frond and the pinnae, less so in the main axis and the pinnules, and (10) the shoot apices are not dissected. The gynoecium may be on the main axis in *R. meagheri*. *Riccardia hymenophylloides* may also belong to subg. *Arceoneura*, but it has not been considered in detail as part of this study.

Two other Patagonian species possess some features of subgenus *Arceoneura*. These two species were placed in their own subgenera by Hässel (1972) but have such strong similarities to subgenus *Arceoneura*, particularly the pigmented stele, that it seems likely that they belong there. *Riccardia fuegiensis* C.Massal. (subgenus *Lophoneura* Hässel) is pendulous to 80 mm long, dendroid and regularly 3-pinnate, has a pigmented stele, and the main axis and branches have a multi-stratose wing. The ventral surface has epidermal hairs of several uniseriate cells. The species is dioicous but fertile branches occur on the main axis as well as on the pinnae.

Riccardia spinulifera C.Massal. (subgenus *Spinella* (Schiffn. & Gottsche) Hässel) is prostrate, 3-pinnate, has a pigmented stele,

and has projecting epidermal cells as in *R. prehensilis* and *R. dendroides*. However, the main axis and branches are unwinged, the species is monoicous and fertile branches are often on the main axis.

Heteroblasty

Heteroblasty is a feature of some plant species where there is an abrupt change of form in the plants, usually between juvenile and adult plants (Goebel 1889; Zotz et al. 2011). It is observed in most major plant lineages but is not often reported in bryophytes. Mishler and de Luna (1991) discuss heteroblastic leaf series in some mosses (see also Crandall-Stotler and Bartholomew-Began 2017). By this they mean a change in form of leaves produced early on, to leaves produced later, on the same axis.

The change in form in *Riccardia eriocaula* may qualify as heteroblasty as there is an abrupt change from prostrate to erect form with accompanying changes from dense to sparse pinnae, a decrease in the degree of branching from 4-pinnate to 3-pinnate, and an abundance to a paucity of geotropically positive branches and rhizoids. The cylindrical stele that is 2 or 3 layers thick in the erect form of *R. eriocaula* is only one layer thick in the prostrate form (Fig. 15). Prostrate plants are not fertile.

It is uncertain whether heteroblasty is a feature of *Riccardia dendroides*. Five of the six collections are of loosely prostrate plants supported by other bryophytes and vascular plants (Fig. 1B). Only one, the type, is erect (Fig. 1A). Erect and prostrate plants can be fertile and the erect form does not arise from prostrate plants as seen in *R. eriocaula*. Prostrate and erect plants have the same degree of pinnateness, pinnule width is the same (270–410 µm wide), and the main axis stele is 3 cells thick in all plants.

However, there are differences: in prostrate plants of *Riccardia dendroides* new axes often form by extension of the main axis pinnae (not seen in the erect specimen), geotropically positive terete branches form from pinnules (not seen in the erect specimen), and prostrate plants are shorter (10–25 mm long, not 30–46 mm long). Prostrate plants have shorter internodes, fewer pairs of pinnae, and more pinnules per pinna.

Likewise, in *Riccardia prehensilis*, it is uncertain whether the erect and prostrate forms described by Hässel (1972) represent heteroblasty. Hässel does not state whether prostrate forms can be fertile, but BA 12123 appears to be the prostrate form and is fertile. In making the prostrate *R. savatieri* (Steph.) A.Evans a new synonym of *R. prehensilis*, Hässel suggests that prostrate and erect forms are a response to environment:

"The concept "*R. savatieri*" corresponds to plants that develop on substrates devoid of other species, or among small-sized plants and in particular, where other examples of the same species are not represented. When their continued growth reduces the available space, the plants separate from the substrate. This results in the erect aspect ..." [translated from Spanish].

Acknowledgements

I thank Greg Napp (Department of Conservation) for collecting fresh material of *Riccardia dendroides* at Amphitheatre Creek. I thank Lara Shepherd for sequencing *Riccardia dendroides* and comparing it with GenBank sequences of *R. prehensilis* and *R. eriocaula*. I also thank Stella Fish for reviewing this paper prior to submission. This work was supported by the Ministry of Business, Innovation and Employment's Strategic Science Investment Fund.

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

Crandall-Stotler BJ, Bartholomew-Began SE (2007) Morphology of mosses (phylum Bryophyta). Flora of North America volume 27. URL accessed 2 Sept 2024.

Evans AW (1921) The genus *Riccardia* in Chile. *Transactions of the Connecticut Academy of Arts and Sciences* 25: 93–209. URL

Glenny D (2024a) *Riccardia dimorpha* sp. nov. (Hepaticophyta, Aneuraceae) from Western Nelson, New Zealand, exhibiting sexually determined morphological dimorphism, an overlooked feature of some liverworts. *Telopea* 27: 73–83. DOI

Glenny D (2024b) *Riccardia sphagnicola* sp. nov. (Marchantiophyta, Aneuraceae), a filamentous penalpine bog species of the New Zealand mountains, compared to six similar New Zealand species. *Telopea* 29: 127–147. DOI

Goebel K (1889) Über die jugendzustände der pflanzen. *Flora* 72: 1–44. URL

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 Naturalis "Bernadino Rivadavia", Botànica* 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

Mishler BD, de Luna E (1991) The use of ontogenetic data in phylogenetic analyses of mosses. *Advances in Bryology* 4: 121–167.

Müller, F. (2023) A new *Riccardia* (Aneuraceae, Marchantiophyta) from Myanmar. *Bryophyte Diversity and Evolution* 46: 51–55. DOI

Rabeau L, Gradstein SR, Dubuisson J-Y, Nebel M, Quandt D, Reeb C (2017) New insights into the phylogeny and relationships within the worldwide genus *Riccardia* (Aneuraceae, Marchantiophytina). *European Journal of Taxonomy* 273: 1–26. DOI

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

Schiffner V (1898) Expositio Plantarum in itinere suo indico annis 1893/94 suscepto collectarum speciminibusque exsiccatis distriburarum, adjectis descriptionibus novarum. Series prima: Hepaticarum partem continens. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-naturwissenschaftliche Klasse* 67: 153–203. URL

Singh D, Singh, DK (2017) Two new species of *Riccardia* (Aneuraceae, Marchantiophyta) from Eastern Himalaya, India with notes on the genus in Sikkim. *Taiwania* 62: 33–42. DOI

Townsend AJ, de Lange PJ, Duffy CAJ, Miskelly CM, Molloy J, Norton DA (2008) *New Zealand Threat Classification System manual*. Wellington, Department of Conservation. PDF

Váňa J, Engel JJ (2013) The liverworts and hornworts of the Tristan da Cunha group. *Memoirs of the New York Botanical Garden* 105: 1–138.

Zotz G, Wilhelm K, Becker A (2011) Heteroblasty–a review. *Botanical Review* 77: 109–151. DOI