

## ***Riccardia dimorpha* sp. nov. (Hepaticophyta, Aneuraceae) from Western Nelson, New Zealand, exhibiting sexually determined morphological dimorphism, an overlooked feature of some liverworts**

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### Abstract

*Riccardia dimorpha* is described from 24 collections made in New Zealand between 1984 and 2020 from Western Nelson, Westland, and Fiordland ecological provinces in the South Island, and from Stewart Island / Rakiura. These specimens were misidentified as *R. browniae* [*R. pusilla* (Steph.) E.A.Br., nom. illeg.], *R. asperulata* R.M.Schust., *R. multivittata* E.A.Br., and *R. perspicua* E.A.Br., or identified only to genus. *Riccardia dimorpha* belongs to the *Riccardia* section *Alcicornia* Hässel and is characterised by having strong striations on the epidermis, a subterete thallus, a monopodial growth form, endomycorrhizae absent from the ventral epidermis, and epidermal cells are the same size as internal cells. Specimens were collected in fire-induced *Leptospermum scoparium* shrublands, on peat soils at lowland to montane elevations. *Riccardia dimorpha* is sexually dimorphic in plant size and number of branches (meristematic tip number), and male and female plants differ to the degree that the sexuality of a plant can be determined without finding sexual branches on a plant. Such dimorphism is rarely reported in liverworts although is common in mosses.

**Keywords:** *Aneuraceae*, *Riccardia*, New Zealand, new species, endemic, liverwort, sexual dimorphism

### Introduction

The genus *Riccardia* was revised by Hewson (1970) for Australia and by Brown and Braggins (1989) for New Zealand. No new species for either country has been described since those treatments were published. The publication in Brown and Braggins (1989) of two new species known at the time only from the Glasgow Range, Western Nelson (*Riccardia pennata* E.A.Brown and *R. intercellula* E.A.Brown) signalled that further undiscovered species were likely in Western Nelson. Of 30 species recognised in New Zealand by Brown and Braggins (1989), 19 are endemic (63%). The non-endemic species are mostly shared with Australia (10 species). As currently circumscribed, *Riccardia crassa* is also widespread in Asia. *Riccardia alcicornis* is present in South America, Australia, and New Zealand, and *R. alba* is present in Fiji, Australia, and New Zealand.

While determining *Riccardia* specimens identified only to genus and checking determinations of other species for the liverwort flora project (Engel and Glenny 2008, 2019a,b) it was noticed that most specimens identified as *R. browniae* A.Hagborg & L.Söderstr. (Hagborg and Söderström, 2022) did not fit that species as described by Brown and Braggins (1989, as *R. pusilla* (Steph.) E.A.Br., nom. illeg.). These anomalous

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specimens did not fit any other New Zealand species treated by them, and are described below as *Riccardia dimorpha*. *Riccardia* collections at CHR were searched to find more overlooked material. Specimens of *R. alcicornis*, *R. asperulata*, *R. crassa*, *R. multicorpora*, *R. perspicua*, *R. browniae*, *Acromastigum anisostomum*, and *Telaranea inaequalis* R.M.Schust. from *Leptospermum* shrublands in the western South Island and Stewart Island / Rakiura were examined, and many more specimens were found in this way. Field trips were made in 2020 to two localities to collect fresh plants.

Sexually determined dimorphism, also termed dimorphism in secondary sexual characteristics (Lloyd and Webb 1977), is well studied in dioecious flowering plants (Delph 1999; Barrett and Hough 2013) but rarely commented on in the liverwort literature. It is well known in the mosses with the phenomenon of dwarf males: one third of dioicous pleurocarpous mosses may have dwarf males (Hedenas and Bisang 2011). However, in the liverworts it is only reported in a few species. *Sphaerocarpos* has male vegetative parts very reduced in size relative to the female. Schuster (1992: 811) describes *S. texanus* Aust. males as 10–20% the size of females. *Cryptothallus mirabilis* Malmb. also has dwarfed male plants (Schuster 1992: 574).

Furuki (1991) reported, “The dioicous species [of *Riccardia*] usually show sexual dimorphism: the male thalli are smaller and less branched than those of the female.” Furuki (1991) in his morphological notes also mentioned sexual dimorphism as present in *R. pusilla* Grolle and *R. marginata* var. *pacifica* Furuki, with male plants of those two taxa less than 2 mm long. However, Furuki did not incorporate the dimorphism in size into his descriptions of the species. Brown and Braggins (1989) say of *Riccardia asperulata* R.M.Schust. “There may be a tendency for male thalli to be smaller than the female ones but very few mixed populations were examined”. Sexually determined dimorphism is not commented on by Hewson (1970) or Hässel de Menendez (1972) however *R. longioleata* Hässel is illustrated as dimorphic with two female plants illustrated as being shorter and more richly branched than a single male plant (Hässel de Menendez 1972: 32, Fig. 6a–c). This dimorphism is of the same type as that observed in *R. dimorpha*. Because of conflicting accounts of sexual dimorphism in *Riccardia*, it is quantified here for *R. dimorpha*.

## 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, stained with 0.2% methylene blue for a few seconds, then rinsed again in water (the ‘bleach and blue’ method of Rico 2011; cited in Reeb and Bardat 2014). This method aims to show surface features such as surface texturing, hyaline papillae, and rhizoids. Reeb and Bardat (2014) 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 photographs were taken with a Leica DMLB400, usually using differential interference contrast. SEM photography was done using a desktop Hitachi TM3050Plus microscope, after sputter-coating the dry specimen with gold.

Terminology follows Brown and Braggins (1989) for most parts, such as stolons and slime papillae. However, the parallel thickenings on the epidermal surface of species such as *R. crassa* and *R. perspicua* are usually referred to as striations (e.g. Hässel de Menendez 1972; Brown and Braggins 1989). Striations are literally scratches (i.e. indentations in the surface) rather than ridges, as occurs in *R. dimorpha*, *R. crassa*, and *R. perspicua*. Furuki (1991) uses the better term ‘striately verrucose’ for the ornamentation of *R. crassa*, and this terminology is used here.

Sexual dimorphism was quantified using characters that are visibly different in male and female plants: plant length from the base of the oldest living tissue of the main axis to the shoot apex furthest from the base, number of meristematic tips per plant, and main axis width measured between pinnae at about halfway between base and apex. In the 32 samples, 11 female plants and 21 male plants were measured. A balanced two-way ANOVA test was performed on measurements from 11 female and a randomly chosen subset of 11 male plants.

## Results

Of 23 collections of *Riccardia dimorpha*, 15 were found to be female, six male, and two had male and female plants mixed.

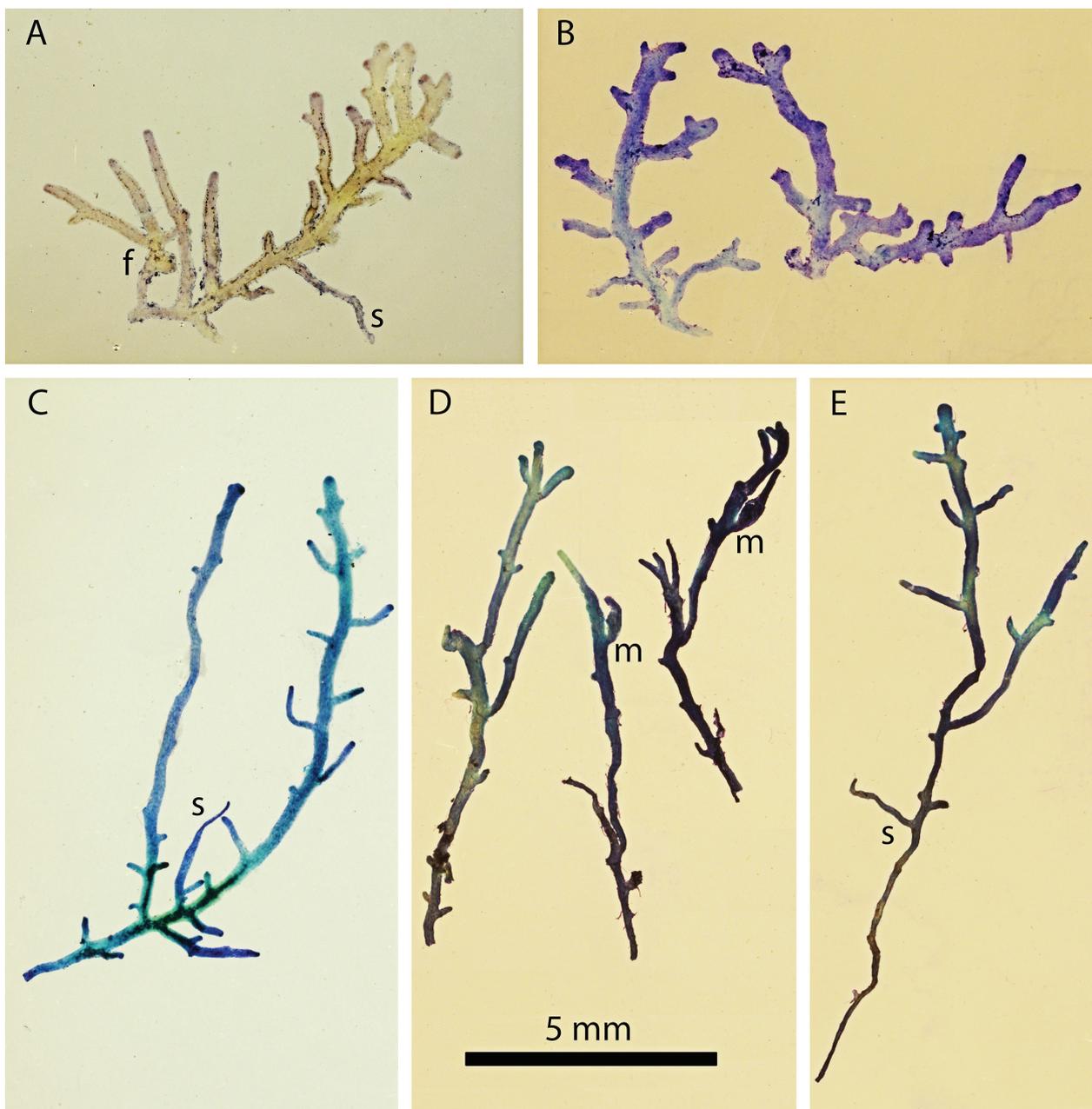
Mean length of male plants was 10.5 mm (range 6–18 mm, n=21) and mean length of female plants was 7.7 mm (range 4.5–13 mm, n=11). Mean number of meristematic tips per plant in male plants was 11.2 (range 4–24, n=21) and mean number of tips per female plant was 25.5 (range 12–42, n=11). Main axis width did not differ. A two-way ANOVA rejected the null hypothesis that male and female plants do not differ in plant length and number of tips per plant do not differ ( $p=0.000147$  and  $p=0.000103$  respectively).

The dark brown cellular inclusions mentioned in the description are not normal oil-bodies as they are relatively unaffected by bleach and do not decay in dried specimens. However, they have a similar granular structure to oil-bodies (Fig. 5c). The inclusions are not stained by lactophenol cotton blue as would be expected for fungal pelotons. Also, they have an unusual intramarginal position that is not usually seen in endomycorrhizae or oil-bodies. They are not mentioned by Hässel de Menendez (1972) or Brown and Braggins (1989) and I have not seen them in other New Zealand *Riccardia* specimens. The inclusions were found in one male and one female collection of the 23 collections examined and were present in all plants in those two collections.

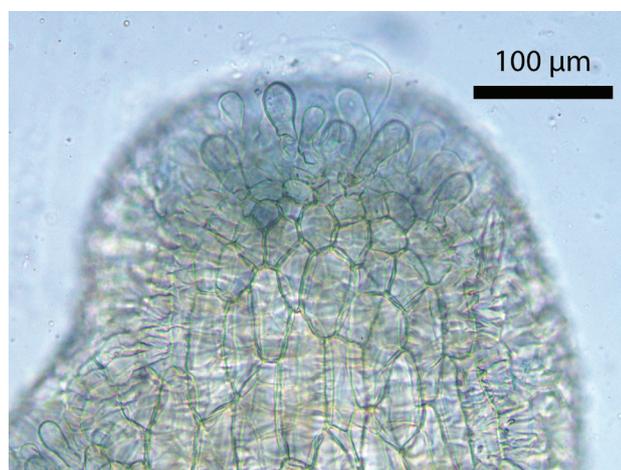
## Taxonomy

***Riccardia dimorpha* Glenny, sp. nov.**

Type: New Zealand: Western Nelson, Stockton Plateau, T35 Stream, 580 m, 171.906°E, 41.661°S, *Chionochoa juncea* – *Leptospermum scoparium* / *Empodisma minus* – *Gleichenia microphylla* low scrub in marsh with open soil areas and shallow temporary pools, with *Kurzia hippuroides*, *Pallavicinia rubristipa*, and *Riccardia crassa*, male plants, brown inclusions present, 28 Oct 2008, D. Glenny 10326 (holotype: CHR 603443; isotype: F).

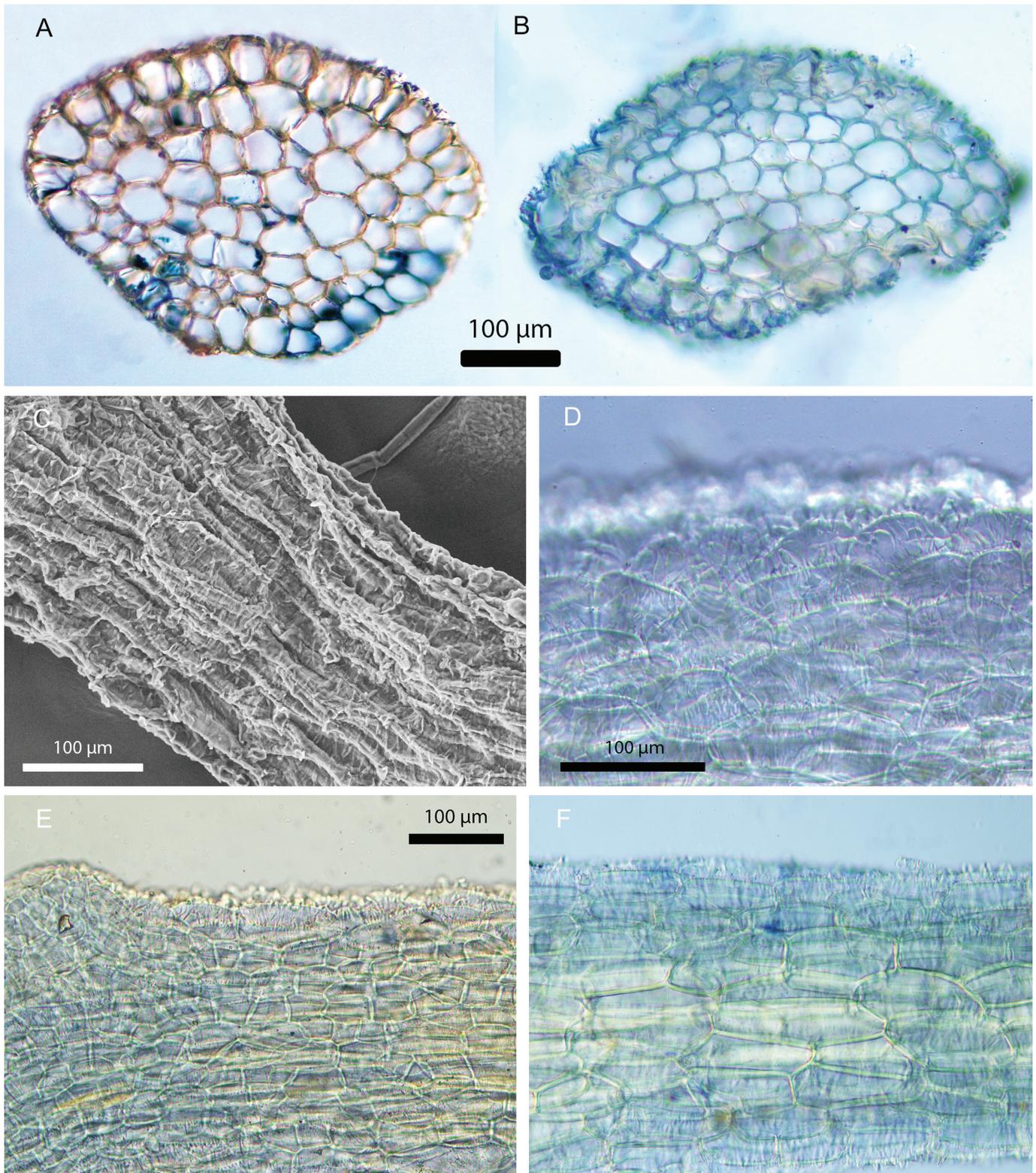


**Fig. 1.** *Riccardia dimorpha*, whole male and female plants. Female plants: A, B. Male plants: C, D, E. A photographed from CHR 668220, B from CHR 638186, C from CHR 603443, D and E from CHR 518930. 5 mm scale bar applies to all. f = female branch, m = male branch, s = stolon.



**Fig. 2.** *Riccardia dimorpha*, ventral view of shoot apex showing clavate slime papillae, the apical meristem cell on the ventral side of the branch. A mucus cap produced by the papillae is just visible. Photographed from CHR 638186.

Plants sexually dimorphic, male plants 6–18 mm long, female plants 4.5–13 mm long (Fig. 1). Meristematic tips per plant (i.e. branch tips) in male plants 4–24 per plant, in female plants 12–42 per plant, plants 1.5–4.5 mm wide including branches, loosely prostrate, green throughout, with a distinct main axis and side branches. Branching alternate to subopposite, with simple pinnae up to 2 mm long, pinnae sparsely branching or showing continued development to 9 mm long. Thallus and apex branches rounded at apex, without an apical sinus. Mucilage papillae in a transverse row at the apex or slightly ventral to the apex and projecting apically, usually not persisting on ventral surface but sometimes persisting to about halfway to the base of the plant and scattered over the whole ventral surface, never in 2 rows, absent from the dorsal surface; 33–45(60) µm long, 13–28 µm diameter at widest, clavate and narrowed to a 10 µm diameter base attachment, outer surface smooth, walls thin to 4 µm thick at apex (Fig. 2). Rhizoids not seen. Stolons occasional (1 or 2 per plant), sometimes developing from normal branches



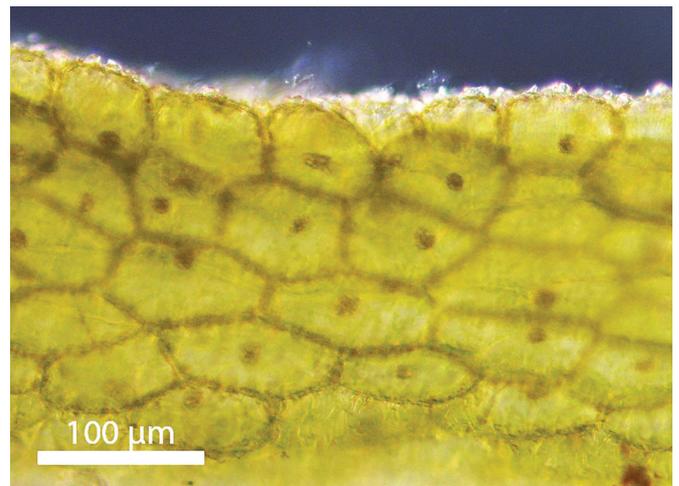
**Fig. 3.** *Riccardia dimorpha*. A, B. Transverse sections of main axis from female and male plants showing a lack of dimorphism in the main axis dimensions. A. Female, photographed from CHR 606646. B. Male, photographed from CHR 603443. C, D. Epidermis ornamentation. C. Dorsal epidermis, SEM view showing striations. D. Ventral epidermis, light microscope view. Both photographed from CHR 526319. E, F. Epidermal cells. E. Dorsal epidermis. F. Ventral epidermis and margin showing verrucose thickenings in side view. Both photographed from CHR 603443. 100 µm scale bar applies to E and F.

and equally frequent at any position on the main axis (Fig. 1). Gemmae absent. Main axis 280–500 µm wide between pinnae, 180–350 µm and (5)7–10 cells thick, subterete in transverse section, width to depth ratio 1.4–1.8:1, unwinged (Fig. 3A,B). Dorsal epidermal cells not smaller in transverse sectional view

than internal cells. Ventral epidermal cells smaller in transverse sectional view than internal cells (typically 30–32 µm deep, not 37–39 µm deep as for internal cells). Epidermal cells sometimes mamillate 0.7 mm below the thallus apex (of main axis or branch) due to bulging of the outer cell wall. Epidermal surfaces with

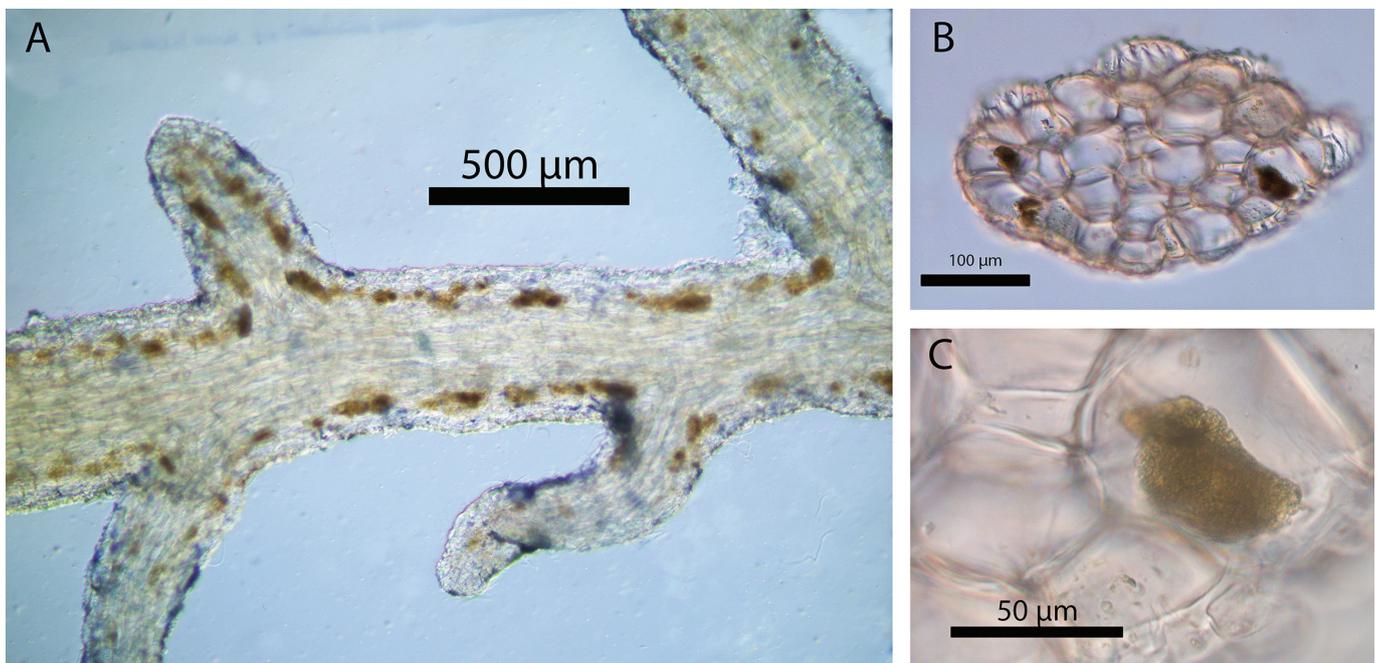
transverse thickenings (striately verrucose) on both dorsal and ventral surfaces (Fig. 3B,C), the outer epidermal wall 4  $\mu\text{m}$  thick, the thickenings 6  $\mu\text{m}$  thick. All thallus cells chlorophyllose. Dorsal epidermal cells quadrate to elongated-rhomboid (2.2–7.0:1), 43–105  $\times$  (28)35–50  $\mu\text{m}$ , 40–50  $\mu\text{m}$  deep, the vertical cell walls 5  $\mu\text{m}$  thick (Fig. 3E). In transverse section view, dorsal epidermal cells rectangular, taller than wide. Ventral epidermal cells hexagonal-elongate with acute cell ends (length to width ratio 2.0–4.0:1), 75–160  $\times$  33–50  $\mu\text{m}$ , 28–45  $\mu\text{m}$  deep, the vertical cell walls near the thallus apices 2  $\mu\text{m}$  thick but in older parts of the thallus 5  $\mu\text{m}$  thick (Fig. 3F). In transverse section view ventral epidermal cells are isodiametric. In transverse section, internal rows of cells are equal in size to epidermal cells. Dorsal subepidermal cells 175–200  $\mu\text{m}$  long, 52–63  $\mu\text{m}$  wide, 40–48  $\mu\text{m}$  deep. Cell walls in transverse sectional view all c. 4  $\mu\text{m}$  thick and slightly thickened at the corners into concave-sided trigones. Oil-bodies invariably one in each dorsal epidermal cell, colourless, coarsely granular (botryoidal), mostly spherical (75%) and 8–16  $\mu\text{m}$  diameter, less often ellipsoidal and 10–30  $\times$  7–10  $\mu\text{m}$  (Fig. 4). Endophytic mycorrhizae absent. Brown, granular, spherical inclusions 9–14  $\mu\text{m}$  diameter occasionally present in 2 discontinuous rows 1–2 cells from the thallus margin and midway between dorsal and ventral epidermis, the inclusions equally present in main axis and branches (Fig. 5). Dioicous. Male and female plants usually separate but occasionally mixed. Male branches originating from main axis or from short side-branches facing obliquely dorsally, 800–1500  $\mu\text{m}$  long, the fertile part 700–1400  $\mu\text{m}$  long, 400  $\mu\text{m}$  wide, a marginal wing present, the dorsal surface between the two wings narrow, sometimes with a sterile extension of the branch beyond the antheridia (Fig. 6A). Antheridia 3–8 per male branch. Antheridia 120  $\mu\text{m}$  diameter, on a uniseriate stalk. Female branches solitary, on pinnae in the distal half of the plant, on a very short branch and facing dorsally, sessile, 500  $\mu\text{m}$  long, with 2–8 archegonia in pairs, the gynoecium surrounded on its dorsal

surface with many unbranched scales c. 400  $\mu\text{m}$  and 8 cells long, 3 cells wide (Fig. 6C). Calyptra 1000  $\mu\text{m}$  long, 320  $\mu\text{m}$  diameter, cylindrical, the calyptra surface covered in projections that have a striate-verrucose surface, umbo absent. Sporophyte not seen.

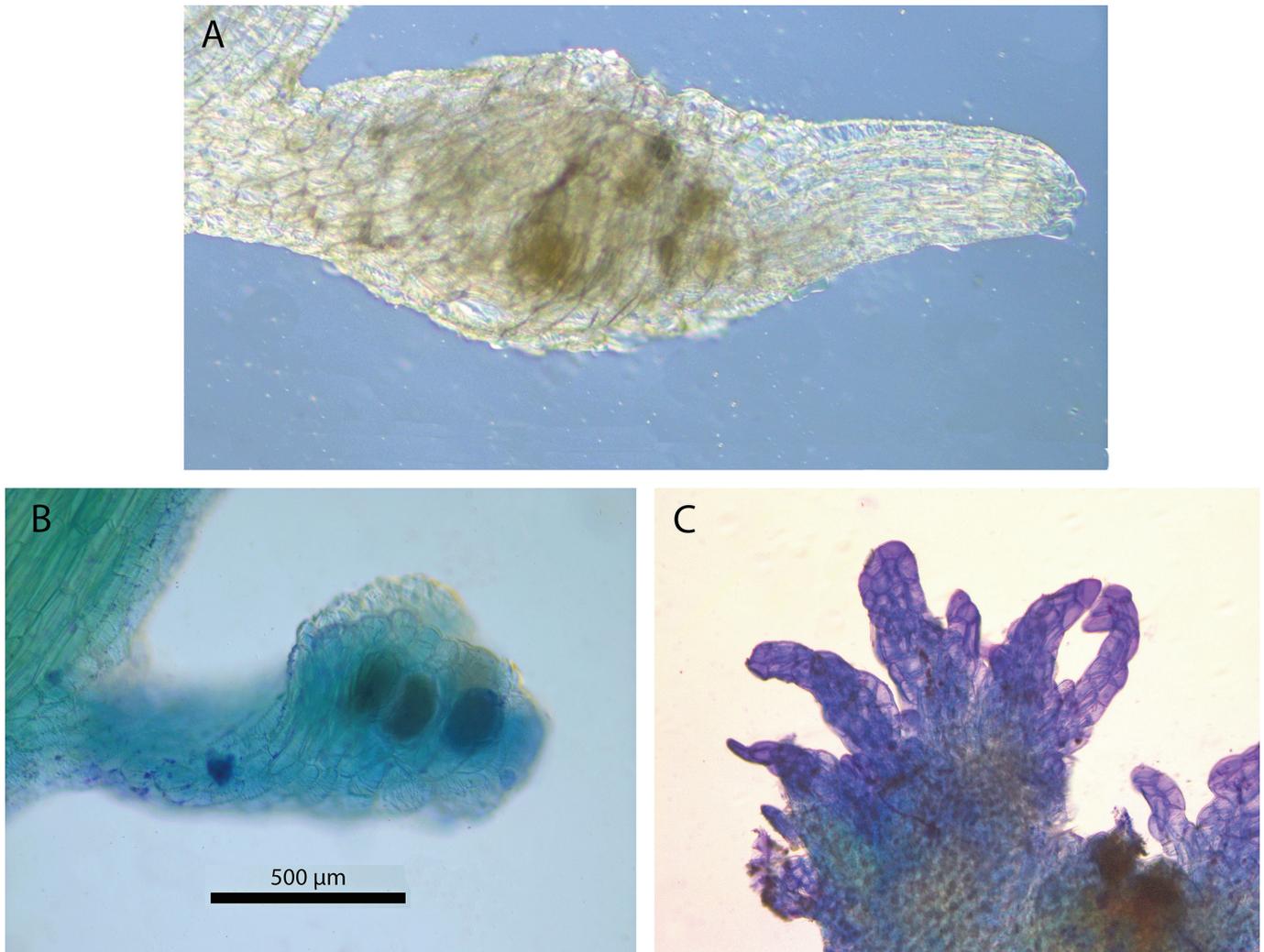


**Fig. 4.** *Riccardia dimorpha*, oil-body, one per cell in dorsal epidermis. Surface verrucae obscure the oil-bodies. Photographed from CHR 668241.

**Diagnosis:** *Riccardia dimorpha* is similar to *R. alcicornis* in that the main axis is subterete, 5–10 cells deep, with dark- and thick-walled cells in several internal layers of old parts of the main axis, and it has a pinnate to bipinnate branching style. Male branches are clam-like in being bilaterally compressed with two wings facing dorsally, and the dorsal branch surface is narrow. It differs from *R. alcicornis* in being dioicous and in having strong transverse striations on the epidermal cell walls, in male and female plants differing in plant length and richness of branching, with female plants being shorter and with more branches per plant than male plants.



**Fig. 5.** *Riccardia dimorpha*, brown cellular inclusions. A. Dorsal view of main axis and branches showing discontinuous lines of inclusions. B. Cross-section of a thallus branch showing three brown cellular inclusions. C. A single cellular inclusion. A–C photographed from CHR 668200.



**Fig. 6.** *Riccardia dimorpha*. A, B. Male branches. C. Female branch. A photographed from CHR 603443, B from CHR 518930, C from CHR 409780. Scale bar applies to A–C.

**Distribution:** Endemic to New Zealand; South Island (35–700 m), Stewart Island / Rakiura (215–305 m). Known from Western Nelson (Stockton Plateau, Mt Frederick, Mt William Range, Te Kuha Ridge, terrace east of Nine Mile Road east of Westport, Tōtara River, Tiropahi River), Westland (Cascade Plateau), Fiordland (Mt Burns), and Stewart Island / Rakiura (Deceit Peaks, Magog).

**Ecology:** The species is nearly always found in low-stature *Leptospermum scoparium* shrublands and openings in *Leptospermum scoparium* scrub, where the vascular species between the shrubs are *Chionochloa juncea*, *Empodisma minus*, *Gleichenia microcarpa*, *G. dicarpa*, *Gahnia rigida*, and *Machaerina teretifolia*. This vegetation is known in New Zealand as pakihi (Mew 1983) and is on flat or low-angled terrain. Soils are gleyed podzols with impeded drainage, resulting in the sites being shallowly inundated by frequent rain. The plants are usually on humic soil formed from the *Leptospermum* and peat-forming monocots. Pakihi results from burning in historical times of tall podocarp forests in which *Dacrydium cupressinum* was the main tree species. *Leptospermum scoparium* scrub develops if the vegetation is not repeatedly burnt, but deliberate burning is commonly done by deer and pig hunters to maintain open

habitat. Many of the plant species of pakihi, both vascular and non-vascular, are fire-adapted. Pakihi in southern Stewart Island / Rakiura (Magog and Deceit Peaks) is very similar in composition and fire history to pakihi in Western Nelson Ecological Province.

One collection, from Te Kuha Ridge, is from *Lepidothamnus intermedius* – *Fuscospora cliffortioides* forest 8 m high. This may have been the common habitat of the species on the Stockton and Denniston plateaux, Mt William, and the Orikaka River before forests were burnt in the historical period.

At Bird's Ferry, Tōtara River, *Riccardia dimorpha* occurs on an old, raised beach surface in *Leptospermum scoparium* / *Machaerina teretifolia* – *Gleichenia dicarpa* fern rushland that has nearby intact forest of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Metrosideros robusta*, *Fuscospora cliffortioides*, and *Lophozonia menziesii*. At this pakihi, *Goebelobryum vermiculare*, *Lethocolea squamata*, and *Riccardia crassa* are accompanying species (Fig 7).



**Fig. 7.** *Riccardia dimorpha*, habitat, growing in bryophyte 'stalactites'. The vascular plant present growing on the stalactites is *Forstera mackayi* and other vascular plant species growing above the stalactites may also have roots in the stalactites. Stockton Plateau. CHR 606646.

At Stockton Plateau and Mt Frederick, the species was interwoven through other small thread-like bryophytes such as *Acromastigum anisostomum*, *Telaranea inaequalis*, and *Zoopsis* in hanging bryophyte 'stalactites', which are kept constantly moist by water seepage from sloping sandstone pavements above the overhangs. These stalactites of bryophytes also contain roots of flowering plants such as *Forstera mackayi*, and are a distinctive feature of the incised streams of the plateau (Fig. 8).

Borland Bog in eastern Fiordland is a raised mire in which *Leptospermum scoparium*, *Empodisma minus*, and *Sphagnum cristatum* are the dominant species (Mark et al. 1979). The bog does not appear to result from historical burning of forest, but most of the *Leptospermum* has been burnt repeatedly (Mark et al. 1979).

**Etymology:** The epithet 'dimorpha' refers to the difference between male and female plants in secondary sexual characteristics, namely plant length and number of meristems (shoot tips) per plant. The difference among sexes is such that, with familiarity, it is often possible to correctly predict the sex of an individual before reproductive structures are observed.

**Conservation status:** The species was neither formally nor informally recognised at the time of the most recent threatened

plant listing (de Lange et al. 2020). A status of 'not threatened' is recommended as the species is widely distributed on the western side of the South Island and on Stewart Island / Rakiura and is commonly found in *Riccardia* specimens from pakihi.

**Specimens examined: NEW ZEALAND: Western Nelson:** Mangatini Stream, 540 m, 171.893°E, 41.653°S, on 4 m-high rock wall at back of overhang kept wet by seepage, associated with *Ceramanus tuberifera*, *Kurzia hippuroides*, *Lepidozia spinosissima*, *Leucobryum javense*, *Neolepidozia patentissima*, *Psiloclada clandestina*, *Rhizogonium pennatum*, *Riccardia cochleata*, *Telaranea inaequalis*, and *Tetracymbaliella decipiens*, female, 13 Sept 2005, D. Glenny 9611 (CHR 573608); Mangatini Stream, 330 m, 171.918°E, 41.628°S, on soil over rock overhang with hanging bryophyte stalactites, on stream bank, *Metrosideros umbellata* – *Lepidothamnus intermedius* – *Dacrydium cupressinum* / *Phormium tenax* / *Gahnia rigida* – *Empodisma minus* – *Gleichenia microphylla* scrub 5 m tall, with *Acromastigum anisostomum*, *Kurzia hippuroides*, *Psiloclada clandestina*, and *Telaranea inaequalis*, male, 15 Sept 2005, D. Glenny 9662 (CHR 580023); southern slopes of Mt Frederick, Deep Creek, 550 m, 171.836°E, 41.745°S, on bryophyte stalactites on vertical rock wall dangling almost into pool of water, female, 28 Jan 2009, D. Glenny 10578 (CHR 606646); Stockton Plateau, north of T31 Stream, 670 m, 171.888°E, 41.666°S, *Leptospermum*



**Fig. 8.** *Riccardia dimorpha* female plant habit, with *Goebelobryum vermiculare* and *R. crassa*, Birds Ferry pakihī. CHR 668200.

*scoparium* – *Chionochloa juncea* – *Metrosideros umbellata* – *Phormium cookianum* shrubland on sandstone pavement, male, 16 Dec 2010, D. Glenny 11096 (CHR 618714); Denniston Plateau, Waimangaroa River, 680 m, 171.787°E, 41.763°S, on peat soil in *Leptospermum scoparium* shrubland 10 cm tall, female, 20 Mar 2019, D. Glenny 14579 & M. Renner (CHR 657812, NSW, F). Westport, pakihī east of Nine Mile Road, 110 m, 171.658°E, 41.799°S, *Gahnia rigida* – *Gleichenia dicarpa* fern rushland on terrace, with *Kurzia calcarata* and *Lethocolea pansa*, female, 19 Jan 1996, D. Glenny 6313 (CHR 509835); Stockton Plateau, Cypress Stream, 700 m, 171.881°E, 41.706°S, hummock and pool system on terrace, male and female, 27 Nov 1998, D. Glenny 7579b (CHR 518930); Orikaka River, 345 m, 171.966982°E, 41.732°S, *Leptospermum scoparium* – *Epacris pauciflora* shrubland, on soil with *Telaranea herzogii*, male, 23 Oct 2004, T. Hay s.n. (CHR 583069); Mt William Range, 688 m, 171.910°E, 41.687°S, 50 cm tall *Leptospermum scoparium* shrubland on sandstone pavement, with *Chionochloa juncea*, female, 14 Dec 2010, D. Glenny 11104 (CHR 618720); Te Kuha Ridge, 600 m, 171.684°E, 41.812°S, *Leptospermum scoparium* 50 cm high / *Gleichenia microcarpa* + *Empodisma minus* sedge shrubland, on peat soil, female, 19 Mar 2001, D. Glenny 8416 (CHR 526319); Te Kuha Ridge, 600 m, 171.684°E, 41.812°S, *Lepidothamnus intermedius* – *Fuscospora cliffortioides* forest 8 m tall, with *Acromastigum cavifolium*, *Neolepidozia tetradactyla*, *Riccardia crassa*, and *Zoopsis setulosa*, female, 19 Mar 2001, D. Glenny

8466 (CHR 526368); Westport, pakihī east of Nine Mile Road, 120 m, 171.644°E, 41.800°S, [*Leptospermum scoparium*] / *Machaerina teretifolia* – *Gleichenia dicarpa* fern rushland, with *Drosera spatulata*, *Goebelobryum vermiculare*, *Lycopodiella diffusa*, female, 10 March 2020, D. Glenny 14750 & K. Frogley (CHR 668241, F); Charleston, 171.436°E, 41.935°S, 150 m, sparse *Gahnia rigida* – *Gleichenia microphylla* / *Lycopodiella diffusa* sedgeland on terrace, female and male, 19 Feb 2000, D. Glenny 8150 (CHR 527490); Tōtara River, Birds Ferry Road, 35 m, 171.490°E, 41.860°S, [*Leptospermum scoparium*] / *Gahnia rigida* – *Gleichenia inclusisora* fern rushland, with *Riccardia alpicornis*, female, 30 May 2020, D. Glenny 14825a (CHR 668258, F); Tōtara River, Birds Ferry Road, 35 m, 171.490°E, 41.860°S, [*Leptospermum scoparium*] / *Machaerina teretifolia* – *Gleichenia dicarpa* fern rushland, with *Goebelobryum vermiculare*, *Kurzia hippuroides*, *Lycopodiella diffusa*, *Riccardia multicorpora*, and *Telaranea herzogii*, female, 1 June 2020, D. Glenny 14832 (CHR 668200, F); Tōtara River, Birds Ferry Road, 35 m, 171.490°E, 41.860°S, *Leptospermum scoparium* / *Machaerina teretifolia* – *Gleichenia inclusisora* fern rushland, female, 31 May 2020, D. Glenny 14833 (CHR 668267, F); Tōtara River, Birds Ferry Road, 35 m, 171.490°E, 41.860°S, *Leptospermum scoparium* / *Machaerina teretifolia* – *Gleichenia inclusisora* fern rushland, female, 30 May 2020, D. Glenny 14827 (CHR 668267); Tiropahi River, 145 m, 171.464°E, 41.977°S, *Leptospermum scoparium* / *Gahnia rigida* – *Gleichenia dicarpa* / *Riccardia crassa* fern rushland, female, 31 May 2015, D. Glenny 12899b (CHR 638186, STU); Tiropahi River, 136 m, 171.422°E, 41.953°S, *Leptospermum scoparium* / *Machaerina teretifolia* – *Gleichenia dicarpa* / *Riccardia crassa* fern rushland, on soil, female, 31 May 2015, D. Glenny 12889a (CHR 638171); **Westland:** Cascade Plateau, Donald Creek, 250 m, 168.433°E, 44.023°S, [*Leptospermum scoparium* – *Halocarpus bidwillii*] / *Gleichenia* – *Empodisma minus* rushland, with *Riccardia crassa* and *R. multicorpora*, female, 29 Jan 2018, H. Speight s.n. (CHR 684781); **Fiordland:** Borland Bog, 200 m, c. 167.553°E, 45.787°S, growing in *Sphagnum cristatum*, male, 10 Jan 1984, J. Child H5175 (CHR 409759); **Stewart Island / Rakiura:** SW of Deceit Peaks, 167.655°E, 47.091°E, 305 m, *Leptospermum scoparium* – *Lepidothamnus intermedius* – *Halocarpus biformis* shrubland, on soil, with *Lycopodiella diffusa* and *Telaranea herzogii*, female, 20 March 2005, N. Zviagina s.n. (CHR 503818); Magog, 215 m, 167.575°E, 47.189°S, opening in *Leptospermum scoparium* scrub, with *Acromastigum anisostomum*, *A. cavifolium*, *A. mooreanum*, *Clasmatocolea notophylla*, *Riccardia pusilla*, *Tetracymbaliella decipiens*, *Telaranea inaequalis*, and *Trichotemnomma corrugatum*, male, 10 Jan 2005, D. Glenny 9332 (CHR 574651).

## Discussion

### Comparison with similar New Zealand species

A strongly striately verrucose epidermis is shared with *Riccardia crassa* and *R. perspicua*. *Riccardia dimorpha* is easily distinguished from those two species by its much narrower thallus. In addition, *R. intercellula* E.A. Brown and *R. browniae* have a lightly striately verrucose surface. All five are compared in Table 1. The two most notable differences between *R. dimorpha* and the other four species are, firstly its narrow thallus with almost no overlap with the minimum main axis width of the other four species, and secondly, *R. dimorpha* is dioicous while of the other four, only *R. crassa* is dioicous. *Riccardia dimorpha* is easily distinguished from *R. crassa* on thallus width.

**Table 1.** Comparison of *Riccardia dimorpha* with other New Zealand species that have a striately verrucose epidermis. Data from Brown and Braggins (1989), supplemented with author’s observations.

	<i>R. dimorpha</i>	<i>R. perspicua</i>	<i>R. crassa</i>	<i>R. intercellula</i>	<i>R. browniae</i>
plant length (mm)	10–18	10–15	15–45	7–10	5–17
thallus width (µm)	250–320	(400)500–3700	960–2250	570–810	300–1000
thallus depth (µm)	180–340	85–117	147–860	147–177	105–295
thallus cell row depth	5–10	5–6	4–15	6	(4)5–9(10)
epidermis cell contents	chlorophyllose	echlorophyllose in older parts of thallus	chlorophyllose	echlorophyllose	chlorophyllose
slime papillae length × width (µm)	35–45 × 25	80–150 × 20–33	97–450 × 21–63	100–200 × 16–25	100–140(230) × 15–33
slime papilla persistence	usually not persisting	not persisting	persisting	persisting	persisting
slime papilla position	ventral only	ventral only	ventral only	ventral and dorsal	ventral only
slime papilla ornamentation	smooth	smooth	striately verrucose	smooth	smooth
ectomycorrhizae	absent	present within ventral epidermal cells, scattered in dorsal epidermis and subepidermis	absent	present, between ventral cells	present in ventral epidermal and subepidermal cells
epidermal ornamentation	strongly striately verrucose	strongly striately verrucose and castellate	strongly striate	very lightly striate	lightly striate
sexuality	dioicous	monoicous	dioecious, rarely monoicous	monoicous	monoicous

New Zealand has four species belonging to sect. *Alcicornia*: *Riccardia alcicornis*, *R. furtiva* E.A.Br. & Braggins, *R. umida* E.A.Br., and *R. multicorpora* E.A.Br. (Brown and Braggins 1989). They are compared in Table 2. Mostly notably, *R. dimorpha* is the only species of the five that has striately verrucose epidermal ornamentation.

*Riccardia dimorpha* is similar to *R. alcicornis* in that the main axis is subterete, with dark-brown- and thick-walled cells in several inner cell layers in older parts of the main axis, and the branching is pinnate to bipinnate (see Brown and Braggins 1989: Fig 4:1 and 4:2). The male branches are very similar in being bilaterally compressed so that the dorsal face is in a groove between the lateral wings (see illustrations in Brown and Braggins 1989: Fig. 4:12; and Hässel de Menendez 1972: Fig. 7j). The mucilage papillae of both species are shortly clavate. *Riccardia dimorpha* differs from *R. alcicornis* in being dioicous and in having strong

epidermal cell ornamentation. The ventral epidermal cells of *R. dimorpha* are hexagonal-elongate with a length to width ratio of 2.0–4.0:1, while those of *R. alcicornis* are less elongate (length to width ratio 1.1–1.7:1).

The key to New Zealand species in Brown and Braggins (1989: 20–25) can accommodate *Riccardia dimorpha* by modifying couplet 13 and adding a new couplet before their couplet 14:

- 13 Monoicous, epidermis lightly striately verrucose, endomycorrhizae present .....*R. browniae*
- 13 Dioicous, epidermis strongly striately verrucose, endomycorrhizae absent ..... 13'
- 13' Main axis flattened, 960–2250 µm wide; slime papillae 100–230 µm long, papilla surface striate ..... *R. crassa*
- 13' Main axis subterete, 250–320 µm wide; slime papillae 35–45 µm long, papilla surface smooth .....*R. dimorpha*

**Table 2.** Comparison of *R. dimorpha* with New Zealand species of *Riccardia* sect. *Alcicornia*. Data from Brown and Braggins (1989).

	<i>R. dimorpha</i>	<i>R. alcicornis</i>	<i>R. furtiva</i>	<i>R. umida</i>	<i>R. multicorpora</i>
sexual dimorphism	present	absent	absent	unknown	absent
main axis width (µm)	280–500	190–590	141–366	225–310	255–446
main axis depth (µm)	180–340	185–260	90–268	110–155	177–215
main axis cell depth	5–10	10–15	7–13	7–8	9–11
epidermal ornamentation	striately verrucose	smooth	smooth	smooth	smooth
ectomycorrhiza	absent	absent or present	present or absent	present	present in lower 3–4 layers
sexuality	dioicous	monoicous	monoicous	dioicous	dioicous
slime papilla length (µm)	35–45	40	25	18–170	40 × 20

## Dimorphism

Patches of female plants of *Riccardia dimorpha* were more than twice as common as patches of male plants. Female-biased sex ratios in dioecious species of bryophytes are common (Longton and Schuster 1983) but not universal (McLetchie and Puterbaugh 2000).

Female plants of *Riccardia dimorpha* had more meristematic tips than male plants. This has also been observed in *Marchantia inflexa* Nees & Mont., where female plants have greater meristematic tip production than males (McLetchie and Puterbaugh 2000). They reported that “Females grew faster, produced more meristematic tips and had lower levels of asexual reproduction than males. Number of meristematic tips was negatively correlated with asexual reproduction and positively correlated with growth rate. These sex-specific patterns may lead to the high frequency of single sex patches as well as biased adult population sex ratios that are observed in the field.”

*Riccardia dimorpha* has male plants less branched than female plants, in accord with the Patagonian species *Riccardia longioleata* and with Furuki’s (1991) observation. However, the male plants of *R. dimorpha* and *R. longioleata* are longer than female plants contrary to Furuki’s observation of sexual dimorphism in *R. pusilla* Grolle and *R. marginata* var. *pacifica*, in which the males were dwarfed.

## Relationships with extra-territorial species

*Riccardia dimorpha* belongs in *Riccardia* subg. *Riccardia* sect. *Alcicornia* Hässel (Hässel de Menendez 1972), which is defined as having a thallus filamentous, biconvex, semi-terete, 120–160 µm wide (width to depth ratio 1.0–2.5:1), without ribs or wings. In southern South America there are five species in section *Alcicornia* (Hässel de Menendez 1972): *R. fuscobrunnea* (Steph.) A.Evans, *R. corralensis* (Steph.) A.Evans, *R. conimitra* (Steph.) A.Evans, *R. longioleata* Hässel, and *R. alcicornis* (Hook.f. & Taylor) Trevis, which are compared to *R. dimorpha* in Table 3. None of these South American species have a striately verrucose epidermis. One species, *R. fuscobrunnea*, has an ectomycorrhiza present.

**Table 3.** Comparison of *Riccardia dimorpha* with southern South American species of *Riccardia* sect. *Alcicornia*. Data on South American species from Hässel de Menendez (1972).

	<i>R. dimorpha</i>	<i>R. alcicornis</i>	<i>R. fuscobrunnea</i>	<i>R. corralensis</i>	<i>R. longioleata</i>	<i>R. conimitra</i>
sexual dimorphism	present	absent	absent?	absent?	present	absent?
main axis width (µm)	280–500	120–260	252–324	540–1000	240–624	180–600
main axis depth (µm)	180–340	130–190	160–200	168–204	168–257	156–204
main axis cell depth	5–10	8–11	6–8	6–7	5–6	5–8
epidermal ornamentation	striately verrucose	absent	absent	absent	absent	absent
ectomycorrhiza	absent	absent	present	absent	absent	absent
sexuality	dioicous	monoicous	dioicous	dioicous	dioicous	dioicous
slime papilla length (µm)	35–45	19–24	31–35	36–48	24–45	24–36

Hewson’s (1970) revision of Australian and New Guinean *Riccardia* preceded Hässel de Menendez’s (1970) publication of the name sect. *Alcicornia* Hässel. However, Australia has *Riccardia alcicornis*, type of the section, and *R. geniana* Hewson (Hewson 1970) of Papua New Guinea probably also belongs in the section. *Riccardia geniana* has a smooth epidermis. *Riccardia pindauensis* Hewson of Mt Wilhelm, Papua New Guinea, has a “cuticle armed with fine dentition” (Hewson 1970: 78) but has a main axis only 3–6 cells deep, not (5–)7–10 cells deep as in *R. dimorpha*.

In summary, comparison with species of New Zealand, southern South America, Australia, and New Guinea shows that it is unlikely that *Riccardia dimorpha* has been previously described.

The description of *Riccardia* sect. *Alcicornia* can be expanded with these characters: surface ornamentation striately verrucose (in *R. dimorpha* only), sexuality usually dioicous (monoicous in two of ten species).

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