



A new species of *Didymodon* (Pottiaceae, Bryophyta) and a key to New Zealand representatives of the genus

JESSICA E. BEEVER¹ & ALLAN J. FIFE²

¹ c/o Landcare Research, Private Bag 92170, Auckland 1142, New Zealand

Email: Beeverj@landcareresearch.co.nz

² Allan Herbarium, Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

Email: Fifea@landcareresearch.co.nz

Abstract

A new species of moss, *Didymodon novae-zelandiae*, is described and illustrated. A key is provided to the six New Zealand species of genus *Didymodon*, together with the single New Zealand species of the related genus *Gymnostomum*. The key distinguishing features of *D. novae-zelandiae* are its gymnostomous capsule with a mammillate operculum, and its diminutive size. This study is a contribution to the preparation of the eFlora of New Zealand, Mosses.

Key words: *Gymnostomum calcareum*; moss; taxonomy

Introduction

A minute pottiaceous moss, growing on sea-cliffs on the northern shore of the Manukau Harbour, Ihumatao, Auckland, was first noted by the senior author in 1982. The plants were gregarious on vertical, damp, SW-facing cliffs composed of scoriaceous tuff produced by the nearby volcanic cone, Maungataketake (Fig. 1). The site was lightly shaded by a remnant fringe of pōhutukawa (*Metrosideros excelsa* J.Gaertner 1788: 172) coastal forest. Microscopic examination of the moss, with particular attention to morphology of its axillary hairs, costal anatomy and the ornamentation of the laminal cells, has convinced us that the plant is best placed in the genus *Didymodon* Hedwig (1801: 104), but that it cannot be assigned to any currently known New Zealand or Australian member of that genus. Identification was sought from a noted authority on the Pottiaceae, R.H. Zander, who was likewise unable to name it. The plant is therefore here described, and a key is provided to New Zealand members of genus *Didymodon*, together with the somewhat similar, and easily confused pottiaceous moss, *Gymnostomum calcareum* Nees & Hornschuch in Nees *et al.* (1823: 153).

Taxonomy

Didymodon novae-zelandiae J.E.Beever & Fife, *sp.nov.*

Holotype:—NEW ZEALAND. North Auckland Land District: northern shore of Manukau Harbour, Ihumatao, ca. 1.5 m elev., 37°0.048'S, 174°45.108'E; on SW-facing, damp, vertical sea-cliff of volcanic tuff, lightly shaded under high pōhutukawa canopy, 15 May 1982, *J.E. Beever 11-61* (WELT M040251).

Paratypes:—at type locality, 17 February 2008, *J.E. Beever 110-36* (CHR 611390); at type locality, 2 June 2008, *J.E. Beever 110-88* (AK 356397); North Auckland Land District, northern shore of Manukau Harbour, Kaitarakihi Bay, 37°1'S, 174°35'E, on bare, eroding, fully exposed coastal cliff, in seepages, 15 September 2012, *P.J. & T.J. de Lange 11094* (AK 356398); Hawke's Bay Land District, Kiwi [Station] near Wairoa, damp papa face in light bush, 6 January 1955, *G.O.K. Sainsbury D2* (WELT M029610); Wellington Land District, Mākiekie Scenic Reserve, ca. 70 km ESE of Āpiti township, 20 January 2009, *J.E. Beever 113-50c* (CHR 637235).



FIGURE 1. Type locality of *Didymodon novae-zelandiae* on Manukau Harbour foreshore. *D. novae-zelandiae* (position arrowed) on the cliff face, below a denser band of vegetation (mainly *Bryum clavatum*), some 1.5 m above high tide mark. The remains of trunks of trees buried by eruption of nearby Maungataketake can be seen in the cliff base both to the right and left of the standing figure. The large pōhutukawa tree (*Metrosideros excelsa*) to the right, above, has now fallen from the cliff. Photo R.E. Beever, 17 Feb. 2008.

Description:—(Fig. 2). Plants brownish-green, gregarious, on damp vertical banks. Stems simple or sparsely branched, ca. 1–2 mm in length, brown, in cross-section rounded, without differentiated central strand, sclerodermis or hyalodermis. Leaves 0.5–1.0 mm, imbricate and appressed-incurred when dry, erect-spreading when moist, lingulate, concave in mid-leaf cross-section, obtuse-rounded and more or less flat at apex, with lamina unistratose throughout; margins papillose and crenulate by bulging laminal cells, plane or very weakly recurved at mid-leaf; upper laminal cells clear in outline, irregularly rounded-subquadrate to oblate, firm-walled, (7–)7.5–13.5(–15) × (7.5–)8–11(–15) μm, unipapillose or bipapillose on both surfaces, with papillae simple, rounded, and low (projecting ca. 3–5 μm); KOH colour reaction of upper laminal cell walls yellow; upper marginal cells not differentiated; basal cells differentiated, oblong-rectangular, mostly 2–4:1, more or less thin-walled, smooth, gradually transitioning to upper lamina. Costa failing several cells below leaf apex, with both abaxial and adaxial surface cells more or less oblong (from near base to mid-leaf), becoming quadrate on the abaxial face distally, but elongate adaxially; in cross-section at mid-leaf with 2–3(–4) guide cells and a weakly differentiated abaxial group of 4–6 smaller, thick-walled cells. Axillary hairs of ca. 4 cells, basal 1–2 usually brown. Sexuality presumed dioicous. Perichaetia terminal, the inner leaves sheathing the seta base and otherwise not differentiated from adjacent vegetative leaves. Male plants smaller, with stems ca. 0.4–0.7 mm, simple or branched (apparently by innovation), with perigonia terminal or on very short innovative branches, with bracts red-brown, the largest ca. 0.3 mm, lingulate from a broadly ovate base, surrounding ca. 2 antheridia and few paraphyses. Setae slender, twisted to the left, dark red at base, lighter or yellow above, becoming darker with age, 3–6 mm; capsules erect, short-cylindric, not constricted below the mouth, yellow-brown, becoming darker with age, 0.5–0.9 mm long; exothecial cells thin-walled, irregular; stomata apparently absent; annulus absent; operculum mammillate. Peristome absent. Calyptra cucullate. Spores spherical, smooth, (7.5–)10.5–14.0(–19.5) μm in diameter.

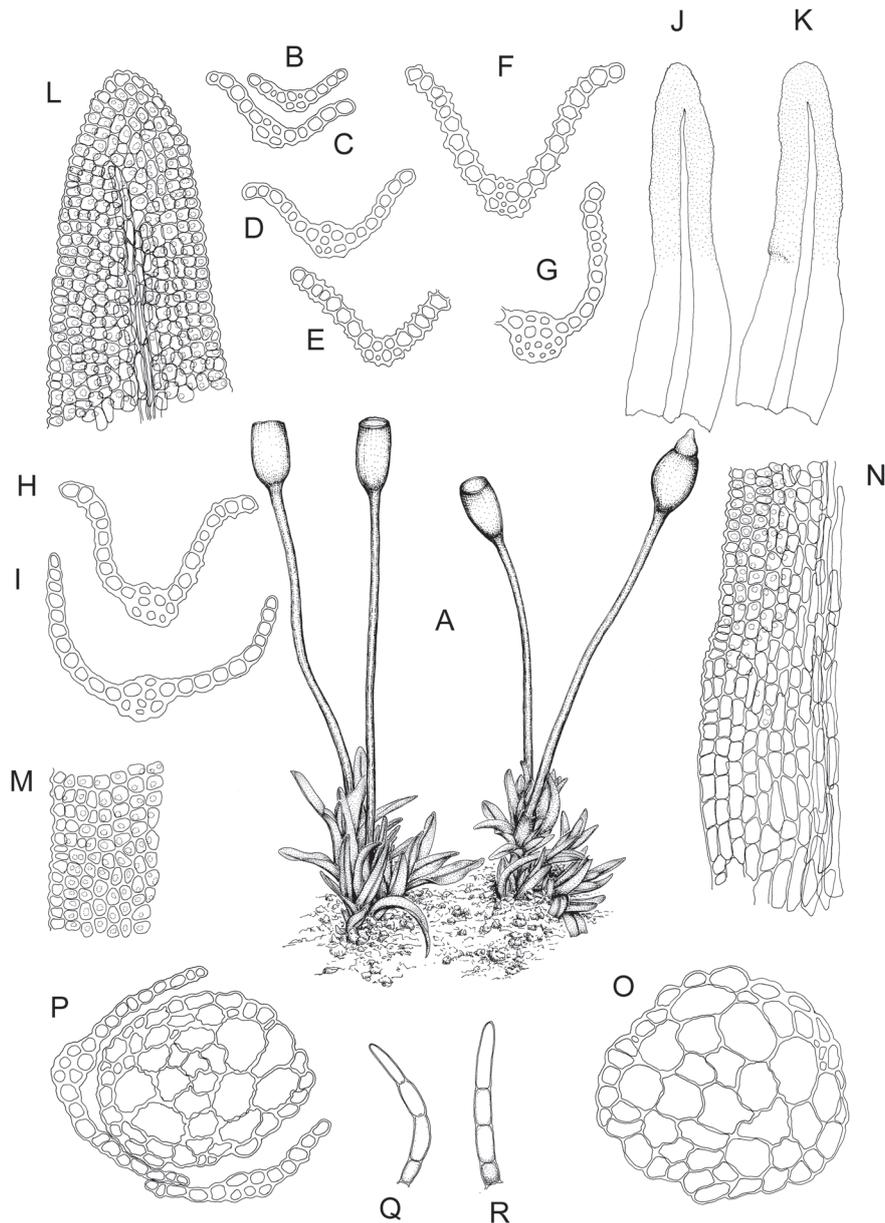


FIGURE 2. *Didymodon novae-zelandiae*. A, habit with capsules. B–I, leaf cross-sections. J–K, stem leaves. L, leaf apex. M, mid laminal cells, at margin. N, lower laminal cells, margin to costa. O–P, stem cross-sections. Q–R, axillary hairs. Drawn from paratype material *J.E. Beever 110-36*, CHR 611390, by R. D. Seppelt.

Etymology:—the epithet “*novae-zelandiae*” refers to the New Zealand provenance of the species. A tag name “*Didymodon Ihu Pott*” has previously been used *in herb.* for this taxon.

Ecology:—At the type locality (Fig. 1) *Didymodon novae-zelandiae* was found on a vertical sea-cliff formed of consolidated volcanic ash (tephra) from the eruption of nearby Maungataketake (Ellet’s Mountain) some 29,000 years ago (Hayward & Hayward 1995). Present-day vegetation consists of a very thin strip of pōhutukawa at the top of the cliff, with associated coastal shrubs, including kawakawa (*Piper excelsum* G.Forster (1786: 5)) and karamū (*Coprosma macrocarpa* Cheeseman (1888: 147)). A detailed account of the vascular vegetation of the site is provided by Cameron (1997).

Didymodon novae-zelandiae was found in bare areas on the tephra cliff face, with scattered *Lobelia anceps* Carl von Linnæus *filius* (1782: 395), and wīwī (*Ficinia nodosa* (C.F.Rottbøll 1772: 24) A.M.Muasya, D.A.Simpson & P.Goetghebeur (2000: 133)). In slightly damper sites adjacent, the moss *Bryum clavatum* (Schimper 1836: 148) Müll. Hal. (1848: 292) formed dense swards. *Didymodon novae-zelandiae* has not been positively identified during recent site visits (April 2012 and Feb. 2015), although minute non-fruiting *Didymodon* plants (not confidently identifiable to

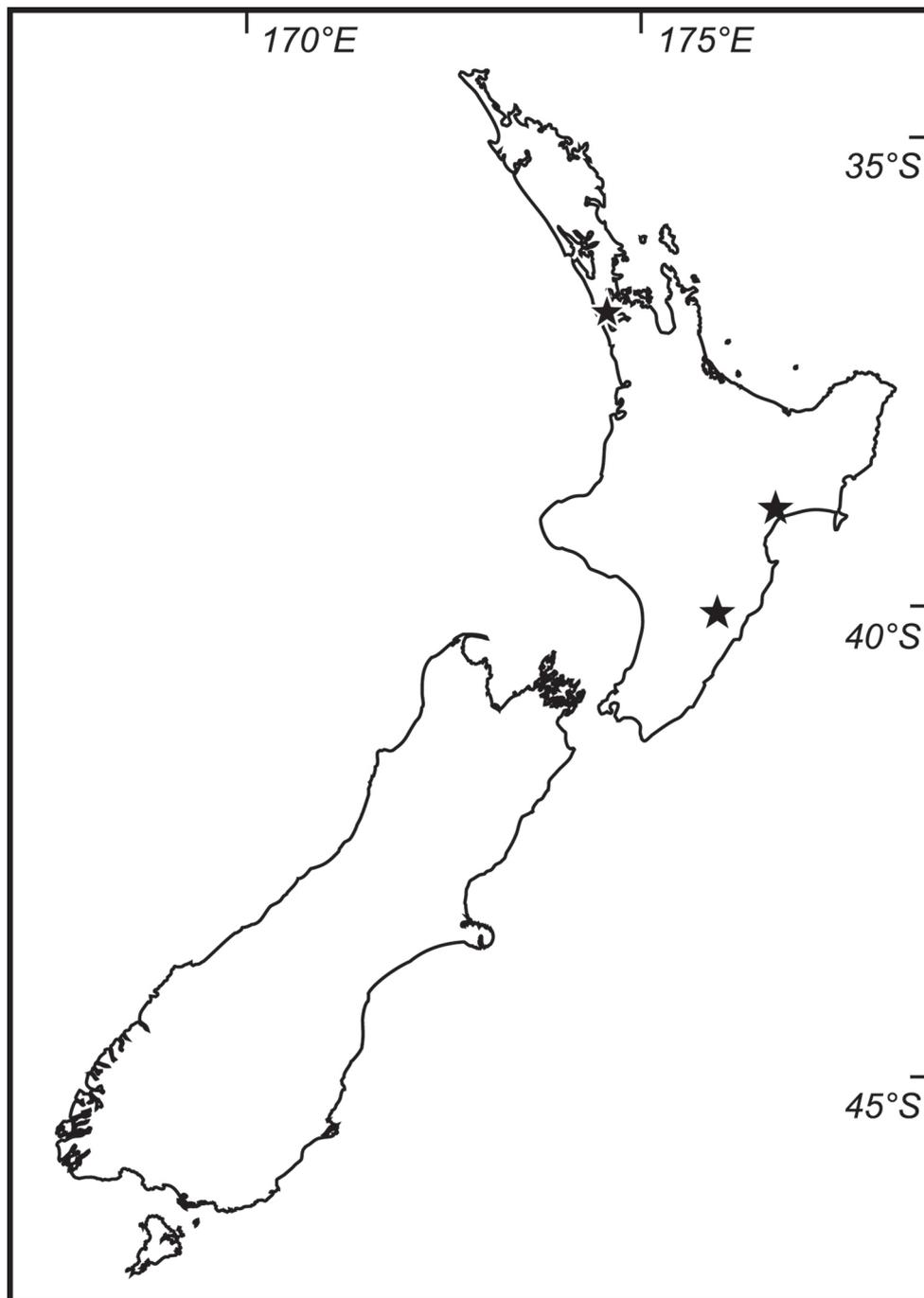


FIGURE 3. Distribution map of *Didymodon novae-zelandiae*. The two northernmost sites are covered by a single symbol. Figure prepared by C. Pan.

species level) were present among shoots of *B. clavatum*. Observations indicated that the much larger and denser *B. clavatum* may be extending its coverage and competing with the smaller moss. However, the cliff surface is exfoliating in patches, creating new moss-free areas, which could be suitable for colonisation by *D. novae-zelandiae* if spores were available. Potentially more disruptive to the site of the moss at Ihumatao are the changes wrought by wholesale collapse of sections of the cliff as mature pōhutukawa fall, and the establishment of the invasive grass kikuyu (*Cenchrus clandestinus* (C.F.Hochstetter ex E.Chiovenda 1903: 41) Morrone in Chemisquy *et al.* 2010:127) on the colluvium. A search for the species along the Manukau Harbour northern foreshore located another colony, on eroding rock, ca. 14 km W of the type locality (P.J. & T.J. de Lange 11094, AK 356398). Here the substrate was fine silty material, in part derived from andesitic breccia and in part sedimentary (P.J. de Lange pers. comm. Sep. 2012).

A further specimen of *D. novae-zelandiae* has been located in the herbarium of G.O.K. Sainsbury (WELT M029610), collected by him near Wairoa (ca. 330 km SE of the type locality). A more recent collection (CHR 637235)

was made from a damp cut roadside bank at the Mākiekie Scenic Reserve, ca. 100 km further south. Both of these specimens were from damp banks composed of the soft, blue-grey mudstone known regionally as ‘papa rock’.

Mosses found growing with *D. novae-zelandiae* include three other pottiaceous mosses: *D. tophaceus*, *D. weymouthii* and *Tridontium tasmanicum* Hook.f. in Hook. (1840: 248).

Conservation status:—Although known from only four sites (Fig. 3), the moss is on a variety of substrates, in habitats that are not rare in the North Island of New Zealand. However, *Didymodon novae-zelandiae* is very small, even when fruiting, and therefore easily overlooked. A classification of ‘Data deficient and endemic’, according to the scheme of Townsend *et al.* (2008), is therefore recommended.

Discussion

Features of this undescribed moss suggested placement in the family Pottiaceae as circumscribed by Brotherus (1924), and in more modern treatments by Saito (1975) and by Zander (1993, 2007). Critical familial features are its small stature, erect habit (of both gametophyte and theca), long single costae, more or less subquadrate and papillose upper laminal cells, and spores mostly 10–14 µm in diameter. Features of its habitat and habit are reminiscent of those of the genera *Gymnostomum* and *Didymodon*. In addition, the possession of short axillary hairs with brown basal cells is a feature of both these genera; quadrate abaxial cells covering the costa in its distal part, and a yellow laminal cell wall reaction with 2% KOH (all features of the new species) may also be found in either genus (Zander 1993). The following features, however, align the undescribed moss with *Didymodon* spp. rather than with *Gymnostomum* spp.: the gregarious nature of the shoots (shoots in turf or cushions for *Gymnostomum*); the lack of papillae on the abaxial face of the costa (abaxial costal papillae present in *Gymnostomum*); papillae 1–2 per laminal cell, centred over the cell lumen (papillae 2–5 per laminal cell, and scattered in *Gymnostomum*—well illustrated in Scott & Stone (1976) Pl. 33).

Although there are features of the undescribed moss that are not typical of genus *Didymodon*, including the absence of both a central strand and a sclerodermis in the stem, lingulate leaves, more or less plane leaf margins, and the absence of a peristome, all these character states are accepted as occurring in some species of the genus *Didymodon* by Zander (1993). Indeed, the New Zealand endemic *Weissia weymouthii* R. Brown bis (1899: 439) was transferred (Zander 1993) into *Didymodon* (as *D. weymouthii*), despite its having lingulate leaves and lacking a central strand in the stem.

For the all above reasons we choose to describe the new moss as a species of *Didymodon*.

Gymnostomum and *Didymodon* showed a close relationship, based on analysis of 75 morphological characters by Zander (1993), and were both placed by him in Tribe Barbulae of Subfamily Merceyoideae. Later this close relationship was maintained (Zander 2006) when Tribe Barbulae was transferred to Subfamily Barbuloideae. An alternative placement of these two genera was suggested by Werner *et al.* (2004), who analysed chloroplast *rps4* sequence data, for a single species of each genus. They concluded that the genera belong in separate Subfamilies; Trichostomoideae and Pottioideae respectively. Regardless of the correct placement, and taxonomic proximity of the two genera, in a New Zealand context the most likely confusion of *Didymodon novae-zelandiae* would be with *Gymnostomum calcareum*, rather than with any other member of the genus *Didymodon*. In addition to generic differences given above, useful distinguishing features between the two species are the colour and height of gametophyte plants (brownish-green shoots, ca. 1–2 mm high in *D. novae-zelandiae*; bright yellow-green shoots, 3–20 mm high, in *G. calcareum*). Microscopically, the nature of the upper laminal cells will easily separate the taxa (upper laminal cells more or less flat and bearing 1–3(–4) low, inconspicuous papillae in *D. novae-zelandiae*; upper laminal cells bulging, and bearing 4–6 conspicuous papillae per cell in *G. calcareum*). In addition, *G. calcareum* has a stouter costa, which bulges strongly on the abaxial leaf surface.

Didymodon is a large and cosmopolitan genus, widely diversified in temperate and montane regions, with ca. 122 species accepted worldwide (Zander 1993; 2007); six have now been recorded in New Zealand. Werner *et al.* (2005) interpreted their molecular data as supporting the monophyly of the genus, contrary to the conclusion of Zander (1993) that the genus “is clearly heterogeneous”, a conclusion in part based on its being “suspiciously heterogeneous in KOH colour reactions”. This latter character thus becomes a useful identification tool at species level within *Didymodon*; it allows separation of *D. novae-zelandiae* (yellow) from two of its New Zealand congeners, namely *D. torquatus* (Taylor 1846: 50) Catcheside (1980: 174) and *D. weymouthii* (both orange). *Didymodon tophaceus* (Brid. 1819: 84) Lisa (1837: 31), which can occur in the same habitats as *D. novae-zelandiae* (and is also KOH yellow), is distinguished by a central strand in the stem, by often having leaves with an ovate base, and (usually) a well-developed peristome.

From his annotations on the packet, it is clear that G.O.K. Sainsbury puzzled over the Wairoa specimen (WELT M029610) that we have identified as *Didymodon novae-zelandiae*. He suggested only that it belonged to genus *Desmatodon* Bridel (1818: 86), whose New Zealand species are now variously placed in *Didymodon* and *Tortula* Hedwig (1801: 122). Later the specimen was tentatively identified as *Tortula viridipila* Dixon & Sainsbury (1933: 218), by an unknown worker. However, that taxon differs markedly from *D. novae-zelandiae*: its leaves have a long flexuose arista formed from the excurrent costa (rather than costa failing several cells below the leaf apex), setae are longer (ca. 10 mm versus 3–6 mm) and opercula are obliquely rostellate (rather than mammillate). This last feature of *D. novae-zelandiae*, a mammillate operculum, is unique among New Zealand Pottiaceae.

Notwithstanding the unique combination of characters that *D. novae-zelandiae* possesses, plants lacking mature sporophytes cannot always be identified with confidence.

Key to New Zealand species of *Didymodon* and *Gymnostomum*

As is the case in North America (Zander 1998), some species of the genus *Didymodon* in New Zealand are common and often difficult to distinguish. The colour reaction of the walls of upper laminal cells with 2% KOH is a useful identification character. As noted by Zander (1993, p. 3), to assess the colour reaction accurately it is necessary to focus on cell walls under high power of the compound microscope.

1. Plants forming dense, bright yellow-green turves, on calcareous substrates; mid-laminal cells papillose, with 4–6 conspicuous papillae per cell; leaf margins plane; leaf apex flat, unistratose, acute to rounded-obtuse and often variable on the same plant; costa failing below the leaf apex *Gymnostomum calcareum*
- Plants forming dense turves or loosely to densely gregarious, of various dark colours and not bright yellow-green, on various mineral substrates including calcareous; mid-laminal cells papillose, with 1–3(–4) low, often inconspicuous, papillae, or papillae lacking; leaf margins recurved at least in part, or rarely plane (if plane, plants brownish green); leaf apex flat or cucullate, unistratose or otherwise, acute to rounded-obtuse (but not on the same plant); costa failing below the leaf apex, or percurrent to excurrent
..... 2 *Didymodon*
2. Leaves lingulate, scarcely tapered from base to apex; lamina unistratose throughout; stem in cross-section without a central strand 3
- Leaves lanceolate or lingulate from an ovate base, widest near the leaf base; lamina unistratose throughout or bistratose at distal margins; stem in cross-section with a well-developed central strand 4
3. Leaf margins plane or weakly recurved in mid-leaf; KOH reaction of walls of upper laminal cells yellow; setae 3–6 mm; operculum mammillate with a blunt central projection; peristome absent *Didymodon novae-zelandiae*
- Leaf margins recurved, at least below; KOH reaction of walls of upper laminal cells orange; setae 6–12 mm; operculum rostrate with a long oblique beak; peristome present *Didymodon weymouthii*
4. Laminal cells smooth; perichaetial leaves strongly differentiated, with sheathing base narrowing abruptly to a subula; species known only from Hawke’s Bay and Wellington Land Districts, not seen since 1956 *Didymodon calycinus* Dixon (1915: 95)
- Laminal cells papillose, with low, rounded, simple papillae; perichaetial leaves weakly differentiated, base may be sheathing but leaves gradually narrowing to their apex, not subulate; common species, widespread in New Zealand 5
5. Leaves lingulate from an ovate base; leaf apex obtuse-rounded; costa clearly failing ca. 4–8 cells before unistratose leaf apex
..... *Didymodon tophaceus*
- Leaves linear-lanceolate to broadly lanceolate; apex acuminate to bluntly acute; costa percurrent, excurrent, or terminating obscurely in pluristratose leaf apex 6
6. Leaves linear-lanceolate; basal laminal cells strongly differentiated, elongate, thin-walled and hyaline in ca. 10 rows (discernible as a white leaf base with 10× hand-lens); stem in cross-section with cells of outer layer not strongly differentiated, thin-walled (at least on outermost wall); peristome not spirally twisted, teeth erect and incurved when dry
..... *Didymodon australasiae* (Hooker & Greville 1824: 301) R.H.Zander (1978: 21)
- Leaves broadly lanceolate; basal laminal cells not strongly differentiated except in 1 or 2 rows at extreme base, not hyaline (not discernible with 10× hand-lens); stem in cross-section with a differentiated outer layer of thick-walled, narrow-lumened stereid cells; peristome spirally twisted *Didymodon torquatus*

Acknowledgements

We are grateful to Richard Zander for his opinion that *Didymodon novae-zelandiae* is a new species, to Peter de Lange for his efforts in locating a second site for *D. novae-zelandiae* on the Manukau Harbour foreshore and providing information on its substrate, and to Rod Seppelt for his skilled illustration (Fig. 2). Our thanks to staff of herbaria AK, BM, CHR, NY, PDD, and WELT for accessioning and/or loaning of specimens. Thanks too to Sue Gibb for much assistance in tracing bibliographic references, to Christine Bezar and Leah Kearns for editing, and to Cissy Pan for preparing the distribution map (Fig. 3). JEB is grateful to Stephanie Parkes, Ewen Cameron and the late Ross Beaver for assistance in the field. This research was supported by Core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment’s Science and Innovation Group, and its predecessors.

References

- Beever, J.E. (2014) The mosses of Te Haupa (Saddle Island), Mahurangi, Hauraki Gulf. *Auckland Botanical Society Journal* 69: 143–146.
- Brotherus, V.F. (1924) Musci. In: Engler, A. (Ed.) *Die natürlichen Pflanzenfamilien*. Engelmann, Leipzig, pp. 143–478.
- Brown, R. (1899) Notes on the New Zealand Musci. *Transactions and Proceedings of the New Zealand Institute* 31: 437–442.
- Bridel, S.E. (1818) *Muscologia Recentiorum Supplementum* 4. C.G. Ettinger, Gotha, 220 pp.
- Cameron, E.K. (1997) Native vegetation of Ihumatao cliffs, Mangere. *Auckland Botanical Society Journal* 51: 9–12.
- Catcheside, D.G. (1980) *Mosses of South Australia*. Government Printer, Adelaide, 364 pp.
- Cheeseman, T.F. (1888 “1887”) Notes on the Three Kings Islands. *Transactions and Proceedings of the New Zealand Institute* 20: 141–150.
- Chioyenda, E. (1903) Graminaceae (2). *Flora della colonia Eritrea*. In: *Annuario del Reale Istituto Botanico di Roma*. 8: 21–70.
- Dixon, H.N. (1915) New and rare Australian mosses, mostly from Mitten’s herbarium. *Bulletin of the Torrey Botanical Club* 42: 93–110.
<http://dx.doi.org/10.2307/2479777>
- Dixon, H.N. & Sainsbury, G.O.K. (1933) New and rare species of New Zealand mosses. *Journal of Botany, British and Foreign* 71: 213–220.
- Forster, G. (1786) *Florulae insularum Australium Prodrromus*. Dietrich, Göttingen, 103 pp.
- Gaertner, J. (1788) *De Fructibus et Seminibus Plantarum*. Vol. 1. Stuttgart, 384 pp.
- Hayward, J.J. & Hayward, B.W. (1995) Fossil forests preserved in volcanic ash and lava at Ihumatao and Takapuna, Auckland. *Tane* 35: 127–142.
- Hedwig, J. (1801) *Species Muscorum Frondosorum*. Barth., Leipzig, pp. 1–353.
- Hooker, W.J. (1840) *Icones Plantarum; or figures, with brief descriptive characters and remarks, of new or rare plants, selected from the author’s herbarium*. Vol. 3. Longman, Rees, Orme, Brown, Green & Longman, London, pls 201–300.
- Hooker, W.J. & Greville, R.K. (1824) On the genus *Tortula*, of the order Musci. *Edinburgh Journal of Science* 1: 287–302.
- Linnaeus, C. von filius (1782) *Supplementum Plantarum Systematis Vegetabilium*. Orphanotrophe, Braunschweig, 467 pp.
- Lisa, D. (1837) *Elenco dei Muschi raccolti nei contorni di Torino*. Dalla Stamperia Reale, Turin, 62 pp.
- Morrone, O., in Chemisquy, M.A., Giussani, L.M., Scataglini, M.A., Kellogg, E.A. & Morrone, O. (2010) Phylogenetic studies favour the unification of *Pennisetum*, *Cenchrus* and *Odontelytrum* (Poaceae): a combined nuclear, plastid and morphological analysis, and nomenclatural combinations in *Cenchrus*. *Annals of Botany* 106: 107–130.
<http://dx.doi.org/10.1093/aob/mcq090>
- Muasya, A.M., Simpson, D.A. & Goetghebeur, P. (2000) New Combinations in *Trichophorum*, *Scirpoides*, and *Ficinia*. *Novon* 10: 132–133.
<http://dx.doi.org/10.2307/3393013>
- Müller, C. (1848–1849) *Synopsis Muscorum Frondosorum omnium hucusque cognitorum*. Vol. 1. Alb. Foerster, Berlin, 812 pp.
- Nees, C.G.D., Hornshuch, C.D.F. & Sturm, J. (1823) *Bryologia Germanica* Vol.1, Nürnberg, 373 pp.
- Rottbøll, C.F. (1772) *Descriptionum et Iconum Rariores*. Societas typographicae, Copenhagen, 71 pp.
- Scott, G.A.M. & Stone, I.G. (1976) *The mosses of southern Australia*. Academic Press, London, 495 pp.
- Saito, K. (1975) A monograph of the Japanese Pottiaceae (Musci). *Journal of the Hattorii Botanical Laboratory* 39: 373–537.
- Schimper, W.P. (1836) Muscorum chilensium species novae descripsit. *Annales des Sciences Naturelles; Botanique, sér. 2* 6: 145–149.
- Taylor, T. (1846) The distinctive characters of some new species of Musci, collected by Professor William Jameson, in the vicinity of Quito, and by Mr. James Drummond at Swan River. *London Journal of Botany* 5: 41–67.
- Townsend, A.J., de Lange, P.J., Duffy, C.A.J., Miskelly, C.M., Molloy, J. & Norton, D.A. (2008) *New Zealand threat classification system manual*. Department of Conservation, Wellington, 35 pp.
- Werner, O., Jiménez, J.A., Ros, R.M., Cano, M.J. & Guerra, J. (2005) Preliminary investigation of the systematics of *Didymodon* (Pottiaceae, Musci) based on nrITS sequence data. *Systematic Botany* 30: 461–470.
<http://dx.doi.org/10.1600/0363644054782198>
- Werner, O., Ros, R.M., Cano, M.J. & Guerra, J. (2004) Molecular phylogeny of Pottiaceae (Musci) based on chloroplast *rps4* sequence data. *Plant Systematics and Evolution* 243: 147–164.
<http://dx.doi.org/10.1007/s00606-003-0076-0>
- Zander, R.H. (1978) New combinations in *Didymodon* (Musci) and a key to the taxa in North America north of Mexico. *Phytologia* 41: 11–32.

<http://dx.doi.org/10.5962/bhl.part.20773>

- Zander, R.H. (1993) Genera of the Pottiaceae: mosses of harsh environments. *Bulletin of the Buffalo Society of Natural Sciences* 32: i–vi, 1–378.
- Zander, R.H. (1998) A phylogrammatic evolutionary analysis of the moss genus *Didymodon* in North America north of Mexico. *Bulletin of the Buffalo Society of Natural Sciences* 36: 81–115.
- Zander, R.H. (2006) The Pottiaceae *s. str.* as an evolutionary Lazarus taxon. *Journal of the Hattorii Botanical Laboratory* 100: 581–602.
- Zander, R.H. (2007) Pottiaceae. *Flora of North America north of Mexico* 27: 476–640.