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Didymodon fuscus (Müll.Hal.) J.A.Jiménez & M.J.Cano: a South American—Cape winter-rainfall disjunct and a key to South African species of the genus

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With about 127 species worldwide the genus *Didymodon* Hedw. is among the most diverse of the Pottiaceae (Zander, 1993, 2007). Jiménez *et al.* (2017) have commented on the poor representation of the genus in Africa, where only 19 species are recorded. Of these, 6 (*D. australasiae* (Hook. & Grev.) R.H.Zander, *D. jackvancei* R.H.Zander, *D. tophaceopsis* R.H.Zander, *D. tophaceus* (Brid.) Lisa, *D. umbrosus* (Müll.Hal.) R.H.Zander, and *D. xanthocarpus* (Müll.Hal.) Magill) are recorded from South Africa and Lesotho (O'Shea, 2006).

Recent collections from the winter-rainfall area of South Africa yielded several specimens that could not be assigned to any of the species known from the area. Revision of these collections (as well as specimens from other herbaria) by the second author, in the course of a world revision of the genus, revealed their identity as *Didymodon fuscus* (Müll.Hal.) J.A.Jiménez & M.J.Cano, a species previously known only from Chile and a single locality in the adjacent Argentina (Jiménez & Cano, 2006).

A detailed description of *D. fuscus* is provided by Jiménez & Cano (2006), and the South African specimens match this very closely. Although we have not analysed them statistically, there would appear to be a few quantitative differences between the specimens from the two areas. For example, the range in costa width is smaller in South Africa, and the average is slightly less. In the South American populations, dorsal costa cells are quadrate to short-rectangular, whilst in South Africa they tend more often to be short-rectangular to rectangular. Also, South African plants are more often greenish-brown rather than the reddish-brown typical of the South American populations, but exceptions occur in both areas.

Didymodon fuscus is readily distinguished from all other South African species except *D. xanthocarpus* in the combination of lanceolate leaves with firm-walled basal cells, bulging, smooth, lamina cells, orange KOH reaction, and the costa covered by bulging, quadrate cells on the ventral surface, with numerous guide cells in 3 layers but lacking ventral stereids. It shares these characters with *D. xanthocarpus,* but the two are readily separated by a number of features (Figure 1). One of the most prominent is the difference in the basal leaf cells. These are strongly differentiated, elongate and narrow in *D. xanthocarpus*, extending to about a $\frac{1}{4}$ of the leaf length. In many specimens they form a weak, often orange, shiny sheath that is easily seen with a hand lens. In *D. fuscus* the basal cells are scarcely differentiated (often only juxtacostally) and usually quadrate to short-rectangular. In addition, the costa is usually excurrent as a stout point in *D. fuscus* (rarely percurrent in some leaves), whilst in *D. xanthocarpus* it is typically percurrent. Furthermore *D. xanthocarpus* has larger leaves with a more rectangular base and the margins broadly recurved to revolute rather than narrowly recurved.

In South Africa, the species occurs only in the winter-rainfall area (Figure 2), where it is restricted almost entirely to nutrient-rich soils derived from shale in Succulent Karoo (vegetation types follow Mucina & Rutherford, 2006). Exclusion from fynbos is likely an edaphic phenomenon, as this vegetation type usually

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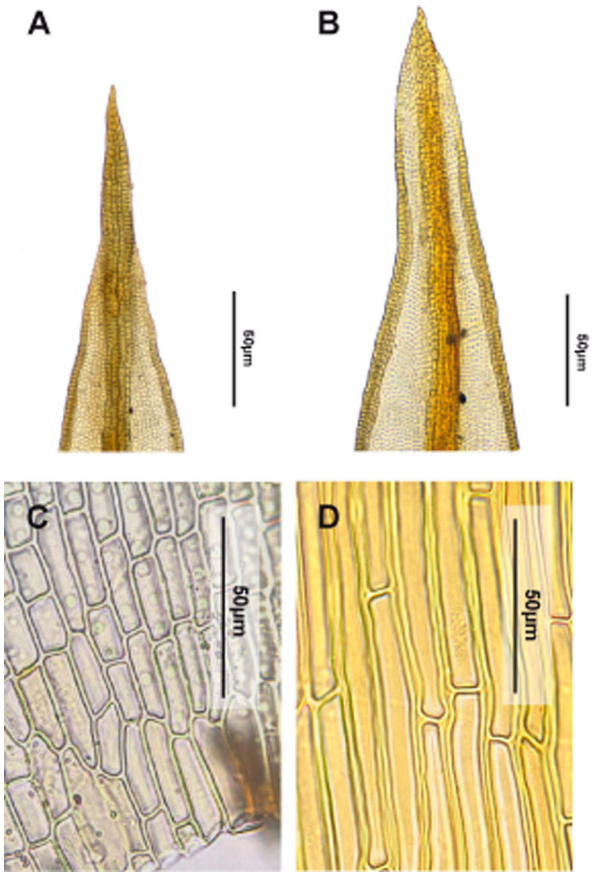

Figure 1 Comparison of leaf apices and basal cells of *Didymodon fuscus* (A, C) and *D. xanthocarpus* (B, D). (A) and (C) from *Hedderson 17060* (BOL), (B) and (D) from *Hedderson 16443a* (BOL).

occurs on nutrient-poor quartzitic sandstones; soils derived from these tend to be extremely sandy and loose, with very poor development of soil crust communities as a result of frequent burial and disturbance. The only fynbos type in which the species is recorded is the Limestone Fynbos of the southern coastal plain where nutrient levels are more similar to those of shale-derived soils, and the substrate is more stable.

As currently known, *Didymodon fuscus* exhibits a disjunctive distribution between the winter-rainfall (Mediterranean climate) areas of South Africa and South America. Whilst disjunctions between Africa and South America are fairly common and well documented, these usually involve tropical forest, grassland, or alpine species (e.g. Delgadillo, 1993). The Cape winter-rainfall bryophyte flora, and especially that of Succulent Karoo and Renosterveld vegetation types, rather exhibits strong links with that of Australia, and many species, or pairs of sister species, are disjunct between these two areas (see for e.g. Magill, 1981; Hedderson, 2012). More rarely, as in the case of *Triquetrella* Müll.Hal. (Hedderson & Zander, 2007) genera have representatives in all five of the world's main Mediterranean climate regions. This is the first example that we know of where a disjunction is shared between South America and Africa to the exclusion of the other winter-rainfall areas. The Cape winter-rainfall mega-niche is thought to be relatively recent (2–5 mya), and most clades within it appear to have begun diversification within the last 0.5–2.5 million years (Klak *et al.*, 2004; Hedderson & Zander, 2007). Thus the disjunction documented here is likely to be a recent one and the result of long-distance dispersal. Molecular data could help establish a time line for its establishment and also determine the extent and direction of ongoing gene flow between the two regions.

The addition of *D. fuscus* brings the total number of *Didymodon* species recorded from South Africa to seven. However, *Didymodon jackvancei* (≡ *Husnotiella plicata* Magill) is gametophytically indistinguishable from *D. tophaceus*, and in our opinion represents a gymnostomous form of that species. We propose the following synonymy:

Didymodon tophaceus (Brid.) Lisa, Elenc. Musch. 31. 1837. *Trichostomum tophaceum* Brid., Muscol. Recent. Suppl. 4: 84. 1818 [1819].

Type: [Germany]. 'Comburgi', February 1808, [sine collector] (lectotype, designated by Jiménez *et al.*, 2005, Hb. Bridel in B!).

= *Husnotiella plicata* Magill, Fl. S. Africa, Bryophyta 1: 222. 1981. ≡ *Didymodon jackvancei* R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 162. 1993, *syn. nov.* **Type:** 'Lesotho. 1 km E of Taung, 210 km E of Maseru along Mountain Road, in small canyon above the Orange River', 1 December 1977, *R.E Magill 4216* (holotype, PRE!; isotypes: H!, MO, NY).

The remaining six species can be separated by the following key:

Key to South African species of *Didymodon*:

1. Ventral cells of the costa in upper leaf elongated . . . . . *D. tophaceus*
1. Ventral cells of the costa in upper leaf short rectangular to quadrate 2
2. Basal laminal cells hyaline, very thin-walled, usually bulging; leaf margins bistratose in 1-several rows above midleaf 3
2. Basal laminal cells not hyaline, slightly to strongly thick-walled, not bulging; leaf margins unistratose, very rarely bistratose above midleaf 4
3. Leaves long-lanceolate; basal marginal cells clearly differentiated, long-rectangular to elongate in 2–6 rows; stems with hyalodermis . . . . . *D. umbrosus*
3. Leaves oblong-lanceolate to lanceolate, ovate or triangular; basal marginal cells not or weakly differentiated, quadrate to shortly rectangular; stems without hyalodermis or occasionally present in patches . . . . . *D. australasiae*
4. Leaves lingulate to widely ovate-lanceolate, apex obtuse or rounded; costa ending several cells

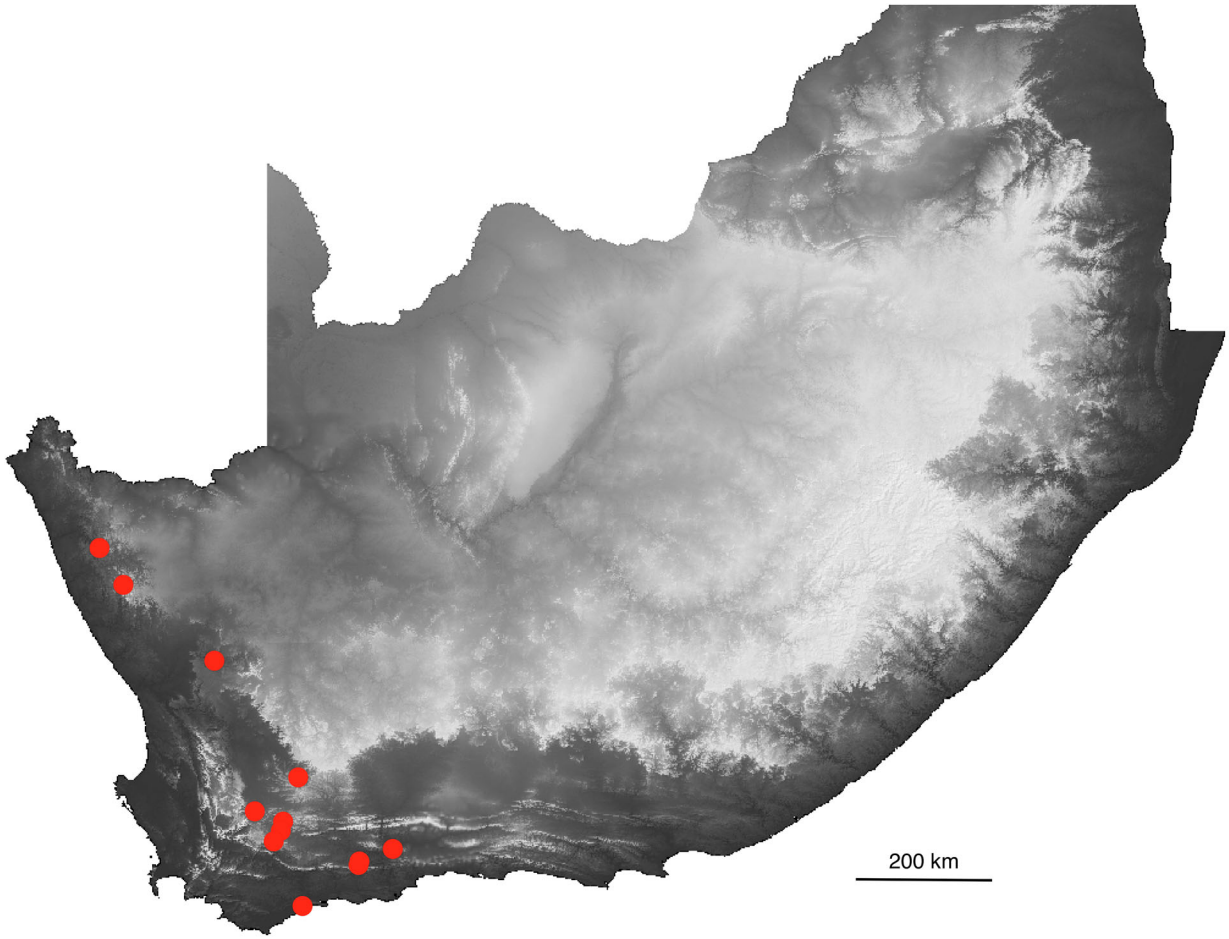

Figure 2 Map of South Africa and Lesotho showing the African distribution of *Didymodon fuscus*.

below the apex; upper and middle laminal cells flat . . . . . *D. tophaceopsis*

4. Leaves lanceolate or oblong-lanceolate, apex acute; costa percurrent or excurrent; upper and middle laminal cells bulging 5
5. Leaves oblong-lanceolate or long-lanceolate, apex mucronate, leaf margins broadly revolute; costa percurrent or rarely weakly excurrent; basal laminal cells clearly differentiated from the rest, elongate, reaching to *ca* 1/4 leaf length . . . . *D. xanthocarpus*
5. Leaves lanceolate, apex not mucronate, leaf margins narrowly recurved; costa usually excurrent; basal laminal cells not or weakly differentiated from the rest, quadrate to shortly rectangular . . . *D. fuscus*

South African specimens of *Didymodon fuscus* seen: All at BOL unless otherwise indicated. See Figure 2.

Northern Cape Province: Namaqualand, Spektakelberg 23.4 km W of Springbok, 2917DA, 13 September 1977, *E. A. Schelpe 7733*; Namaqualand, Kamieskroon area on road to Liliefontein, near top of Kamiesberg Pass, 30°11′17″S, 17°59′01″E, 3017BB, 1030 m, 29 September 2007, *T. A. J. Hedderson 16553*; Niewoudtville, 22 km NE of town on road to Loeriesfontein, 11 April 1978, *D. S. Hardy 4311* (MO); Along the R356 between Sutherland and Ceres, 32°44′06.4″S, 20°21′40.5″E, 3220CB, 700 m, 22 June 2006, *T. A. J. Hedderson 16095*. **Western Cape Province:** Along the R356 between Sutherland and Ceres, just after Karoo Poort, 33°11′04″S, 19°46′15″E, 3319BB, 680 m, 09 September 2009, *T. A. J. Hedderson 17060*; Touwsrivier District, Pienaarskloof, Karookop, 33°13′15.7″S, 20°09′20.9″E, 3320AA, 930 m, 08 September 2011, *T. A. J. Hedderson 17748*; Worcester District, Touwsrivier, farm de Bron, dry Slangrivier gully, August 1977, *D. S. Hardy 4245* (MO); Touws Rivier area, road from R318 to Nougaspoort, at Drie Kuilen, 33°34′55.3″S, 20°01′41.6″E, 3320CA, 1025 m, 22 September 2013, *T. A. J. Hedderson 18474*; Calitzdorp area, Rooiberg Pass, 33°40′55″S, 21°38′49″E, 3321DA, 790 m, 03 September 2007, *T. A. J. Hedderson 16473c*; Doornkloof Farm, *ca* 48 km south of Ladismith on the Ladismith-Riversdale road, 33°50′52″S, 21°11′38″E, 3321CC, 01 July 2001, *M. T. Hoffman UCT03;* Southern Little Karoo, dirt road from R323 to Barrydale, near edge of Grootvadersbosch (Thornhill) WWF reserve, 33°53′38″S, 21°10′53″E, 3321CC, 380 m, 03 September 2007, *T. A. J. Hedderson 16474*; De Hoop Nature Reserve, road from cottages to entrance, 34°26′11.8″S, 20°25′10.1″E, 3420AD, 55 m, 23 August 2009, *T. A. J. Hedderson 17033*.

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Taxonomic Additions and Changes: *Didymodon tophaceus* (Brid.) Lisa (*Husnotiella plicata* Magill, *syn. nov.*).

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