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Reinstatment of species rank for *Didymodon gelidus* (Bryophyta, Pottiaceae)

Juan A. JIMÉNEZ[a*] *& Ryszard OCHYRA*[b]

[a]*Departamento de Biología Vegetal (Botánica), Facultad de Biología, Universidad de Murcia, Campus de Espinardo, 30100-Murcia, Spain*

[b]*Department of Bryology, Institute of Botany, Polish Academy of Sciences, ul. Lubicz 46, 31-512 Krakow, Poland*

Abstract – The Antarctic subendemic moss species *Didymodon gelidus* Cardot has been considered to be identical to the Holarctic *D. brachyphyllus* (Sull.) R.H.Zander. On the basis of a detailed analysis of the type and very many non-type specimens of the two species, the reinstatement of species rank for *D. gelidus* is proposed. Diagnostic characters of *D. gelidus* and its distinction from some closely related species, with which it may be confused, are discussed and illustrated. The species that shares all taxonomically important characters with *D. gelidus* is the Antarctic endemic *Barbula byrdii* E.B.Bartram and consequently the names of these two species are considered synonymous, the former having priority.

Antarctica / *Didymodon* / distribution / endemism / Îles Kerguelen / Musci / South Georgia / Subantarctica / taxonomy

INTRODUCTION

Didymodon Hedw. is one of the most diverse genera of Pottiaceae, with approximately 126 species, that are represented on all continents in a wide range of habitats (Zander, 1993, 2007). Its large number of species, extensive distribution and high degree of morphological variation make this genus taxonomically complex. At present, no monograph of the whole genus exists and only some regional taxonomic revisions have been published for some areas in the Northern Hemisphere, including China (Li *et al.*, 2001), Central America (Allen, 2002), Europe, North Africa, Southwest and Central Asia (Jiménez, 2006), and North America (Zander, 1994, 2007). In contrast, the knowledge of the genus in the Southern Hemisphere is less refined and many species are still poorly understood, since so far there are only two regional treatments of the genus available for southern Africa (Magill, 1981) and Antarctica (Ochyra *et al.*, 2008a).

In the austral polar regions the genus *Didymodon* is poorly represented and actually only one species, *D. gelidus* Cardot, has long been known from this biome, being described by Cardot (1907) from a single collection made by the British National Antarctic Expedition of 1901-1904 under the leadership of Robert F. Scott on the ship *Discovery*. The material was found in Granite Harbour (77°00′S, 162°35′E), a bay located on the coast of Southern Victoria Land in the Ross Sector

* Corresponding author: jajimene@um.es

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of continental Antarctica. Cardot (1907) provided a brief description and illustrations of the new species and compared it to the northern *D. luridus* Hornsch., from which it should differ in its smaller size, plane or slightly recurved leaf margins and more lax basal cells.

For nearly a century *Didymodon gelidus* has not been taxonomically assessed and was treated to be an Antarctic endemic (Seppelt & Green, 1998; Ochyra *et al.*, 1998; Ochyra, 1998), but finally it was considered to be conspecific with the northern *D. brachyphyllus* (Sull.) R.H.Zander (Zander & Ochyra, 2001). This taxonomic conclusion established *D. brachyphyllus* as a bipolar species, which outside the Antarctic has a wide but scattered distribution in western North America north of Mexico, extending from Alaska to California, Arizona and New Mexico (Zander, 2007), and with some scattered occurrences elsewhere in the Northern Hemisphere, including Mexico (Zander, 1994), Greenland (Zander, 2007), Europe (Jiménez, 2006), and Russia (Afonina *et al.*, 2010).

Didymodon brachyphyllus has been recorded from numerous localities in the maritime Antarctic where it occurs on the Antarctic Peninsula and in the adjacent peri-Antarctic archipelagoes, whilst in continental Antarctica it is very rare. So far, it has been found only in Southern Victoria Land from whence it was described as *D. gelidus* (Cardot, 1907; Seppelt & Green, 1998) and in Marie Byrd Land. The material from the latter area was originally described by Bartram (1938) as a separate species, *Barbula byrdii* E.B.Bartram, which was subsequently considered identical to *D. brachyphyllus* (Zander & Ochyra, 2001) and this taxonomic conclusion was later supported by Sollman (2016). Outside the Antarctic *D. brachyphyllus* is exceedingly rare in the austral polar region and hitherto it is known only from subantarctic South Georgia (Blockeel *et al.*, 2005) and Îles Kerguelen (Ellis *et al.*, 2015).

The other species of *Didymodon* discovered in the austral polar region was *Didymodon austroalpigenus* (Müll.Hal.) Broth. from Îles Kerguelen which was originally described from this archipelago as *Trichostomum austroalpigenum* Müll. Hal. (Müller, 1883, 1889). However, this species proved to be conspecific with *Bryoerythrophyllum rubrum* (Jur. *ex* Geh.) P.C.Chen. Accordingly, the genus *Didymodon* is currently represented in the cold regions of the Southern Hemisphere by two species, namely *D. brachyphyllus* whose distribution was described in detail above and *D. australasiae* (Hook & Grev.) R.H.Zander which is known from only a single station from South Georgia (Blockeel *et al.*, 2007; Sollman, 2016).

In the context of a worldwide taxonomic revision of *Didymodon* carried out by the first author, the types of *D. gelidus*, *D. brachyphyllus* and *Barbula byrdii* were re-examined, along with numerous non-type collections of these species deposited at AAS, BM, CAS, FH, ICEL, KRAM, MUB, NY, PC, S, UB and UBC.

RESULTS AND DISCUSSION

At first sight, the Antarctic specimens designated as *Didymodon brachyphyllus* appear to be very closely similar to those from the Northern Hemisphere. However, a careful study of this material revealed that the Antarctic plants exhibited a suite of characters which do not fit well with the northern plants of *D. brachyphyllus* and should be reinstated as a distinct species.

All populations of *Didymodon gelidus* are sterile but the species is well characterised by a set of gametophyte characters. These include (*1*) dense turfs with

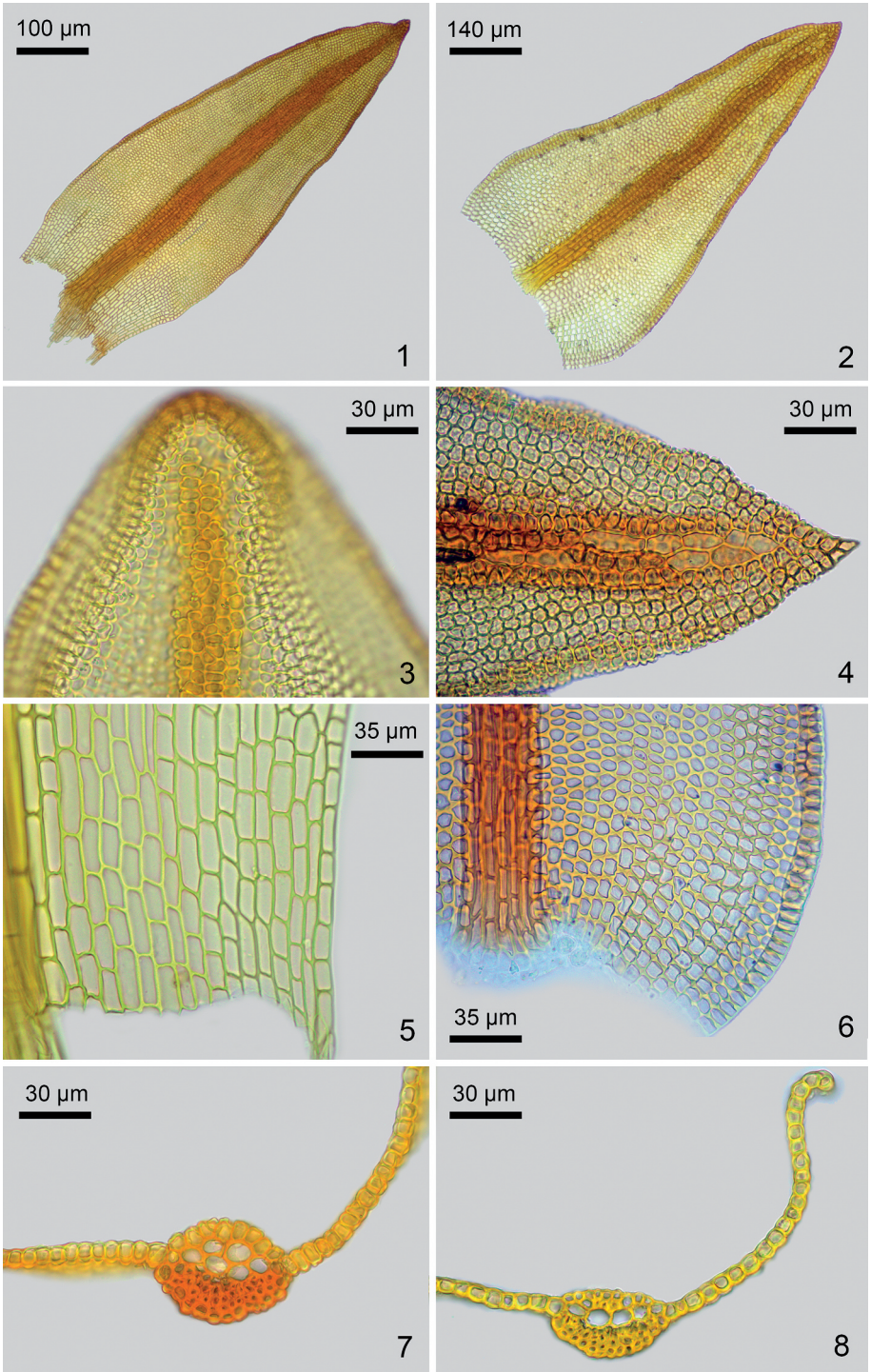
a reddish cast; (*2*) ovate, ovate-lanceolate or oblong-lanceolate leaves (Fig. 1) that are appressed and slightly incurved distally when dry; (*3*) an obtuse or widely acute, usually cucullate leaf apex; (*4*) unistratose leaf margins, weakly recurved in the upper two thirds, sometimes strongly recurved at the leaf apex and giving it a thick appearance; (*5*) unistratose lamina with a reddish orange colour in KOH; (*6*) subpercurrent costa, usually ending several cells below the apex (Fig. 3) which is rather broad and adaxially protuberant and papillose (Fig. 3), in transverse section rounded, with 2-3 layers of guide cells, lacking adaxal stereids and with an adaxial costal pad of papillose cells (Fig. 7); (*7*) slightly bulging and papillose upper and middle laminal cells, becoming shortly rectangular to rectangular and lax, smooth, and evenly thin-walled in the basal part (Fig. 5); (*8*) numerous multicellular gemmae present in the leaf axils.

Didymodon gelidus is a little variable species, although it is worth noting that the specimens from subantarctic South Georgia and Îles Kerguelen have larger leaves (up to 1.7 mm long) and much thickened costae (up to 110 μm wide at the base) than other specimens examined, but their key diagnostic characters remain stable. A complete description and illustrations of *D. gelidus* (as *D. brachyphyllus*) are provided by Ochyra & Zander (2002) and Ochyra *et al.* (2008a).

Didymodon brachyphyllus and *D. gelidus* share some morphological features such as the overall appearance, reddish coloration, the size, shape and papillosity of the upper and middle laminal cells, colour of the lamina with KOH, and production of axillary gemmae. However, *D. brachyphyllus* can be separated from *D. gelidus* by its (*1*) ovate to ovate-triangular leaves that are shortly acuminate (Fig. 2); (*2*) leaf apices that are usually apiculate by one or more conical cells (Fig. 4); (*3*) semicircular costa in transverse section, lacking an adaxial costal pad of cells and generally with 1 layer of guide cells and a small adaxial stereid band (Fig. 6); and (*4*) quadrate, oblate or shortly rectangular basal laminal cells with transversely thick-walled, especially towards the margins (Fig. 8).

Nevertheless the best character for distinguishing *Didymodon brachyphyllus* is the absence of adaxial surface cells of the costa below the apex and the differentiation of rectangular cells in the channeled apex, which are visible as an area of hyaline and smooth cells (Fig. 4). This feature is characteristic of the *Didymodon* section *Vineales* (Steere) R.H.Zander, recently elevated to genus rank as *Vinealobryum* R.H.Zander (Zander, 2013), to which *D. brachyphyllus* belongs, and it is also diagnostic in other groups of Pottiaceae such as *Erythrophyllopsis* Broth. (Cano *et al.*, 2010). In contrast, *D. gelidus* has a superficial layer of cells on the adaxial surface of the costa below the apex, and therefore hyaline cells are not visible (Fig. 3). This character excludes a close relationship of the two species.

Zander and Ochyra (2001) considered *Barbula byrdii* as a synonym of *Didymodon brachyphyllus*. This name refers to a species described by Bartram (1938) from Marie Byrd Land on the basis of the specimens collected during the American Second Byrd Antarctic Expedition of 1934. In a short discussion Bartram (1938) stated that he could know of "no species in particular with which these plants [of *Barbula byrdii*] might be closely compared" but he evidently overlooked *D. gelidus*. The holotype and several paratypes of *B. byrdii* are entirely sterile but they perfectly match the type material of *D. gelidus* in the overall appearance of the plants and all details of leaf morphology and anatomy. Accordingly, *B. byrdii* was considered conspecific with *Didymodon brachyphyllus* along with *D. gelidus* (Zander & Ochyra, 2001). Because the latter is now treated as a species of its own, *B. byrdii* and *D. gelidus* must be regarded synonyms, the latter name having priority.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Didymodon gelidus Cardot

In F.J.Bell, *Nat. Antarct. Exped 1901-04, Nat. Hist.* 3 *Musci*: 4, *pl. 1, f. 1-11*. 1907. **Type citation:** [Antarctica, Southern Victoria Land] Granite Harbour, Jan. 20, 1902. **Lectotype** (*vide* Ochyra *et al.* 2008a: p. 335): "Herb. J. Cardot. Didymodon (?) gelidus Card. sp. nova. Terre Victoria: Granite Harbour, L. S. 77º. Exped. de la Discovery, 20 janvier 1902" – PC!; **isolectotypes**: BM!, S!

Barbula byrdii E.B.Bartram, *Ann. Missouri Bot. Gard.* 25: 720. 1938 ≡ *Bryoerythrophyllum byrdii* (E.B.Bartram) R.H.Zander, *Bull. Buffalo Soc. Nat. Sci.* 32: 115. 1993. **Type citation:** [Antarctica] Marie Byrd Land, Edsel Ford Range, Lichen Peak, *P. Siple & S. Corey G. 51a*. **Lectotype** (*vide* Ochyra *et al.* 2008a: p. 335): "Byrd Antarctic Expedition II Mosses of Marie Byrd Land, Antarctica No. G Type Barbula Byrdii Bartr. sp. nov. Locality: Mt. 73 Collected by: Paul A. Siple Determined by: Edwin B. Bartram" – FH-Bartram!; **isolectotypes**: AAS!, BM!, NY!), ***syn. nov.***

Didymodon cardotii (Dusén) R.H.Zander, a rare and poorly known taxon from eastern Patagonia of Argentina (Chubut and Santa Cruz provinces), appears to be rather closely related to *D. gelidus*. Both species share a similar leaf shape and areolation, colour of the lamina with KOH, the anatomical structure of the costa, the papillosity of the upper and middle laminal cells, and the presence of gemmae in the leaf axils. However, *D. cardotii* differs from *D. gelidus* by having revolute leaf margins from apex to base and a shortly excurrent costa.

Didymodon australasiae is the second species of the genus reported from the Antarctic region where it is only known from the subantarctic island of South Georgia (Blockeel *et al.*, 2007). Although it is rather a non-descript species, it can be recognised easily from *D. gelidus* by its crisped, twisted or incurved leaves when dry, bistratose distal leaf margins and hyaline basal laminal cells which are clearly differentiated.

Didymodon gelidus is superficially similar to small forms of any of the three species of *Bryoerythrophyllum* P.C.Chen reported from the Antarctic, namely *B. antarcticum* (L.I.Savicz & Smirnova) P.Sollman, *B. rubrum* and *B. recurvirostrum* (Hedw.) P.C.Chen (Sollman, 2015). *Bryoerythrophyllum antarcticum* is the easiest to confuse with to *D. gelidus*. The two species occur in the same habitats and sometimes they are found in mixed stands in the same turfs. In addition, *B. antarcticum* like *D. gelidus* may have ovate leaves with an obtuse or widely acute leaf apex, weakly recurved and edentate leaf margins and a subpercurrent costa. Nevertheless, the three species of *Bryoerythrophyllum* are readily distinguishable from *D. gelidus* by their entirely hyaline axillary hairs and C-shaped papillae on the upper laminal cells.

Another species with which *Didymodon gelidus* could be confused is *Ceratodon purpureus* (Hedw.) Brid. The latter species shows high variability in size, leaf shape and aerolation, excurrency of the costa and curvature of the leaf margins in the Antarctic (Ochyra *et al.*, 2008a). Additionally, it has axillary hairs with brown basal cells like *Didymodon* species. Some of these phenotypes with ovate leaves, obtuse leaf apices, weakly recurved leaf margins and subpercurrent costa may imitate *D. gelidus*, but they are immediately distinguished by their epapillose laminal cells and the clear yellow colour of the lamina in KOH.

◀ Figs 1-8. **1, 3, 5, 7.** *Didymodon gelidus* Cardot (isolectotype, BM). **1.** Leaf. **3.** Leaf apex, adaxial side. **5.** Basal laminal cells. **7.** Cross-section of the leaf. **2, 4, 6, 8.** *Didymodon brachyphyllus* (Sull.) R.H. Zander (isolectotype, BM). **2.** Leaf. **4.** Leaf apex, adaxial side. **6.** Basal laminal cells. **8.** Cross-section of the leaf.

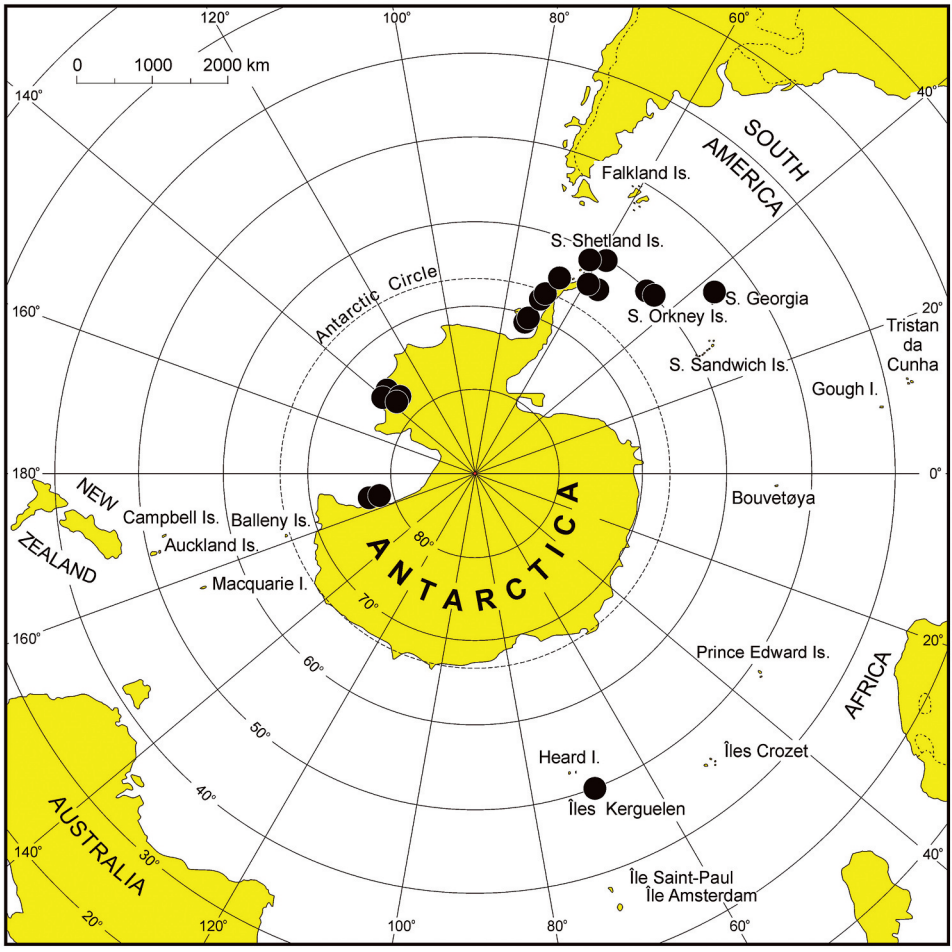

Fig. 9. Known geographical distribution of *Didymodon gelidus*.

PHYTOGEOGRAPHICAL IMPLICATIONS

The reinstatement of *Didymodon gelidus* as a distinct species in its own right does not affect directly species richness of the moss flora of Antarctica since it is merely a replacement of a species with a different phytogeographical status. Since the publication of the handbook of Antarctic mosses, in which 111 species and two varieties have been recorded from this biome (Ochyra *et al.*, 2008a, b), four species have been added to the moss flora of Antarctica (Ellis *et al.*, 2013a, b; Sollman, 2015), so currently it consists of 115 species and two varieties.

Didymodon gelidus was initially considered as one of the few endemic mosses present in Antarctica (Ochyra *et al.*, 1998; Seppelt & Green, 1998). However, it changed its phytogeographical status for a bipolar species as a result of its conspecificity with *D. brachyphyllus*. Until now only twelve species had been

accepted as Antarctic endemics which are classified into four subelements (Ochyra *et al.*, 2008a; Sollman, 2015). Initially, *D. gelidus* was included within the pan-Antarctic subelement, along with *Bryoerythrophyllum antarcticum* and *Syntrichia sarconeurum* Ochyra & R.H.Zander, which are widespread in both West and East Antarctica. However, at present it must be considered as an Antarctic subendemic penetrating into the Subantarctic where its currently known geographical range covers South Georgia and Îles Kerguelen. This distribution pattern was formerly designated as Antarctic-South Georgian subelement and it was exhibited by four species of moss only (Ochyra *et al.*, 2008a). Discovery of *Didymodon gelidus* in Îles Kerguelen indicate that some Antarctic species are not restricted in their distribution to subantarctic South Georgia only but may have a wider distribution in the Subantarctic and therefore it seems wiser to rename this distribution pattern for an Antarctic–Subantarctic subelement. A similar type of distribution shows also the liverwort *Hygrolembidium ventrosum* (Mitt.) Grolle which, however, is absent from South Georgia (Ochyra & Váňa, 1989a, b; Bednarek-Ochyra *et al.*, 2000).

Didymodon gelidus is widely distributed, but not abundant, throughout the continental and maritime Antarctic (Fig. 9). It has maximum occurrence in the West Antarctic where it occurs along the western coast of the Antarctic Peninsula, ranging from the Danco Coast to central Alexander Island and the adjacent archipelagoes of the South Shetland Islands and South Orkney Islands. Moreover, it is relatively frequent in the James Ross Island group on the northern part of the eastern Antarctic Peninsula (Ochyra *et al.*, 2008a). In continental Antarctica, *D. gelidus* is very rare and so far it is known only from Southern Victoria Land from whence it was described (Cardot, 1907; Seppelt & Green, 1998) and Marie Byrd Land where it was recorded at several stations and the material was originally described as *Barbula byrdii*. The record of *D. gelidus* from Cape Hallett on the Borchgrevink Coast in Northern Victoria Land (Ochyra & Zander, 2002; Ochyra *et al.*, 2008a) is based upon the misdetermined material.

It is likely that *Didymodon gelidus* may have a wider distribution, possibly occurring in suitable places in the southernmost parts of South America. The species prefers dry to moist sites in a wide range of habitats. It usually grows on rocks with accumulated soil, sheltered soils and volcanic ash and more detailed information can be found in Ochyra *et al.* (2008a).

Selected specimens examined.

SUBANTARCTICA. **SOUTH GEORGIA**. Scree slope below Pirner Point, on south side of Whale Valley, *ca* 350 m, 31 January 1972, *Bell 1160* (AAS, KRAM, MUB). **ÎLES KERGUELEN**. Golfe Du Morbihan, Presqu'île Jeanne d'Arc, north-westernmost part of the peninsula, an unnamed stream north of le Dôme Rouge, debouching into Baie des Swains at the base of Halage des Swains, *ca* 45 m, 5 December 2006, *Ochyra 1481/06* (KRAM, MUB).

ANTARCTICA. **WEST ANTARCTICA**. South Orkney Islands. ***Signy Island***. Jebsen Rocks, 1976-1977, *Lewis Smith 1793* (BM); south of North Point, 50 m, 29 September 1966, *Lewis Smith 655* (AAS, KRAM); W side of Stygian Cove, *ca* 30 m, 10 January 1966, *Lewis Smith 492 & 661* (AAS, KRAM). South Shetland Islands. ***King George Island***. Admiralty Bay, Klekowski Crag between Lange Glacier and Polar Committee Glacier, 110 m, 20 February 1980, *Ochyra 2286A/80* (KRAM). ***Deception Island***. NE Neptunes Windows, *ca* 60 m, 9 December 1964, *Longton & Lewis Smith 868* (AAS, KRAM); Whalers Bay, Ronald Hill, above the destroyed British Station, 40 m, 20 March 1980, *Ochyra 2785/80* (BM, KRAM); Whalers Bay, foundations of building at N end of site of former BAS station, 5-6 m, 3 February 2005, *Lewis Smith 11919A* (AAS, KRAM); west side of Ronald Hill, 25 m, 12 March 1987, *Lewis Smith 5778B* (AAS, KRAM); lower slopes of Ronald Hills, 22 December 1960, *Taylor 252b* (KRAM); Port Foster, Pendulum Cove, Mooring Post, south

of the destroyed Chilean Station, 10 m, 20 March 1980, *Ochyra 2790/80* (BM, KRAM); E face of N summit of Mt. Pond, 480 m, 22 March 1987, *Lewis Smith 5820B* (AAS, KRAM); N of Spindrift Rocks, 8 March 1989, *Lewis Smith 8062B* (AAS, KRAM); Whales Bay, 65 m, 10 January 2015, *Bordin & Fechina 2535* (MUB, UB). ***Livingston Island***. Hurd Peninsula, in the vicinity of Juan Carlos I Station, February 1992, *Schulz s.n.* (KRAM 219437). WEST ANTARCTIC PENINSULA. **Graham Coast**. Cape Tuxen, 15 m, 26 November 1964, *Corner 676* (AAS, KRAM); Argentine Islands, Skua Island, north coast, *ca* 8 m, 7 March 1965, *Longton 1335* (AAS, KRAM). **Loubet Coast**. North side of Léonie Island, 25 m, 16 February 1995, *Lewis Smith 8940* (AAS, KRAM). **George VI Sound**. ***Alexander Island***. Northern part of Waitabit Cliffs, *ca* 10 miles south of Fossil Bluff, *ca* 165 m, 21 March 1962, *Taylor 512* (AAS, KRAM). EAST ANTARCTIC PENINSULA. **James Ross Island Group**. ***Vega Island***. N end of False Island Point, 25-40 m, 4 February 1989, *Lewis Smith 7842* (AAS, KRAM). ***James Ross Island***. Terrapin Hill, 540 m, *Lewis Smith 7714* (AAS, KRAM); E side of Lachman Crag, 3-50 m, *Lewis Smith 7330 & 7384* (AAS, KRAM). ***Cockburn Island***. Between Adelie colony and foot of cliff, 120 m, *Lewis Smith 7914* (AAS, KRAM). **EAST ANTARCTICA**. VICTORIA LAND. **Scott Coast**. Granite Harbour, 20 Jan 1902, *Discovery Expedition s.n.* (BM, PC, S – type of *Didymodon gelidus*); Cape Roberts, *Steere & Greene 65020* (AAS, KRAM). MARIE BYRD LAND. **Saunders Coast**. ***Edsel Ford Ranges***: Lichen Peak, *Siple & Corey G* (AAS, BM, FH, NY - type of *Barbula byrdii*); Skua Gull Peak, *Siple & Corey 1A, 4, 8 & 99A* (FH, NY); Mt. Donald Woodward, *Siple, Wade, Corey & Standcliff 97* (FH, NY); Mt. Marujupu, *Perkins 129A* (FH, NY).

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