

Notes from the BBS Workshop on *Didymodon*, 2018

Tom Blockeel and Jan Kučera summarise the presentations to last year's BBS workshop on this tricky genus

At the BBS *Didymodon* Workshop held at Leicester Botanic Garden in October 2018, Jan Kučera (University of South Bohemia) made a series of presentations about the genus, including the European as well as British and Irish species. Some species of the genus have not been well understood in these islands and have been mis-recorded. At the same time molecular studies, including many by Jan himself, have clarified some problems and revealed many new ones. In this note we summarise some of the key points from the Workshop, especially concerning the British and Irish species, in the hope that it will help with identification and provide some general background to the current state of our knowledge.

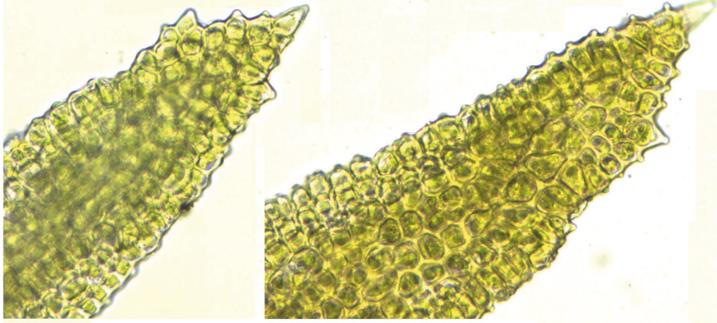
Introductory comments

Molecular analysis has shown that the definition of the genus *Didymodon* in the important paper on Japanese Pottiaceae by Saito (1975) and subsequently in the account of the genera of Pottiaceae by Zander (1993) is essentially correct, while the more recent segregation of the genera *Geheebia*, *Vinealobryum*, *Exobryum*,

Fuscobryum, and the re-establishment of *Trichostomopsis*, as proposed by Zander (2013), are essentially unnecessary or unsupported. JK's own data indicate that the genus is monophyletic only if certain other genera are included in it (e.g. *Tridontium*). The European species fit into five lineages that are fairly well defined morphologically. These lineages are best treated as sections of a single genus, rather than distinct genera, because (1) some species do not make a good fit morphologically with the species to which they are most closely related phylogenetically, and (2) the well-known and generally accepted sections that we describe here form together a monophyletic unit.

Many of the individual species of the genus are variable morphologically, and deviant specimens are occasionally found (unfortunately even quite regularly in certain species). Therefore a combination of characters is usually necessary to recognise a species morphologically. This makes it difficult to construct a reliable key to the species. In the following paragraphs, therefore, we provide some notes on the five sections of the genus, as well as the individual species.

Fig. 1. *Didymodon sinuosus*, showing denticulate leaf apices.



Note that sections of the costa are taken in the lower part of the leaf, at about 1/5 to 1/3 from the base.

Section *Rufiduli*

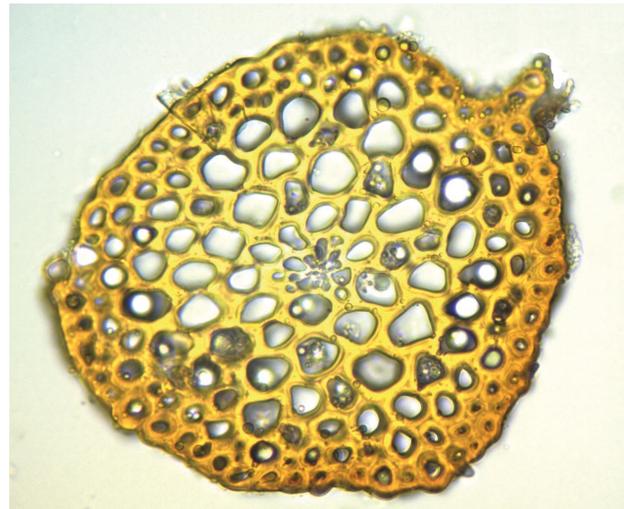
This section is characterised by the frequent presence of rufous coloration, lamina cells that are mammillose and bulging on both surfaces, and the common presence of vegetative means of propagation (e.g. fragile leaf laminae, swollen caducous leaf apices). *D. sinuosus* is the only British/Irish species of the section and is usually easy to identify because of a unique character, the presence of denticulate leaf apices (Fig. 1), best observed in young intact leaves. Even in older leaves the margins are notched and the lamina is usually fragile and broken. But be aware that other species may sometimes have broken leaves (e.g. *D. insulanus*).

Section *Fallaces*

Species of this section (*D. fallax*, *D. tophaceus* and related species) typically have keeled leaves that are often recurved when moist, and with a tendency to be arranged in three rows. The leaf base is often decurrent. The leaf cells of many species have angular/triangular lumens, and the ventral cells of the costa are elongate (except in *D. luridus*). The presence of rufous coloration is variable in this section.

D. ferrugineus and the rare *D. maximus*

have strongly squarrose-recurved leaves in which the 3-rowed arrangement is usually very distinct. The leaf base is decurrent and the margins are broadly recurved below. These characters are shared with *D. giganteus*, the type species of the genus *Gebeebia*, a species very similar in habit to *D. maximus*, but never recorded from Britain or



△Fig. 2. *Didymodon ferrugineus*: stem section with narrow central strand.

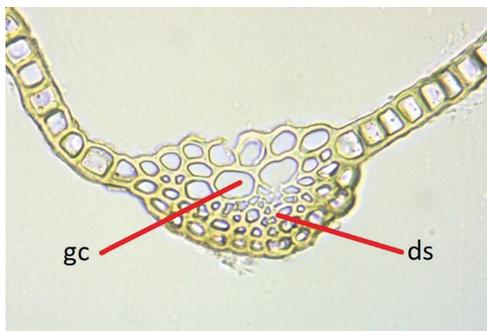
Ireland. Occasionally *D. ferrugineus* can be difficult to separate from *D. fallax*, but it differs in having a weak stem central strand (Fig. 2), and more distinctly decurrent leaves.

D. fallax and *D. spadiceus* have less markedly squarrose leaves that are not distinctly 3-ranked and not or hardly decurrent. The stem central strand is stronger than in *D. ferrugineus* (Fig. 3). The main distinctions between the two species are:

D. fallax: peristome twisted, leaves with recurved margins in the upper part, and archegonia shorter (mostly 400-500 μm).

D. spadiceus: peristome straight, leaves with plane margins in the upper part, and archegonia longer (mostly 700-800 μm).

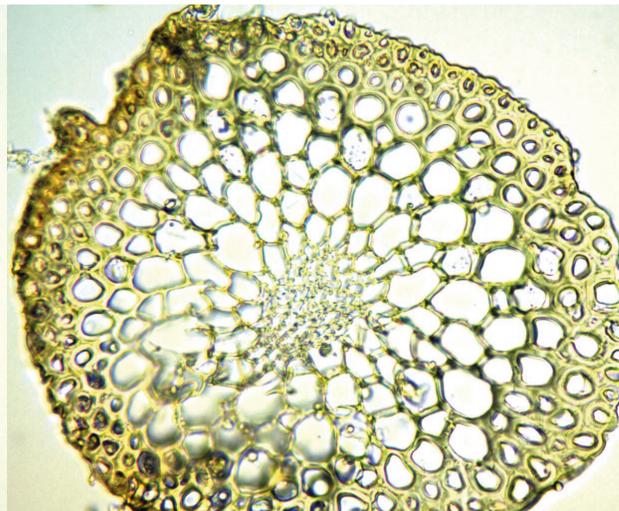
Molecular data have shown that *D. luridus* is the closest relative of *D. fallax* and *D. spadiceus*. This was unexpected because the ventral cells of



△Fig. 4. *Didymodon luridus*: section of costa with dorsal but not ventral stereids, and with a single row of guide cells (ds = dorsal stereids; gc = guide cells).

other species, e.g. *D. acutus*, *D. nicholsonii*, *D. vinealis*. The costa of *D. luridus* provides some useful diagnostic characters: it has only a single row of guide cells and lacks ventral stereids (Fig. 4), whereas there are two rows of guide cells in well-developed leaves of *D. nicholsonii* (Fig. 5) and often in *D. vinealis*, and ventral stereids are present in *D. acutus*.

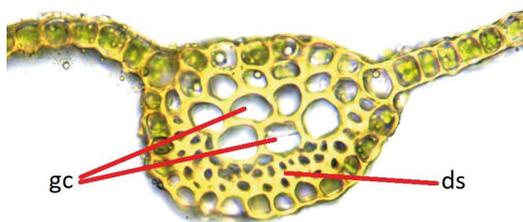
D. tophaceus is a variable and complex species, characteristic of moist substrates, and with extreme variability in the gametophyte and sporophyte. Typical forms have elongate cells on the ventral surface of the costa, as in *D. fallax*. Other characters include (1) costa typically (but not always) ending well below the apex, (2) leaf base clearly decurrent, (3) leaf cells with simple conical papillae. It is known to produce rhizoidal tubers, but they appear to be very rare. Large forms of *D. tophaceus* can be similar to *D. spadiceus*. The decurrent leaf base of *D. tophaceus* can be a helpful distinguishing character.



△Fig. 3. *Didymodon fallax*: stem section with wide central strand

the costa are isodiametric, and the leaves are not keeled. It is characterised by (1) costa percurrent or sometimes excurrent, without a ventral groove at the apex (compare section *Vineales*), (2) leaf margins narrowly and evenly recurved, (3) cells of lamina rounded, completely smooth, (4) perichaetial leaves obtuse, with the costa ceasing well below the apex. Often it has short, nearly triangular leaves, but some forms have longer, narrower leaves and can be confused with

▽Fig. 5. *Didymodon nicholsonii*: section of costa with dorsal but not ventral stereids, and with two rows of guide cells (ds = dorsal stereids; gc = guide cells).



Two closely related taxa are *D. sicculus* and *D. erosus*, recently reduced to subspecies rank under *D. tophaceus* (Kučera *et al.*, 2018). Both are likely to occur in Britain and Ireland but are not yet recorded here. Not all specimens can be identified confidently using morphological characters. *D. erosus* has (1) the ventral cells of the costa mostly isodiametric to shortly rectangular, (2) leaves tending to be eroded at the margin near the apex, (3) costa percurrent. It is less hygrophilous than *D. tophaceus*. *D. sicculus* also has the ventral cells of the costa mostly isodiametric to shortly rectangular but has somewhat broader leaves, similar in shape to *D. luridus*. The plants are mostly small with a rather narrow percurrent costa; they often grow on saline soils.

Section *Vineales*

This section includes *D. nicholsonii*, *D. vinealis* and related species. Typical characteristics of the section are (1) a reddish cell-wall coloration (particularly with KOH), (2) multiple leaf-cell papillae, (3) cells on ventral surface of costa quadrate, (4) costa lacking ventral stereids and with guide cells typically in 2 rows. Many of the species have a narrow groove on the ventral side of the costa at the leaf apex (Fig. 6), and a group of enlarged cells is often visible on the floor of the groove.

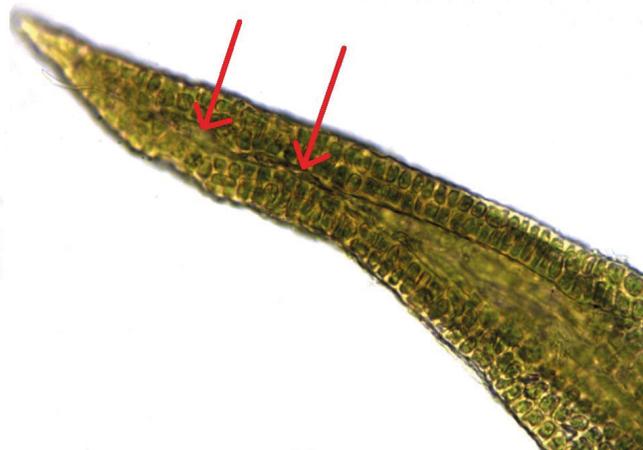
D. nicholsonii has bi- to multi-stratose leaf margins, and the leaf apex is usually boat-shaped. The leaves are sub-erect when moist and weakly curved when dry. It seems to vary little in Britain and Ireland, but it is morphologically very variable elsewhere. It can be distinguished from short-leaved forms of *D. rigidulus* (which has similar leaf margins) by the absence of ventral stereids in the costa and the presence of two or more rows of guide cells (Fig. 5), and it never has

axillary gemmae (they have been reported but their presence needs to be substantiated).

The *D. vinealis* aggregate is a nightmare! Serious taxonomic study into the delimitation of the species is needed and we can expect the description of additional taxa. *D. insulanus* is moderately well differentiated from the rest of the aggregate by (1) its denser leaf papillae and more opaque areolation, (2) the leaf margins not recurved in the upper part of the leaf, (3) the leaf section in the upper part keeled with the lamina straight (giving a V-shaped section). It tends also to have elongate cells on the dorsal surface of the costa. The curvature of the leaves is **not** a constant character separating it from *D. vinealis*; forms with straight leaves are common.

D. vinealis is what is left over in Britain and Ireland after the separation of *D. insulanus*. It is extremely variable morphologically, though less so in these islands than in other parts of Europe, and there are several more or less cryptic taxa. These include *D. eckeliae*, which has been

▽Fig. 6. *Didymodon vinealis*: leaf apex with ventral groove (arrowed).



recorded from Europe, although the use of this name for the European plants is probably incorrect. *D. vinealis* s.str. can be separated from *D. insulanus* by its less densely papillose leaf cells, the margins recurved in the upper part of the leaf, and the dorsal surface of the costa with quadrate cells. The leaves are typically straight (not curved) when moist. It has sometimes been confused with *D. acutus/icmadophilus* in Britain. The costa of the latter lacks a ventral groove at the apex of the leaf (Fig. 7) and has ventral stereids in section (Fig. 9), except in depauperate forms. *D. vinealis* lacks ventral stereids, or almost so.

Section *Asteriscium*

Formerly treated as a separate genus (*Trichostomopsis*), this section includes *D. umbrosus* and *D. australasiae*. It is characterised by (1) leaf margins bistratose, often tending to be erect, not recurved, (2) basal leaf cells thin-walled, hyaline, inflated, (3) costa with guide

▽ Fig. 7. *Didymodon icmadophilus*: leaf apex lacking ventral groove.



cells in multiple rows, (4) ventral stereids absent, (5) numerous rhizoidal tubers regularly present. Although Jiménez *et al.* (2005) reduced the number of species in *Trichostomopsis* to two, the taxonomy appears to be more complicated. *D. umbrosus* seems to be fairly clear-cut, but *D. australasiae*, as the molecular data suggest, is a complex of morphologically very similar taxa. The differentiating characters of *D. umbrosus* given by Jiménez *et al.* (2005) are (1) stems with a hyalodermis of thin-walled cells (lacking or almost so in *D. australasiae*), (2) marginal basal cells clearly differentiated, elongate, in 2-6 rows (not or weakly so in *D. australasiae*). The leaves of *D. umbrosus* are also said to have a narrower, long-lanceolate shape. However all these characters appear to be more variable than indicated by Jiménez *et al.*, and the identification of *D. australasiae* remains rather problematic. The relative frequency of the two species is not yet known in Britain, but the following specimens of *D. australasiae* have been confirmed by molecular analysis:

West Cornwall (vc 1): unshaded open sandy ground with patchy short vegetation by path near cliff top, Gwithian Towans, 15 m alt., SW57904155, D.T. Holyoak 04-481, 7 December 2004; Isles of Scilly, forming mat over gravel and low rocks at base of N.-facing wall of ruin, almost unshaded, St Mary's, near Hugh Town, Harry's Walls, SV90951092, D.T. Holyoak 03-71, 11 April 2003.

Carmarthenshire (vc 44): dirt zone of roadside verge, Dafen, Llanelli, SN53100107, B. Stewart, 17 January 2018.

Camlad moss

Mark Lawley found a strange moss by the R. Camlad in Montgomeryshire in 2015 (Lawley, 2016). Molecular analysis puts it as a sister

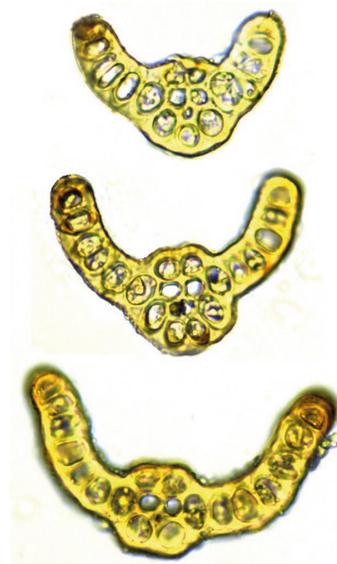
lineage to the genus *Tridontium*, which is nested in *Didymodon*. It appears to be an undescribed species, and its status as a native or introduced plant is unclear. It is a tiny moss with lingulate leaves rounded at the apex, growing on soil. It is very easily overlooked.

Section *Didymodon*

This is a large section, with many European species. The following features are characteristic of the section as a whole, but exceptions can be found to all of them in different species: (1) costa often excurrent, in cross-section with both ventral and dorsal stereids and only 1 row of guide cells (Fig. 9), (2) ventral cells of costa isodiametric in surface view, (3) leaf margins recurved evenly along most of the leaf length, (4) no rufous or reddish coloration, cell walls not red in KOH, (5) leaf-cell papillae mostly simple, (6) axillary gemmae often present.

D. rigidulus is generally well known to British and Irish bryologists. The leaves have bistratose margins and the apex tends to be elongate and subulate. The costa has ventral stereids, and axillary gemmae are commonly present. Molecular data indicate that it is not closely related to other species of the section, except perhaps *D. maschalogenus*. *D. nicholsonii* can be confused with short-leaved forms of *D. rigidulus* but differs in the absence of a ventral stereid band in the costa (Fig. 5).

Didymodon maschalogenus occurs in the Alps and southern Norway but is not yet known from Britain or Ireland. Its occurrence in southern Norway suggests that it might be found in Scotland. It resembles *D. rigidulus* and has numerous axillary gemmae but is clearly distinguished by the presence of elongate cells on the ventral surface of the costa and always unistratose leaf margins. A description with

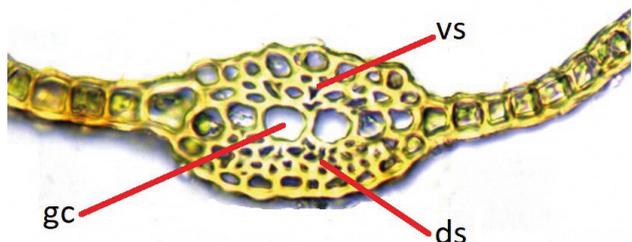


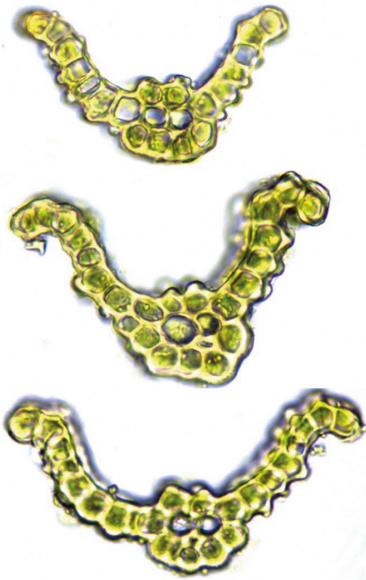
△Fig. 8. *D. acutus*: U-shaped upper leaf sections (leaf margins erect).

illustrations can be found in the paper by Köckinger & van Melick (2007), which can be read on-line free at <https://www.jstor.org/stable/20150235>.

Didymodon aff. *subandreaeoides* is a very interesting moss known only from Clogwyn du'r Arddu in Snowdonia (vc 49). It is discussed briefly in the paper on *D. subandreaeoides* by Kučera & Köckinger (2000). True *D. subandreaeoides* is not known in Britain or Ireland. It resembles *D. rigidulus* but lacks axillary gemmae and produces innovations with reduced cochleariform leaves. A detailed description can be found in Kučera

▽Fig. 9. *Didymodon icmadophilus*: section of costa with ventral and dorsal stereids, and one row of guide cells(ds = dorsal stereids; vs = ventral stereids; gc = guide cells).





△Fig. 10. *Didymodon icmadophilus*: upper leaf sections not U-shaped (leaf margins spreading or recurved); note also the papillose leaf cells.

& Köckinger's paper. The moss from Clogwyn du'r Arddu differs in the presence of axillary gemmae. It has innovations with reduced leaves, but they are not cochleariform, and it differs in other respects from *D. rigidulus*. It is distinct molecularly and is thought to be an undescribed species. It is still not known from any other localities.

Didymodon glaucus possibly survives at only one British locality. It is typically bluish-green in colour and has very narrow leaves. The axillary gemmae are borne on long rhizoids and are smaller than in *D. rigidulus*. The basal cells are rather thin-walled, ± inflated and the leaf margins mostly unistratose. Only female plants are known. An unresolved problem with this species is its relationship to *D. verbanus* of Central and Southern Europe, which has the appearance of a male version of *D. glaucus*, but without axillary gemmae and with relatively shorter and broader leaves.

Didymodon acutus is one of several species with excurrent costae. The apex of the costa lacks the ventral groove that is usually present in *D. vinealis*. Although morphologically similar to *D. icmadophilus*, *D. validus* and some other taxa, it is an isolated lineage according to molecular

data. Key differentiating characters are: (1) smooth leaf cells with thick walls and rounded cell lumens, (2) leaf section broadly U-shaped in upper part of leaf, with erect leaf margins (Fig. 8), (3) colour of the plants often with brownish or reddish-brown undertones (which is unusual in this section of the genus). Although widely recorded in Britain, it actually appears to be very rare here. Most of our populations belong to *D. icmadophilus*, and at present we have only two confirmed records of *D. acutus*:

North Somerset (vc 6): short turf, edge of golf course, between castle and road, Clevedon, ST415727, Peter Martin & Ron Porley, 5 May 1991.

South Hants (vc 11): at base of a north-facing shallow ridge next to a bare chalky path, Fort Widley, Portsdown Hill, SU665170647, J.A. Norton, 13 December 2014.

Didymodon icmadophilus consists of several distinct lineages based on molecular data, but they are morphologically nearly cryptic, with most of the morphological characters overlapping. Most of the British and Irish records of *D. acutus* belong to *D. icmadophilus*, including those from the southern chalk and limestone. In recent years there has been a steady flow of records from ruderal habitats. Important morphological characters for the lineage that occurs in Britain and Ireland are: (1) leaf cells papillose with rounded-quadrate lumens, (2) costa long-excurrent (>15% of leaf length), (3) upper part of leaf not U-shaped in section (Fig. 10), (4) widest part of the leaf at 1/4-1/3 from the base, (5) colour of the plants lacking reddish-brown undertones. In addition the cells of the annulus are inflated and separating (but sporophytes are extremely rare).

The *Didymodon validus* complex is very close morphologically to *D. icmadophilus* and includes

a number of separate cryptic lineages. They have the widest part of the leaf at 15–20% from the base and the excurrent part of the costa does not exceed 15% of the leaf length, but the overlap in these characters with the *D. icmadophilus* complex is rather large. The true *D. validus* s.str. is a rather robust plant and is perhaps restricted in Europe to the eastern Alps. A specimen from Scotland (Water of Ailnack, vc 94, T.L. Blockeel, 29 July 2008) has proved to belong molecularly to one of the lineages that resembles small forms of *D. validus*, but much more work is needed to resolve the taxonomy of this complex.

Didymodon cordatus does not present any problems in Britain, being known from only one site in Devon. The British population belongs to the true *D. cordatus* s.str., which is characterised by: (1) costa broad, dorsally shiny, excurrent, (2) leaf margins broadly revolute, (3) leaf cells small and smooth, (4) axillary gemmae numerous, smaller and not protuberant as in *D. rigidulus*. In Europe and elsewhere, however, there is a problematic complex of taxa around *D. cordatus* which forms part of the same complex as *D. validus*, with several undescribed species even in central and southern Europe.

Didymodon tomaculosus is now known to be close to *D. acutus*, both morphologically and molecularly. Its most distinctive character is the presence of rhizoidal tubers, but it also has somewhat elongate cells on the ventral surface of the costa. In its preferred habitat in Britain and Ireland (arable fields) the plants are small and typically have abundant tubers, but in continental Europe (where very few localities are known) larger forms sometimes occur on more stable substrates, and they may have fewer tubers.

References

- Jiménez, J.A., Ros, R.M., Cano, M.J. & Guerra, J. (2005).** A new evaluation of the genus *Trichostomopsis* (Pottiaceae, Bryophyta). *Botanical Journal of the Linnean Society* 147: 117–127.
- Köckinger, H. & van Melick, H. (2007).** *Didymodon maschalogenus* (Pottiaceae), a novelty in the European moss flora, reported from the Austrian Alps and southern Norway. *Lindbergia* 32: 62–68.
- Kučera, J. & Köckinger, H. (2000).** The identity of *Grimmia andreaeoides* Limpr. and *Didymodon subandreaeoides* (Kindb.) R.H.Zander. *Journal of Bryology* 22: 49–54.
- Kučera, J., Blockeel, T.L., Erzberger, P., Papp, B., Soldán, Z., Vellak, K., Werner O. & Ros, R.M. (2018).** The *Didymodon topiaceus* complex (Pottiaceae, Bryophyta) revisited: new data support the subspecific rank of currently recognized species. *Cryptogamie, Bryologie* 39: 241–257.
- Lawley, M. (2016).** An unknown *Didymodon*, our latest “must-see” moss. *Field Bryology* 115: 31–34.
- Saito K. (1975).** A monograph of Japanese Pottiaceae (Musci). *Journal of the Hattori Botanical Laboratory* 39: 373–537.
- Zander, R.H. (1993).** Genera of the Pottiaceae: mosses of harsh environments. *Bulletin of the Buffalo Society of Natural Sciences* 32: 1–378.
- Zander, R.H. (2013).** *A framework for post-phylogenetic systematics*. Zetetic Publications, St Louis, Missouri.

Tom L Blockeel

e Tblockeel@aol.com

Jan Kučera

e kucera@prf.jcu.cz