

Didymodon tophaceus subsp. *erosus* new to Britain

Seán O’Leary and **Jan Kučera** describe a recent find extending the known European range of this subspecies

In February 2023, on the invitation of the owners, SVOL carried out a survey of the bryophytes in the beautiful private gardens of Medmenham Mill in Buckinghamshire (vc 24). A small acrocarpous moss was collected from shaded bricks and mortar in a mill race channel, next to a water mill wheel at SU808844. The moss was not recognised in the field and was taken back for microscopic examination. Even then, it remained puzzling. It was evidently a *Didymodon*, but SVOL was unable to assign it to any of the species described by Smith (2004). The nearest taxon was perhaps the familiar *Didymodon tophaceus* (Brid.) Lisa, a variable plant of calcareous habitats well-known to many bryologists. However, the moss differed in some key features: the leaf shape was more lanceolate than is typical for this species and the cells overlying the ventral surface of the nerve were often quadrate to short-rectangular near the tip.

A specimen was sent to Peter Martin and to Tom Blockeel for their opinions, but both of these bryologists confessed that they were unsure of its identity. It was decided to send a sample to JK, a specialist in *Didymodon*, who led the BBS workshop on the genus at Leicester Botanic Garden in 2018. He tentatively identified the specimen, on morphological grounds, as sharing characters of both *D. tophaceus* subsp. *tophaceus* and subsp. *erosus* (J. A. Jiménez & J. Guerra) Jan Kučera. The leaf shape and ventral cells over the

nerve resembled those of subsp. *erosus*, but the leaf margins lacked the strongly erose border often found in this plant.

It was decided to investigate further using molecular barcoding. This confirmed that the Medmenham plants belong to *D. tophaceus* subsp. *erosus*. It is the first time that this taxon has been recorded in Britain or Ireland (O’Leary & Kučera, 2024) and represents a significant extension to its range within Europe. It has previously been recorded in Spain, Portugal, France, Germany, Austria, Albania and Hungary (Hodgetts & Lockhart, 2020). There is a single record outside Europe, from Ecuador (Kučera *et al.*, 2018).

The *D. tophaceus* complex

For the field bryologist, of course, the key point of interest is how one might detect this plant in the hand and under the microscope, as few of us will have access to DNA analysis. A detailed description is given by Kučera *et al.* (2018), so we will describe here the features which catch the eye as being unusual and different from the more familiar *D. tophaceus* subsp. *tophaceus* and other taxa in the *D. tophaceus* complex.

Kučera *et al.* (2018), based on genetic and morphological evidence, considered the complex to comprise three subspecies: subsp. *tophaceus*, subsp. *erosus* and subsp. *sicculus* (M.J. Cano, Ros, García-Zam. & J. Guerra) Jan Kučera. Subsp. *tophaceus* in turn comprises two varieties, var.

tophaceus and var. *anatinus* Hamm.

In subsp. *tophaceus* the cells overlying the nerve on the ventral face are elongate (length/width ratio greater than 3:1), and the costa on well-grown plants is greater than 100 µm wide. The leaves are lingulate, lanceolate to oblong-lanceolate and up to 2.2(–3) mm long. The two varieties of subsp. *tophaceus* are distinguished by the length of the costa, excurrent in var. *anatinus* (not confirmed in Britain and Ireland as yet) but ending below the apex in var. *tophaceus*, the familiar taxon described by Smith (2004).

D. tophaceus subsp. *sicculus* was recorded, new to Britain and Ireland, on Lundy Island off the North Devon coast (vc 4), by Peter Martin in April 2021. A description of this plant, comparing it with subsp. *tophaceus*, can be found in his article in *Field Bryology* (Martin, 2021). It shows a narrower nerve than subsp. *tophaceus* (less than 70 µm wide on well-developed plants) and cells over the ventral face of the nerve which are short-rectangular to irregularly quadrate (length/width ratio mostly < 2:1). The leaves are ovate, ovate-lanceolate to ovate-lingulate (length/width ratio 1.8–3.4:1), and up to 1.45 mm long.

D. tophaceus subsp. *erosus* is very similar to subsp. *sicculus*, sharing the narrow nerve and quadrate cells overlying the ventral face of the nerve, but the leaves are lanceolate to lingulate (length/width ratio 2.3–5.2:1) and up to 1.9 mm long. Its leaves may be strongly erose above. KOH reaction distinctions between the subspecies seem to be somewhat inconclusive and subject to environmental conditions (Martin, 2021).

The ecological requirements of the three subspecies, summarised by Kučera *et al.* (2018), seem to overlap, according to current knowledge. Subsp. *sicculus* is most often recorded in Europe from periodically wet but seasonally dry saline grasslands, but it can also grow on seasonally or permanently wet calcareous sites which are not saline. The British material grew between granite blocks of a wall, about 200 m from the sea. The ecological range of subsp. *tophaceus* overlaps with that of subsp. *sicculus*, but it prefers wetter sites. Subsp. *erosus* has been recorded from wet and dry calcareous sites and from saline grassland.

Sporophytes have not been found on European material of subsp. *erosus* and the British material also lacked them. The Ecuadorean specimen did

have sporophytes, and these are described and illustrated by Kučera *et al.* (2018).

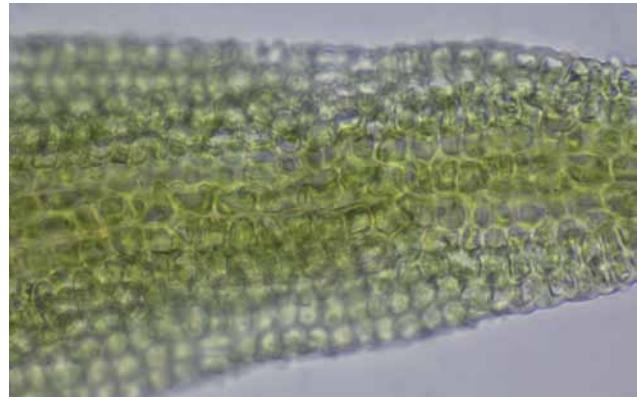
From these descriptions it is clear that it is not possible to be completely sure, based solely on morphological and



◁ Figure 1. Shoots from Medmenham plant (scale bar 1 mm). All photographs Seán O'Leary



△ Figure 2. Leaf of typical shape and size from Medmenham plant (scale bar 0.1mm).



△ Figure 3. Quadrate cells over the ventral surface of nerve in upper part of leaf of Medmenham plant.

ecological evidence, where the boundaries are between the subspecies. Particular difficulty lies in separating subsp. *sicculus* from subsp. *erosus* – leaf shape and size are our best guides here, but molecular barcoding may be necessary to provide more reliable information.

The Medmenham plants

The Medmenham plants were growing in shaded conditions and may have been somewhat stunted. They grew in a wet site on bricks and mortar, so probably in calcareous conditions, although no pH measurements were made. Shoots were typically about 5 mm tall (Fig. 1) with lanceolate leaves up to 1.4 mm long (Fig. 2), and about 0.3 mm wide. The length/width ratio was up to 4.3 but often less. The nerve was up to 70 μm wide at the leaf base. Some leaves had an excurrent nerve. The leaf margins were not erose above. The ventral cells over the nerve were often quadrate (Fig. 3), especially towards the leaf tip, but this was not the case in every leaf – some leaves had elongated cells over the nerve.

It is clear, from this description of the Medmenham plant, why JK and other bryologists found the specimen confusing initially. It does not fit exactly into any of the

above morphological descriptions and shares the span of possible habitat requirements of both subsp. *erosus* and subsp. *tophaceus*, while subsp. *sicculus* was unlikely to match this plant both on ecological and morphological grounds. Safe assignment of the material to *D. tophaceus* subsp. *erosus* in this case was possible only with the help of DNA barcoding.

The subspecific rank of *D. tophaceus* subsp. *erosus* reflects the partly overlapping morphological traits with the other two subspecies and the complex phylogenetic pattern revealed among the specimens of the *D. tophaceus* complex studied so far (Kučera *et al.*, 2018). The lineage which has been interpreted as subsp. *erosus* contains three clades. The first includes the majority of analysed plants, the second contains a single specimen collected in southern Austria, together with the Medmenham plant, and the third contains a single analysed specimen from Ecuador. The Ecuadorian plants differ from the rest of subsp. *erosus* plants in the rather regularly elongated ventral surface cells of the costa, while the Austrian and Medmenham plants share the hardly erose margins of the leaf apex, but neither of these traits is invariable in subsp. *erosus* (Werner *et al.*, 2009; Kučera *et al.*, 2018).

Concluding observations

Clearly subsp. *erosus* is a difficult plant to identify. It is necessary to pick out a moss looking similar to *D. tophaceus* of Smith (2004) in leaf shape and size, but with quadrate cells overlying the ventral face of the narrower nerve. A feature which may prove helpful is that subsp. *erosus* often has rhizoidal gemmae (illustrated by Kučera *et al.*, 2018), a feature shared with subsp. *sicculus*. However, these were not observed in the Medmenham material. The leaf margin may be strongly erose above, as emphasised in Jiménez *et al.* (2004), but this character should not be taken as diagnostic according to Werner *et al.* (2009) – it can be absent, as in the Medmenham material. It is important to search for well-developed plants, if available, as stunted plants may have elongated cells over the ventral surface of the nerve, as in the Medmenham plants, and stunted specimens of subsp. *tophaceus* may match moderately developed plants of subsp. *erosus* in leaf shape and size.

A potential source of confusion in calcareous habitats is small plants of *D. sinuosus* (Mitt.) Delogne. This familiar plant has erose leaf margins, but differs clearly from *D. tophaceus* subsp. *erosus* in several features: the leaves are much more crisped when dry, usually much longer (up to 5 mm), dentate near the apex (invariably so in younger leaves), with a ventral groove near the apex and lacking ventral stereids in the nerve section. The lamina cells are clearly bulging-mammillose in cross section.

In conclusion, *D. tophaceus* subsp. *erosus* has been recorded for the first time in Britain and Ireland. Hopefully this will help to stimulate collection of material of the *D. tophaceus* complex in order to help to build a clearer picture of the morphological, ecological and, if possible, genetic differences between the subspecies.

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