



Bryoerythrophyllum campylocarpum (Müll.Hal.) H.A.Crum, a tropical and subtropical moss new to Ireland and Britain

Tom Ottley^a, Tom L. Blockeel^b and Jan Kučera^c

^aValley Forge, Goginan, Aberystwyth SY23 3PD, Wales, UK; ^b9 Ashfurlong Close, Dore, Sheffield S17 3NN, UK; ^cFaculty of Science, University of South Bohemia, České Budějovice, Czech Republic

ABSTRACT

Introduction. An unfamiliar member of the Pottiaceae discovered near Goginan in Cardiganshire, Wales, UK, was identified as *Bryoerythrophyllum campylocarpum* sensu lato. An earlier collection from a wood in East Cork, Ireland, was subsequently confirmed as belonging to the same species. This moss is primarily a tropical and subtropical species and is very rare in Europe.

Methods. Both the Irish and Welsh plants were initially identified by morphological comparison with herbarium specimens of *Bryoerythrophyllum campylocarpum* from other areas of its distribution. Identification was confirmed by assessment of molecular affinities using two chloroplast markers, *rps4* and *trnM-trnV*.

Key results and conclusions. Molecular and morphological affinities are presented and discussed. Comparisons are made with similar species and notes on identification are presented. *Bryoerythrophyllum campylocarpum*, as currently circumscribed, is confirmed as a member of the Irish and British bryophyte floras; however, both the molecular and morphological variation of specimens attributed to this species suggest that it is a collective taxon comprising at least three lineages which will probably need to be described as species in the future. The possible origins of the Irish and Welsh plants are considered.

ARTICLE HISTORY

First Published Online 20 December 2021

KEYWORDS

Bryoerythrophyllum campylocarpum; Cardiganshire; cryptic species; East Cork; *rps4*; *trnM-trnV*

Introduction

A chance find in Wales in January 2021, during one of the lockdown responses to the Covid-19 pandemic, led to T.O. being puzzled by a moss that appeared to be a very unusual *Barbula*. A sample was sent to T.L.B., who identified it as probable *Bryoerythrophyllum campylocarpum* (Müll.Hal.) H.A.Crum, a species he had studied during his work on *B. duellii* in Greece (Blockeel et al. 2017). He also noted that it was similar in many respects to an unusual *Bryoerythrophyllum* that he had collected in southern Ireland in 2002 but which had never been satisfactorily identified. Both the Irish and the Welsh specimens were sent to the third author, J.K., who confirmed their close molecular affinities to previously studied specimens of *B. campylocarpum*. The two populations are genetically identical in the loci studied, despite having minor morphological differences (described below). The species is therefore an addition to both the Irish and British bryophyte lists.

The initial discovery in Wales was from crumbling soil on an embankment of a forest track in coniferous planted woodland near Goginan in Cardiganshire. A typical patch of the moss is illustrated in Figure 1. Further records and samples were obtained subsequently from several other sites in northern Cardiganshire, a frequent habitat being on thin soil

accumulated around small rocks set in tracks and paths under trees where it can be locally abundant, as at the Waterfall Walk, a tourist attraction at Devil's Bridge (Pontarfynach). Known localities for this moss in Wales extend geographically from Hafod in the south to Cwm Einion in the north, a distance of about 23 km.

The sole Irish record is from the edge of a gravel path through Glenbower Wood near Killeagh in East Cork in the south of the country. As this was a chance collection made during a walking holiday, there is relatively little additional information available on its ecology at this site. Part of the collected sample is shown in Figure 2.

Eight species of *Bryoerythrophyllum* are currently known from Europe (Hodgetts et al. 2020). The latest one to be added was *B. duellii* (Blockeel et al. 2017), which has a very restricted distribution in the Eastern Mediterranean. *Bryoerythrophyllum campylocarpum* is similarly rare in Europe; Hodgetts and Lockhart (2020) accept it only for Portugal and Madeira, but Koppe and Düll (1986) cite a locality in the Canary Islands (La Palma). The unlocalised reference to its presence in the Azores by Garcia et al. (2013) is erroneous (C. A. Garcia, University of Lisbon, personal communication). Unlike *B. duellii*, *B. campylocarpum* is primarily a tropical and



Figure 1. *Bryoerythrophyllum campylocarpum* on gravel at the edge of a forest track in Cardiganshire, Wales. Photograph: Tom Ottley.



Figure 2. The appearance of the plants in the Irish population of *Bryoerythrophyllum campylocarpum* at Glenbower Wood, near Killeagh in East Cork, when moist. Photograph: Tom Ottley.

subtropical species, with many sites in Central America, South America, sub-Saharan Africa and several oceanic islands.

Nomenclature

The names of European bryophytes mentioned in the text follow Hodgetts et al. (2020).

Materials and methods

Molecular analysis

Molecular sampling included two chloroplast loci used successfully in previous treatments dealing molecularly with the genus (Blockeel et al. 2017; Kučera et al. 2020): the *rps4* gene with the adjoining *rps4-trnS* spacer and the *trnM-trnV* spacer with the variable *trnV* intron. The selection of taxa for the analysis also followed these treatments, and comprised

representatives of the genera *Bryoerythrophyllum*, *Saitobryum*, *Mironia* and *Erythrophyloopsis*, which together form a monophyletic unit (Kučera et al. 2020). Newly obtained sequences were derived from additional samples of *B. campylocarpum* sensu lato (see Appendix), following the laboratory protocols described in detail by Kučera et al. (2019). Sequence data were edited and aligned following the procedures described by Kučera et al. (2020). Concatenated plastid data including indels scored by the simple coding method (Simmons and Ochoterena 2000) were analysed in phylogenetic context using Bayesian inference (BI) and Maximum Likelihood (ML) methods. Both were run at the cluster computer facilities of MetaCentrum VO (see Funding), using the MrBayes v. 3.2.7a (Ronquist et al. 2012) and RAxML v. 8.2.12 (Stamatakis 2014) software packages. Details of analysis settings followed Kučera et al. (2020).

Morphological study

Specimens of the Welsh and Irish populations were examined using light microscopy. They were compared with material of *Bryoerythrophyllum campylocarpum* sensu lato from Portugal, Madeira, Mexico, Costa Rica, Cameroon and South Africa present in the private herbaria of T.L.B., Ron Porley and Howard Matcham and the institutional herbaria CBFS and E.

Results

Molecular affinities

The two specimens from Wales and Ireland (Ottley 21012201 and Blockeel 31/306) are fully identical in the studied chloroplast loci but differ from the Portuguese and Mexican specimens in two *rps4* substitutions, three *trnM-trnV* substitutions, and two *trnM-trnV* indels (one 1-bp deletion and one 6-bp insert). Similarly, they differ from the two analysed samples from Cameroon in one *rps4* substitution, one 26-bp insert in the *rps4-trnS* spacer, and four substitutions and two 1-bp deletions in the *trnM-trnV* locus. They also differ from the sample from Colombia in three *rps4* substitutions, but that specimen was neither analysed nor examined morphologically by us, and *trnM-trnV* data were not available for the GenBank accession.

These relatively large molecular differences are reflected in the tree topology derived from the phylogenetic analysis (Figure 3). All accessions named *Bryoerythrophyllum campylocarpum* form a highly supported monophyletic lineage with a posterior probability from Bayesian Inference (PP) of 1 and bootstrap support from Maximum Likelihood analysis (BS) of 92. This clade is further branched into an unresolved trichotomy of highly or fully supported lineages, represented by the accessions from (i) Britain

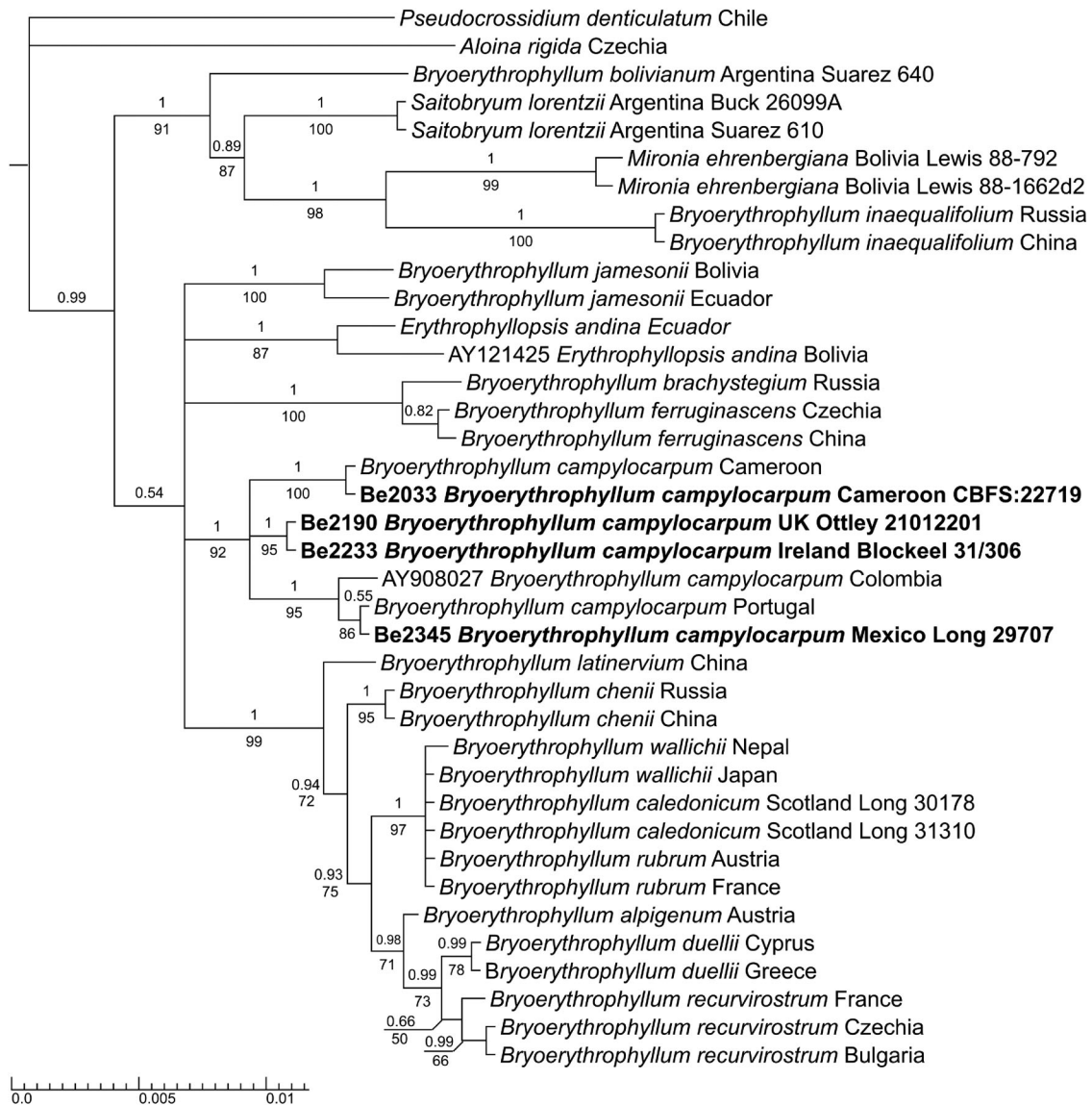


Figure 3. Bayesian consensus tree inferred from concatenated chloroplast *rps4-trnS* and *trnM-trnV* sequence data, illustrating the molecular affinities of the Irish and Welsh populations of *Bryoerythrophyllum campylocarpum*. The matrix was partitioned using DNA and indel data scored by the simple coding method (Simmons and Ochoterena 2000). Numbers above branches are Bayesian posterior probabilities; numbers below branches correspond to bootstrap support (500 replicates) of branches obtained from Maximum Likelihood analysis of the same, equally partitioned dataset. Newly obtained sequences are marked in bold.

+ Ireland, (ii) Cameroon, and (iii) Portugal + Mexico + Colombia. The divergence between these three lineages within *B. campylocarpum* sensu lato appears greater than between any other pair of congeneric *Bryoerythrophyllum* species within any of the other clades, and stands in particular contrast to the absence of molecular differentiation in these loci between the morphologically disparate *B. rubrum* and *B. wallichii* (Mitt.) P.C.Chen sensu lato.

Morphology

Because the two populations in Britain and Ireland thus far discovered were found to be dissimilar in a few respects, and because *Bryoerythrophyllum campylocarpum* is present at numerous sites in Cardiganshire,

the Welsh plants are described in detail below and minor differences between the Welsh and Irish populations are noted separately.

Welsh population. Plants forming loose patches up to a few centimetres across and 4–10(–18) mm in height, light green above becoming pale orange in some patches, appearing matt due to the presence of abundant papillae on the leaves. Stems erect to decumbent, unbranched or branched at the base, to about 220 μm in width, \pm circular in section, with an irregularly shaped central strand and lacking a hyalodermis. Stems turning an orange-brown colour with age and covered by appressed, hyaline leaf bases. Axillary hairs abundant towards shoot apices, to 500 μm in length, 10–12 μm wide, and comprising up to about

10 cells, faintly chlorophyllose apart from basal 1 (or 2) cells and a sometimes slightly wider apical cell. When well developed, shoots show leaves increasing in length up the stem and forming a moderately distinct comal tuft to about 3 mm across but in smaller plants leaves more uniform in length.

Lower leaves narrowly ovate, dark green becoming browner with age. Upper leaves linear to lingulate to about $1.6(-2.0) \times 0.3$ mm, slightly narrowing at the base, otherwise either parallel-sided or widest near the middle and tapering above to an acute apex. Smaller plants may have shorter, more ovate-lanceolate leaves. Leaves plane, slightly flexuose and patent to spreading when moist from an appressed, erect base; when dry, leaves incurved and moderately crisped, the smooth dorsal surface of the costa then becoming conspicuous. Leaf apex with a smooth mucro strongly contrasting with the densely papillose laminal cells. Laminal cells quadrate, often nearly square but otherwise tending to be oblate, thin-walled, usually arranged in rows, $(7-11-13(-15)) \mu\text{m}$ across, with numerous small papillae per cell. Margins papillose-crenulate, often irregular in outline towards leaf apex, unistratose, recurved towards the base. Edges of leaf sometimes eroded, fracturing quite readily both along the costa and across the lamina, the fractured edges appearing papillose. Basal part of leaf strongly differentiated with 3–6 median rows formed of hyaline, thin-walled, inflated, rectangular cells $(15-30-50 \times (12-15-20)) \mu\text{m}$. Towards the margin are 2–6 rows of narrower, smooth, thicker-walled, chlorophyllose cells, $23-60 \times 6-9 \mu\text{m}$, and on larger mature leaves, a marginal row composed of up to about 12, rarely to 20, hyaline, thick-walled, elongate cells, $20-50 \times 5-9 \mu\text{m}$, ascending the basal margin, with a partial second row forming sometimes (Figure 4).

Costa to $100 \mu\text{m}$ wide at the very base of the leaf, where becoming brown in older leaves, rapidly narrowing to about $50 \mu\text{m}$ by mid-leaf and percurrent at leaf apex, which terminates in a smooth mucro to about $60 \mu\text{m}$ in length, composed of 1–4 cells with the apical cell up to $50 \mu\text{m}$ long. Occasionally, the mucro can itself have a spine on one side or indeed be equally forked. Dorsal surface cells of the costa smooth and striate from the base nearly to the apex, where they become papillose. Ventral surface smooth in lower part of leaf, where the epidermal cells, visible in surface view, are elongate to about $50 \mu\text{m}$, but with progressive encroachment of quadrate papillose cells from the edges and entirely covered by such cells towards the leaf apex. In section, costa very convex on dorsal side with 3–4(–5) guide cells and weakly differentiated epidermal cells dorsally and ventrally as well as corresponding bands of stereids. Hydroids present in some sections towards the base of the leaf. A transverse section across the base of a mature leaf is shown in Figure 4.

Rhizoids reddish brown, smooth. On samples from fine silt at Devil's Bridge, rhizoidal tubers are plentiful on short side branches of the larger rhizoids. The tubers are broadly ellipsoidal, $100 \times 50 - 250 \times 130 \mu\text{m}$, dark reddish brown and nearly smooth. Constituent cells large to $90 \mu\text{m}$ long, with 3–6 visible in surface view. An example, partially ruptured, is shown in Figure 4.

Sporophytes were not seen in the Welsh (or Irish) material, but immature archegonia were observed at the shoot apices of a few of the larger plants. The species is known to be dioicous.

Irish population. In contrast to the Welsh population, within which there is very little morphological variation, the Irish plants have a strikingly orange-brown colour (see Figure 2); this was one of the characteristics that attracted attention to them in the field at the time of discovery. The other noticeable difference is that the leaves of the Irish specimen do not spread much on hydration, tending to stay erect to patent when moist.

Other differences are minor. In the Irish population, the upper cells are about the same size ($9-12 \mu\text{m}$) as those of the Welsh plants but the cells of the mucro are smaller, the apical cell being up to about $30 \mu\text{m}$ in length. The mucro lacks any additional spine that is present on some leaves from Welsh plants. The cells on the dorsal surface of the costa just below the mucro are often less papillose. The basal cells are smaller, $15-40 \times 12-18 \mu\text{m}$ and less inflated, but the basal marginal cells are similar in most respects.

It was not possible to confirm the presence of chlorophyll in the submarginal basal rows. However, some fragments contained in those cells indicated that it could have been present in fresh material.

Other studied specimens. Examination of specimens from other geographical regions show them to differ from the British and Irish plants in several respects, briefly summarised here. The plants from Portugal and Mexico are very similar to each other, consistent with their molecular affinity. They share with the British and Irish material broadly linear leaves with the leaf base hardly expanded, but the apex is broadly acute or obtuse-cuspidate with a few to several sharp, hyaline marginal teeth. The lamina cells are significantly smaller, $6-8(-9) \mu\text{m}$, but the structure and shape of the basal cells are largely similar, differentiated between the external narrow cells in several rows and the wider, longer and inflated juxtacostal cells in well-differentiated 'windows'. A specimen from Madeira is almost identical morphologically to plants from the Welsh population, having a very similar leaf apex, even with occasional leaves exhibiting a forked mucro as described above, although the cells are a little smaller, at $8-11 \mu\text{m}$. In the material from Costa Rica

(Cleef & Fournier 10220), which was not investigated molecularly, the leaf shape, basal cell differentiation and upper lamina cell size are similar to those in Mexican and Portuguese material, but it is more robust with laxer foliage and nearly squarrosely spreading leaves when moist, possibly reflecting its more humid habitat. In addition, the denticulation is perhaps the best developed of these three populations, but still restricted to the very apex of the leaves.

The plants from the rich collection from Mount Cameroon differ in having an expanded leaf base with markedly inflated basal cells in a large group, whereas the marginal basal cells are rather reduced in number and mostly do not form a well-differentiated border. The leaf margins are not parallel but rather slightly tapering to the apex, which is mostly

broadly cuspidate, sometimes lingulate, and lacking teeth, although the margins near the apex may be irregularly notched. The specimen from Malawi may represent the same lineage, but here the plants are more robust, with laxer foliage, nearly parallel leaf margins, and the leaf base less expanded and with a more pronounced differentiation between the juxtacostal and marginal basal cells. The more robust habit may reflect milder, more humid conditions (forest at 1740 m) as compared with the exposed habitat of lava fields at 3200 m or more at Mount Cameroon. The South African plants are very similar to the sample from Malawi; the leaves are \pm lingulate with slightly expanded bases but, as in other African plants, the broadly cuspidate to lingulate apex is at most irregularly notched rather than toothed. All non-British/Irish plants, with the exception of the

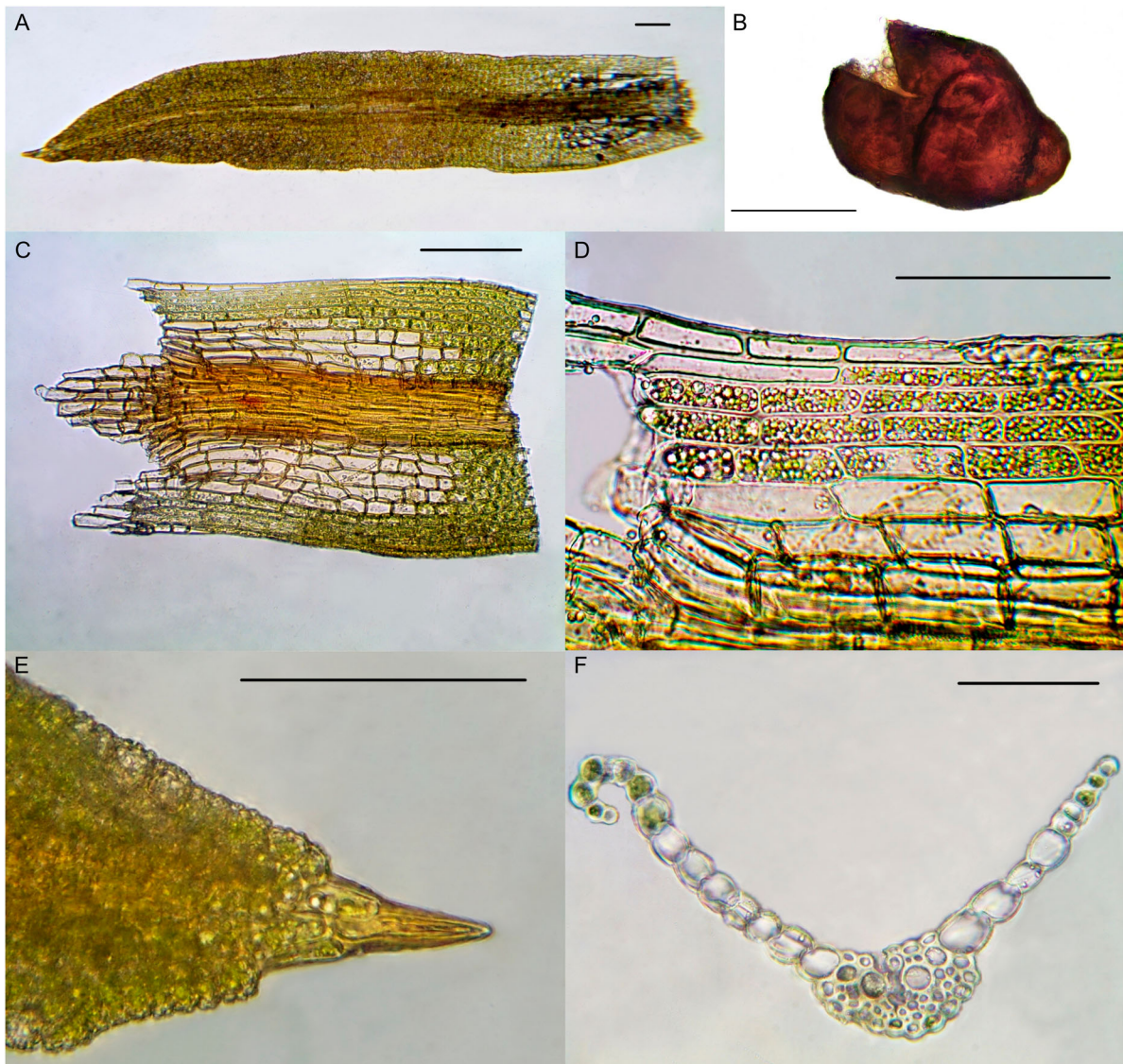


Figure 4. *Bryoerythrophyllum campylocarpum* (Müll.Hal.) H.A.Crum. (A) Leaf. (B) Slightly crushed rhizoidal tuber, showing the oil droplets contained within. (C) Base of a leaf. (D) Detail of alar region. (E) Apex of leaf. (F) Transverse section near base of leaf. All scale bars = 100 μ m. Photographs from samples collected in Cardiganshire, Wales. Photographs: Tom Ottley (A, C–F) and Claire Halpin (B).

specimen from Madeira noted above, share the narrower upper lamina cells averaging about 7–8 µm.

Differentiation

In the moist state, the overall appearance of the plants found so far in Wales is perhaps superficially similar to that of a small *Trichostomum* (Garcia et al. 2013), but they are surely more likely to be mistaken for a species of *Barbula* or *Streblotrichum*, and the frequently recurved lower leaf margins would seem to support that view. In particular, smaller forms of *Barbula unguiculata* can come very close in appearance in the field, even having reddish stems on occasion, but they usually have slightly broader leaves, generally lacking orange tints. When dry, the crisped, erect shoots so closely resemble a *Barbula* or a *Didymodon* that they are very likely to be overlooked, particularly when growing on gravel tracks. Once a leaf is examined under the microscope, however, the highly distinctive basal cells (see Figure 4) should preclude most other species of European moss, although there are potential similarities to *Bryoerythrophyllum recurvirostrum*, as described below, and species of *Syntrichia* can share many of the same features, albeit in a differently shaped leaf. The enlarged median basal cells may also suggest *Didymodon umbrosus* but, among many differences, the leaf shape in that moss is uniformly tapering, it is a significantly smaller plant, and the habitats would not usually overlap.

Although the usual habitats of *Bryoerythrophyllum recurvirostrum*, such as walls, bridges and tree roots, should make it an unlikely candidate for significant confusion, it does occasionally grow on compacted soil or coarse gravel on tracks and so is considered here. The leaf margins of *B. recurvirostrum* are much more strongly recurved, reaching far up the leaf, and this provides the simplest and most obvious distinction between it and *B. campylocarpum*. In *B. recurvirostrum*, the wider, ovate leaf base does have a somewhat similar arrangement of cells but there are many more rows of hyaline median cells (often more than 20) in the significantly broader base, and these are less obviously enlarged and less wide at 9–12(–15) µm. Similarly, there are also a few rows of narrower, faintly chlorophyllose cells towards the margin, sometimes with a row of hyaline marginal cells extending up to about 10 cells above the base, but in both cases with less clearly thickened walls. The leaf apex shows both similarities and differences: in both species the presence of strongly papillose cells on both surfaces of the costa immediately below the mucro gives the effect of the smooth mucro emerging from a 'ruff' of papillose cells (see Figure 4). This is less noticeable on the specimen from the Irish population of *B. campylocarpum*, in which the dorsal cells in particular are less strongly papillose. In *B. recurvirostrum*, the leaf

apex generally lacks an obvious mucro although the costa is usually shortly excurrent in a smooth apiculus, which can consist of up to three cells but more often only one. A monoicous inflorescence can often be demonstrated in *B. recurvirostrum*, and it frequently produces sporophytes.

Bryoerythrophyllum ferruginascens occurs widely on gravelly tracks, where it may be increasing (Blockeel et al. 2014), but it typically needs a more base-rich habitat than that of *B. campylocarpum*. It is a smaller plant but not dissimilar in habit, having similarly plane upper parts of the leaves, although the basal part of the leaf has a more broadly ovate shape. It has much less differentiated basal cells, however, and even though the basal marginal cells may be narrower, the transition from the hyaline median cells is gradual. Although the colour differs from most colonies of *B. campylocarpum* in Wales, it can certainly be similar to the Irish plants in being rusty orange. *Bryoerythrophyllum ferruginascens* nearly always has abundant rhizoidal tubers, but these are a different shape to those seen in *B. campylocarpum*, both as described here and also as reported in specimens collected in Ecuador (Arts and Sollman 1998).

Bryoerythrophyllum caledonicum was described by Long (1982), and the differences from *B. campylocarpum* are discussed therein. In view of the very restricted range and habitat of *B. caledonicum* in Britain, where it is confined to wet calcareous rock in the mountains of the Central Highlands and Inner Hebrides, it is unlikely to present identification problems. It does, however, differ in several important characters: *B. caledonicum* has a pronounced translucent border of a few rows of smooth cells in the upper part of the leaf, contrasting with the otherwise densely papillose laminal cells in which the cell walls are obscured; the upper margins are strongly dentate; the basal cells are hyaline but are not inflated and only gradually reduce in width towards the margins. In addition, *B. caledonicum* invariably develops strong orange coloration which is more similar to the Irish specimen of *B. campylocarpum*.

Habitat

The track in Wales where the first patches of *Bryoerythrophyllum campylocarpum* were found is made of compacted shale, and at the place of discovery there are relatively few trees but the bank is steep and faces north so is substantially shaded. After the identity of the moss had been confirmed, further scattered populations were found along the middle and edges of the same track (which is shown in Figure 5), and it is noticeable that it only occurs where at least partially shaded by trees. Several other sites have been located in this same area, including one in a somewhat different habitat of shale rocks set in a ditch bank by



Figure 5. Banc y Castell, Goginan, Cardiganshire, Wales. *Bryoerythrophyllum campylocarpum* forms small patches along the middle and edges of this track. Photograph: Tom Ottley.

a minor road through a wood; a few of these rocks support patches of very small plants of the *Bryoerythrophyllum*, suggesting recent colonisation at this site.

The track at the original locality is believed to have been created for forestry work in the 1960s. It is currently frequently used by cyclists as part of a network of forest trails. As is common in this part of Wales, the track is surfaced with shale chippings, which give rise to generally acidic conditions. Associated bryophytes are typical of many such tracks in the area: *Polytrichum juniperinum*, *Pogonatum urnigerum*, *Campylopus subulatus* (abundant), *Pohlia annotina*, *Pleuroidium acuminatum*, *Kindbergia praelonga*, *Solenostoma gracillimum*, *Nardia scalaris* and *Calliergonella cuspidata*. A more unusual moss, *Pohlia flexuosa*, is present only on the steep embankment of crumbling soil where *Bryoerythrophyllum campylocarpum* was first found.

Several kilometres away, *Bryoerythrophyllum campylocarpum* is locally abundant on accumulated silt between rocks set in the paths at Devil's Bridge, from where visitors view a well-known series of waterfalls. Associated species in the humid environment here include the liverworts *Hygrobiella laxifolia*, *Jungermannia pumila* and *Marsupella emarginata*. The overriding perception is that *Bryoerythrophyllum campylocarpum* is highly adaptable and likely to be found growing near a wide range of other bryophytes but mainly acidophiles. It can tolerate habitats that dry out in the summer months as well as places that are more or less permanently damp. The rhizoidal tubers are likely to be an effective mode of dispersal.

In Ireland, ecological surveys of Glenbower Wood are available (Wallace 2010) and indicate the soil to be neutral to acid, with very few basiphile bryophytes recorded. The collected sample consists of more than 60 stems of *Bryoerythrophyllum campylocarpum*,

although many are small and poorly developed, along with much *Archidium alternifolium* and a single shoot of *Philonotis fontana*. Other bryophytes collected nearby but not necessarily in direct association with *B. campylocarpum* were *Pohlia drummondii* and *Fossombronia caespitiformis* subsp. *multispira*. It is not known to what extent the site was shaded.

In Serra de Monchique, Portugal, most sites are on or by tracks (R. D. Porley, Aljezur, Portugal, personal communication), but further north in the country the species also occurs on rocks (Garcia et al. 2013), thus demonstrating a similar ecological range to that so far established in Britain and Ireland. Associated mosses on tracks include *Pohlia annotina*, *Kindbergia praelonga*, *Hypnum cupressiforme*, *Epipterygium tozeri*, *Fissidens curvatus*, *Claopodium whippleanum* and *Pleuroidium acuminatum*.

Discussion

The presence of a mainly tropical species of moss in the cool, damp climate of West Wales is certainly surprising. However, the climate in this part of Wales, west of the Cambrian Mountains, is strongly influenced by oceanic factors, and there are many examples of hyperoceanic species of bryophyte in the surrounding area; for example, *Campylopus setifolius* is present on rocks immediately adjacent to the site where *Bryoerythrophyllum campylocarpum* was first found. All records in Wales have been from woodland sites with significant shade. This not only helps to retain moisture levels during dry spells but also has an ameliorating effect during cold weather (Zellweger et al. 2019). The climate in southern Ireland is similarly influenced by the Atlantic Ocean (the site is only 8 km from the sea), and the locality there is likewise in woodland. Oceanic factors are likely also to be significant in the ability of the moss to survive in Tristan da Cunha in the South Atlantic and even in subantarctic islands (Ellis et al. 2013).

It is thought likely that *Bryoerythrophyllum campylocarpum* has been introduced to both Ireland and Wales, but this assumption is mainly based on the absence of earlier records. Bearing in mind the difficulties associated with identifying a moss not hitherto known to exist in Britain and Ireland and indeed rare even within Europe, it is possible that it has been overlooked even though the Devil's Bridge site in particular has been visited by many competent bryologists. Thus there remains a possibility of it being native.

The genetic similarity between the Irish and Welsh plants suggests either a common source or that one population is derived from the other. Within the local population in Wales, there is evidence that it is being spread on vehicle (including bicycle) tyres and footwear, as it has been found only on or near well-used

tracks and footpaths. This might add weight to the suggestion that it is an introduction, but some of its native associates, for example *Solenostoma gracillimum*, are much commoner on tracks than elsewhere, and at the Devil's Bridge site *Hygrobrella laxifolia* is rare apart from on rocky paths.

As described here, *Bryoerythrophyllum campylocarpum* exhibits substantial variation in both molecular and morphological characters. Some forms with exceptionally denticulate leaf apices can approach *B. jamesonii* (Taylor) H.A.Crum, and this has led several authors to assume that the two species are synonymous (Bartram 1949; Zander 1978; Magill 1981). However, that species differs in having denticulate to serrate margins in the whole upper third of the leaf, in lacking a differentiated border of marginal cells at the leaf base, and in possessing an erect capsule in contrast to the curved capsules in *B. campylocarpum* (Long 1982). Based on the molecular data presented here, *B. jamesonii* is clearly distinct from *B. campylocarpum*.

Even after the exclusion of *Bryoerythrophyllum jamesonii*, *B. campylocarpum* remains a variable taxon. The clear molecular divergence between the three lineages illustrated in Figure 3, and supported by the morphological differences described here, could be formalised by the description of at least three species. However, the variability of *B. campylocarpum* sensu lato in parts of its geographical range will require broader sampling to enable a proper understanding of both the morphology and the genetics of these taxa. As described in published accounts, there is clearly much variability in the tothing of the leaf apex of *B. campylocarpum* sensu lato from both South Africa (Magill 1981) and Central America (Allen 2002). Even the Portuguese populations may not prove to be homogeneous. In the protologue of *Hyophila crenulata* Guim. (nom. illeg., \equiv *H. machadoana* Sérgio), described from Portugal and now considered a synonym of *B. campylocarpum*, Machado (1917) states that the leaves are crenulate and not toothed near the apex, and this stands in contrast to the studied material from the Algarve. In addition, apparent differences between the rhizoidal tubers found by us in the Welsh material and those illustrated by Arts and Sollman (1998) from Ecuador suggest that tuber morphology is similarly variable across the different lineages.

Bryoerythrophyllum campylocarpum is considered very rare in Europe and Macaronesia, where it is currently assessed as Vulnerable with evidence of a continuing decline (Sim-Sim et al. 2019). However, the population appears to be stable on tracks in the Serra de Monchique area of mainland Portugal (R. D. Porley, personal communication). On Madeira, it has not been seen since 1996, although it is unclear whether the site of the 1968 specimen seen by the authors and published by Koppe and Düll (1986) has been searched recently. The new additional

territories for *B. campylocarpum* described in this paper are therefore important in the European part of its geographical range.

Acknowledgements

The authors would like to thank Ron Porley for lending samples of *Bryoerythrophyllum campylocarpum* collected from Serra de Monchique, Portugal, and providing photographs and notes about the sites. We also thank Howard Matcham, who lent to us a sample he had collected in KwaZulu-Natal. Sue Rubinstein made helpful comments about the leaf structure of *B. recurvirostrum*, and Claire Halpin managed to obtain good photomicrographs of rhizoidal tubers, which had defeated the authors. Jan Kučera acknowledges the molecular laboratory work carried out by Dr Alžběta Manukjanová (University of South Bohemia). César Garcia (University of Lisbon) is thanked for information regarding *Bryoerythrophyllum* in the Azores.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Jan Kučera acknowledges the support by the SYNTHESYS programme (GB-TAF-3543), which enabled the study of Royal Botanic Garden Edinburgh collections (E). Molecular analyses were funded by the University of South Bohemia. Computational resources (Metacentrum VO) were supplied by the Ministry of Education, Youth and Sports of the Czech Republic under the Projects CESNET (Project No. LM2015042).

Notes on contributors

Tom Ottley is the Cardiganshire Recorder for Bryophytes for the British Bryological Society and has wider interests in taxonomy. Before moving to Wales, he discovered *Pterygoneurum papillosum* in Sussex, new to Britain, and recently wrote a paper on the taxonomy of *Racomitrium obtusum*, published in *Field Bryology*. His current research interests are in *Leucobryum*.

Tom Blockeel read Classical History and Literature at the University of Oxford, from which he graduated in 1972. He is an independent researcher with a lifelong interest in bryophytes, especially concerning taxonomy and floristics. In addition to his studies on the British and Irish flora, he has explored many parts of Greece and published widely on the bryophytes of that country.

Jan Kučera is an associate professor at the Department of Botany at the Faculty of Science, University of South Bohemia, in the Czech Republic. His main research areas are the taxonomy and molecular phylogeny of mosses, particularly the haplolepidous family Pottiaceae; however, he has recently also started several projects on pleurocarpous mosses. He continues to study the biology of rare bryophytes and is active in local bryofloristic research.

ORCID

Jan Kučera  <http://orcid.org/0000-0002-0230-5997>

References

- Allen B. 2002. Moss flora of Central America. Part 2. Encalyptaceae-Orthotrichaceae. St Louis (MO): Missouri Botanical Garden Press.
- Arts T, Sollman P. 1998. A contribution to the moss flora of Ecuador. *Tropical Bryology*. 14:43–52.
- Bartram EB. 1949. Mosses of Guatemala. *Fieldiana: Botany*. 25:1–442.
- Blockeel TL, Bosanquet SDS, Hill MO, Preston CD, editors. 2014. Atlas of British and Irish Bryophytes. 2 volumes. Newbury: Pisces Publications.
- Blockeel TL, Kučera J, Fedosov VE. 2017. *Bryoerythrophyllum duellii* Blockeel (Bryophyta: Pottiaceae), a new moss species from Greece and Cyprus, and its molecular affinities. *Journal of Bryology*. 39:247–254.
- Ellis LT, Bednarek-Ochyra H, Ochyra R, Benjumea MJ, Saïs LV, Caparrós R, Lara E, Mazimpaka V, Dulin MV, Garilletti R, et al. 2013. New national and regional bryophyte records, 35. *Journal of Bryology*. 35:129–139.
- Garcia CA, Sérgio C, Vieira C, Hespanhol H, Stow S, Sim-Sim M, Long D. 2013. An update on the distribution in mainland Portugal of bryophytes of the European Habitats Directive. *Journal of Bryology*. 35:306–309.
- Hodgetts NG, Lockhart N. 2020. Checklist and country status of European bryophytes – update 2020. *Irish Wildlife Manuals*, No. 23. Dublin: National Parks and Wildlife Service, Department of Culture, Heritage and the Gaeltacht, Ireland.
- Hodgetts NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim M, et al. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*. 42:1–116.
- Koppe F, Düll R. 1986. Beiträge zur Moosflora Madeiras. *Bryologische Beiträge*. 6:32–48.
- Kučera J, Kuznetsova OI, Manukjanová A, Ignatov MS. 2019. A phylogenetic revision of the genus *Hypnum*: towards completion. *Taxon*. 68:628–660.
- Kučera J, Sollman P, Afonina OM, Ignatova EA, Fedosov VE, Shevock JR, Tubanova DY, Ignatov MS. 2020. Range extensions for *Bryoerythrophyllum sollmanianum* and *Tortula yuennanensis* (Pottiaceae, Musci) with reconsideration of their phylogenetic affinities including *Pararhexophyllum*, gen. nov. *Nova Hedwigia, Beihefte*. 150:273–292.
- Long DG. 1982. *Bryoerythrophyllum caledonicum*, a new moss from Scotland. *Journal of Bryology*. 12:141–157.
- Machado A. 1917. Notas de briologia Portuguesa. *Brotéria, Série Botânica*. 15:8–11.
- Magill RE. 1981. Flora of Southern Africa. Bryophyta. Part 1. Mosses. Fascicle 1. Sphagnaceae–Grimmiaceae. Pretoria: Botanical Research Institute.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*. 61:539–542.
- Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology*. 49:369–381.
- Sim-Sim M, Gabriel R, Hodgetts NG, Martins A. 2019. *Bryoerythrophyllum campylocarpum*. The IUCN Red List of Threatened Species 2019: e.T85839356A87715427. [accessed 2021 Mar 24]. <https://www.iucnredlist.org/species/85839356/87715427>.
- Stamatakis A. 2014. RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*. 30:1312–1313.
- Wallace JFK. 2010. Ecological assessment of Glenbower Wood [MSc dissertation]. Cork: Department of Zoology, Ecology and Plant Science, University College Cork.
- Zander RH. 1978. A synopsis of *Bryoerythrophyllum* and *Morinia* (Pottiaceae) in the New World. *The Bryologist*. 81:539–560.
- Zellweger F, Coomes D, Lenoir J, Depauw L, Maes SL, Wulf M, Kirby KJ, Brunet J, Kopecký M, Máliš F, et al. 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*. 28:1774–1786.

Appendix

Specimens examined

GenBank accession numbers for newly obtained sequences (ordered *rps4*, *trnM–trnV*) follow the herbarium codes in square brackets. Details for other sequences used in the present study can be found in Kučera et al. (2020).

***Bryoerythrophyllum campylocarpum*: Cameroon.** Mt Cameroon, 5 specimens collected at ca 3200 m a.s.l., and one at 3820 m a.s.l., 2 December 2013, *M. Dančák et al.* (CBFS: 16797, 22644, 22647, 22681, 22690, 22719 [MZ148280, MZ148277]). **Costa Rica.** San José, Cordillera de Talamanca, Cerro de la Muerte, Carretera Interamericana. Orilla de un chorro, mucha sombra, sitio humedo, *A.M. Cleef & L.A. Fournier 10220* (E). **Ireland.** Glenbower Wood nr. Kill-eagh, East Cork, W9978, by gravelly path with *Archidium*, 9 August 2002, *T. L. Blockeel 31/306* (BBSUK, CBFS [MZ148278, MZ148275]). **Madeira.** (as *B. machadoanum*) Passo di Poiso, between Monte and Poiso, on slopes and rocks of the path, 11 November 1968, *A. v. Hübschmann* (Herb. Blockeel ex Herb. R. Düll). **Malawi.** Mulanje Mt, Lichenya, on bank in forest below hut, 1740 m, *N.G. Hodgetts M2506b* (E). **Mexico.** Queretaro: near El Tejamanil, Sierra Gorda 21° 06'54"N 99°39'57"W, on soil in road cutting in dry *Pinus/Quercus* forest, 2480 m alt., 20 March 2001, *D. G. Long & C. Delgadillo 29707* (CBFS [MZ254662, MZ254663], Herb. Blockeel). **Portugal.** Algarve: Peso, N of Monchique, Serra de Monchique, 29S 0538775 4131523, on compacted soil of path through *Castanea sativa–Quercus suber* mixed woodland, 620 m alt., 1 April 2016, *R. D. Porley* (CBFS, Herb. Porley); Algarve: road to Picota summit, Serra de Monchique, 29S 0540458 4129990, on compacted soil path in *Quercus suber* woodland, 482 m alt., 8 March 2017, *R. D. Porley* (Herb. Porley). **South Africa, KwaZulu-Natal.** Drakensberg: nr Cathedral Peak Hotel, W of Winterton, 28°57'N 29°11'E, on silty soil above stream, 2000 m alt., 24 January 1995, *H. W. Matcham with J. G. Duckett, N. G. Hodgetts & L. G. Matcham* (Herb. Matcham). **Wales.** Esgair Nantyrarian, Cardiganshire, SN70908184, on soil and gravel on steep slope below track, 150 m alt., 22 January 2021, *T. W. Ottley 21012201* (BBSUK, CBFS [MZ148279, MZ148277]); Banc y Castell, Goginan, Cardiganshire, SN70078172, on shale forest track, 120 m alt., 15 February 2021, *T. W. Ottley 21021502* (Herb. Ottley); Devil's Bridge, Cardiganshire, SN74227728, fine silt between rocks set in path of Waterfall Walk, 16 April 2021, *T. W. Ottley 21041601* (Herb. Ottley).

***Bryoerythrophyllum caledonicum*: Scotland.** Aonach Beag nr Fort William, NN1971, wet base-rich schist in gully, 29 July 1986, *D. G. Long & T. L. Blockeel* (Herb. Blockeel).