



Integrative taxonomy sheds light on an old problem: the *Ulota crispa* complex (Orthotrichaceae, Musci)

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The combined use of morphological and molecular analyses has been proven to be useful in resolving taxonomic complexes with hidden diversity. In bryology, however, integrative taxonomy has rarely been employed to revisit relevant old, unresolved problems. One of these classical controversies is whether the *Ulota crispa* complex comprises one or three species. To elucidate this, an exhaustive morphological revision, based on numerous herbarium and fresh specimens from most of the Holarctic areas in which *U. crispa* has been reported, and molecular analyses, using one nuclear (ITS2) and three plastid (*trnG*, *trnL-trnF*, *atpB-rbcL*) loci on a selection of representative specimens, have been performed. The results unambiguously point to the existence of three morphotypes, ascribable to the previously described *Ulota crispa* s.s., *U. crispula* and *U. intermedia*, which can be differentiated by an ample set of qualitative and quantitative morphological characters. A phylogenetic reconstruction based on molecular data is proposed, including samples of these morphotypes in a framework of another ten *Ulota* spp. and two *Orthotrichum* and two *Zygodon* spp. According to the results, the samples belonging to these morphotypes are placed in three independent and coherent monophyletic clades, indicating that they represent three closely related, but independent, species. The origin and development of the taxonomic debate around *U. crispa* and related taxa are discussed to illuminate the reasons for this historical confusion. The analysis of the geographical origin of the studied samples shows that all three species are widely distributed throughout the Northern Hemisphere, although with different ranges. *Ulota crispula* has an amphi-Atlantic range, whereas *U. crispa* and *U. intermedia* display broader disjunct ranges; only in Europe do the three species co-occur. A key to the three species and updated detailed descriptions are provided. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, 180, 427–451

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INTRODUCTION

Integrative taxonomy (Dayrat, 2005; Padial *et al.*, 2010; Schlick-Steiner *et al.*, 2010) and, in particular, the combined approach of thorough morphological studies and DNA sequence-based phylogenetic analysis for the determination of species boundaries are allowing taxonomic problems in various biological groups to be solved satisfactorily (e.g. Grismer *et al.*, 2013; Malekzadeh-Viayeh *et al.*, 2014; Vigalondo *et al.*, 2015; Zamora, Calonge & Martín, 2015).

Among bryophytes, many cryptic species (*sensu* Bickford *et al.*, 2007) have been uncovered thanks to this methodology (e.g. Vanderpoorten *et al.*, 2010; Damayanti *et al.*, 2012; Medina *et al.*, 2012, 2013; Buchbender *et al.*, 2014; Hedenäs *et al.*, 2014; Draper *et al.*, 2015; Heinrichs *et al.*, 2015). In these organisms, integrative taxonomy has been used mainly for the study of complexes in which a hidden diversity has been suspected, but for which no critical morphological analyses have been undertaken in recent times. In that sense, the combined use of morphological and molecular analyses has rarely been applied to old taxonomic conflicts. The target of this

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study is precisely one of these old problems: the delimitation of taxa in the *Ulota crispa* (Hedw.) Brid. complex.

Ulota D.Mohr is a large genus with 69 recognized taxa (Garilleti, Mazimpaka & Lara, 2015), mainly distributed in temperate oceanic areas all around the globe, but with a few species living in montane habitats in tropical or subtropical regions. These taxa mostly grow as epiphytes on a wide diversity of trees and shrubs, although some species are primarily saxicolous or can live on rocks. They usually form part of diverse epiphytic communities and can be the dominant species on trees or shrubs under oceanic hyper-humid conditions (Garilleti, Mazimpaka & Lara, 2012; Garilleti *et al.*, 2015).

The nomenclatural history of the genus is complicated, as the strong morphological similarity with *Orthotrichum* Hedw. has led to numerous changes in taxa between both genera, including the repeated consideration of *Ulota* as a section or subgenus of *Orthotrichum* (Müller, 1849; Mitten, 1869; Boulay, 1884). Even the most outstanding monographer of *Ulota*, N. Malta, considered that the generic separation was doubtful, although he maintained it (Malta, 1927, 1932). Since then, few taxonomic treatments of the genus have been published, and all have been regional revisions without a wide territorial or systematic scope that could contribute to a better understanding of the inner structure or relationships of the genus, and thus we have no constancy of any posterior questioning of the status of this genus as an independent entity. Moreover, molecular data also point to the close relationship of *Ulota* with *Orthotrichum* spp. with superficial stomata. According to Goffinet *et al.* (2004) and Sawicki, Plásek & Szczecińska (2010), the monophyly of *Ulota* and the phaneroporous *Orthotrichum* spp. is ambiguous. The fact that the molecular evidence gathered so far is not taxonomically conclusive with regard to *Ulota* emphasizes the need for the combination of molecular and morphological approaches for any taxonomic or systematic study.

Ulota crispa is not only the type of the genus, but also one of the species with the widest range, as it has been reported from both the Palaearctic and the Nearctic. It seems to be a common species in humid oceanic forests in parts of Asia and North America, and it has been extensively reported from Europe, where it is considered to be the most common *Ulota* sp., and its predominance over other species of this genus has been regionally demonstrated (Albertos *et al.*, 2000).

This dual condition of type species with an extensive range has contributed to make *U. crispa* a model species in the genus. This moss, so variable in its current concept, presents most of the

commonest traits that define a large number of frequently sympatric species in the genus, the differences among them sometimes being subtle. Because of such morphological variability and wide distribution, many species have been described or discussed by comparison (e.g. *U. fulva* Brid., *U. bruchii* Hornsch.) and some have been synonymized (e.g. *U. intermedia* Schimp.). An inevitable consequence of this has been that the concept of the species has become confused and many synonymizations have been made. In its wider concept, *U. crispa* is the species in the genus with by far the longest list of synonyms. In recent years, some confusion has been resolved on the basis of classic morphological studies alone, by the analysis of characters not or only rarely used previously, e.g. in cases of *U. bruchii* (Garilleti *et al.*, 2000) and *U. crispula* Bruch (Caparrós, Garilleti & Lara, 2014). Despite these advances, a degree of uncertainty remains over the general validity of the morphological characters used to distinguish these species and on the relationships among them. Some doubtful synonyms that have elusive morphological differences remain under *U. crispa* and a new integrative approach is needed to resolve the true nature of these names. Two of them represent the most important cases: *U. crispula* and *U. intermedia*.

The protologue of *U. crispa* by Hedwig (1801), as *Orthotrichum crispum* Hedw., is somewhat ambiguous, as this moss was described as having crowded, crisped when dry linear leaves with a wide base, and a long exerted ovate capsule, a vague set of traits that fit most of the currently recognized species in the genus. Some years later, Bruch (in Bridel, 1827) was able to recognize a form sufficiently different to define a new species, *U. crispula* Bruch in Brid., considering his new species as being close to *U. crispa*. Later, Schimper (1876) proposed a new species, *U. intermedia* Schimp., explicitly stating its intermediate morphology between *U. crispa* and *U. crispula*. Although the traits used by these authors when describing their species are still used to discriminate *Ulota* spp., the extension and limits of their variability are imprecise in the protologues, which makes the species discrimination difficult. Moreover, the three supposedly different mosses share ecological preferences and it is common to find two growing together, which has made the interpretation of the true nature of these taxa even more difficult. This situation, with two species apparently discriminated only by subtle morphological differences, and a third with intermediate character states, has created a long-standing controversy around the nature of the two latter taxa. In fact, this old problem has been revisited several times over the last century (Smith & Hill, 1975;

Rosman-Hartog & Touw, 1987) without achieving an entirely satisfactory solution.

The goal of the present work is to determine whether the forms grouped into the so-called *U. crisper* complex correspond to a single species or whether it is possible to differentiate definitively several taxa within it. To this end, a detailed morphological study has been made to evaluate the traits traditionally used in the taxonomy of the genus, and to find new characters to define the variability and distinction of the different species more accurately. We then contrasted the morphological entities against clades inferred from phylogenetic analyses of molecular data to infer the existence of monophyletic, morphologically diagnosable taxa (see Medina *et al.*, 2012, 2013).

MATERIAL AND METHODS

MORPHOLOGICAL STUDIES

The morphological approach was an unbiased study including a large number of samples matching the concept of the problem group of species. Specimens from herbaria all around the world (BCB, BM, BP, DUKE, FCO, G, H, HIRO, LISU, MA, MAUAM, MHA, MO, MUB, NICH, NY, S, TU and VIT, and personal herbaria of P. Boudier and D. Callaghan) were included in the analyses. In addition, specimens doubtfully identified as belonging to different species of this complex were also included. As the synonymization of *U. crispula* and *U. intermedia* with *U. crisper* is an old topic, many of the herbarium samples were kept under the last name and only in rare cases were they found under the other names. In addition to herbarium specimens, the research team collected a large number of fresh material from the west coast of North America, Japan and Europe. The scope of this broad specimen sampling was intended to represent the entire distribution and ecological range of the species. In total, c. 800 samples were studied and a selection is listed in Appendix 1.

Nearly 100 morphological traits were scored, selected on the basis of the experience of the research team on *Uloa* and related groups of Orthotrichaceae (Medina *et al.*, 2012, 2013; Caparrós *et al.*, 2014). The variation in these characters across the studied samples led to the identification of different morphotypes. These were considered as potential species candidates and their characteristics were cross-checked with the type material available for *U. crisper* and related taxa (for the detailed study, see Caparrós *et al.*, in press) to give the nomenclaturally correct name to each morphotype.

DNA EXTRACTION, POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION AND SEQUENCING

For the molecular study, we sampled several specimens covering the geographical range of each morphotype: 11 specimens morphologically assigned to *U. crisper s.s.*; seven specimens assigned to *U. crispula*; and seven specimens assigned to *U. intermedia*. Other Northern Hemisphere *Uloa* spp. were also included to provide a phylogenetic framework: *U. bruchii*, *U. coarctata* (P.Beauv.) Hammar, *U. curvifolia* (Wahlenb.) Lilj., *U. drummondii* (Hook. & Grev.) Brid., *U. macrospora* Baur & Warnst., *U. megalospora* Venturi, *U. obtusiuscula* Müll. Hal. & Kindb., *U. phyllantha* Brid., *U. rehmannii* Jur. and *U. reptans* Mitt. Specimens of other members of Orthotrichaceae were also included to complete the outgroup sampling: *Orthotrichum affine* Brid., *O. rupestre* Schleich. ex Schwägr., *Zygodon pentastichus* (Mont.) Müll. Hal. and *Z. viridissimus* (Dicks.) Brid. A complete list and details of the specimens can be found in Appendix 2.

Total DNA was extracted from a single individual in each sample using a Plant DNeasy Mini Kit from Qiagen. PCR was performed in an Eppendorf Mastercycler using PuReTaq™ Ready-To-Go™ PCR Beads (GE Healthcare, Madrid, Spain) in a reaction volume of 25 µL, according to the manufacturer's instructions. Four molecular regions were amplified, one from the nuclear genome (ITS2) and three from the plastid genome (*trnG*, *trnL-trnF* and *atpB-rbcL*).

For ITS2, the primers used were ITS2 forward and ITS2 reverse (Ziolkowski & Sadowski, 2002), and the amplification protocol included one melting step of 1 min at 94 °C, followed by 30 cycles (up to 35 in samples that were difficult to amplify) of 1 min at 94 °C, 1 min at 59 °C and 1 min 30 s at 72 °C, and a final extension period of 5 min at 72 °C. For *trnG*, the primers used were *trnGf_leu* (Stech *et al.*, 2011) and *trnGr* (Pacak & Szweykowska-Kulinska, 2000), and the PCR program included one melting step of 5 min at 94 °C, followed by 40 cycles of 30 s at 94 °C, 40 s at 52 °C and 1 min 30 s at 72 °C, and a final extension period of 8 min at 72 °C. For *trnL-trnF*, the primers used were *trnLc-104* and *trnFF-425* (Vigalondo *et al.*, 2016). The PCR program included one melting step of 5 min at 94 °C, followed by 38 cycles of 30 s at 94 °C, 1 min at 47 °C, 30 s at 72 °C and 30 s at 94 °C, and a final extension period of 1 min at 72 °C. For *atpB-rbcL*, the primers used were *atpB* and *rbcL* (Chiang, Schaal & Peng, 1998), and the PCR program included one melting step of 5 min at 94 °C, followed by 30 cycles of 30 s at 94 °C, 1 min at 52 °C and 30 s at 68 °C, and a final extension period of 7 min at 68 °C.

After visualization on 1% agarose gels, successful amplifications were purified using the Exo/SAP protocol (Thermo Fisher Scientific, Madrid, Spain). Samples were incubated with 1 µL Exo1 enzyme and 4 µL FastAP following the manufacturer's instructions. Cleaned PCR products were sequenced by Macrogen (www.macrogen.com).

SEQUENCE EDITING, ALIGNMENT AND PHYLOGENETIC ANALYSIS

Nucleotide sequences were edited and assembled for each DNA region in PhyDE v0.9971 (Müller *et al.*, 2006). The assembled sequences were manually aligned and the primer annealing sites and regions with incomplete data at the 5' and 3' ends of the sequences were excluded from subsequent analyses: for ITS2, 36 positions at the 3' end; for *trnG*, 26 positions at the 5' end/72 positions at the 3' end; for *trnL-trnF*, 12/20 positions; and for *atpB-rbcL*, 73/60 positions.

Phylogenetic reconstructions were made on the basis of three different optimality criteria [maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI)] to assess whether there were any differences in the trees recovered with regard to the method used. The analyses were performed with the programs TNT 1.1 (Goloboff, Farris & Nixon, 2008) for MP, MEGA 6 (Tamura *et al.*, 2013) for ML and MrBayes 3.2.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist *et al.*, 2012) for BI. Among the outgroup taxa (Appendix 2), *Z. pentastichus* was considered to be the furthest outgroup and was used to root the consensus tree recovered by BI.

The swapping algorithm selected in TNT was tree bisection–reconnection (TBR), with ten trees held in memory. All characters were equally weighted. Clade support in MP analyses was assessed via non-parametric bootstrapping (bootstrap support, BS) using the default settings in TNT, except for the number of replicates, which was set to 1000. The output results requested were the absolute frequencies. For all generated MP trees, the consistency index (CI), retention index (RI) and tree length were calculated.

The nucleotide substitution models used for the ML and BI analyses were selected for each locus separately using jModeltest 2.1.4 (Posada, 2008; Darriba *et al.*, 2012) and based on the Akaike and Bayesian information criteria. These were HKY + I + G for ITS2 and HKY + G for the three plastid markers (*trnG*, *trnL-trnF*, *atpB-rbcL*). On the basis of these results, the matrix for the final analyses was partitioned in two, one partition corresponding to the nuclear and the other to the plastid regions. Clade support in ML was assessed using 1000 bootstrap

replications, and the ML heuristic method selected was nearest-neighbour interchange.

The BI analyses used one cold and three incrementally heated Monte Carlo Markov chains (MCMCs) on two simultaneous runs. MCMC runs continued until the standard deviation of the split frequencies was below 0.01 (3 000 000 generations), with one tree sampled every 1000th generation, each using a random tree as a starting point and a temperature parameter value of 0.2 (the default in MrBayes). The first 25% of the total sampled trees of each run were discarded as 'burnin' to achieve the MCMC log-likelihoods that had become stationary and converged. Clade support in these analyses was assessed as the posterior probability (PP).

Insertions and deletions (indels) in non-coding regions are sometimes difficult to assess (e.g. Kelchner, 2000) and can lead to ambiguous alignments. This is the case in part of the ITS regions, and to determine the effect of their inclusion, all the analyses were run with the indels considered as missing information and with indels coded as informative characters. The indel coding strategy was the simple method of Simmons & Ochoterena (2000), as implemented in SeqState (Müller, 2004), and the model selected for the indel partition in MrBayes was F81, as recommended by Ronquist, Huelsenbeck & Teslenko (2011). The analyses were run with the same parameters indicated for the datasets without coded indels.

Initially, the four regions (ITS2, *trnG*, *trnL-trnF* and *atpB-rbcL*) were analysed separately, using the three different optimality criteria (MP, ML and BI). The matrices used have been deposited in TreeBASE (<http://purl.org/phylo/treebase/phylovs/study/TB2:S18716>). The results were visually compared to try to find possible incongruence among regions, between the datasets (coding or treating the indels as missing data) or among the different reconstruction methods. After this inspection, the four regions were combined in a single matrix.

RESULTS

MORPHOLOGICAL APPROACH

The analysis of morphological variability led to the identification of three different morphotypes in the *U. crispa* complex. The study of the appropriate type material enabled each of these three morphotypes to be related to one of the three principal names of the complex: *Orthotrichum crispum* (\equiv *U. crispa*), *U. crispula* and *U. intermedia*. Results from the study of the type material, including the detailed lectotypification, are presented in Caparrós *et al.* (in press). The differentiation of these species

is based on a broad set of characters (see Taxonomic section and Table 1), including several qualitative macro- and microscopic characters.

MOLECULAR SEQUENCE VARIATION

The length variation in the four DNA regions is shown in Table 2, with the information content of each data partition. No incongruence in terms of well-supported clades was observed in separate analyses of the four molecular loci, and therefore all the markers were combined in a single matrix that had a total length of 1944 bp, with 206 variable sites (95 potentially parsimony informative, 19 in *U. crispera*, *U. crispula* and *U. intermedia*). Simple indel coding increased the number of potentially parsimony-informative characters by three within the ingroup and recovered trees with identical topology, but slightly higher support, than those obtained when the indels were treated as missing data.

PHYLOGENETIC RECONSTRUCTION

The MP analyses yielded 96 (without considering the indels) or 16 (with the indels coded) most parsimonious trees (length: 725/440; CI = 0.78/0.81; RI = 0.83/0.84). The consensus tree had a congruent topology with that obtained in the ML and BI analyses, although both MP and ML resolved fewer clades than BI, as shown in Figure 1. We hereafter refer to the support values in the text following the scheme (PPindels/PP/BSindels in MP/BS in MP). ML analyses recovered trees with low support, which are not shown.

The molecular data resolve all of the included samples of *Ulota* in a monophyletic well-supported group according to BI (0.94/0.99/–/–), which is placed as the sister clade of the outgroup species belonging to *Orthotrichum*. In *Ulota*, the ingroup samples are gathered in three separate well-supported clades that correspond to the three morphotypes: *U. crispera* (1/1/79/78), *U. crispula* (1/1/79/79) and *U. intermedia* (0.99/0.95/64/65). The molecular data gathered for the present study are not sufficient to fully resolve the relationships within *Ulota*. According to the tree recovered when the indels are considered as informative, *U. crispula* and *U. crispera* could be closely related. This sister relationship is poorly supported (0.7) and, when the indels are treated as missing information, the tree recovered suggests a closer relationship between *U. crispula* and *U. intermedia* (0.86). All of the analyses indicate that sister species to the clade including the ingroup samples, are *U. curvifolia* and *U. obtusiuscula* (1/0.77/82/79). Other species closely related to this group are *U. reptans* and *U. drummondii* (1/1/86/–). However,

U. rehmannii, *U. megalospora*, *U. bruchii*, *U. coarctata* and *U. macrospora* are gathered in a well-supported sister clade (1/1/94/–). Finally, *U. phyllantha* is located in an early-branching grade according to BI (0.94/0.99).

DISCUSSION

The species belonging to the *U. crispera* complex are conspicuous mosses common on trees in temperate regions of Europe and North America, and hence they have been extensively collected, including in the early days of bryology. Dillenius (1742) and Linnaeus (1763) had already referred to these plants, and the first species validly published of what became the genus *Ulota*, *Orthotrichum crispum*, was in the opus that has been chosen as the nomenclatural starting point for most mosses (Hedwig, 1801). Before long, Mohr (1806) created the genus *Ulota* and Bridel (1818) made the combination *U. crispera*. Subsequently, *U. crispula* was described (Bruch in Bridel, 1827), accurately discussing its most outstanding differences from *U. crispera*. Bruch, the author of that species, had a clear concept of these two species and their differences, including the characters that later led him to recognize *in schedula* (BM 000852210!) a new moss, first considered as an *Orthotrichum* sp. (*O. intermedium*, cf. Caparrós *et al.*, in press). Schimper published the valid description of *U. intermedia* after the death of Bruch (Schimper, 1876), with whom he had collaborated intensively. Schimper partially based the description of the species on the above-mentioned specimens of Bruch, but he added several materials identified by himself that were not always correctly interpreted. Although *U. intermedia* became well defined, Schimper's incorrect mixture of materials complicated the establishment of its clear morphological delimitation. Moreover, this could maintain or increase the existing uncertainties about the distinction of *U. crispera* and allied forms, and revitalize the increasing controversy on the taxonomic value of these forms. Indeed, *U. crispula* had already been proposed at variety rank (Hammar, 1857). After the work of Schimper (1876), some classical authors recognized all three species (Limpricht, 1890–1895; Husnot, 1892–1894), but others regarded them as forming a single species with varieties (Braithwaite, 1888–1895; Dixon, 1924) or two different species with a transitional form corresponding to *U. intermedia* (Boulay, 1884). Paradoxically, most of these authors properly differentiated the three taxa but, independent of the taxonomic rank considered, they regarded 'crispula' and 'intermedia' as forms of doubtful value because of the difficulties in a clear allocation of

Table 1. Main morphological characters for the differentiation of *Ulotia crispata*, *U. crispula* and *U. intermedia*

	<i>Ulotia crispata</i>	<i>Ulotia crispula</i>	<i>Ulotia intermedia</i>
Sporophyte			
Sporophyte total length (mm)	(3.0–)3.2–6.8(–7.4)	(1.8–)2.0–3.8(–4.0)	(3.0–)3.2–6.5
Spores	(12–)14–23(–25)	(18–)20–29(–30)	(15–)18–35(–38)
Capsule shape	Cylindrical to ellipsoid	Short cylindrical to ovoid or somewhat urceolate	Ellipsoid to cylindrical-ellipsoidal, rarely long ovoid
Capsule when dry and full of spores	Urceolate	Short cylindrical to somewhat urceolate or obconic	Cylindrical, oblong-cylindrical, obconic or elongate-ovoid
Urn shape when dry and empty	Strongly constricted	Not or slightly constricted	Not constricted
Constriction below mouth when dry and empty			
Capsule furrows (spaces between ribs)	Commonly uniformly narrow, collapsed at the constricted area of the urn	Usually broad, somewhat sinuous or irregular, not collapsing anywhere	Broad, not collapsing anywhere
Width of furrows when dry and empty			
Exothecial bands			
Number of cell rows	4–5(–6)	2–4	2–4(–5)
Cell colour	Evenly yellow to pale orange	Evenly pale yellow	Hyaline with pale yellow incrassated lateral walls
Differentiation at capsule mouth	Neatly reaching the mouth or obscurely separated by a ring of small, thin-walled cells in 1–3(4) layers	Not reaching the mouth, visibly separated by a ring of small, thin-walled cells in (1)2–4(5) layers	Not reaching the mouth, visibly separated by a ring of small, thin-walled cells in (1)2–6(7) layers
Peristome: exostome teeth			
Tendency of teeth pairs to split	No, most teeth remain tightly fused in pairs even in old capsules	Yes, teeth split easily after being recurved	Yes, teeth tend to split after being recurved
External visibility of principal peristomial layer (PPL) at marginal parts of teeth	Yes, as a smooth hyaline halo (sometimes not visible in deteriorate teeth)	No	No
Peristome: endostome segments			
Segment appearance and durability	Robust and persistent	Slender and fragile	Robust and usually persistent
Segment position when dry	Incurved	Irregular (some incurved, other erect or patent)	Incurved
Segment shape	Long triangular to subulate	Almost linear with a more or less widened base	Broadly linear with a more or less widened base or subulate
Segment cell pattern at the inner peristome layer (IPL)	Uniseriate, with transversal walls variably incrassate	Uniseriate or irregularly biseriate, with thin transversal walls	Uniseriate, with incrassate and prominent transversal walls

Table 1. *Continued*

	<i>Ulota crispera</i>	<i>Ulota crispula</i>	<i>Ulota intermedia</i>
Internal ornamentation (IPL)	Smooth to finely papillose below, variably papillose above, but never opaque because of the papillae density	Densely covered by a reticulum of striae, perceived above as an opaque, almost smooth ornamentation	Smooth to very finely papillose below, variably reticulate above, but never opaque because of the ornamentation density
Operculum			
Colour	Yellowish, without a differentiate basal rim	Yellowish, usually with an orange to reddish basal rim	Yellowish, without a differentiate basal rim
Gametophyte			
Habit and aspect when dry	Medium to large cushions, generally strongly crisped	Small to large cushions, slightly to markedly crisped	Medium to large cushions, markedly crisped
Leaves			
Leaf shape when dry	Tortuose or circinate, occasionally falcate	Curved to tortuose, more rarely circinate	Tortuose or circinate, occasionally falcate-tortuose
Leaf base	Mostly obovate, distinctly concave, abruptly narrowing into the lamina	Mostly elliptical, not obviously concave, gradually narrowing into the lamina	Mostly obovate, distinctly concave, abruptly narrowing into the lamina
Leaf basal marginal cells			
Width of band with differentiated cells	Broad, (5–7–16–20) cell rows	Usually narrow, (1–)3–8(–10) cell rows	Narrow to broad, (2–)3–14(–16) cell rows

Table 2. Length variation, number of variable and potentially informative sites and most suitable substitution model for the nuclear (ITS2) and plastid (*trnG*, *trnL-trnF* and *atpB-rbcL*) sequences used in this study

	ITS2	<i>trnG</i>	<i>trnL-trnF</i>	<i>atpB-rbcL</i>
Length variation				
<i>Orthotrichum affine</i>	460	512	305	Incomplete
<i>Orthotrichum rupestre</i>	460	514	305	493
<i>Ulota bruchii</i>	452	513	306	494
<i>Ulota coarctata</i>	474	513	Incomplete	494
<i>Ulota crispa</i>	449–450	511–517	304–305	484–485
<i>Ulota crispula</i>	449	511	303–305	484–495
<i>Ulota curvifolia</i>	449	512	306	484
<i>Ulota drummondii</i>	474	512	306	483–484
<i>Ulota intermedia</i>	449–450	511–512	305–306	484
<i>Ulota macrospora</i>	488	513	Incomplete	494
<i>Ulota megalospora</i>	471	513	306	494
<i>Ulota obtusiuscula</i>	Incomplete	512	306	485
<i>Ulota phyllantha</i>	Incomplete	509	305	493
<i>Ulota rehmannii</i>	515	513	306	494
<i>Ulota reptans</i>	485	512	307	484
<i>Zygodon pentastichus</i>	Incomplete	518	319	491
<i>Zygodon viridissimus</i>	446	524	318	494
Variable sites	80	52	36	38
Variable sites (ingroup)	6	5	3	9
Informative sites	33	22	20	20
Informative sites (ingroup)	5	4	3	7
Indel sites	68	25	11	9
Indel sites (ingroup)	3	1	2	0
Indel informative sites	31	11	6	5
Indel informative sites (ingroup)	0	1	2	0
Positions in data matrix	1–585	586–1115	1116–1443	1444–1944
Substitution model	HKY + I + G	HKY + G	HKY + G	HKY + G

some exemplars to any of the three taxa. The situation worsened during the 20th century, when *U. crispula* and *U. intermedia* were generally considered as unimportant forms or merely synonyms of *U. crispa* (Grout, 1935; Nyholm, 1956; Smith & Hill, 1975; Rosman-Hartog & Touw, 1987). Finally, Smith & Proctor (1993) did not consider *U. crispula* or *U. intermedia* in their revision of the *U. crispa* complex, which, in fact, consisted of the distinction of *U. crispa* and *U. bruchii*, a question later resolved by Garilleti *et al.* (2000). Only recently, Caparrós *et al.* (2014) reinstated *U. crispula* based on significant morphological differences, leading to the current study.

Qualitative macroscopic characters that differentiate the three species can be observed with a hand lens, even in the field, whenever samples are in dry conditions and have ripe capsules (Table 1). These traits include: the capsule shape both when full of spores and when dry and empty; the eventual constriction of the urn below the mouth when dry and empty and the subsequent collapse of the capsule

ribs at the constricted area or the more or less uniform separation of ribs by broad furrows; in the peristome, the possible tendency of teeth pairs to split, the segment shape and its durability in empty capsules; and the potential differentiation of a coloured basal rim in the operculum. Additional quantitative macroscopic characters, such as the sporophyte total length, the size of the cushions and the degree of crispature of leaves when dry, eventually can help in the identification of these species, even in the field.

A complementary set of diagnostic microscopic characters allows a safe discrimination in the laboratory of specimens in a good state of preservation and with the necessary morphological structures. These include some qualitative traits related to the peristome, such as the existence or not of a thin hyaline membrane-like margin bordering the exostome teeth, or the precise structure, ornamentation and position of the endostome segments when dry. To this type of discriminant characters also belong the form of the leaf bases (shape, type of narrowing towards the lamina and concavity), the structure of the exothelial

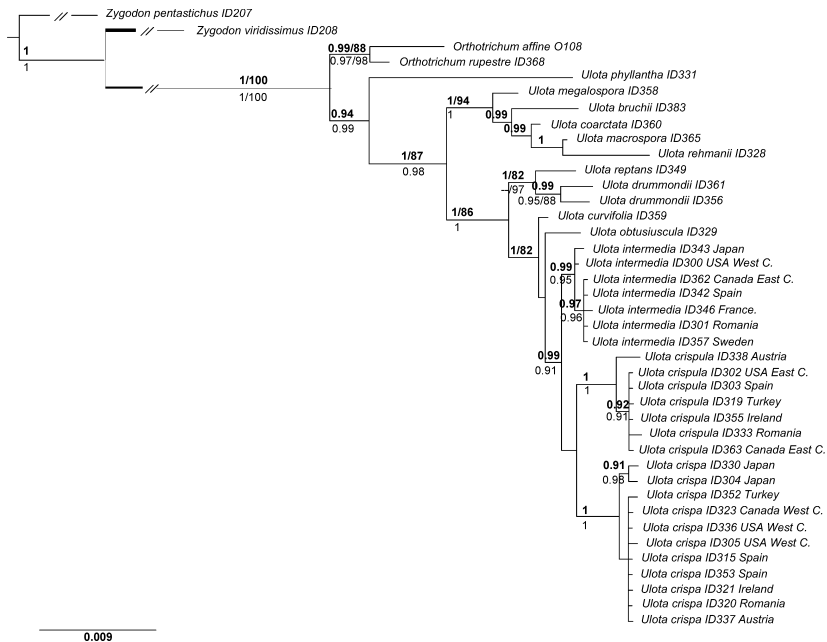


Figure 1. Consensus phylogram based on Bayesian inference (BI) resulting from the analysis of the matrix combining ITS, *trnG*, *trnL-trnF* and *atpB-rbcL* datasets, treating indels as missing information. The numbers above the branches indicate node supports when indels were coded and considered in the analyses; the numbers below the branches indicate node supports when the indels were treated as missing data. The first value indicates BI support (posterior probability, values shown are those > 0.9); the second value indicates maximum parsimony (MP) (bootstrap support, values shown are those > 80). The tree was rooted using *Zygodon pentastichus* as outgroup. Sample numbers are indicated in Appendix 2.

bands (number of cell rows and cell colour) and their potential reach to the mouth. Finally, some microscopic quantitative traits have representative ranges of values for the different species, namely the spore size and the width of the band of leaf basal marginal cells (Table 1).

Our phylogenetic reconstruction based on molecular data places samples identified as *U. crista*, *U. crispula* or *U. intermedia* in independent clades that are coherent with the morphological placement. The congruent results obtained with all the different phylogenetic methods employed (BI, MP and ML) and from the morphological study increase the support for the recognition of the three morphotypes at the species level. Despite the lack of a complete phylogenetic analysis of the genus, the results suggest that these species are closely related. According to Bickford *et al.* (2007), this could be considered as a true complex of cryptic species, in the sense that three distinct species have been erroneously classified (and hidden) under one species name (*U. crista*) by most bryologists during the last century. The results of specific studies carried out by Smith & Hill (1975) and Rosman-Hartog & Touw (1987), searching for differences between these species, also point in the same direction. However, according to

our results, each of these three entities can be diagnosed on the basis of morphological traits (Table 1), several of them being decisive. In consequence, specimens in good condition can be unequivocally ascribed to the corresponding species in the complex (see Taxonomic section).

Not all the differential traits highlighted here for the differentiation of the species in the *U. crista* complex are new. Indeed, many have been used previously for the distinction of these taxa, although not always exactly as we do. It is unclear why the delimitation of the species in the complex has been unsatisfactory in the past, but it could rely on difficulties related to the interpretation of characters. On the one hand, it seems that some of the most useful traits considered here were poorly or ambiguously defined. This was the case for the features related to the capsule shape and appearance. Capsule outline and colour, its constriction below the mouth and the aspect of the capsule ribs, although of great interest for the distinction of these species (Table 1), show a wide variation that depends on the capsule condition (full or empty of spores, dry or wet state and degree of ripeness). Our conclusion is that, to be informative, these features must be referred to a specific condition (wet or dry, full of spores or empty). A similar situa-

tion has occurred with the leaf base, as its shape must be specified in terms of outline and, in particular, by the degree of narrowing towards the lamina and concavity. However, most quantitative traits used previously, such as the capsule and seta lengths or leaf crispature, show a broad variability and should not be used as main differential characters, although they can help in the identification as complementary features in many cases. The degree of leaf crispature when dry could be useful to separate *U. crispula*, which normally is evidently less crisped than *U. crispera* and *U. intermedia*. However, it is not uncommon to find more strongly crisped exemplars of *U. crispula* and exceptionally slightly crisped forms of *U. crispera*, which seem to be especially frequent in Japan.

Most of the authors who supported the distinction of the taxa in the *U. crispera* complex based it on a misleading interpretation of the morphological variability, without finding significant qualitative characters for a sharp distinction. As a consequence, they could only establish typical trends of morphological variation for each taxon and, at the same time, indicated the existence of intermediate forms. This fact was decisive for more synthetic taxonomists or those who knew the complex less well and gave little relevance to the differences shown by the extreme forms. In both cases, the result was the classification of all forms under a single species name. However, as pointed out above, qualitative differential characters for the distinction of the three *Ulota* spp. exist and, in most cases, they are related to structures that were studied only superficially, e.g. the peristome and the exothecial bands. Other differences have been completely overlooked, e.g. spore size and the differentiation of a basal rim in the operculum. In our opinion, the sum of differential morphological traits found in this study should be sufficient for the definitive recognition of *U. crispula* and *U. intermedia* as distinct species.

The molecular evidence provided in this study adds support to the recognition of the three taxa. Even in the cases in which thorough morphological investigations provide convincing taxonomic evidence, integrative taxonomy offers the opportunity to obtain strong support for the conclusions (e.g. Medina *et al.*, 2013; Hedenäs *et al.*, 2014). For such a purpose, molecular evidence is the most used and convincing today (Heinrichs *et al.*, 2015). Nevertheless, other sources of evidence are also possible (Bickford *et al.*, 2007). In the case of the *U. crispera* complex, an additional taxonomic signal comes from phenology and has been known for a long time. Bruch & Schimper (1837) stated that sporophytes of *U. crispera* and *U. crispula* mature at different times: in late summer for the former vs. usually in late spring for the latter. This was

also highlighted by other bryologists (Wilson, 1855; Schimper, 1876) and specifically treated by Jones (1951), who confirmed previous data and further suggested that the maturation of capsules in *U. intermedia* and *U. crispera* occurred at the same time. Although Smith & Hill (1975) later provided data that seemed to blur these phenological trends, our observations agree with those of Jones (1951).

TAXONOMIC SECTION

As discussed above, the three species considered here have an important set of differential characters. However, the identification of *Ulota* samples can be a complex task depending on the degree of development of the plants, the availability of mature sporophytes and the status of preservation of the material under study. The following artificial key can be used for the identification of samples in good condition, i.e. well-developed cushions with mature capsules bearing complete peristomes, belonging to the involved species. For samples in suboptimal conditions, a wider set of characters might be needed. Table 1 summarizes the most useful traits to be taken into account when discerning between *U. crispera*, *U. crispula* and *U. intermedia*, but careful evaluation of the full set of traits provided in the descriptions of these species could also be necessary before naming some particularly difficult samples.

KEY TO SPECIES

- 1 Capsules when dry and empty strongly constricted below mouth, with ribs separated by narrow furrows, collapsed at the constricted area of the urn; exothecial bands formed by four to six rows of cells, reaching the mouth or nearly so; exostome teeth remaining tightly fused in pairs in empty capsules, bordered by a hyaline halo. *U. crispera* s.s.
- 1' Capsules when dry and empty not or slightly constricted below mouth, with ribs separated by more or less broad furrows in the upper half of urn; exothecial bands formed by two to four (five) rows of cells, visibly separated from the mouth by a ring of small thin-walled cells; pairs of exostome teeth partially splitting in empty capsules, teeth not bordered by a hyaline halo 2
- 2 Endostome segments incurved when dry, uniseriate with incrassate and prominent transverse walls; all the cells of the exothecial bands hyaline with pale yellow incrassate lateral walls; leaves markedly crisped when dry, abruptly narrowing from a concave base *U. intermedia*

2' Endostome segments variably bent when dry, uniseriate or irregularly biseriate with thin transverse walls; cells of the exothecial bands evenly pale yellow, at least in the two central rows; leaves slightly or moderately crisped when dry, gradually narrowing from a plane to slightly concave base *U. crispula*

≡ *Orthotrichum crispum* Hedw., Sp. musc. frond. 162. 1801 (basionym).
 ≡ *Bryum crispum* (Hedw.) With., Syst. arr. Brit. pl. (ed. 4) 3: 810. 1801.
 ≡ *Weissia crispata* (Hedw.) P.Gaertn., B.Mey. & Scherb., Oekon. Fl. Wetterau 3(2): 94. 1802.
 ≡ *Systegium crispum* (Hedw.) Schur, Enum. pl. Transsilv. 866. 1866. *hom. illeg.* [non *S. crispum* (Hedw.) Schimp. - 1860].

SPECIES DESCRIPTIONS

Ulota crispata (Hedw.) Brid., Muscol. recent. suppl. 4: 112. [1818] 1819.

Type: In saxis, arborum truncis per omnem Europam. **Lectotype:** *s. loc.*, *s. coll.* (G 00040001!, herb.

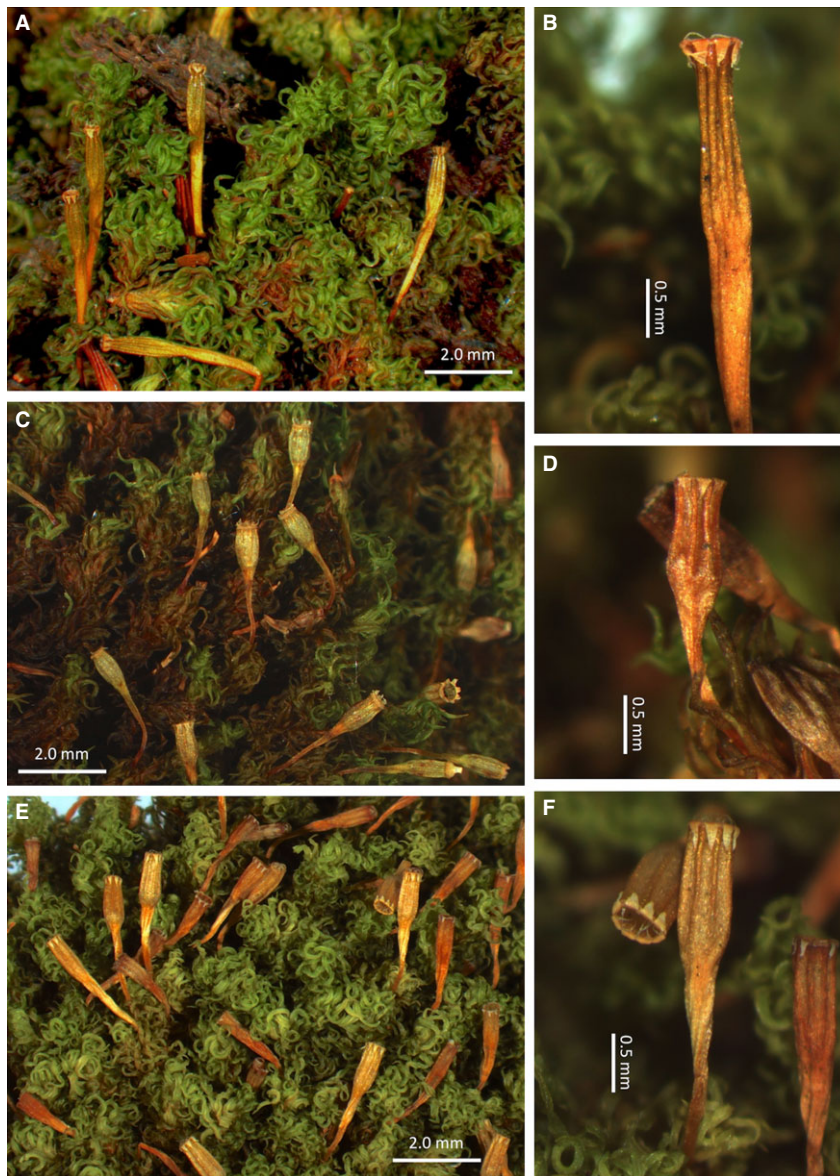


Figure 2. Comparison of general habit and capsule shape when dry and empty of *Ulota crispata* (A, B; MAUAM-Brio 4441), *U. crispula* (C, D; MAUAM-Brio 4439) and *U. intermedia* (E, F; MAUAM-Brio 4749).

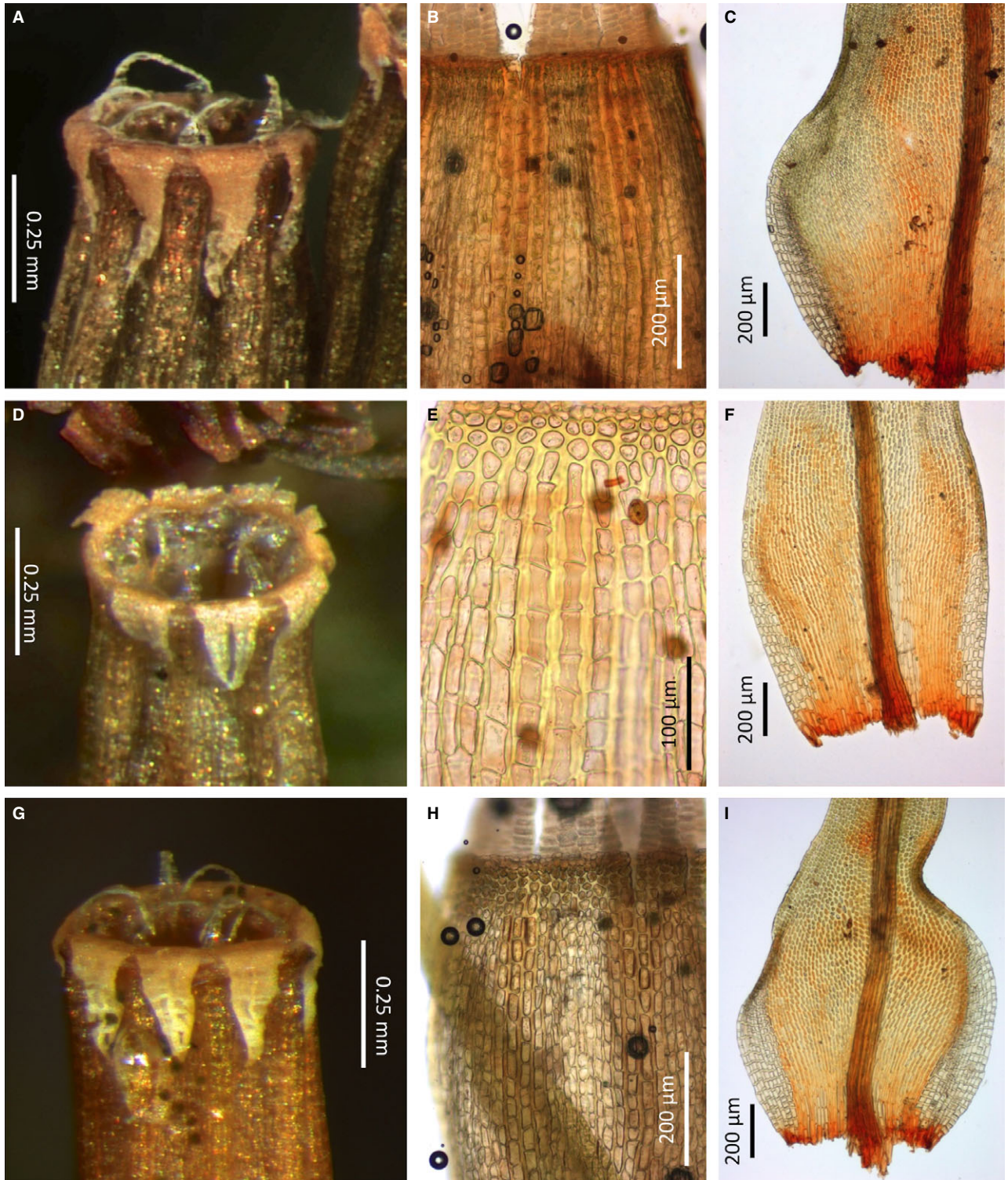


Figure 3. Comparison of *Ulota crispula* (A–C; MAUAM-Brio 4441), *U. crispula* (D–F; MAUAM-Brio 4439) and *U. intermedia* (G–I; MAUAM-Brio 4749). A, D, G, Details of the capsule mouth with well-preserved peristome teeth and segments; in D, the characteristic teeth splitting of *U. crispula* can be observed in the frontal tooth pair. B, E, H, Images of the exothecial bands; note the thinnest band in *U. crispula*, only two cells wide, and the suboral ring of short cells in *U. crispula* and *U. intermedia*. C, F, I, Different transitions from leaf base to lamina: abruptly narrowing in *U. crispula* and *U. intermedia*, and gradual in *U. crispula*.

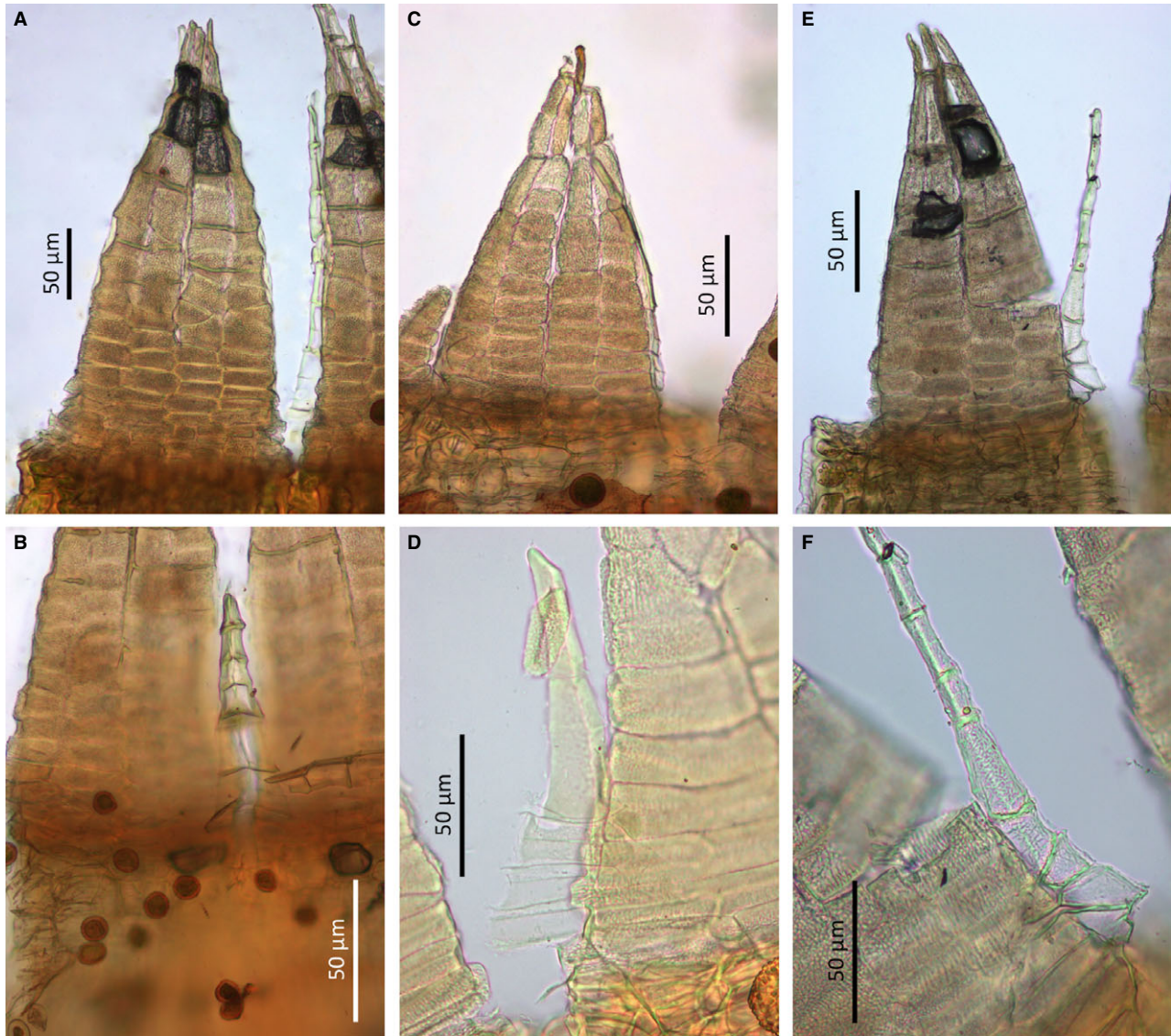


Figure 4. Comparison of peristome of *Uloata crispa* (A, B; MAUAM-Brio 4441), *U. crispula* (C, D; MAUAM-Brio 4439) and *U. intermedia* (E, F; MAUAM-Brio 4749). A, C, E, Views of exostome tooth pairs and a principal endostome segment. B, D, F, Details of an endostome segment; in B and F, transversal walls are clearly incrassate. The hyaline halo of the peristome of *U. crispa* can be observed in the central part of the tooth (A); in this case, the halo is not particularly well developed. The trabeculae of the primary peristomial layer (PPL) of *U. crispa* (A) and *U. intermedia* (E) cause the retention of the air droplets that appear in these photographs; the trabeculae are also apparent in Figure 3A, G.

Hedwig-Schwägrichen). Lectotypified by Caparrós *et al.* (in press).

Figures 2A, B; 3A–C; 4A, B.

Plants to 3.3 cm high, usually strongly crisped, growing in dense, medium to large cushions, olivaceous to dark green above, brownish to reddish below. **Stems** abundantly branched. **Rhizoids** common at stem base, frequently also scattered along stems, brown-reddish, smooth. **Leaves** mostly tortuose or circinate, occasionally falcate when dry,

erect-patent to squarrose when wet, (1.3–)1.4–3.7 (–3.8) × 0.3–0.9(–1.0) mm; **leaf lamina** lanceolate to narrowly lanceolate, unistratose, variably keeled; **leaf base** wide, obovate, rounded or oblate, distinctly concave, abruptly narrowing into lamina. **Apex** acuminate, sometimes channelled or with one margin irregularly incurved. **Margins** weak and variably recurved on one or both sides of lamina. **Costa** ending at some distance from apex. **Median and upper leaf cells** rounded to elliptic, (6–)9–16(–

22) × (6–)9–12(–17) µm, with moderately incrassate cell walls, with one or two low and simple, frequently inconspicuous papillae; **basal leaf cells** long rectangular to linear, (15–)25–45(–74) × (5–)7–11(–14) µm, with incrassate, sinuous, sometimes porose cell walls; **differentiated basal marginal cells** in (5–)7–16(–20) rows, forming a broad marginal band along leaf base. **Goniautoicous. Perichaetial leaves** differentiated, clearly longer and with wider and more elongated base than vegetative leaves, apex acute to acuminate, and costa frequently percurrent. **Vaginula** naked or variably hairy, with hairs partially two- to four-seriate, papillose, hyaline. **Sporophyte** (3.0–)3.2–6.8(–7.4) mm long. **Seta** (0.3–)0.5–4.4(–5.0) mm long. **Capsule** long exserted. **Urn** cylindrical to ellipsoid when dry and full of spores; clearly urceolate, strongly constricted below mouth when dry and empty, then with eight long and prominent ribs separated by narrow furrows, collapsed at the constricted area of urn; (0.5–)0.8–1.7(–2.0) mm long, yellowish brown to reddish brown with concolorous ribs. **Neck** usually long, 0.5–3.0 times as long as urn, gradually tapering into seta. **Exothecial bands** four or five (six) cells wide, almost as long as urn, reaching the mouth or obscurely separated from it by a thin ring, 8–33(–38) µm tall, formed by one to three (four) layers of small, thin-walled cells; differentiated cells of the band evenly yellow to pale orange, not concolorous with other exothecial cells. **Stomata** located in urn base and upper part of neck. **Peristome** double. **Prostome** frequent, usually incomplete and low, more rarely well developed. **Exostome** of eight pairs of teeth remaining tightly fused even in old capsules, yellowish to orange, recurved and lying on the exothecium when dry; outer surface outer peristome layer (OPL) densely ornamented by thin papillae, weakly striate in the distal portion; inner surface (exostomial Principal Peristome Layer [PPL]) smooth or finely papillose, frequently with distinct trabeculae; PPL visible externally as a hyaline halo as OPL edges partially retract. **Endostome** of eight robust and persistent segments, occasionally with up to eight additional intermediate, sometimes shorter processes; principal segments *c.* two-thirds the length of teeth, long triangular to subulate, uniseriate with transversal walls variably incrassate, incurved when dry, translucent and shiny; external surface (endostomial PPL) smooth; internal surface inner peristome layer (IPL) smooth to finely papillose below, variably papillose above, but never opaque because of the papillae density. **Operculum** plane-convex to conic, rostrate, yellowish without differentiated basal ring. **Calyptra** hairy, hairs one- to four- (to five-) seriate, exceeding the beak. **Spores** (12–)14–23(–25) µm in diameter.

Distribution: West coast of North America, common and widespread throughout Europe, south-west Asia (Pontic Mountains, Caucasus), China, Russian Far East, Japan and Taiwan.

- Ulota crispula* Bruch**, Bryol. Univ. 1: 793. 1827.
 ≡ *Orthotrichum crispulum* (Bruch) Hornsch., Bryol. Eur. fasc. 2-3: 23. 1837.
 ≡ *Ulota crispa* var. *crispula* (Bruch) Hammar, Monogr. Orthotrich. Ulot. Suec. 24. 1852.
 ≡ *Orthotrichum crispum* ssp. *crispulum* (Bruch) Nyl. & Saelan, Herb. Mus. Fenn. 66. 1859.
 ≡ *Systegium crispula* (Bruch) Schur, Enum. pl. Transsilv. 866. 1866.
 ≡ *Weissia crispula* (Bruch) Lindb., Acta Soc. Sci. Fenn. 10: 12. 1871. *Illegitimate, later homonym* [non *W. crispula* Hedw. - 1801].
 ≡ *Orthotrichum ulophyllum* ssp. *crispulum* (Bruch) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 121. 1883.
 ≡ *Orthotrichum cupulatum* ssp. *crispulum* (Bruch) Boulay, Musc. France, mousses 344. 1884.
 ≡ *Weissia ulophylla* var. *crispula* (Bruch) Braithw., Brit. moss Fl. 2: 94. 1889.
 ≡ *Orthotrichum cupulatum* var. *crispulum* (Bruch) Dalla Torre, Z. Ferdinandeums Tirol 35: 241. 1891. *Hom. illeg.*
 ≡ *Ulota crispa* ssp. *crispula* (Bruch) Hérib., Mém. Acad. Sci. Clermont-Ferrand 14: 333. 1899.
 ≡ *Ulota ulophylla* var. *crispula* (Bruch) Weim., Förteckn. Skand. Växt., moss. (ed. 2) 40. 1937.
 ≡ *Ulota ulophylla* ssp. *crispula* (Bruch) Giacom., Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia, Atti 4: 249. 1947.

Type: In arboribus sylvaticis *c.* Bipontium clar. Bruch detexit; a quo ut et a Funckio amice communicatum habemus. **Lectotype:** [Germany, Rheinland-Pfalz: Zweibrücken]. ‘An Waldbäumen bey Zweibrücken/(Bruch) [s.n.]’ (B 31 0251 01!). Lectotyped by Caparrós *et al.* (in press).

Figures 2C, D; 3D–F; 4C, D.

Plants to 4.2 cm high, variably crisped, growing in dense, small to large cushions, olivaceous above, brown-reddish to dark brown below. **Stems** abundantly branched. **Rhizoids** abundant at stem base and frequently ascending along stems, brown-reddish, smooth. **Leaves** curved to tortuose, more rarely circinate when dry, erect-patent to squarrose-recurved when wet, (0.7–)1.2–2.8(–3.0) × (0.1–)0.3–0.6(–0.7) mm long; **leaf lamina** lanceolate to narrowly lanceolate, unistratose, variably keeled; **leaf base** elliptical, sometimes oblong to obovate, slightly concave, usually gradually narrowing into lamina. **Apex** acuminate to long acuminate, frequently channelled or with one margin irregularly

incurved. Margins weak and variably recurved on one or both sides. **Costa** ending at some distance from apex, sometimes close to it. **Median and upper leaf cells** rounded to elliptic, (5–)8–18 (–31) × (5–)8–12(–18) μm, with moderately incrassate walls, smooth or with one or two low and simple, frequently inconspicuous papillae; **basal leaf cells** long rectangular to linear, (11–)25–40(–60) × (5–)6–10(–13) μm with incrassate, sinuous, sometimes porose cell walls; **differentiated basal marginal cells** in (1–)3–8(–10) rows, forming a relatively narrow marginal band along leaf base. **Goniautoicous**. **Perichaetial leaves** somewhat differentiated, lanceolate to widely lanceolate, longer and wider than regular leaves, leaf base oblong to obovate, variably sheathing. **Vaginula** hairy, sometimes densely, with hairs partially two- or three-seriate, papillose, hyaline. **Sporophyte** (1.8–)2.0–3.8(–4.0) mm long. **Seta** 0.9–2.1(–3.0) mm long. **Capsule** exserted. **Urn** short cylindrical to ovoid or slightly urceolate when dry and full of spores; short cylindrical, somewhat urceolate, or obconic (gradually tapering from mouth to seta), not or slightly constricted below mouth when dry and empty, then with eight prominent ribs usually separated by broad, somewhat sinuous or irregular furrows; (0.6–)0.7–1.2 mm long, pale yellow to brownish yellow, with darker ribs. **Neck** long, 0.4–2.0 times as long as urn, gradually tapering into seta. **Exothecial bands** two to four cells wide, almost as long as urn, separated from the mouth by a conspicuous ring, (12–)18–65(–75) μm tall, formed by (one–)two to four(–five) layers of small, thin-walled cells; differentiated cells of the band evenly pale yellow and not concolorous with other exothecial cells, rarely hyaline and concolorous (eastern North America). **Stomata** located in urn base and upper part of neck. **Peristome** double. **Prostome** frequent, usually incomplete and low, sometimes developed up to one-third to one-half of teeth length. **Exostome** of eight pairs of teeth with marked tendency to split into 16, yellowish to pale orange, recurved and lying on the exothecium when dry; outer surface (OPL) ornamented by thick papillae, sometimes becoming longitudinally striate or with crests in upper one-half to one-third; inner surface (exostomial PPL) smooth, occasionally with sparse, sometimes aligned, papillae in upper half; PPL not externally visible at tooth margins. **Endostome** of eight slender and fragile segments, occasionally with up to eight additional intermediate, sometimes shorter processes; principal segments almost as long as teeth, almost linear with variably widened base, irregularly biseriate, with thin transversal walls, incurved, erect or patent when dry, variably translucent at base or lower half, more or less opaque in upper part; external surface (endostomial PPL) smooth; internal surface (IPL)

with a dense reticulum of striae which, in extreme cases, may look like an opaque and almost smooth ornamentation. **Operculum** plane to convex, rarely conic, rostrate, yellowish, usually with an orange to reddish basal ring. **Calyptra** hairy, hairs two- or three- (four-) seriate, variably exceeding the beak. **Spores** (18–)20–29(–30) μm in diameter.

Distribution: Amphi-Atlantic, widespread throughout eastern North America, Europe and south-western Asia (Pontic Mountains, Caucasus).

***Ulota intermedia* Schimp.** Syn. musc. Eur. (ed. 2): 305. 1876.

≡ *Orthotrichum ulophyllum* var. *intermedium* (Schimp.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 121. 1883.

≡ *Ulota crispa* var. *intermedia* (Schimp.) Cardot, Bull. Soc. Roy. Bot. Belgique 24(2): 26. 1885.

≡ *Weissia ulophylla* var. *intermedia* (Schimp.) Braithw., Brit. moss Fl. 2: 94. 1889. *Illegitimate, earlier name included.*

≡ *Weissia intermedia* (Schimp.) Tolf, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 16 Afd. 3(9): 70. 1891.

≡ *Orthotrichum ulophyllum* ssp. *intermedium* (Schimp.) Kindb., Eur. N. Amer. Bryin. 2: 307. 1897.

≡ *Ulota crispa* ssp. *intermedia* (Schimp.) Hérib., Mém. Acad. Sci. Clermont-Ferrand 14: 333. 1899.

≡ *Orthotrichum intermedium* (Schimp.) Kindb. ex Paris, Index bryol. (ed. 2) 3: 331. 1905. *nom. inval.*

≡ *Ulota ulophylla* var. *intermedia* (Schimp.) Jansen & Wacht., Ned. Kruidk. Arch. 53: 215. 1943.

Type: Hic illic per Europam *D. crispae* et *crispulae* associata: in Hassia superior ad *Fagos* male evolutas (Bruch), prope Jever Oldenburgiae, ipse copiose legi ad arborum, praepremis *Fraxini* et *Aceris* truncos in valle Scotiae Loch Lomond. **Lectotype:** [Germany, Hesse: Marburg-Biedenkopf]. ‘Ludwigshütte. Jul Aug. 41. Bruch m. Nov. 41’ (BM 000852210!). Lectotypified by Caparrós *et al.* (in press).

Figures 2E, F; 3G–I; 4E, F.

Plants to 3.5 cm high, crisped, growing in dense, medium to large cushions, olivaceous to dark green above, dark brown below. **Stems** abundantly branched. **Rhizoids** at stem and branch bases, sometimes ascending along stems, brown-reddish, smooth. **Leaves** tortuose or circinate, occasionally falcate-tortuose when dry, erect-patent to squarrose-recurved when wet, (1.0–)1.5–3.4(–3.7) × 0.3–0.7(–0.8) mm; **leaf lamina** lanceolate to narrowly lanceolate, unistratose, variably keeled; **leaf base** obovate to orbicular, rarely oblate or elliptic, distinctly concave, abruptly narrowing into lamina. **Apex** acuminate to long acuminate, sometimes acute, frequently channelled. **Margins** weak and irregularly recurved on one or both sides, crenulate to crenulate-papillose.

Costa ending at some distance from apex. **Median and upper leaf cells** rounded to elliptic, 7–16(–17) × (6–)7–13 µm, with moderately incrassate walls, with one or two simple or bifurcate papillae; **basal leaf cells** long rectangular to linear, (18–)20–63(–68) × 5–10(–12) µm, with incrassate, sinuous, sometimes porose cell walls; **differentiated basal marginal cells** in (2–)3–14(–16) rows, forming a broad marginal band along leaf base. **Goniautoicous**. **Perichaetial leaves** differentiated, clearly longer than regular leaves, leaf base long ellipsoidal to oblong-ellipsoidal, sometimes obovate or almost orbicular, frequently sheathing, apex acute to shortly acuminate. **Vaginula** naked or hairy, with hairs partially one- or two- (three-) seriate, papillose, hyaline. **Sporophyte** (3.0–)3.2–6.5 mm long. **Seta** 1.0–4.0(–5.5) mm long. **Capsule** long exserted. **Urn** ellipsoidal to cylindrical-ellipsoidal, rarely long ovoid when dry and full of spores; cylindrical, oblong-cylindrical, obconic or elongate-ovoid, not constricted below the mouth when dry and empty, then with prominent ribs separated by broad furrows; (0.6–)0.8–1.5(–1.7) mm long, pale yellow to brownish yellow, with darker ribs. **Neck** long, 0.5–2.0 times as long as urn, gradually tapering into seta. **Exothecial bands** two to four (five) cells wide, almost as long as urn, separated from the mouth by a conspicuous ring, (15–)18–113(–238) µm tall, formed by (one-) two to six (–seven) layers of small, thin-walled cells; differentiated cells of the band hyaline with pale yellow incrassate lateral walls, concolorous with other exothecial cells. **Stomata** located in urn base and upper part of neck. **Peristome** double. **Prostome** frequent, incomplete and low or with fragments irregularly sparse along teeth, sometimes well developed. **Exostome** of eight teeth pairs with tendency to split into 16, pale yellow with bases sometimes becoming darker, brown–orange, recurved and lying on the exothecium, except sometimes at their bases, when dry; outer surface (OPL) with a dense papillose reticulum, sometimes the papillae fused into transverse striae in lower part or into longitudinal weak striae in upper third; inner surface (exostomial PPL) smooth or finely papillose, sometimes the papillae forming thin lines in lower half, frequently with marked trabeculae and fenestrate in upper third; PPL not visible externally at tooth margins. **Endostome** of eight robust and usually persistent segments, occasionally with up to eight additional intermediate, sometimes shorter processes; principal segments three-quarters as long as teeth, broadly linear with variably widened base to subulate, uniseriate, usually with incrassate and prominent transverse walls, incurved when dry, hyaline and usually shiny; external surface (endostomial PPL) smooth; internal surface (IPL) smooth

or finely papillose in lower half, variably reticulate above but never opaque because of the ornamentation density. **Operculum** plane to convex, sometimes conic, rostrate, yellowish without differentiated basal ring. **Calyptra** variably hairy, hairs (one-) two- to four- (five-) seriate, not or scarcely exceeding the beak. **Spores** (15–)18–35(–38) µm in diameter.

Distribution: Western and eastern North America, northern Europe and southern European cordilleras, Altai, Russian Far East and Japan.

SPECIES DISTRIBUTION

Ulota crispa s.l. has been reported from several, mainly oceanic, areas in both the Nearctic and Palaearctic. In North America, it is currently recognized for the eastern third of the continent (Vitt, 2014), although Grout (1935, 1946) also signalled records from the west coast in southern Alaska. In Europe, it is considered to be widespread, being scarce or absent in different inland and Mediterranean territories (Lewinsky-Haapasaari, 1998; Ignatov *et al.*, 2006; Ros *et al.*, 2013). In Asia, *U. crispa* has been reported from four disjunct territories (Noguchi, 1989; Ignatov & Ochyra, 1994; Ignatov *et al.*, 2006; Jia, He & Guo, 2011; Wang & Jia, 2012): south-western Asia, in mountainous areas bordering the Black and Caspian seas; Altai and the neighbouring Central Asian mountains; Russian Far East and Japan; and subtropical China and surroundings. Thus, *U. crispa* is present in all or most of the centres of diversity of *Ulota* in the Holarctic kingdom, as defined in Garilieti *et al.* (2015). In addition, for North America and Europe, a number of mainly ancient records have reported *U. intermedia* or *U. crispula* at specific or variety levels (e.g. Lesquereux & James, 1884; Husnot, 1892–1894; Grout, 1935; Nyholm, 1956).

The results of our taxonomic revision draw a substantially different biogeographical panorama, as each of the three recognized species shows a different Holarctic disjunct distribution (Fig. 5). *Ulota crispula* displays an amphi-Atlantic area, being widespread throughout eastern North America (southern Canada and USA, except southernmost areas), most of Europe (rare in northernmost and Mediterranean areas) and south-western Asia (Pontic Mountains, Caucasus). *Ulota intermedia* shows a much more wider and fragmented area, being present in western North America (mainly Alaska and Canada), eastern North America (mainly Canada), northern Europe, European cordilleras (North Iberian ranges, Alps, Carpathians, etc.), Altai, Russian Far East and Japan (most main islands, not recorded from Kyushu). This species seems to prefer high elevational

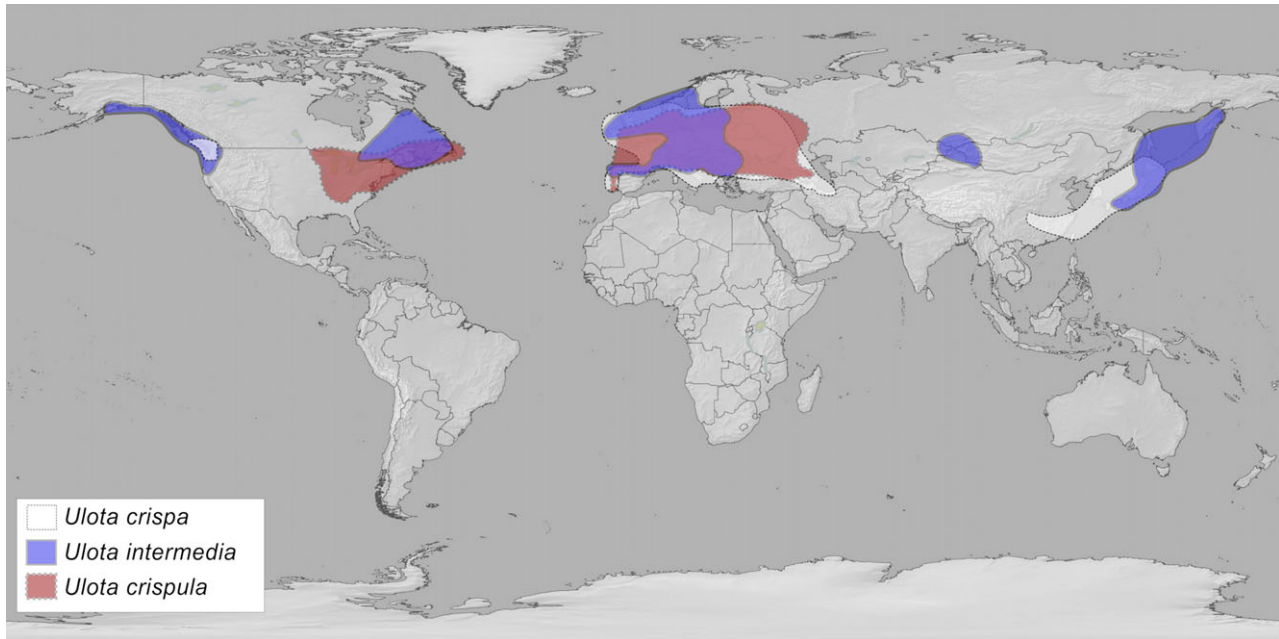


Figure 5. World approximate distribution of the different species in the *Ulota crisper* complex, based on the studied material (see Appendix 1).

or altitudinal areas in the temperate zone. Finally, *U. crisper s.s.*, although displaying a wide and disjunct distribution throughout the Holarctic, is not present in all the territories in which it has formerly been recognized. Although uncommon, it is present along the west coast of North America (from British Columbia to Oregon), where no previous records seem to exist. In contrast, we have not found any sample ascribable to this species from eastern North America, which, in turn, always corresponded either to *U. crispula* or, usually in northern areas, to *U. intermedia*. In Europe, *U. crisper s.s.* is a common and widespread species and frequently coexists with *U. crispula*, as has been verified recently for the Iberian Peninsula (Caparrós *et al.*, 2014). Finally, in Asia, *U. crisper s.s.* is confirmed for the south-western part of the continent (Pontic Mountains, Caucasus), China, Russian Far East, Japan (all main islands) and Taiwan; we have no evidence of its presence in Central Asian mountains where, however, *U. intermedia* occurs.

For a taxonomic work like this, the revision of all existing records related to the *U. crisper* complex is an unattainable goal. However, the importance of these species for most North American and Eurasian floras implies that, before long, a much more accurate drawing of the distribution of these three *Ulota* spp. will be available, based on the re-evaluation of samples under the new taxonomic light by trained bryologists around the world.

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- Appendix 1**
- All specimens listed below are a selection of the samples used for morphological analyses.
- Ulota crispa* (Hedw.) Brid.** - AUSTRIA, Oberösterreich: beim Ht. Langbathsee, alt. 750 m, S-B177772; Oberösterreich: im unteren Stammbachthal bei Goisern, c. 510 m, S-B225053; BELGIUM, Liège, Reinardstein, (près Malmeady), 2.xi.1913, *Toussaint s.n.*, BM; CANADA, British Columbia, Regional District of Mount Waddington, Vancouver Island, Winter Harbour, Kwaksistah Regional Park, around the campsite, 50°31'01"N, 128°02'23"W, alt. 2 m, MAUAM-Brio 4806; Clayoquot District, Ucluelet, Vancouver Island, 48°55'00"N, 125°34'00"W, NY 156768; CHINA, Hunan, Sangzhi Co., Badagongshan, Liaoyewan, c. 1 km NE of the administration office, collecting locality 43, 29°46'N, 110°03'E, alt. 1400 m, S-B176297; CROATIA, Lika-Senj, Velebit in sylvia Jasikovac, prope Gospić, BP 43305; FRANCE, Aquitaine, La Rhume, alt. 900 m, BCB 19166; Centre, Saint-Denis-des-Puits, Etangs de la Gatine, en rive droite du dernier étang, alt. 200 m, Herb. Boudier 2389; Haute-Normandie, Forêt de Brotonne (Seine inférieure), 1891, *Thériot s.n.*, BM; Lorraine, *Hooker s.n.*, BM; Midi-Pyrénées, Luchon, Vallée de Lys, BCB 19165; Poitou-Charentes, Forêts des Lus-sac et de Châteauneuf, *Schimper 457*, BM; Région Basse Normandie, 1.iv.1912, *Douin s.n.*, BM; Vogesen-gebiet, An Naldlaement, *P. Beaub s.n.*, BM; GEORGIA, distr. Chokhatauri, montes Meskhedski khrebet, in viciniis pagi Nabeglavi, alt. 1000 m, 21.vii.1979, *Vašák s.n.*, G 00124254; Abkhazia, distr. Gulripsh, in vicinitate pagi Lata, in valle fluminis Kodori, alt. 500 m, G 00124247; GERMANY, Baden-Württemberg, Baden-Baden, Cascade de Geroldsau près de Baden-Baden, 17.ix.1858, *Jack s.n.*, BM; Oberbayern, Baiern: Reichenhall, alt. 480 m, 10.ix.1909, *Schiffner s.n.*, BM; Turingia, Saalfeld, Thuringes Wald, *Reinsch s.n.*, BM; HUNGARY, Fejer, In vallis Határvölgy prope pag Pálháza, BP 26366; Somogy, In silvis vs. stationem pagi Szentá, alt. 157 m, BP 121748; Szabolcs-Szatmár Bereg, In sylvia Megykerék-erdő prope Kőmörő, alt. 110 m, BP 121586; Vas, In silva Nagy-erdő ad Métnepusztá prope Gödörháza, alt. 250 m, BP 121736; IRELAND, Leinster, aparcamiento del centro de visitantes Glendalough, MAUAM-Brio 4802; Munster, Tork Cascade, m. Killarney (Hibernia), vi.1865, BM; ITALY, Trentino-Südtirol, Kohlern Wald, BM; JAPAN, Kyoto, Honshu, Ine-cho, Yoza-gun, Kamanyu, alt. 100 m, *Deguchi 34159*, HIRO; Fukushima, Honshu, Bandaisan National Park, Urubandai, alrededores del Urubandai Royal Hotel, 37°39'17"N, 140°05'37"E, alt. 775 m, MAUAM-Brio 4744; Hiroshima, Honshu, Geihoku-cho, Yamagata-gun, Higashi-yawatabara, Mt. Garyu, alt. 1200–1223 m, 19.x.1999, *Kitamura 410*; HIRO; Tottori, Honshu, Chizuchó, Sugijinja, MAUAM-Brio 4805; Yamanashi, Honshu, Fuji Hakone Izu National Park, vertiente norte del Monte Fuji, 35°23'26"N, 138°42'59"E, alt. 2270 m, MAUAM-Brio 4749; Iburi, Hokkaido, Shikotsu-Toya National Park, lago Toya, Toyako Onsen, parque junto a la orilla del lago, 42°34'00"N, 140°48'29"E, alt. 87 m, MAUAM-Brio 4742; Kushiro, Hokkaido, Akan National Park, orillas del lago Akan, alrededores de Akanko Onsen, 43°26'15"N, 144°05'51"E, alt. 436 m, MAUAM-Brio 4804; Kumamoto, Kyushu, Aso Kuju National Park, carretera 265, c. Soyo-machi, 32°41'14"N, 131°08'31"E, alt. 582 m, MAUAM-Brio 4759; Miyazaki, Kyushu, Kunishi Dake Area, Motoyashiki, estación de esquí Gokase Highland, 32°34'44"N, 131°07'05"E, alt. 1290 m, MAUAM-Brio 4760; Tokushima, Shikoku, Mt. Tsurugisan, 33°51'59"N, 134°05'33"E, alt. 1420 m, MAUAM-Brio 4756; Ehime, Shikoku, Ishizuchisan Quasi National Park, Mt. Kamegamori, inicio del camino de subida junto a la carretera, 33°47'11"N, 133°11'25"E, alt. 1690 m, MAUAM-Brio 4765; Yagoshima, Yakushima, Kirishima-Yaku National Park, Hadogawa Trail, Hananoego, inicio del camino a Ishizuka hat, 30°19'20"N, 130°30'40"E, alt. 1650 m, MAUAM-Brio 4762; NORWAY, *Hübener s.n.*, BM; POLAND, Podkarpackie, East Carpathians, Polish Eastern Beskids, Slonne Góry Hills, in hornbeam forest near Mt. Sobién, alt. 400 m, 13.v.1973, *Ochyra s.n.*, BM; PORTUGAL, Beira Litoral, Lousã, Espigão, Volta da Lomba, UTM 29TNE6435, alt. 890 m, LISU 204647; Douro Litoral, Serra da Freita, Senhora da Lapa, UTM 29TNF5825, alt. 820 m, LISU 204593; Estremadura, Serra de Sintra, Pen-

inha, UTM 29TMC5991, alt. 417 m, LISU 222040; Minho, Corno do Bico, Travassos, próximos de Coutos, UTM 29TNG4137, alt. 640–650 m, LISU 198665; Tras-os-Montes, Vila Real, Parque Natural do Alvão, próximo de Lamas de Ólo, UTM 29TNF9878, alt. 1092 m, MAUAM-Brio 4783; ROMANIA, Alba, in valle Kőköz prope Nyirmező = Poiana Aiudului, montes Bihar, BP 77356; Beszterce-Naszód, Mt. Radnay havasok, in ramis Piceae excelsae declivium valis V. Rosu, pr, pag. Borberek, BP 8437; Buzău, Mts. Apuseni, Pietroase, desvío a Poiana Florilor, alt. 400 m, MAUAM-Brio 4810; Sibiu, Carpat. Merid. In valle Podragu, montes Fogarasi havasok, alt. 1400 m, BP 72068; RUSSIA, Caucasus, Kapa-Cy-Bezengi River, 43°18'N, 43°26'E, alt. 850 m, 3.viii.2004, *Ignatov, Ignatova & Kharzinov s.n.*, MHA; Caucasus occidentalis, Sochi, distr. Sochi, in colle Bytkha, in valle fluminis Macesta ad cataractas rivi Zmeika prope pagun, Kraievo Armianskoye, alt. 300–400 m, G 00124249; SLOVAKIA, Košice, Mts Slovenský Raj, Vel'ký Sokol dolina Valley, 20°20'5"N, 48°55'53.4"E, alt. 700 m, BP 176055; Žilina, in ramulis Piceae in Piceetis vallis, alt. 1000–1100 m, BP 121697; SPAIN, Asturias, Río Purón, MAUAM-Brio 4800; Burgos, Angostina, ribera del Arceniega, UTM 30TVN8573, alt. 290 m, VIT5789; Cantabria, Picos de Europa, S^a de la Corta, Monte de la Llama, MAUAM-Brio 4809; León, Sierra de Ancares, MAMusci 4223; Girona, Vilallonga de Ter, Torrent de Vallvigil, UTM DG48, alt. 1200 m, BCB 24461; Castellón, El Esprio, Penyagolosa, BCB 10211; Orense, Devesa do Caurel, Sierra do Caurel, 42°36'N, 07°6'W, alt. 900–1000 m, MUB 43446; Navarra, Orbaiceta, Bosque de Irati, Bco. Erlan, UTM 30TXN4863, alt. 980 m, VIT 34922; Vizcaya, Abadiano, Gorosarri, UTM 30TWN3075, alt. 230 m, VIT 14697; SWITZERLAND, Jura, La Dôle, 18.vii.1869, *Bernet s.n.*, BM; Vaud, Hinter St. Cergue, G 00124244; TAIWAN, Nantou, Ren-ai Village, Mei-feng Shan (Mt.), 24°07'N, 121°10'E, alt. 2000–2200 m, MO 5355215; TURKEY, Rize, near main-road about 4 km W of Ardesen, alt. ± 20 m, S-B99508; Trabzon, carretera de Macka al Monasterio de Sümela, 40°41'06"N, 39°39'56"E, alt. 1500 m, MAUAM-Brio 4801; carretera de Maçka a Torul, 40°42'32"N, 39°27'56"E, alt. 1450 m, MAUAM-Brio 4770; UK, Scotland, New Galloway (73) Scotland, S-B17776; Wales, c. 3.5 km SSW Machynlleth, Llyf-nant Valley, UTM SN753975, alt. 91 m, BCB 12364; UKRAINE, Transcarpathia, In silvis vallis Hoverla prope Tiszabogdány, alt. 1–1400 m, BP 121548; USA, Oregon, Tillamook State Forest, Elk Creek, 46°36'43"N, 123°28'00"W, alt. 300 m, MAUAM-Brio 4807; Corbett, Columbia Gorge, Along Big Cr., NY 524159; Washington, Olympic National Park, Lake Crescent, Storm King Ranger Station, 48°03'30"N, 123°47'16"W, alt. 190 m, MAUAM-Brio 4808; Gifford Pinchot National Forest, Sunset Campground, along E Fork of Lewis River, upriver from campground, alt. 325 m, NY 432308; *Ulotia crispula* Bruch - AUSTRIA, Burgenland, sö von Güssing bei Gr. Mürbisch, alt. 275–300 m, S-B177769; Oberösterreich, Ob.Ost.: im unteren Stammbachtal bei Goisern, alt. 510 m, S-B177773; BELGIUM, Namur, Louette-Saint-Pierre, vi.1872, *Gravet s.n.*, BM; BULGARIA, Burgas, Southern Black Sea coast, Strandzha National Park, Marina reka reserve at Balgari village, 42°07'1"N, 27°45'54.4"E, alt. 255 m, BP 180189; Montana, Stara Planina Mts, Varsec, Zanozhene village, valley of Stara reka river, above Byalata voda shelter house, under Todorini Kukli peak, 43°08'1.5"N, 23°12'45"E, alt. 1190 m, BP 173885; CANADA, British Columbia, Westminster Junction, NY 224932; New Brunswick, Albert Co., Fundy National Park, trail to Third Vault Falls, 45°38'N, 65°00'W, NY 224956; Newfoundland & Labrador, Avalon Peninsula, Whitbourne, NY 156715; Nova Scotia, Annapolis Co., Kejimikujik National Park, Mill Falls on Mersey River, 44°29'N, 65°08'W, NY 224977; Ontario, Bruce Co., Fathom National Marine Park, Flowerpot Island, along trail from Beachy Cove to Marl Bed, 45°17'50"N, 81°37'38"W, NY 1206493; Prince Edward Island, Queens Co., 1 mile north of Argyle Shore, 46°10'N, 63°21'W, NY 224983; Quebec, Laurentian Mts., Vicinity of St. Jerome, NY 152119; CAUCASUS, 1836, *Dollinger s.n.*, BM; DENMARK, Zealand, G 00124259; ESTONIA, Pärnu, Kreis Pernau, Fich Tenhochwalde 1 km SO von der Station Surrie, 21.viii.1909, *Mikutowicz s.n.*, BM; FRANCE, Aquitaine, Gan, v.1847, *Spruce s.n.*, BM; Bretagne, Côtes-du-Nord, Gorges du Corong, Wène, alt. 200 m, G 00047155; Centre, Saint-Denis-des-Puits, Etangs de la Gatine, en rive droite du dernier étang, alt. 200 m, BOUDIER 2389; Jura, Les Fourgs, entre la Petit Vitiau et les Prises, formation du pre-bois, alt. 1140 m, BOUDIER 3905B; Limousin, Forêt de Crozat, 7.vii.1871, BM; Pays de la Loire, Forêt de Perseignes, BM; Poitou-Charentes, Rognac, Comm. De Charras, SE Angoulême, Charente, alt. 130 m, G 00124241; Pyrénées-Atlantiques, La Rhume, alt. 900 m, BCB 19166; Rhône-Alpes, carretera de N.A Bellecombe (entre Chamonix y Albertuille), 45°47'56.7"N, 6°29'15.0"E, alt. 832 m, MAUAM-Brio 4710; GEORGIA, distr. Chokhatauri, in viciniis pagi Nabeglavi, montes Meskhedski khrebet, alt. 1000 m, G 00124254; Abkhazia, distr. Gulripsh, in vicinitate pagi Lata, in valle fluminis Kodori, alt. 500 m, G 00124247; GERMANY, Baden-Württemberg, Emmendingen, alt. 260 m, G 2747; Bayern, Waldmünchen, G 00124261; Hesse, Ludwigshutte, *Bruch*, vii.1841, BM; Rheinland-Pfalz, in valle Rhennana prope St Goar, 1874, *Herpell s.n.*, BM; Sylva

negra, prope Griesbach, Jun, *Sch. L s.n.*, BM; HUNGARY, Baranya, alt. 125 m, BP 168437; Heves, in silvis montis Hosszabérc supra vallem Iona-völgy prope Parádfürdő, alt. 330 m, BP 121758; Somogy, in silvis 'Urasági-erdő' prope Zákány, alt. 200 m, BP 121722; Szabolcs-Szatmár-Bereg, 'Éretthegy-erdő' prope Mánd, alt. 110 m, BP 121588; Zala, in silva 'Nyírlakosai-erdő' prope Várfölde, alt. 200 m, BP 121723; IRELAND, Leinster, aparcamiento del centro de visitantes Glendalough, MAUAM-Brio 4814; MONTENEGRO, Žabljak, Durmitors Mts, Durmitor NP, Žabljak, between Crno jezero and Poljana, 43°08'52,0"N, 19°05'48"E, alt. 1421 m, BP 178715; NORWAY, Telemark, Sannidal, Lislau (farmer), 23.vii.1946, *Lid s.n.*, BM; POLAND, Malopolskie, Tatry zachodnie: Dolina Kościeliska, na zeschlych galeziach świerku, BP 83187; Podkarpackie, East Carpathians, Polish Eastern Beskids, Slonne Góry Hills, alt. 400 m, BP 160736; PORTUGAL, Beira Litoral, Lousã, Antenas, UTM 29TNE6939, alt. 1115 m, LISU 205975; Douro Litoral, Serra da Freita, Senhora da Lapa, UTM 29TNF5825, alt. 820 m, LISU 204593; Minho, Corno do Bico, Travassos, próximos de Coutos, UTM 29TNG4137, alt. 640-650 m, LISU 198665; Tras-os-Montes e Alto Douro, Carvalhal de Sezelhe, UTM 29TNG9228, alt. 1000 m, LISU 236060; ROMANIA, Alba, in valle Kőköz prope Nyirmező-Poiana Aiudului, montes Bihar, BP 77356; Buzău, Mts. Apuseni, Pietroase, desvío a Poiana Florilor, alt. 400 m, MAUAM-Brio 4815; Harghita, ad 'Medvebarlang' prope Borszék, alt. 900 m, BP 121669; Sibiu, in valle Podragu, montes Fogarasi havasok, alt. 1400 m, BP 72067; Szeben, in rupibus schist. Silvat. Supra Zibinklamm/Cheia, Riulmare/infra Hohe Rinne = Paltinis, alt. 900-1000 m, BP 121813; RUSSIA, Caucasus, Cherek Bezengijskij River, 1 km upstream Dumala Creek mouth, 43°10'N, 43°14'E, alt. 1650 m, 1.viii.2004, *Ignatov, Ignatova & Kharzinov s.n.*, MHA; Caucasus occidentalis, (Sochi) in faucibus fluminis. Psakho infra vicum Kamenka, alt. 200-300 m, G 00124251; ad cataractas in faucibus rivi Agura, alt. 350-400 m, G 00124252; in vicinitate pagi Loo, 6 km ab ostio fluminis Loo, alt. 30-150 m, G 00124257; SERBIA, Golija Biosphera Reserve, Golija Biosphera Reserve, at Orlov kamen, between Bele Vode and Kumanica villages, 43°27'38"N, 20°15'42.8"E, alt. 950 m, BP 171951; Tara National Park, Jokića potok, Ljuti breg reserve area, alt. 960 m, BP 168279; SLOVAKIA, Banská Bystrica, Tatra Humiliore, in ripa rivi Bisztra prope Tále, alt. 800 m, BP 121717; Prešov, prope pag Tátrafűred (Smokovec) monte Visoky Tatry, alt. 1000 m, BP 66758; Žilina, in ramulis Piceae in Piceetis vallis, alt. 1000-1100 m, BP 121697; SPAIN, Asturias, próximo al nacimiento del río Purón, MAUAM-Brio 4788; Cantabria, Picos de Europa, S^a

de la Corta, Monte de la Llama, MAUAM-Brio 4813; León, Los Ancares, valle del Cuiña, UTM PH84, BCB 19875; Girona, Sant Llorenç de la Muga, BCB 6332; A Coruña, Parque Natural de las Fragas del Eume, MAUAM-Brio 4794; Huesca, Arguís, Sierra de Gratal, hayedo calcícola de Peiró, UTM 30TYM0788, alt. 1400 m, VIT 27399; Navarra, Lapiaz de Larra a 800 m. al norte del refugio, alt. 1335 m, MAUAM-Brio 4787; Álava, Sierra de Urbasa, bajando del puerto de Opakua, alt. 980 m, MAUAM-Brio 4780; SWITZERLAND, Soleure, Hagendorf, 23.v.1896, *Dresler s.n.*, BM; Ticino, Roncaccio, preso Locarno, BM; Vaud, Hinter St. Cergue, G 00124244; TURKEY, Rize, Kaçkar Dağları Milli Parkı, Ayder, 40°56'52"N, 41°08'08"E, alt. 1550 m, MAUAM-Brio 4811; Trabzon, carretera de Of a Uzungöl, en la salida de Taşhanpazari, 40°50'15"N, 40°16'33"E, alt. 140 m, MAUAM-Brio 4774; UK, North West England, Windermere, Westmoreland, Amie's wood, BM; UKRAINE, Transcarpathia, in monte Magurica prope Turjaremete, alt. 350 m, BP 64679; USA, Alleghanay Mts., NY 507792; Connecticut, Mansfield, Joshua's Trust, next to Knowlton Pond, MAUAM-Brio 4766; Delaware, Farmhurst Station near Wilmington, NY 991745; Georgia, Chattahoochee National Fores, Cohutta Wilderness, Tearbitches Trail from Forest Serv. Rd. 68 to Bald Mountain, NY 507804; Indiana, Clifty Falls State Park, NY 507812; Kentucky, Ezel Quad, Rough Br. (tributary of Spaws Cr.), 1.1 miles north of Dan, 37°58'12"N, 83°27'51"W, alt. 274.32 m, DUKE 0127685; Maine, Spruce Point c. 1.5 miles SE of Boothbay Harbor, NY 507783; Grafton Notch State Park, 44°25'24"N, 70°56'44"W, MAUAM-Brio 4768; Massachusetts, Cape Cod. Brewster, MAUAM-Brio 4767; Michigan, along Carp Creek at the Iron Bridge Douglas Lake Region, NY 795404; Big Stone, NY 507721; New Hampshire, Mt. Willard, NY 507799; New York, Adirondack Mts., along trail east of Henderson Lake, 30 miles N. Tahawus, NY 507845; Catskill Mountains, NY 507719; North Carolina, Tanawha Trail, near Wilson Creek overlook, Blue Ridge Parkway, NY 507776; Great Smoky Mountains National Park, Andrews Bald Trail, NY 507814; Ohio, Bog north of Springfield, NY 507817; Pennsylvania, between Mt. Hope and Penryn, on the Lancaster and Lebanon County Line, NY 507801; Rhode Island, border of towns of Exeter and South Kingstown, Marion Eppley Wildlife Sanctuary, c. 1.5 miles NE of Usquepaug, along Queens River, 41°31'06"N, 71°35'33"W, NY 840619; Vermont, Green Mountain National Forest, between Woodford and Bennington, 42°53'12"N, 73°06'15"W, alt. 419 m, MAUAM-Brio 4812; Virginia, Jefferson National Forest, Whitetop Mountain, 36°38'17"N, 81°36'21"W, alt. 1675 m, NY 986405; West Virginia, Monongahela National Forest, upper

slopes of Spruce Mountain, vicinity of Blue Knob, Lobelia Quad., 38°10'32"N, 80°16'47"W, alt. 1158–1311 m, NY 954721; Wisconsin, Highlands, NY 507808; *Ulotia intermedia Schimp.* - AUSTRIA, Kärnten, Kā.: nächst Ossia... w des Meierhof... Tauern, alt. 890 m, S-B177775; Salzburg, am Ufer des Attersees zw. Burgau u. Unterach, alt. 480 m, S-B177776; CANADA, British Columbia, Central Coast Regional District, Bella Coola, pista que sube por la Clynton Fall Creek, 52°19'58"N, 126°49'19"W, alt. 335 m, MAUAM-Brio 4720; New Brunswick, Lepreau Parish, New River Beach Provincial Park, Barnaby Head Trail between Raspberry Cove and Chitticks Beach, 46°07'50"N, 66°31'31"W, NY 01220922; Newfoundland & Labrador, Bay Bulls, 47°18'57"N, 52°48'37"W, 1.x.1892, *Aron 22*, BM; Nova Scotia, Lake Weir, 7.5 miles NW of Halifax, NY 152129; Ontario, Ottawa, 45°25'00"N, 75°42'00"W, *Macoun s.n.*, BM; Quebec, Jupiter River, 49°28'01.2"N, 63°37'01.2"W, NY 152104; Gasp-Sud Co., Ile Bonaventure, NY 224972; Saskatchewan, Glen Harbour, 15.v.1883, *Waghorne s.n.*, BM; CROATIA, Lika-Senj, Velebit, Rusajča Crakoviae prope Mesak, BP 43226; DENMARK, Copenhagen, Dyrehaven, 4.viii.1902, *Hesselbo s.n.*, BM; FRANCE, Aquitania, subida a Col d'Aubisque, carretera de 918, alt. 1500 m, MAUAM-Brio 4818; Miquelon Island, 47°05'40"S, 56°22'00"W, vii.1883, *Delamare s.n.*, BM; Rhône-Alpes, Villard de Lans, Forêts des Jarrands, G 00124268; GERMANY, Bayern, Ludwigshütte, *Bruch*, viii.1837, BM; Hesse, Braunfels, *Faurie s.n.*, BM; HUNGARY, Borsod-Abaúj-Zemplén, in sylva prope pag Telkibánya, montes Sátorhegység, BP 62776; Nográd, in valle rivi ... prope Királyháza, montes Borzsöny, BP 59613; Zala, in silva 'Nyírlakosai-erdő' prope Várfolde, alt. 200 m, BP 121723; IRELAND, Munster, Muckross, *Braithwaite s.n.*, BM; JAPAN, Hokkaido, prov. Sôya, Isl. Rishiri, Mt. Rishiri, alt. 100–500 m, 8.viii.1954, *Hasegawa s.n.*, H; Kamikawa, Hokkaido, Daisetsuzan National Park, Sounkio valley, al SO de Sounkio, Obako, 43°41'58"N, 143°00'57"E, alt. 715 m, MAUAM-Brio 4817; Kushiro, Hokkaido, Akan National Park, laderas del monte del lago Mashu, carretera 52 hacia Teshikaga, 43°32'23"N, 144°30'23"E, alt. 370 m, MAUAM-Brio 4736; Tokachi, Hokkaido, Daisetsuzan National Park, Nukabira National Hwy, Horoka, unos 15 km al NNW de Nukabira, 43°29'41"N, 143°08'44"E, alt. 650 m, MAUAM-Brio 4730; Yamanashi, Honshu, Fuji Hakone Izu National Park, vertiente norte del Monte Fuji, 35°23'26"N, 138°42'59"E, alt. 2270 m, MAUAM-Brio 4750; MAUAM-Brio 4746; Tokushima, Shikoku, Ichiu-mura, Mima-gun, Mt. Tsurugi, alt. 1800–1900 m, *Taoda 5621*, HIRO; NORWAY, Telemark, Sannidal, Lislau (farmer), 23.xii.1946, *Lid s.n.*, BM; POLAND, voivodato de la Pequeña Polonia,

Zacopane (al pie de los Tatra), Dolina Strazinska, MAUAM-Brio 4711; PORTUGAL, Minho, Viana do Castelo, Melgaço, Lamas de Mouro, UTM 29TNG6654, alt. 863 m, LISU 215261; Tras-os-Montes, Vila Real, Parque Natural do Alvão, próximo de Lamas de Ólo, UTM 29TNF9878, alt. 1092 m, MAUAM-Brio 4785; Tras-os-Montes e Alto Douro, Serra do Alvão, Lamas de Olo, pr. Bouça do Ribeiro, UTM PF0081, alt. 1000–1050 m, LISU 213870; ROMANIA, Alba, in valle Kóköz prope Nyirmező = Poiana Aiudului, montes Bihar, BP 77356; Braşov, in faucem Taminaszakadék in pede montis Nagyköhavas, alt. 1100 m, BP 69049; Buzău, Apuseni Mountains, c. Plateau de adis, alt. 1200 m, MAUAM-Brio 4824; Cluj, ad caverna Skerisora prope pag. Aranyosfő = Scarisoara, BP 77351; Szeben, montes Szeben, valle del río Degeneasa cerca de Paltinis, alt. 1300 m, BP 74062; RUSSIA, Altai, northern shore of Teletzkoye, Yailyu, 51°45'N, 87°35'E, alt. 450 m, 24.vi.1991, *Ignatov s.n.*, MHA; Kamchatskaya oblast, Syd-Kamtchatka, Nikolajevsk, S-B193307; Óblast de Sajalín, viii.1933, *Sakurai s.n.*, BM; SERBIA, Tara National Park, at Tepih Livada, Crveni potok reserve area, alt. 1050 m, BP 168240; SLOVAKIA, Košice, Mts Slovenský Raj, Veľký Sokol dolina Valley, 20°20'5"N, 48°55'53.4"E, alt. 700 m, BP 176055; Prešov, 'Három tócsa' supra Tátralomnic = Tatranska Lomnica, alt. 990 m, BP 121707; Žilina, Porubka Liptovska, alt. 681 m, BP 76404; SLOVENIA, Notranjska, In monte Sněžník supra Lasač, *Baumgartner*, BP 43224; SPAIN, Álava, Salvatierra, Uburin, UTM 30TWN5538, alt. 980 m, VIT 13953; Asturias, Sierra del Sueve, MAUAM-Brio 4798; Cantabria, Cahecho, La ermita del Santo, alt. 825 m, MAUAM-Brio 4778; A Coruña, Parque Natural de las Fragas del Eume, MAUAM-Brio 4795; Huesca, Linza, UTM 30TXN8051, alt. 1500 m, VIT 29563; Navarra, Lapiaz de Larra a 800 m. al norte del refugio, alt. 1335 m, MAUAM-Brio 4786; Álava, San Millán, Ocariz, Puerto Opacua, UTM 30TWN5441, alt. 920 m, VIT 3547; SWEDEN, Södermanland, Utö, Ålö nature reserve, Söderskog, 200 m S of Vreta, 58°55,225' N, 18°12,660' E, S-B176729; Bahusiae, *Thedenius s.n.*, BM; Blekinge, Rödeby, Spjutsbygd, 56°15'N, 15°36'E, 25.vii.1888, *Arnell 120*, BM; Östergötland, Borgs Udde, S-B81846; Skåne, Hjarsås, Sibbhult, 0.5 km NE of Tykatorp, S-B179352; Södermanland, Ösmo, Hammersta. Just N of Frugrottan, 59°1.323'N, 18°0.316'E, S-B184625; SWITZERLAND, Fribourg, Foret des Reposoirs, near la Valsainte, alt. 1030 m, 29.vi.1923, *Rhodes 1961*, BM; Jura, La Dôle, 18.vii.1869, *Bernet s.n.*, BM; UK, Escocia, New Galloway (73) Scotland, S-B177766; USA, Alaska, Kenai Lake cerca de Primrose (1.7 km al NW), en la 9 Hwy, 60°23'07"N, 149°21'11"W, alt. 157 m, MAUAM-Brio 4715; picnic site, Lowe River,

12 miles E of Valdez, alt. 609.6 m, NY 156791; Oregon, Tillamook State Forest, Elk Creek, 46°36'43"N, 123°28'00"W, alt. 300 m, MAUAM-Brio 4713; Wash-

ington, Junction of Little River Road and Olympic Hot Springs Road, along Little River, 48°07'N, 123°35'W, alt. 70 m, NY 524160.

Appendix 2

Specimens included in the molecular analyses, with corresponding GenBank accession numbers.

Taxon	Herbarium voucher	Geographical origin	ITS2	<i>trnG</i>	<i>trnL-trnF</i>	<i>atpB-rbcL</i>
Ingroup taxa						
<i>Uloa crispa</i>	MAUAM-Brio 4805 (ID304)	Japan	KT804262	KT804301	KT804340	KT804380
	MAUAM-Brio 4808 (ID305)	USA, Western Coast	KT804266	KT804305	KT804344	KT804383
	MAUAM-Brio 4809 (ID315)	Spain	KT804267	KT804306	KT804345	KT804384
	MAUAM-Brio 4810 (ID320)	Romania	KT804270	KT804309	KT804348	KT804386
	MAUAM-Brio 4802 (ID321)	Ireland	KT804269	KT804308	KT804347	–
	MAUAM-Brio 4806 (ID323)	Canada, West. Coast	KT804264	KT804303	KT804342	–
	MAUAM-Brio 4804 (ID330)	Japan	KT804261	KT804300	KT804339	KT804379
	MAUAM-Brio 4807 (ID336)	USA, Western Coast	KT804265	KT804304	KT804343	KT804382
	S-B225053 (ID337)	Austria	KT804271	KT804310	KT804349	–
	MAUAM-Brio 4801 (ID352)	Turkey	KT804263	KT804302	KT804341	KT804381
	MAUAM-Brio 4800 (ID353)	Spain	KT804268	KT804307	KT804346	KT804385
	MAUAM-Brio 4812 (ID302)	USA, Eastern Coast	KT804272	KT804311	KT804350	KT804387
	MAUAM-Brio 4813 (ID303)	Spain	KT804273	KT804312	KT804351	KT804388
	MAUAM-Brio 4811 (ID319)	Turkey	KT804274	KT804313	KT804352	–
<i>Uloa crispula</i>	MAUAM-Brio 4815 (ID333)	Romania	–	KT804315	KT804354	KT804390
	S-B177773 (ID338)	Austria	KT804276	–	KT804355	KT804391
	MAUAM-Brio 4814 (ID355)	Ireland	KT804275	KT804314	KT804353	KT804389
	NY 1206493 (ID363)	Canada, East Coast	KT804277	KT804316	KT804356	–
	MAUAM-Brio 4715 (ID300)	USA, Western Coast	KT804283	KT804322	KT804362	KT804397
	MAUAM-Brio 4824 (ID301)	Romania	KT804286	KT804325	KT804365	KT804400
<i>Uloa intermedia</i>	VIT 3547 (ID342)	Spain	KT804284	KT804323	KT804363	KT804398
	MAUAM-Brio 4817 (ID343)	Japan	KT804281	KT804320	KT804360	KT804395
	MAUAM-Brio 4818 (ID346)	France	KT804285	KT804324	KT804364	KT804399
	S-B176729 (ID357)	Sweden	KT804287	KT804326	KT804366	KT804401
	NY 01220922 (ID362)	Canada, East Coast	KT804282	KT804321	KT804361	KT804396
	MAUAM-Brio 4329 (O-108)	Spain	KT804255	JQ836900	JQ836985	JQ836694
	MAUAM-Brio 4444 (ID383)	Spain	KT804259	KT804298	KT804337	KT804377
MAUAM-Brio 4438 (ID360)	Spain	KT804260	KT804299	KT804338	KT804378	
MAUAM-Brio 4826 (ID359)	Russia	KT804278	KT804317	KT804357	KT804392	
MAUAM-Brio 4816 (ID356)	Japan	KT804280	KT804319	KT804359	KT804394	
MAUAM-Brio 4825 (ID361)	Canada	KT804279	KT804318	KT804358	KT804393	
P. Boudier 7595-B (ID365)	France	KT804288	KT804327	KT804367	KT804402	
MAUAM-Brio 4819 (ID358)	Canada	KT804289	KT804328	KT804368	KT804403	
MAUAM-Brio 4820 (ID329)	Canada	KT804290	KT804329	KT804369	KT804404	
MAUAM-Brio 4821 (ID331)	USA	KT804291	KT804330	KT804370	KT804405	
MAUAM-Brio 4822 (ID328)	Turkey	KT804292	KT804331	KT804371	KT804406	
MAUAM-Brio 4823 (ID349)	Japan	KT804293	KT804332	KT804372	KT804407	
Outgroup taxa						
<i>Orthotrichum affine</i>	MAUAM-Brio 4329 (O-108)	Spain	KT804255	JQ836900	JQ836985	JQ836694
<i>Orthotrichum rupestre</i>	VAL-Brief 11631 (ID368)	Cyprus	KT804256	KT804295	KT804334	KT804374
<i>Uloa bruchii</i>	MAUAM-Brio 4444 (ID383)	Spain	KT804259	KT804298	KT804337	KT804377
<i>Uloa coarctata</i>	MAUAM-Brio 4438 (ID360)	Spain	KT804260	KT804299	KT804338	KT804378
<i>Uloa curvifolia</i>	MAUAM-Brio 4826 (ID359)	Russia	KT804278	KT804317	KT804357	KT804392
<i>Uloa drummondii</i>	MAUAM-Brio 4816 (ID356)	Japan	KT804280	KT804319	KT804359	KT804394
	MAUAM-Brio 4825 (ID361)	Canada	KT804279	KT804318	KT804358	KT804393
<i>Uloa macrospora</i>	P. Boudier 7595-B (ID365)	France	KT804288	KT804327	KT804367	KT804402
<i>Uloa megalospora</i>	MAUAM-Brio 4819 (ID358)	Canada	KT804289	KT804328	KT804368	KT804403
<i>Uloa obtusiuscula</i>	MAUAM-Brio 4820 (ID329)	Canada	KT804290	KT804329	KT804369	KT804404
<i>Uloa phyllantha</i>	MAUAM-Brio 4821 (ID331)	USA	KT804291	KT804330	KT804370	KT804405
<i>Uloa rehmannii</i>	MAUAM-Brio 4822 (ID328)	Turkey	KT804292	KT804331	KT804371	KT804406
<i>Uloa reptans</i>	MAUAM-Brio 4823 (ID349)	Japan	KT804293	KT804332	KT804372	KT804407

Table . Continued

Taxon	Herbarium voucher	Geographical origin	ITS2	<i>trnG</i>	<i>trnL-trnF</i>	<i>atpB-rbcL</i>
<i>Zygodon pentastichus</i>	MAUAM-Brio 2981 (ID207)	Argentina	KT804257	KT804296	KT804335	KT804375
<i>Zygodon viridissimus</i>	MAUAM-Brio 2910 (ID208)	UK, England	KT804258	KT804297	KT804336	KT804376