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Three species for the price of one within the moss *Homalothecium sericeum* s.l. --Manuscript Draft--

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Corresponding Author:	Lars Hedenäs Swedish Museum of Natural History Stockholm, SWEDEN
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Swedish Museum of Natural History
Corresponding Author's Secondary Institution:	
First Author:	Lars Hedenäs
First Author Secondary Information:	
Order of Authors:	Lars Hedenäs
	Aurélie Désamoré
	Benjamin Laenen
	Beata Papp
	Dietmar Quandt
	Juana Maria González-Mancebo
	Jairo Patiño
	Alain Vanderpoorten
	Michael Stech
Order of Authors Secondary Information:	
Abstract:	<p>Phylogenetic analyses within the moss <i>Homalothecium sericeum</i> resolved two clades and four haplotypes lacking any molecular synapomorphy. Because they exhibit comparable levels of genetic divergence to those observed among sister species in the genus, significant morphological differences, and distinct geographic distributions, they are recognised as three distinct species. Discriminant analysis was employed to assign the types of 'forgotten' taxa previously recognized within <i>H. sericeum</i> s.l. to one of those three species based on their morphology. While a growing number of 'cryptic species' has been mentioned in the literature, the results suggest that thorough morpho-anatomical investigations are likely to reveal morphological discontinuities among such taxa and trigger their formal description at the appropriate taxonomic level. <i>Homalothecium sericeum</i> s.str., <i>H. mandonii</i> (Mitt.) Geh. and <i>H. mediterraneum</i> Hedenäs stat. et nom. nov. clearly differ in sporophytic traits but the identification of sterile specimens is challenged by the overlap in gametophytic characters. As a consequence, 8-37% of the specimens were mis-classified in discriminant analyses in an attempt to find the best combination of gametophytic traits to identify specimens that were assigned to one of the three species on the basis of their genotype. This points to the necessity of developing easy-to-use molecular identification tools in taxonomically challenging plant groups, such as bryophytes. <i>Homalothecium mandonii</i> is the second case of an endemic Macaronesian bryophyte species whose range encompasses the Cape Verde Islands, the Canary Islands, Madeira, and the Azores. <i>Homalothecium</i></p>

Three species for the price of one within the moss *Homalothecium sericeum* s.l.

**Lars Hedenäs¹, Aurélie Désamored², Benjamin Laenen², Beata Papp³, Dietmar Quandt⁴,
Juana Maria González-Mancebo⁵, Jairo Patiño^{2,5}, Alain Vanderpoorten^{2*} & Michael
Stech^{6*}**

1 Swedish Museum of Natural History, Department of Cryptogamic Botany, Box 50007, SE-104 05 Stockholm, Sweden.

2 Institute of Botany, University of Liège, B22 Sart Tilman, B-4000 Liège, Belgium

3 Botanical Department, Hungarian Natural History Museum, 1476 Budapest, Hungary.

4 Nees Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany.

5 Department of Botany, University of La Laguna, La Laguna, Tenerife (Canary Islands), Spain.

6 Naturalis Biodiversity Center, Leiden University, PO Box 9517, 2300 RA Leiden, The Netherlands.

** contributed equally to this paper*

Author for correspondence: Lars Hedenäs, lars.hedenas@nrm.se

Abstract. Phylogenetic analyses within the moss *Homalothecium sericeum* resolved two clades and four haplotypes lacking any molecular synapomorphy. Because they exhibit comparable levels of genetic divergence to those observed among sister species in the genus, significant morphological differences, and distinct geographic distributions, they are recognised as three distinct species. Discriminant analysis was employed to assign the types

of ‘forgotten’ taxa previously recognized within *H. sericeum* s.l. to one of those three species based on their morphology. While a growing number of ‘cryptic species’ has been mentioned in the literature, the results suggest that thorough morpho-anatomical investigations are likely to reveal morphological discontinuities among such taxa and trigger their formal description at the appropriate taxonomic level. *Homalothecium sericeum* s.str., *H. mandonii* (Mitt.) Geh. and *H. mediterraneum* Hedenäs stat. et nom. nov. clearly differ in sporophytic traits but the identification of sterile specimens is challenged by the overlap in gametophytic characters. As a consequence, 8-37% of the specimens were mis-classified in discriminant analyses in an attempt to find the best combination of gametophytic traits to identify specimens that were assigned to one of the three species on the basis of their genotype. This points to the necessity of developing easy-to-use molecular identification tools in taxonomically challenging plant groups, such as bryophytes. *Homalothecium mandonii* is the second case of an endemic Macaronesian bryophyte species whose range encompasses the Cape Verde Islands, the Canary Islands, Madeira, and the Azores. *Homalothecium mediterraneum* is circum-Mediterranean and was reported from one locality in Lanzarote in the Canary Islands, while *H. sericeum* occurs across Europe, eastern North America, and western Asia. The distributions of the segregate species within *H. sericeum* s.l. reinforce the notion that many disjunctions typically observed in moss distribution ranges are due to taxonomic shortcomings and call for the necessity of substantial taxonomic revisions of previously broadly defined bryophyte species.

Key words: Bryophytes; Cryptic species; Discriminant analysis; DNA-barcoding; Europe; Macaronesia; Mediterranean

Running head: Species within *Homalothecium sericeum* s.l.

INTRODUCTION

The acquisition of the different properties defining daughter species (when they become phenotypically diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, etc.) is not simultaneous. Before the acquisition of any one of those properties, everyone will agree that there is a single species, and after the acquisition of all, everyone will agree that there are two (De Queiroz, 2007). With the increasing use of molecular characters in systematics, a growing number of studies have revealed the existence of lineages that are well-defined genetically but appear to be indistinguishable by normally used morphological features, and are hence termed ‘cryptic taxa’ (see Bickford & al., 2007, for review). Cryptic taxa have increasingly been mentioned in the recent literature (Bickford & al., 2007), but are almost never formally described, typified, and named. This reflects the reluctance of taxonomists to describe species only based on molecular characters. As Oliver & Lee (2010) claimed, taxonomists need taxa that can be separated visually, because ‘portable DNA barcoding probes are many years away, at best’. However, cryptic taxa do not necessarily share a common ancestor (e.g., Goffinet & al., 2007), and in such cases recognition of the genetically divergent but morphologically similar lineages is necessary when species are defined based on the criterion of monophyly (Hutsemékers & al., 2012). By showing that different entities exist, molecular analyses can help to detect species that would otherwise have remained hidden and call for the careful search of morphological differences among seemingly cryptic taxa, which is an essential step towards their effective recognition (e.g., Szweykowski & al., 2005; Vanderpoorten & al., 2010; Sukkharak & al., 2011; Bell & al., 2012; Medina & al., 2012).

Here, we re-analyze previously published molecular data to revisit the significance of morphological variation and taxonomy of the pleurocarpous moss *Homalothecium sericeum* (Hedw.) Schimp. Within *H. sericeum* s.l., numerous taxa were described during the second

half of the 19th and in the beginning of the 20th Century. These were later all synonymised with *H. sericeum* (Hofmann, 1998), and this taxonomic position has been adopted in the most recent check-lists of mosses of European and Macaronesian mosses (Hill & al., 2006; Ros & al., 2013). Recent phylogenetic analyses (Désamoré & al., 2012) showed that accessions of *H. sericeum* s.l. from its entire distribution range belong to three molecular groups, including two sister clades hereafter referred to as *H. mandonii* and *H. sericeum* s.str., and four haplotypes that did not share any synapomorphy and are hereafter referred to as *H. mediterraneum* (Fig. 1).

In the present study, we compare the level of divergence of the molecular lineages identified within *H. sericeum* s.l. with those observed among other species in the genus. We then use the phylogenetic identity of a representative number of accessions to seek for differences in morphological characters among lineages of the *H. sericeum* s.l. clade. Because relevant type material is too old for sequencing, we compute a discriminant function that optimizes morphological identification from the sample of molecularly analysed specimens, and assign each type specimen to one of the molecular lineages. Finally, we make the appropriate taxonomic changes based on the morphological and molecular data.

MATERIAL AND METHODS

Specimens representing each haplotype based on *rpl16* and *atpB-rbcL* sequences from all 130 accessions of *H. sericeum* s.l. included in Désamoré & al. (2012) were combined with those generated for multiple accessions of each species of the genus by Huttunen & al. (2008). The dataset thus created included 68 accessions in total (Appendix 1). *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen was employed as outgroup. Indels were scored using simple index coding (Simmons & Ochoterena, 2000) as implemented in the plugin SeqState (Müller, 2004) of PhyDE v0.995 (Müller & al., 2006).

The data matrix was submitted to a MP analysis using DNAPars as implemented by Seaview 4.4.2 (Gouy & al., 2010) with 10 random starts, saving a maximum of 50000 most parsimonious trees and using gaps as informative characters. Support for the branches was assessed through a non-parametric bootstrap analysis with 100 replicates.

Forty-three out of the 130 specimens of *Homalothecium sericeum* s.l. included by Désamuré & al. (2012) were sampled to represent the morphological variation and distribution range of *H. mediterraneum* (11 accessions), *H. mandonii* (12 accessions), and *H. sericeum* s.str. (20 accessions) (see the Taxonomic treatment below for voucher information). The types of a number of segregate taxa previously recognized within *H. sericeum* s.l., namely *Camptothecium aureolum* Kindb., *Homalothecium sericeum* var. *meridionale* M.Fleisch. & Warnst., *Hypnum mandonii* Mitt., and *Homalothecium barbelloides* Dixon & Cardot, were also examined. We did not score morphological characters of the type of *Leskea sericea* Hedw. (Hedwig, 1801). In addition to the fact that Hedwig's type material should not be sampled unless absolutely necessary, the type of *L. sericea* exhibits the long and narrow leaves that are typical for *H. sericeum* s.str. Furthermore, Hedwig's European type material originates mainly from the non-Mediterranean regions where only the latter occurs. As a dioicous species, *H. sericeum* s.l. is infrequently found with sporophytes and only three specimens included in Désamuré & al. (2012) indeed bore them. Therefore, a further 12 specimens with sporophytes were selected from herbarium material and assigned to one of the three lineages on the basis of their gametophytic traits: six *H. mediterraneum*, five *H. mandonii*, and one *H. sericeum* s.str. Sporophytes were only studied in one additional specimen of the latter since their character states were already largely studied in previous studies (Hedenäs, 2001, 2012). All morphologically studied specimens are cited under the Taxonomic treatment.

Seven gametophytic traits were scored: leaf length (mm); leaf width (mm); leaf length to width ratio; median leaf lamina cell length (μm); median leaf lamina cell width (μm); median leaf lamina cell length to leaf length ratio; and leaf margin denticulation (finely denticulate, denticulate, strongly denticulate). Initial measurements were made in both stem and branch leaves in three arbitrarily selected specimens of each lineage (*H. mediterraneum*: H69, H78, H86; *H. mandonii*: H28, H29, H30; *H. sericeum* s.str.: H16, H19, H91; specimens cited under Taxonomic treatment). Three stem and branch leaves that had reached their final size were measured, for median lamina cells the total size range was noted, and for all measurements the mid-point (median) values were used in the comparisons (cf. Hedenäs, 1996). These characters showed parallel patterns of variation in the two kinds of leaves, and since it was substantially easier to obtain undamaged branch leaves than stem leaves (results not shown), it was decided to use only branch leaves in order to potentially find distinguishing characters among the three lineages. Leaf lamina cell width did not distinguish the lineages based on the initial three specimens per entity due to too great overlap (branch leaf lamina cell width 4.4-6.9 μm in *H. mediterraneum*, 4.2-8.4 in *H. mandonii*, and 4.6-8.4 in *H. sericeum* s.str.). This feature was therefore not measured in the remaining material, as it seemed unlikely that it would be a useful character for taxon identification.

Shapiro Wilk's W-test and Brown & Forsythe's test showed that the continuous gametophytic variables branch leaf length, leaf width, leaf length to width ratio, median lamina cell length, and median leaf lamina cell length to leaf length ratio did not significantly depart from a normal distribution and did not exhibit significant differences in variance, respectively. Morphological differences between *H. sericeum*, *H. mandonii*, and *H. mediterraneum* depending on the five variables were thus sought using parametric statistics, namely Analysis of variance (ANOVA) and Fisher's Least Significant Difference (LSD) test as implemented by STATISTICA 8.0 (StatSoft, 2008). Linear discriminant analysis (LDA)

was then employed, using the same program, to identify which is the best combination of morphological variables to identify *H. sericeum*, *H. mandonii*, and *H. mediterraneum*. Variables were selected using backward selection with a probability to stay in the model of $p = 0.01$. The discriminant functions were employed to assign the types of taxa previously recognized within *H. sericeum* s.l. to one of the three species based on their morphological features. To determine what is the actual error rate when attempting at identifying specimens from morphological characters only, a cross-validation procedure, during which each specimen was successively removed from the matrix, was employed.

RESULTS

The datamatrix included 1273 characters, of which 94 (22 indels) were parsimony-informative. The MP analysis of *rpl16* and *atpB-rbcL* in *Homalothecium* resulted in 887 equally parsimonious trees of 121 steps, whose strict consensus is presented in Fig. 1. Within *H. sericeum* s.l., a large polytomy comprising four haplotypes labelled as *H. mediterraneum* as well as a clade holding the accessions of reciprocally monophyletic *H. mandonii* and *H. sericeum* s. str. were recovered. Most branches did not receive bootstrap support >50%.

Branch leaf length (*H. mediterraneum*, mean \pm standard deviation: 1.74 ± 0.30 ; *H. mandonii*: 1.60 ± 0.19 ; *H. sericeum* s.str.: 1.74 ± 0.28 ; $p = 0.17$ – 0.98 , Fisher's LSD test) and lamina cell width (see above) did not significantly differ among lineages, leaving four continuous characters (leaf width, leaf length to width ratio, median lamina cell length, and median lamina cell length to leaf length ratio; Table 1) as well as denticulation of leaf margins for consideration as potentially discriminative gametophytic characters. Specimens of *H. sericeum* s.str. exhibited significantly narrower leaves and a higher leaf length to width ratio than those of the other clade and the grade according to Fisher's LSD test (Table 1). In *H. mandonii*, the lamina cells were significantly longer and the lamina cell length to leaf

length ratio was significantly higher than in *H. mediterraneum* and *H. sericeum* s.str. (Table 1). All of the investigated characters were, however, overlapping among the three, with an overlap of 9% in the lamina cell length to leaf length ratio to 61% in leaf width (Table 1). *Homalothecium sericeum* s.str. was further characterized by the strong denticulation or sometimes weak dentation of the leaf margin in the alar region, with at least some of the teeth distinctly bent outwards (Fig. 2).

Two variables, namely the leaf length to width ratio and the median lamina cell to leaf length ratio, were selected in the LDA. On average, 79% of the specimens were assigned to the correct taxa after cross-validation, which corresponds to a correct classification rate of 63%, 92%, and 80% in *H. mediterraneum*, *H. mandonii* and *H. sericeum* s.str., respectively. The type specimens of *H. sericeum* var. *meridionale* and *Hypnum mandonii* were assigned to *H. mediterraneum* and *H. mandonii*, respectively, while the types of *Camptothecium aureolum* and *H. barbelloides* were assigned to *H. sericeum* s.str..

Sporophytic characters, when available, further distinguished the three taxa. The seta was rough throughout its length in *H. mandonii* and *H. sericeum* s.str., but completely rough, smooth in the upper 1/4, or occasionally completely smooth, in *H. mediterraneum*. The outer exostome ornamentation was clearly cross-striolate in *H. sericeum* s.str., but smooth or only weakly cross-striolate in *H. mediterraneum* and *H. mandonii*. Finally, the exostome border in the lower portion of the teeth was broad in *H. mediterraneum* but narrow in the two clades (Fig. 3A, E).

Among the three plastid loci (*atpB-rbcL*, *rpl16*, *trnG*) investigated by Désamuré & al. (2012), *rpl16* exhibited three substitutions and one indel (Table 2) within the *H. sericeum* complex, allowing for the unambiguous identification of any specimen that is recent enough for DNA amplification. *TrnG* included one synapomorphic substitution for *H. sericeum* s.l.,

while in *atpB-rbcL* one synapomorphic substitution supports *H. sericeum* s.str. and *H. mandonii*.

DISCUSSION

The analyses confirmed the monophyly of accessions assigned to *H. mandonii* and *H. sericeum* s. str. Levels of divergence between these two clades were similar to those observed among other species of the genus. Although these relationships were supported by the strict consensus resulting from the MP analysis of two cpDNA loci and are further fully consistent with those resolved in other species-level phylogenies of the genus (Huttunen & al., 2008) and with analyses of the *H. sericeum* s.l. clade (Désamoré & al., 2012), they lacked bootstrap support in the present analyses. Although a complete set of ITS sequences was produced, we refrained from combining them with the chloroplast data as accessions of morphologically unambiguously identified species were resolved in completely unrelated clades with ITS. Such a strong incongruence among partitions could result from the amplification of paralogous ITS copies, as recently evidenced in mosses (Kosnar & al., 2012), and further studies are therefore required to explore the utility of that locus in the genus.

Although variation in *rpl16* and *atpB-rbcL* was sufficient to discriminate all *Homalothecium* species recognized to date, the four haplotypes labelled as *H. mediterraneum* formed a polytomy within *H. sericeum* s.l. One possibility to accommodate those haplotypes taxonomically would be to include them within one of the closely related recognized species, but this would be at odds with their levels of divergence that are of the same order as those observed among sister species in the genus. Alternatively, each of those four haplotypes could be recognized as an individual species. However, as they share the same geographic origin and morphological identity (see below), we rather treat them here as conspecific,

although the lack of any molecular synapomorphy remains unexplained and is at odds with a monophyletic species concept.

The discriminant analysis assigned the types of *H. sericeum* var. *meridionale* and *Hypnum mandonii* to our groups of accessions labelled as *H. mediterraneum* and *H. mandonii*, respectively, which are therefore formally recognized here as *H. mediterraneum* Hedenäs stat. et nom. nov. (see Taxonomic treatment below) and *H. mandonii* (Mitt.) Hedenäs. The new epithet *mediterraneum* was used instead of *meridionale*, since at the species level, the latter is blocked by *H. meridionale* Ravaud, a synonym of *H. sericeum* var. *robustum* Boulay. The recognition of *H. mediterraneum* and *H. mandonii* parallels previous 'resurrections' of ancient taxa (Rycroft & al., 2004) or de novo descriptions of moss species in the light of molecular data (Hutsemékers & al., 2012; Medina & al., 2012). The type of *Camptothecium aureolum* was unambiguously assigned to the *H. sericeum* s.str. clade, supporting the notion that the former is a synonym of the latter (Hofmann, 1998). The isotype of *H. barbelloides* has very narrow leaves, so that the specimen was assigned to *H. sericeum* by the discriminant analysis, but its lamina cells and the shape and margin denticulation of the basal leaf are similar to *H. mandonii*. The specimen appears to have grown as a pendent epiphyte, which would explain the narrow leaves, and we therefore believe that *H. barbelloides* is most likely conspecific with *H. mandonii*. However, the very uncharacteristic leaf shape of this taxon makes us refrain from making a formal reduction into synonymy. Unfortunately, only the old type material is available, and the molecular identity could therefore not be determined.

Gametophytic traits significantly differ among *H. mandonii*, *H. mediterraneum* and *H. sericeum* s.str., but exhibit substantial overlap (Table 1). In mosses, the gametophyte is the dominant phase and gametophytic traits are largely employed for species identification. During its lifetime the gametophyte is permanently exposed to environmental variation, and is hence prone to plasticity and sometimes convergence (Vanderpoorten & al., 2002; Olsson

& al., 2011, 2012; but see Huttunen & al., 2012). Variation in gametophytic traits for
 taxonomy and species identification might therefore be misleading (Zander & Vitt, 1979;
 Olsson & al., 2011, 2012; Bell & Hyvönen, 2012; Câmara & Carvalho-Silva, 2013). In the *H.*
sericeum complex and other moss genera where species differentiation mostly relies on
 continuous characters (e.g., *Leucobryum*, Vanderpoorten & al., 2003; *Rhynchostegium*,
 Hutsemékers & al., 2012), specimen identification is challenged by the overlap in characters
 among species. In the *H. sericeum* complex, this overlap results in a misidentification rate of
 8-37% when only gametophytic characters are used. Sporophytic traits substantially assist
 species identification but, as in many of the about 60% of moss species that are dioecious
 (e.g., Wyatt, 1982; Hedenäs & Bisang, 2011), sporophytes are mostly lacking in the *H.*
sericeum complex. Although a combination of gametophytic and sporophytic characters
 allows distinguishing the three species of the *H. sericeum* complex, as summarised in the
 identification key given below, the present study points to the necessity of developing easy-
 to-use molecular identification tools. Such molecular identification tools (DNA barcoding
 markers) will improve biodiversity assessments and ecological research in taxonomically
 challenging bryophyte groups (e.g., Stech & al., 2013; Lang & Stech, in press). Of the three
 plastid markers (*atpB-rbcL*, *rpl16*, *trnG*) used in the phylogeographic study of Désamoré &
 al. (2012), *rpl16* was the only locus that displayed sufficient levels of variation to on its own
 allow for an unambiguous differentiation between the three species (Table 2). Although
atpB-rbcL and *trnG* were also partly informative, *rpl16* can best serve as an easy molecular
 tool for identifying poorly developed and/or sterile *Homalothecium sericeum* s.l. specimens.
 The locus was similarly shown to exhibit appropriate levels of inter-specific variation in
 other genera, such as *Plagiomnium* (Wyatt & Odrzykoski, 2012), *Forsstroemia* (Olsson &
 al., 2012), *Leptodon* (Sotiaux & al., 2009), and *Cratoneuron* (Hedenäs, 2011). *Rpl16* is not
 among the regions that have been explored as DNA barcoding marker in mosses so far (see

Stech & al., 2013; Lang & Stech, in press; and references therein), but can be considered a potential candidate for distinguishing closely related bryophyte species, although its applicability to a wider range of mosses remains to be tested. Contrary to the original idea of species identification based on a single short, standardized DNA region, recent DNA barcoding attempts of mosses indicate that different markers (or different combinations of markers) may work best in different moss lineages, including standard markers such as *trnL*-*F* and ITS (but see above), but also newly considered regions such as *atpF*–*atpH* (Hassel & al., 2013) or *rps19*–*rpl12* (Lang & Stech, in press). The present results concerning *rpl16* are in line with these observations.

The three *Homalothecium* species exhibit distinct, albeit slightly overlapping geographic ranges. *Homalothecium mandonii* is a strict Macaronesian endemic. It is distributed across the four Macaronesian archipelagos, a pattern that is otherwise found in bryophytes only in *Exsertotheca intermedia* (Brid.) S. Olsson, Enroth & D. Quandt, raising the question of why apparently so vagile organisms failed to reach the North African and South-Western European coasts. *Homalothecium mediterraneum* is a Mediterraneo-Macaronesian endemic that is widespread across the Mediterranean but was found in one locality in Lanzarote in the Canary Islands. Finally, *H. sericeum* is a temperate species distributed across central Europe and the South of Scandinavia, with a few scattered localities in the Mediterranean and eastern North America. The restricted distributions of the segregate species within *H. sericeum* s.l. reinforce the notion that many disjunctions typically observed in moss distribution ranges are due to taxonomic shortcomings (Hutsemékers & al., 2012; Medina & al., 2012) and call for the necessity of substantial taxonomic revisions of previously broadly defined bryophyte species.

Taxonomic treatment

299

300 ***Homalothecium sericeum* (Hedw.) Schimp.**, Bryol. Eur. 5: 93. 456 (fasc. 46–47 Mon. 3. 1).
 301 1851.

302 Basionym: *Leskea sericea* Hedw., Sp. Musc. Frond. 228. 1801.

303 Synonym: *Camptothecium aureolum* Kindb., Rev. Bryol. 22: 85. 1895. Lectotype:

304 Norwegen, Opdal, 22/2 80, C.Kaurin (Herb. N. C. Kindberg 19, Herb. H.Möller in S:
 305 B17069) (Hofmann, 1998).

306 *Plants* medium-sized, sometimes small, irregularly or pinnately branched, branches and
 307 upper shoot ± strongly curved upwards-inwards when dry. *Stem* with central strand, a cortex
 308 (including epidermis) of 2-3(-4) layers of small and incrassate cells, without hyalodermis;
 309 *rhizoids* inserted at or just below costa insertion, red-brown, slightly branched, smooth;
 310 *axillary hairs* 1-2 per axil, strictly axillary, with 1-3 short, hyaline upper cells, 6.0-12.0 µm
 311 wide, basal cells 1-2, quadrate, hyaline or brownish; *pseudoparaphyllia* foliose; *paraphyllia*
 312 absent. *Stem leaves* when moist erect to erecto-patent, when dry erect, straight or slightly
 313 homomallous, from ovate-triangular triangular or narrowly triangular base gradually
 314 narrowed to longly acuminate apex, not or slightly narrowed towards insertion, slightly
 315 concave, plicate; *costa* single, ending 50-65% way up leaf, 29.5-80.0 µm wide near base,
 316 cells on both ad- and abaxial sides linear and similar to adjoining lamina cells, smooth or
 317 often ending in a spine on back, in transverse section near base plano-convex, 3-4-stratose,
 318 cells homogeneous; *margin* plane or on one or both sides shortly recurved or reflexed,
 319 without border, above finely denticulate or denticulate, sometimes partly entire, around upper
 320 alar region mostly distinctly denticulate to dentate, denticles or teeth often spreading or
 321 recurved; *median leaf lamina cells* 36.0-130.0 x 4.0-8.5 µm, linear, with moderately to longly
 322 tapering ends, slightly incrassate, scattered cells sometimes dorsally and distally prorate;
 323 *basal lamina cells* slightly wider and much shorter than median cells, strongly incrassate,

324 more or less porose; *alar cells* triangular, transversely rectangular, quadrate or shortly
 325 rectangular, in basal part rectangular and widened, irregular, incrassate, eporose, forming a
 326 large and well differentiated, \pm isodiametric or approximately triangular group, extending
 327 from leaf margin 25-35% of distance to leaf middle at insertion, decurrent 50-80% way down
 328 to leaf below. *Branch leaves* smaller and more shortly acuminate than stem leaves, widest
 329 0-20% way up, costa ending in a spine, upper margin more strongly denticulate than in stem
 330 leaves, median leaf lamina cells $19.0-119.5 \times 4.5-8.5 \mu\text{m}$, many lamina cells distally and
 331 dorsally prorate; median values (three leaves) for leaf width $0.28-0.54 \mu\text{m}$, length to width
 332 ratio $3.94-5.88$, mid-leaf lamina cell length $49.35-82.95 \mu\text{m}$, lamina cell length (μm) to leaf
 333 length (mm) ratio $29.70-45.64$. *Sexual condition* dioicous, with normal-sized or dwarf male
 334 plants. *Perigonia* lateral on stem, in dwarf males lateral or apical, paraphyses present, in
 335 dwarf males absent. *Perichaetia* lateral on stem; inner perichaetial leaves straight and erect,
 336 from ovate or triangular-ovate base suddenly or gradually narrowed to flexuose acumen,
 337 longly acuminate, plicate; costa single, weak; margin in acumen denticulate or partly strongly
 338 so; paraphyses 6-13 cells long, slightly incrassate. *Calyptra* cucullate, 3-5-stratose, smooth,
 339 naked or with a few basal paraphyses. *Seta* 9-17 mm long, orange or red, rough throughout,
 340 when dry untwisted or dextrorse. *Capsule* longly cylindrical to longly elongate-ovoid,
 341 straight, or slightly curved, not furrowed, not constricted at mouth when moist or dry,
 342 orthotropous or slightly homotropous; exothecial cells $27.5-65.0 \times 15.5-27.5 \mu\text{m}$, quadrate to
 343 elongate-rectangular, evenly incrassate, smooth, below mouth 2-4 rows of isodiametric or
 344 transversely rectangular cells; stomata round-pored; annulus separating, of 2(-3) rows of
 345 relatively small cells; operculum longly conical or short-rostrate, basal cells radial, slightly
 346 incrassate. *Exostome* reduced, teeth narrow, red or pale reddish, lower outside cross-striolate,
 347 not furrowed, upper outside papillose or strongly so, margin entire, border in lower portion of
 348 teeth narrow, gradually narrowed at transition zone, absent above, primary peristomial layer

349 reduced or strongly reduced. *Endostome* basal membrane low, with short and imperfect
 350 processes, hyaline or brownish, papillose, cilia 1-2, short or rudimentary. *Spores*
 351 14.5-23.0(-29.0) μm , papillose, mature in winter half-year.

352 Known geographical distribution: *Homalothecium sericeum* occurs across extra-
 353 Mediterranean Europe, eastern North America, western Asia eastwards to the Himalayas and
 354 in Newfoundland (Hofmann, 1998). Earlier reports from China could not be substantiated
 355 (Wang & Hu, 2008).

356 Specimens studied (except types; 'D' with number = specimens included in Désamoré &
 357 *al.* (2012): **Bulgaria.** Strandzha Mts, Veleka reka at Kachul, 5 June 2009, *B.Papp* (D H82),
 358 BP: 179829; Strandzha Mts., between Kachul and Malko Turnovo, 6 June 2009, *B.Papp* (D
 359 H6), BP: 179866. **Germany.** Rheinland-Pfalz, Kr. Ahrweiler, *Frahm* 8604 (D H39), Herb. J.-
 360 P.Frahm BONN. **Greece.** Chalkidiki, Galatista, 6 April 2006, *B.Papp* (D H77), BP: 174546.
 361 **Hungary.** Veszprém County, Hálóeresztő, 19 June 2007, *B.Papp* (D H76), BP: 175051.
 362 **Norway.** Finnmark, Söröysund, 24 July 2001, *L.Hedenäs* (D H25), S: B59862; Troms,
 363 Lyngen, 18 July 2003, *L.Hedenäs* (D H26), S: B82906. **Poland.** Western Carpathians, Beskid
 364 Maly Range, *A.Stebel* (*Musci Macror. Merid. Pol. Exs. 1476*) (D H23), S: B157625.
 365 **Slovakia.** Mts Slovenský Raj, Vel'ký Sokol dolina Valley, 3 May 2008, *B.Papp* (D H10),
 366 BP: 176082. **Sweden.** Åsele Lappmark, Dorotea, 29 June 2004, *L.Hedenäs* (D H57), S:
 367 B96087; Medelpad, Torp, 3 October 2006, *L.Hedenäs* (D H59), S: B115534; Öland, E of
 368 Skogsby, 28 April 2010, *L.Hedenäs* (D H19), S: B174820; Östergötland, Krokek, 23 October
 369 2006, *L.Hedenäs* (D H56), S: B115519; Södermanland, Kålsö, 5 May 1991, *L.Hedenäs*, S:
 370 B52012; Södermanland, Utö, 15 May 2010, *L.Hedenäs* (D H91), S: B175290. **Switzerland.**
 371 Ct. Valais, Zermatt, 9 August 2007, *L.Hedenäs* (D H46), S: B121137; Ct. Ticino, Cerentino,
 372 18 June 2008, *L.Hedenäs* (D H47), S: B138085. **Russia.** Krasnodar territory, Anapa district,
 373 *M.Ignatov & E.Ignatova* (*Mosses of Russia* 24) (D H16), S: B113876; Caucasus, Malyi

374 Utrish, *Seregin & Lozhkina M-524* D H15), S: B110844. **Turkmenistan**. Aidere, 2 April
 375 1989, *Levitskaya* (D H52), S: B110843. **United Kingdom**. England, Shropshire, 12 October
 376 2008, *L.Hedenäs* (D H48), S: B144673.

377

378 ***Homalothecium mediterraneum* Hedenäs** stat. et nom. nov. Fig. 3A-D

379 Basionym: *Homalothecium sericeum* var. *meridionale* M.Fleisch. & Warnst., Bot.

380 Centralbl. 72: 395. 1897. Isolectotype: (Italy). Sicilia, Mola bei Taormina and

381 Kalkfelsen, 600 m., 6.4.1897, leg. Fleischer (Herb. H.Möller in S: B185199)

382 (Hofmann, 1998). [blocking name at species level: *Homalothecium meridionale*

383 Ravaud, Mém. Soc. Sc. Nat. Cherbourg 37: 303. 1910, *nom. nud. in synon.* (\equiv *H.*

384 *sericeum* var. *robustum* Boulay)]

385 *Homalothecium sericeum* var. *tunetanum* Besch. in Patouillard, Expl. Sci. Tunisie Bot. 8:

386 11. 1897 (lectotype in PC, Hofmann, 1998).

387 *Plants* medium-sized, sometimes small, irregularly or pinnately branched, branches and

388 upper shoot \pm strongly curved upwards-inwards when dry. *Stem* with central strand, a cortex

389 (including epidermis) of 2-4 layers of small and incrassate cells, without hyalodermis;

390 *rhizoids* inserted at or just below costa insertion, red-brown, hardly to moderately strongly

391 branched, smooth; *axillary hairs* 1-2 per axil, strictly axillary, with 1-4 short, hyaline upper

392 cells, 8.5-10.5 μ m wide, basal cells 1-2, transversely rectangular to shortly rectangular,

393 brownish; *pseudoparaphyllia* foliose; *paraphyllia* absent. *Stem leaves* when moist erect to

394 patent, when dry erect, straight or slightly homomallous, from cordate-triangular or rounded-

395 triangular base gradually narrowed to longly acuminate apex, markedly narrowed towards

396 insertion, slightly concave, plicate; *costa* single, ending 55-75% way up leaf, 38.0-73.5 μ m

397 wide near base, cells on both ad- and abaxial sides linear and similar to adjoining lamina

398 cells, smooth or often ending in a spine on back, in transverse section near base plano-

399 convex, 3-4-stratose, cells homogeneous; *margin* plane or on one or both sides entirely or
 400 partly broadly recurved, without border, entire or finely denticulate, denticles around upper
 401 alar region weak or absent, rarely bent slightly outwards; *median leaf lamina cells* 29.5-92.5
 402 x 4.0-7.5 μm , linear, with shortly to moderately tapering ends, slightly incrassate, scattered
 403 cells sometimes dorsally and distally prorate; *basal lamina cells* wider and much shorter than
 404 median cells, incrassate, eporose; *alar cells* quadrate, transversely rectangular, rhomboidal,
 405 especially towards insertion rectangular, in distal portion of group often irregular, slightly
 406 incrassate, eporose, forming a large and well differentiated, \pm isodiametric or along margin
 407 slightly elongate group, extending from leaf margin 25-35% of distance to leaf middle at
 408 insertion, decurrent 20-50% way down to leaf below. *Branch leaves* smaller and more ovate
 409 than stem leaves, widest 15-30% way up, costa ending in a spine, upper margin more
 410 strongly denticulate than in stem leaves, median leaf lamina cells 25.0-115.5 x 4.5-7.0 μm ,
 411 many lamina cells distally and dorsally prorate; median values (three leaves) for leaf width
 412 0.34-0.56 μm , length to width ratio 3.03-4.26, mid-leaf lamina cell length 46.20-81.90 μm ,
 413 lamina cell length (μm) to leaf length (mm) ratio 24.75-48.21. *Sexual condition* dioicous,
 414 with normal-sized or dwarf male plants. *Perigonia* lateral on stem, in dwarf males lateral or
 415 apical, paraphyses present, in dwarf males few. *Perichaetia* lateral on stem; inner perichaetial
 416 leaves straight and erect, from ovate or ovate-oblong base suddenly or gradually narrowed to
 417 flexuose acumen, acuminate, smooth or weakly plicate; costa single, weak; margin in acumen
 418 denticulate or finely so, at shoulder strongly so or partly dentate; paraphyses 8-19 cells long,
 419 slightly incrassate. *Calyptra* cucullate, 3-5-stratose, smooth, naked. *Seta* 8-15 mm long, red,
 420 rough almost throughout or above weakly so or smooth, occasionally smooth almost
 421 throughout, when dry dextrorse. *Capsule* cylindrical, shortly or gradually narrowed towards
 422 mouth, straight, or mouth slightly oblique, not furrowed, often constricted at mouth when
 423 moist but not more so when dry, orthotropous; exothecial cells 21.0-65.0 x 12.5-40.0 μm ,

quadrate or shortly to longly rectangular, evenly incrassate or slightly collenchymatous with superficial thickenings, smooth, below mouth 1-4 rows of isodiametric, shortly transversely rectangular, or rectangular cells; stomata round-pored, occasionally ovate-pored; annulus separating, of 1-3 rows of relatively small cells; operculum conical or rostrate, basal cells radial, incrassate. *Exostome* reduced, teeth short and narrow, yellow-brown or pale yellow-brown, lower outside indistinctly cross-striolate to smooth, not furrowed, upper outside strongly papillose, margin entire or irregular, border in lower portion of teeth broad, gradually narrowed at transition zone, absent above, primary peristomial layer strongly reduced. *Endostome* basal membrane low, with short and imperfect or vestigial processes, hyaline, vestigial processes sometimes brownish, papillose above, sometimes more finely so below, cilia 1-3, vestigial. *Spores* 13.0-21.0 μm , finely or strongly papillose, mature in winter half-year.

According to Hofmann (1998), *H. sericeum* var. *meridionale* (*H. mediterraneum*) and *H. sericeum* var. *tunetatum* differ from *H. sericeum* s. str. only in their smooth seta. Because the often occurring smooth or partly smooth seta is one feature that distinguishes *H. mediterraneum* from the other two species recognized here (Table 2), *Homalothecium sericeum* var. *tunetatum* is considered as a synonym of *H. mediterraneum*.

Known geographical distribution: *Homalothecium mediterraneum* is circum-Mediterranean and is known from one locality in Lanzarote in the Canary Islands (Désamoré & al., 2012).

Specimens studied (except types; 'D' with number = specimens included in Désamoré & al. (2012): **Cyprus**. Trodos Mts, at Pano Platres village, 18 September 2001, *B.Papp* (D H44), BP: 177881; Troodos Gebirge, Pano Platres, *Frahm 200691* (D H31), Herb. J.-P.Frahm BONN. **Greece**. Crete, Chania, *Frahm K-158* (D H34), Herb. J.-P.Frahm BONN; Crete, Irakleion region, 18 April 2001, *B.Papp* (D H86), BP: 170680; Crete, environs de

449 Heraklion, *A.Désamoré, B.Laenen H108* (D H108), LG; Kephissos, Attica, 1873,
 450 *DeHeldreich 138*, S B185184; Péloponnèse, Kalavryta, *A.Désamoré, B.Laenen H110* (D
 451 H110), LG; Péloponnèse, Sella, *A.Désamoré, B.Laenen H115* (D H115), LG; Rhodos Island,
 452 Mt. Profitis Ilias, 7 August 2006, *B.Papp* (D H78), BP: 174611. **Italy**. Sardinia merid.:
 453 Iglesias, *K.Holmen 70-34*, S: B185180; Sardinia merid.: Iglesias, *K.Holmen 71-53*, S:
 454 B185181. **Montenegro**. Lovcen Mts, Njegusi village to Kotor, 12-13 October 2003, *B.Papp*
 455 (D H69), BP: 174306. **Spain**. Granada (Alpujarra de la Sierra). Sierra Nevada, May 2006,
 456 *R.M.Ros, S.Rams* (D H50), S: B135972. **Canary Islands**. Lanzarote, Heleches,
 457 *A.Vanderpoorten HS41* (D HS41), LG. **Tunisia**. Aim Draham, *C.J.Pirad 65*, S: B185187.
 458 **Turkey**. Prov. Aydin, north side of Samsundag, *E.Nyholm 335/71*, S: B99830; Prov. Mugla,
 459 mainroad Marmaris-Mugla, *E.Nyholm 475/71*, S: B99831.

460

461 ***Homalothecium mandonii* (Mitt.) Geh.**, Flora 69: 348. 1886. Fig. 3E-H

462 Basionym: *Hypnum mandonii* Mitt., Nat. Hist. Azores 311. 1870. Isolectotypes: 'Mandon:
 463 Mousees de Madère no. 36. Homalothecium sericeum Sch. Rib. das Cales, Mars' (S:
 464 B8824); 'Homalothecium sericeum, Madeira, Rib. d. Cales, Mandon 36, Mars.' (Herb.
 465 H.Möller in S: B8823) (Hofmann, 1998).

466 *Homalothecium sericeum* var. *meridionale* Schimp. in Geh., Flora 69: 349. 1886, *nom.*
 467 *nud.* (Geheeb, 1886)

468 *Plants* medium-sized, sometimes small, irregularly pinnately branched, branches sometimes
 469 turning to new stems, branching angle relatively narrow, branches straight or curved
 470 upwards-inwards when dry. *Stem* with central strand, a cortex (including epidermis) of
 471 1-2(-3) layers of small and incrassate cells, without hyalodermis; *rhizoids* inserted at or just
 472 below costa insertion, red-brown, not or slightly branched, smooth; *axillary hairs* 1-3 per
 473 axil, strictly axillary, with 1-2 short, hyaline upper cells, 10.0-12.5 µm wide, basal cells 1-2,

474 transversely rectangular to shortly rectangular, brown; *pseudoparaphyllia* foliose;
 475 *paraphyllia* absent. *Stem leaves* when moist erect to patent, when dry erect, straight or
 476 slightly homomallous, triangular or ovate-triangular, from shortly above insertion gradually
 477 narrowed to acuminate apex, distinctly constricted at insertion, concave, strongly plicate;
 478 *costa* single, ending 50-75% way up leaf, 31.5-63.0 μm wide near base, cells on both ad- and
 479 abaxial sides linear and similar to adjoining lamina cells, smooth, in transverse section near
 480 base plano-convex, 4(-5)-stratose, cells homogeneous; *margin* plane or shortly to longly
 481 weakly reflexed, without border, finely denticulate throughout, a few denticles around upper
 482 alar region sometimes stronger, rarely bent slightly outwards; *median leaf lamina cells*
 483 46.0-178.5 x 4.0-8.0 μm , linear, with moderately to longly tapering ends, slightly incrassate
 484 or incrassate, smooth or slightly distally and dorsally prorate; *basal lamina cells* wider and
 485 much shorter than median cells, strongly incrassate, porose; *alar cells* in upper portion of
 486 group transversely rectangular, quadrate, or rectangular, often rounded, below rectangular to
 487 longly rectangular, incrassate, slightly porose, forming a rounded, shortly oblong, or
 488 triangular group, extending from margin 35-40% of distance to leaf middle at insertion,
 489 decurrent or shortly so. *Branch leaves* smaller than stem leaves, widest 15-25% way up, *costa*
 490 occasionally ending in small, obtuse spine, upper margin denticulate, median leaf lamina
 491 cells 33.5-147.0 x 4.0-8.5 μm , occasional lamina cells distally and dorsally prorate; median
 492 values (three leaves) for leaf width 0.37-0.61 μm , length to width ratio 2.96-3.60, mid-leaf
 493 lamina cell length 65.10-103.95 μm , lamina cell length (μm) to leaf length (mm) ratio
 494 44.93-59.64. *Sexual condition* dioicous, with normal-sized or dwarf male plants. *Perigonia*
 495 lateral on stem, in dwarf males lateral or apical, paraphyses present, in dwarf males few.
 496 *Perichaetia* lateral on stem and branch bases; inner perichaetial leaves straight and erect,
 497 narrowly ovate or triangular ovate, above shortly narrowed to acumen, apex narrowly
 498 acuminate, smooth or plicate; *costa* single, weak, indistinct; *margin* in acumen entire or

weakly denticulate, at shoulder denticulate, strongly so, or with single teeth, not or weakly bordered; paraphyses 6-19 cells long, incrassate. *Calyptra* cucullate, 3-5-stratose, smooth or sometimes with one low ridge, naked. *Seta* 11-22 mm long, red, rough throughout, when dry dextrorse. *Capsule* ovoid to cylindrical, not furrowed, not or when dry sometimes weakly constricted below mouth, orthotropous or almost so; exothecial cells 21.0-50.5 x 12.5-31.5 μm , quadrate or rectangular, slightly evenly incrassate or longitudinal walls incrassate, not collenchymatous, smooth, below mouth 1-4 rows of small, rectangular, transversely rectangular, or quadrate cells; stomata round-pored; annulus separating, of 1-3 rows of relatively small cells; operculum shortly rostrate, basal cells radial, incrassate. *Exostome* reduced or strongly so, teeth narrow and sometimes short, light orange-brown, lower outside weakly cross-striolate to smooth, not furrowed, upper outside papillose to almost smooth, margin entire, border absent, or present, narrow, and gradually narrowed upwards, primary peristomial layer strongly reduced. *Endostome* basal membrane low, with short and imperfect or vestigial processes, yellowish or brownish, papillose or finely so, cilia 0-2(-3), absent or vestigial. *Spores* 14.5-22.0 μm , rather strongly papillose, mature in winter half-year.

In the original description of *Hypnum mandonii* Mitt. (Mitten, 1870), this taxon was said to have more closely imbricate leaves than *H. sericeum*, and acute rather than more narrowly pointed leaves. The latter is probably to some degree reflected in the narrower leaves that widen from closer to the leaf insertion in *H. sericeum* than in *H. mandonii*.

Known geographical distribution: *Homalothecium mandonii* is a Macaronesian endemic distributed across Cape Verde, all of the Canary Islands, Madeira, and the Azorean islands São Miguel and Santa Maria (<http://www.azoresbiportal.angra.uac.pt/listagens.php?sstr=3&lang=en>; accessed 15 August 2013).

Specimens studied (except types; 'D' with number = specimens included in Désamuré & al. (2012): **Canary Islands**. El Hierro, Arbol Santo, *I.Hildebrandt 06-13* (D H30), L; El Hierro, El Brezal, *I.Hildebrandt 06-17* (D H29), L; Hierro, Riscos de Sabinosa, March 1906, *C.J.Pitard*, S: B185186; Fuerteventura, *A.Vanderpoorten HS43* (D HS43), LG; La Palma, los Tilos, *A.Vanderpoorten 1577* (D HS25), LG; Lanzarote, Peñas del Cache, *A.Vanderpoorten HS39* (D HS39), LG; Lanzarote, Pico de la Zarza, *A.Vanderpoorten HS32* (D HS32), LG; Tenerife, Anaga-Gebirge, *Abts 6145* (D H33), Herb. J.-P.Frahm BONN. **Cape Verde**. Santo Antão, Ribeira da Torre, *A.Lindlar 193* (D H32), Herb. J.-P.Frahm BONN. **Madeira**. Lapa do Passo, *Mandon 37*, S: B8799; Pico Arieiro to Pico Ruivo, *Stech 04-387* (D H28), L; Rabaçal, Cascata de Risco, *Frahm M-138* (D H67), Herb. J.-P.Frahm BONN; Ribeira Brava, Pico Ferreiro, 8 May 2007, *L.Hedenäs* (D H27), S: B119087; São Jorge, Ribeira Grande, *S.Fontinha, L.Hedenäs MA91-199* (D H88), S: B8835; Ribeiro Frio, 3 January 1880, *R.Fritze*, S: B8831; Ribeiro Frio, 8 April 1864, *L.Kny*, S: B8833.

Taxon with uncertain position

***Homalothecium barbelloides* Dixon & Cardot**, J. Bot. 49: 6. 2. 1911.

Isotype: (Canary Islands). Teno Mts., Teneriffe, Evergreen woods, Dec. 1909, leg. Dr. Salter; No. 52. Ex herb. H.N.Dixon. Orig. spec. (Herbarium G.Roth. 1842-1915, Herb. H.Möller in S; reg. no. B107660) (Hofmann, 1998).

Key to the European and Macaronesian species of Homalothecium sericeum s.l.

1. Branch leaves 3.9-5.9 times as long as wide, mostly widest 0-20% way up leaf; margin denticulation at alar region well developed, with at least some teeth distinctly bent outwards (Fig. 2). Exostome distinctly cross-striolate on lower outside.

H. sericeum s.str.

1. Branch leaves 3.0-4.3 times as long as wide, mostly widest 15-30% way up leaf; margin denticulation at alar region weak or absent, teeth rarely and only slightly bent outwards (Fig. 3C, G). Exostome smooth or weakly cross-striolate on lower outside. 2
2. Ratio between branch leaf lamina median cell length (μm)/median leaf length (mm) 24.7-48.2. Seta frequently partly or entirely smooth; exostome border broad (Fig. 3A).

H. mediterraneum

2. Ratio between branch leaf lamina median cell length (μm)/median leaf length (mm) 44.9-59.6. Seta rough throughout; exostome border narrow (Fig. 3E).

H. mandonii

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LITERATURE CITED

- Bell, N. & Hyvönen, J.** 2012. Gametophytic simplicity in Laurasian and Gondwanan Polytrichopsida — the phylogeny and taxonomy of the *Oligotrichum* morphology. *J. Bryol.* 34: 160--172.
- Bell, D., Long, D.G., Forrest, A.D., Hollingsworth, M.L., Blom, H.H. & Hollingsworth, P.M.** 2012. DNA barcoding of European *Herbertus* (Marchantiopsida, Herbertaceae) and the discovery and description of a new species. *Molec. Ecol. Res.* 12: 36--47.
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I.** 2007. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* 22: 148--155.

- 573 **Câmara, P. & Carvalho-Silva, M.** 2013. The genus *Schroeterella* Herzog
574 (Sematophyllaceae) revisited. *Bryologist* 116: 146--148.
- 575 **De Queiroz, K.** 2007. Species concepts and species delimitation. *Syst. Biol.* 56: 879--886.
- 576 **Désamoré, A., Laenen, B., Stech, M., Papp, B., Hedenäs, L., Mateo, R.G. &**
577 **Vanderpoorten, A.** 2012. How do temperate bryophytes face the challenge of a
578 changing environment? Lessons from the past and predictions for the future. *Global*
579 *Change Biol.* 18: 2915--2924.
- 580 **Geheeb, A.** 1886. Bryologische Fragmente. *Flora* 69: 339—353.
- 581 **Goffinet, B., Buck, W.R. & Wall, M.A.** 2007. *Orthotrichum freyanum* (Orthotrichaceae), a
582 new epiphytic moss from Chile 1. *Nova Hedwigia Beih.* 131: 1--11.
- 583 **Gouy, M., Guindon, S. & Gascuel, O.** 2010. SeaView Version 4: A multiplatform graphical
584 user interface for sequence alignment and phylogenetic tree building. *Mol. Biol. Evol.*
585 27: 221-224.
- 586 **Hassel, K., Segreto, R. & Ekrem, T.** 2013. Restricted variation in plant barcoding markers
587 limits identification in closely related bryophyte species. *Mol. Ecol. Resour.* 13: 1047-
588 -1057.
- 589 **Hedenäs, L.** 1996. On the interdependence of some leaf characters within the *Drepanocladus*
590 *aduncus-polycarpus* complex. *J. Bryol.* 19: 311--324.
- 591 **Hedenäs, L.** 2001. Environmental factors potentially affecting character states in
592 pleurocarpous mosses. *Bryologist* 104: 72--91.
- 593 **Hedenäs, L.** 2011. Relationships among *Cratoneuron curvicaule*, *C. filicinum* var. *filicinum*,
594 and *C. filicinum* var. *atrovirens* (Bryophyta: Amblystegiaceae). *J. Bryol.* 33: 99--104.
- 595 **Hedenäs, L.** 2012. Morphological and anatomical features associated with epiphytism
596 among the pleurocarpous mosses – one basis for further research on adaptations and
597 their evolution. *J. Bryol.* 34: 79--100.

- 598 **Hedenäs, L. & Bisang, I.** 2011. The overlooked dwarf males in mosses - Unique among
599 green land plants. *Perspect. Plant Ecol. Evol. Syst.* 13: 121--135
- 600 **Hedwig J.** 1801. *Species muscorum frondosorum*. Lipsiae: Joannis Ambrosii Barthii.
- 601 **Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J.,**
602 **Flatberg, K.I., Frahm, J.-P., Gallego, M.T., Garilleti, R., Guerra, J., Hedenäs, L.,**
603 **Holyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz, J.**
604 **& Söderström, L.** 2006. An annotated checklist of the mosses of Europe and
605 Macaronesia. *J. Bryol.* 28: 198--267.
- 606 **Hofmann, H.** 1998. A monograph of the genus *Homalothecium* (Brachytheciaceae, Musci).
607 *Lindbergia* 23: 119--159.
- 608 **Hutsemékers, V., Vieira, C.C., Ros, R.M., Huttunen, S. & Vanderpoorten, A.** 2012.
609 Morphology informed by phylogeny reveals unexpected patterns of species
610 differentiation in the aquatic moss *Rhynchostegium riparioides* s.l. *Molec.*
611 *Phylogenet. Evol.* 62: 748--755.
- 612 **Huttunen, S., Hedenäs, L., Ignatov, M.S., Devos, N. & Vanderpoorten, A.** 2008. Origin
613 and evolution of the northern hemisphere disjunction in the moss genus
614 *Homalothecium* (Brachytheciaceae). *Amer. J. Bot.* 95: 720--730.
- 615 **Huttunen, S., Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L. & Quandt, D.** 2012.
616 Phylogeny-based comparative methods question the adaptive nature of sporophytic
617 specializations in mosses. *PloS One* 7: e48268.
- 618 **Košnar, J., Herbstová, M., Kolář, F., Koutecký, P. & Kučera, J.** 2012. A case study of
619 intragenomic ITS variation in bryophytes: Assessment of gene flow and role of
620 polyploidy in the origin of European taxa of the *Tortula muralis* (Musci: Pottiaceae)
621 complex. *Taxon* 61: 709-720.

- 622 **Lang, A. S. & Stech, M.** (in press) What's in a name? Disentangling the *Dicranum*
 623 *scoparium* species complex (Dicranaceae, Bryophyta). *Syst. Bot.*
- 624 **Medina, R., Lara, F., Goffinet, B., Garilleti, R. & Mazimpaka, V.** 2012. Integrative
 625 taxonomy successfully resolves the pseudo-cryptic complex of the disjunct epiphytic
 626 moss *Orthotrichum consimile* (Orthotrichaceae). *Taxon* 61: 1180--1198.
- 627 **Mitten, W.** 1870. Musci. Pp. 288--316 in: Godman, F.D.C. (ed.), *Natural history of the*
 628 *Azores, or western islands*. London: John van Voorst.
- 629 **Müller, K.** 2004. SeqState – primer design and sequence statistics for phylogenetic DNA
 630 data sets. *Applied Bioinformatics* 4: 65--69.
- 631 **Müller, K., Müller, J., Neinhuis, C. & Quandt, D.** 2006. PhyDE – Phylogenetic Data
 632 Editor, v0.995. Program distributed by the authors <http://www.phyde.de>
- 633 **Oliver, P.M. & Lee, M.S.Y.** 2010. The botanical and zoological codes impede biodiversity
 634 research by discouraging publication of unnamed new species. *Taxon* 59: 1201--1205.
- 635 **Olsson, S., Enroth, J., Buchbender, V., Hedenäs, L., Huttunen, S. & Quandt, D.** 2011.
 636 *Neckera* and *Thamnobryum* (Neckeraceae, Bryopsida): paraphyletic assemblages.
 637 *Taxon* 60: 36--50.
- 638 **Olsson, S., Enroth, J., Huttunen, S. & Quandt, D.** 2012. *Forsstroemia* Lindb.
 639 (Neckeraceae) revisited. *J. Bryol.* 34: 114--122.
- 640 **Ros, R.M., Mazimpaka, V. Abou-Salama, U., Aleffi, M., Blockeel, T.L., Brugués, S.M.,**
 641 **Cros, R.M., Dia, M.G., Dirkse, G.M., Draper, I., El-Saadawi, W., Erda, I.,**
 642 **Ganeva, A., Gabriel, R., Gonzalez-Mancebo, J.M., Granger, C., Herrnstadt, I.,**
 643 **Hugonnot, V., Khalil, K., Kürschner, H., Losada-Lima, A., Luis, L., Mifsud, S.,**
 644 **Privitera, M., Puglisi, M., Sabovljevic, M., Sérgio, C., Shabbara, H.M., Sim-**
 645 **Sim, M., Sotiaux, A., Tacchi, R., Vanderpoorten, A., Werner, O.** 2013. Mosses of
 646 the Mediterranean, an annotated checklist. *Cryptog., Bryol.* 34: 99--283.

- 647 **Rycroft, D. S., Groth, H. & Heinrichs, H.** 2004. Reinstatement of *Plagiochila maderensis*
 648 (Jungermanniopsida: Plagiochilaceae) based on chemical evidence and nrDNA ITS
 649 sequences. *J. Bryol.* 26: 37--45.
- 650 **Simmons, M.P. & Ochoterena, H.** 2000. Gaps as characters in sequence-based phylogenetic
 651 analysis. *Syst. Biol.* 49: 369--381.
- 652 **Sotiaux, A., Enroth, J., Olsson, S., Quandt, D. & Vanderpoorten, A.** 2009. When
 653 morphology and molecules tell us different stories: a case-in-point with *Leptodon*
 654 *corsicus*, a new and unique endemic moss species from Corsica. *J. Bryol.* 31: 186--
 655 196.
- 656 **StatSoft, I.** 2008. *STATISTICA (data analysis software system), version 8.0.*
 657 (<http://www.statsoft.com>).
- 658 **Stech, M., Veldman, S., Larraín, J., Muñoz, J., Quandt, D., Hassel, K. & Kruijer, H.**
 659 2013. Molecular species delimitation in the *Racomitrium canescens* complex
 660 (Grimmiaceae) and implications for DNA barcoding of species complexes in mosses.
 661 *PloS One* 8: e53134.
- 662 **Sukkharak, P., Gradstein, S.R. & Stech, M.** 2011. Phylogeny, taxon circumscriptions and
 663 character evolution in the core Ptychanthoideae (Lejeuneaceae, Marchantiophyta).
 664 *Taxon* 60: 1607--1622.
- 665 **Szweykowski, J., Buczkowska, K. & Odrzykoski, I.J.** 2005. *Conocephalum salebrosum*
 666 (Marchantiopsida, Conocephalaceae) - a new Holarctic liverwort species. *Plant Syst.*
 667 *Evol.* 253: 133--158.
- 668 **Vanderpoorten, A., Boles, S. & Shaw, A.J.** 2003. Patterns of molecular and morphological
 669 variation in *Leucobryum albidum*, *L. glaucum*, and *L. juniperoideum*. *Syst. Bot.* 28:
 670 651--656.

- 671 **Vanderpoorten, A., Hedenäs, L., Cox, C.J. & Shaw, A.J.** 2002. Phylogeny and
672 morphological evolution of the Amblystegiaceae (Bryophyta, Musci). *Mol.*
673 *Phylogenet. Evol.* 23: 1--21.
- 674 **Vanderpoorten, A., Schäfer-Verwimp, A., Heinrichs, J., Devos, N. & Long, D.G.** 2010.
675 The taxonomy of the leafy liverwort genus *Leptoscyphus* (Lophocoleaceae) revisited.
676 *Taxon* 59: 176--186.
- 677 **Wang, Y.-f. & Hu, R.-l.** 2008. Brachytheciaceae. Pp. 71--167 in: Hu, R.-l., You, Y.-f.,
678 Crosby, M. R. & He, S. (ed.), *Moss flora of China. English version. Volume 7.*
679 *Amblystegiaceae-Plagiotheciaceae*. Beijing & St. Louis: Science Press & Missouri
680 Botanical Garden.
- 681 **Wyatt, R.** 1982. Population ecology of bryophytes. *J. Hattori Bot. Lab.* 52: 179--198.
- 682 **Wyatt, R. & Odrzykoski, I.J.** 2012. *Plagiomnium floridanum* sp. nov. (Mniaceae), a new
683 moss from the southeastern United States. *The Bryologist* 115: 527--535.
- 684 **Zander, R. H. & Vitt, D.H.** 1979. Gametophytic distinctions of *Zygodon* (Orthotrichaceae),
685 *Anoetangium* and *Leptodontium* (Pottiaceae) and the status of *Anoetangium*
686 *rubrigemmum* of Hawaii. *Canad. J. Bot.* 57: 292--296.
- 687

Table 1 Branch leaf and sporophyte characters that differentiate the three *Homalothecium sericeum* s.l. species. 1--4: Average and standard deviation of the median (mid-point) values of measured characters in *Homalothecium mediterraneum* (n = 11), *H. mandonii* (n = 12), and *H. sericeum* s. str. (n = 20) and median values of the measures from type specimens of *Camptothecium aureolum*, *Homalothecium sericeum* var. *meridionale*, *Hypnum mandonii* and *Homalothecium barbelloides*. Minimum and maximum values for each variable are shown in parentheses. Measurements highlighted in bold in one species indicate a significant difference ($p < 0.05$) from those observed in the two other species according to Fisher's LSD test. 5--9. Other branch leaf and sporophyte characters that differentiate the three *Homalothecium* species.

	1. Leaf	2. Leaf	3. Median	4. Median	5. Leaf	6. Alar leaf	7. Seta	8. Lower	9.
	width	length to	lamina cell	lamina cell	widest at	margin	ornamentation	exostome	Exostome
	(mm)	width ratio	length (μm)	length (μm)		denticulation		outside	border
				to leaf					
				length (mm)					
				ratio					
<i>H. mediterraneum</i>	(0.34)	(3.03)	(46.20)	(24.75)	15-30%	Weak or	Rough, smooth	Smooth or	Broad
	0.48±0.02	3.60±0.11	61.09±3.44	35.92±2.32	above	absent, rarely	in upper ¼, or	weakly	(Fig. 3A)
	(0.56)	(4.26)	(81.90)	(48.21)	leaf base	bent slightly	occasionally	cross-	

						outwards	completely	striolate	
							smooth		
<i>H. mandonii</i>	(0.37)	(2.96)	(65.10)	(44.93)	15-25%	Weak,	Rough	Smooth or	Narrow
	0.49±0.01	3.29±0.06	88.26±3.64	55.05±1.27	above	sometimes a	throughout	weakly	(Fig. 3E)
	(0.61)	(3.60)	(103.95)	(59.64)	leaf base	few stronger		cross-	
						teeth, rarely		striolate	
						bent			
						outwards			
<i>H. sericeum</i>	(0.28)	(3.94)	(49.35)	(29.70)	0-20%	Mostly	Rough	Cross-	Narrow
	0.38±0.01	4.61±0.10	65.31±2.12	37.92±1.02	above	strong,	throughout	striolate	
	(0.54)	(5.88)	(82.95)	(45.64)	leaf base	occasionally			
						dentate, often			
						some teeth			
						bent			
						outwards			
<i>C. aureolum</i>	0.22	4.62	52.50	51.55	-	-	-	-	-

<i>H. sericeum</i> var.	0.50	3.23	71.40	43.87	-	-	-	-	-
<i>meridionale</i>									
<i>H. mandonii</i>	0.48	3.06	95.55	64.54	-	-	-	-	-
<i>H. barbelloides</i>	0.20	5.63	79.80	69.09	-	-	-	-	-

Table 2. Species-specific polymorphisms in the *rpl16* gene among *Homalothecium mandonii*, *H. sericeum*, and *H. mediterraneum*.

Position	594	703	619	832
<i>H. mandonii</i>	C	Poly-A (8 repeats)	T	A
<i>H. sericeum</i>	T	Poly-A (9 repeats)	C	G
<i>H. mediterraneum</i>	T	Poly-A (9 repeats)	T	A

Appendix 1. Voucher information and Genbank accession numbers of the specimens of *Homalothecium* included in the present phylogenetic analysis. *Hap* and *SH* numbers are used in Fig. 1, and refer to haplotypes included in Désamoredé & al. (2012) and specimens in Huttunen & al. (2008), respectively. The GenBank accession numbers for *SH* specimens correspond with *rp116* and *atpB-rbcL*.

Homalothecium aeneum (Mitt.) E.Lawton - *SH308*: EF531042, EF530983. *SH347*:

EF531043, EF530985. *SH348*: EF531045, EF530984. *SH349*: EF531044, EF530986.

Homalothecium aureum (Spruce) H.Rob. - *SH142*: EF531081, EF530969. *SH302*:

EF531082, EF530970. *SH303*: EF531083, EF530967. *SH306*: EF531080, EF530968.

Homalothecium californicum Hedenäs, Huttunen, Shevock & D.H.Norris - *SH345*:

EF531037, EF531016. ***Homalothecium lutescens***(Hedw.) H.Rob. - *SH20*: EF531053,

EF530971. *SH304*: EF531052, EF530974. *SH318*: EF531051, EF530972. *SH321*: EF531050,

EF530973. *SH380*: EF531054, EF530975. ***Homalothecium lutescens* var. *fallax*** (H.Philib.)

Hedenäs & L.Söderstr. - *SH305*: EF531056, EF530977. *SH392*: EF531057, EF531003.

SH397: EF531055, EF530976. ***Homalothecium fulgescens*** (Müll.Hal.) Lawt. - *SH140*:

EF531038, EF530978. *SH320*: EF531040, EF530980. *SH363*: EF531039, EF530979. *SH365*:

EF531041, EF530982. ***Homalothecium mandonii*** (Mitt.) Geh. - *Hap11*, *Hap12*, *Hap13*:

Désamoredé & al. (2012). *SH322*: EF531063, EF531009. *SH357*: EF531064, EF531010.

SH358: EF531065, EF531011. ***Homalothecium mediterraneum*** Hedenäs - *Hap14*, *Hap15*,

Hap16, *Hap21*: Désamoredé & al. (2012). ***Homalothecium megaptilum*** (Sullivant)

Schofield - *SH344*: EF531036, EF531014. *SH346*: EF531035, EF531015. ***Homalothecium***

nevadense (Lesq.) Renauld & Cardot - *SH307*: EF531046, EF530987. *SH309*: EF531048,

EF530989. *SH355*: EF531047, EF530988. *SH356*: EF531049, EF530990. ***Homalothecium***

nuttallii (Wilson) A.Jaeger - *SH68*: EF531077, EF530993. *SH362*: EF531078, EF530991.

SH391: EF531079, EF530992. ***Homalothecium philippeanum*** (Spruce) Schimp. - *SH121*: EF531069, EF530994. *SH310*: EF531074, EF531000. *SH315*: EF531071, EF530996. *SH316*: EF531073, EF530999. *SH317*: EF531070, EF530995. *SH323*: EF531072, EF530997. *SH389*: EF531068, EF531002. *SH390*: EF531076, EF530998. *SH395*: EF531075, EF531001.

Homalothecium sericeum (Hedw.) Schimp. s.str. - *Hap1*, *Hap2*, *Hap3*, *Hap4*, *Hap5*, *Hap6*, *Hap7*, *Hap9*, *Hap10*, *Hap17*, *Hap18*, *Hap20*: Désamuré & al. (2012). *SH35*: EF531061, EF531007. *SH319*: EF531066, EF531012. *SH324*: EF531067, EF531013. *SH359*: EF531060, EF531006. *SH360*: EF531062, EF531008. *SH393*: EF531059, EF531005. *SH394*: EF531058, EF531004. **OUTGROUP: *Brachytheciastrum velutinum*** (Hedw.) Huttunen & Ignatov – *SH78*: EF531033, EF530965.

Figure captions:

Figure 1. Strict consensus of 887 equally parsimonious trees resulting from the MP analysis of *rpl16* and *atpB-rbcL* in the moss genus *Homalothecium*. Thick branches indicate Bootstrap support above 50.

Figure 2. Variation in leaf margin denticulation in the alar region of branch leaves in *Homalothecium sericeum* s.str. (Sweden. Södermanland, Utö, 15 May 2010, *L.Hedenäs*, S: B175290). Scale: 50 µm.

Figure 3. A-D: *Homalothecium mediterraneum* (Greece. Crete, Chania, *Frahm K-158*, Herb. J.-P.Frahm BONN); E-H: *H. mandonii* (Canary Islands. El Hierro, Riscos de Sabinosa, March 1906, *C.J.Pitard*, S: B185186). A, E: lower exostome seen from the outside – note the exostome borders, visible as semi-translucent marginal portions of each tooth; B, F: branch leaves; C, G: leaf margin in alar region; D, H: median leaf lamina cells. Scales: a: 50 µm (A, E); b: 1 mm (B, F); c: 50 µm (C, D, G, H).

Figure 1

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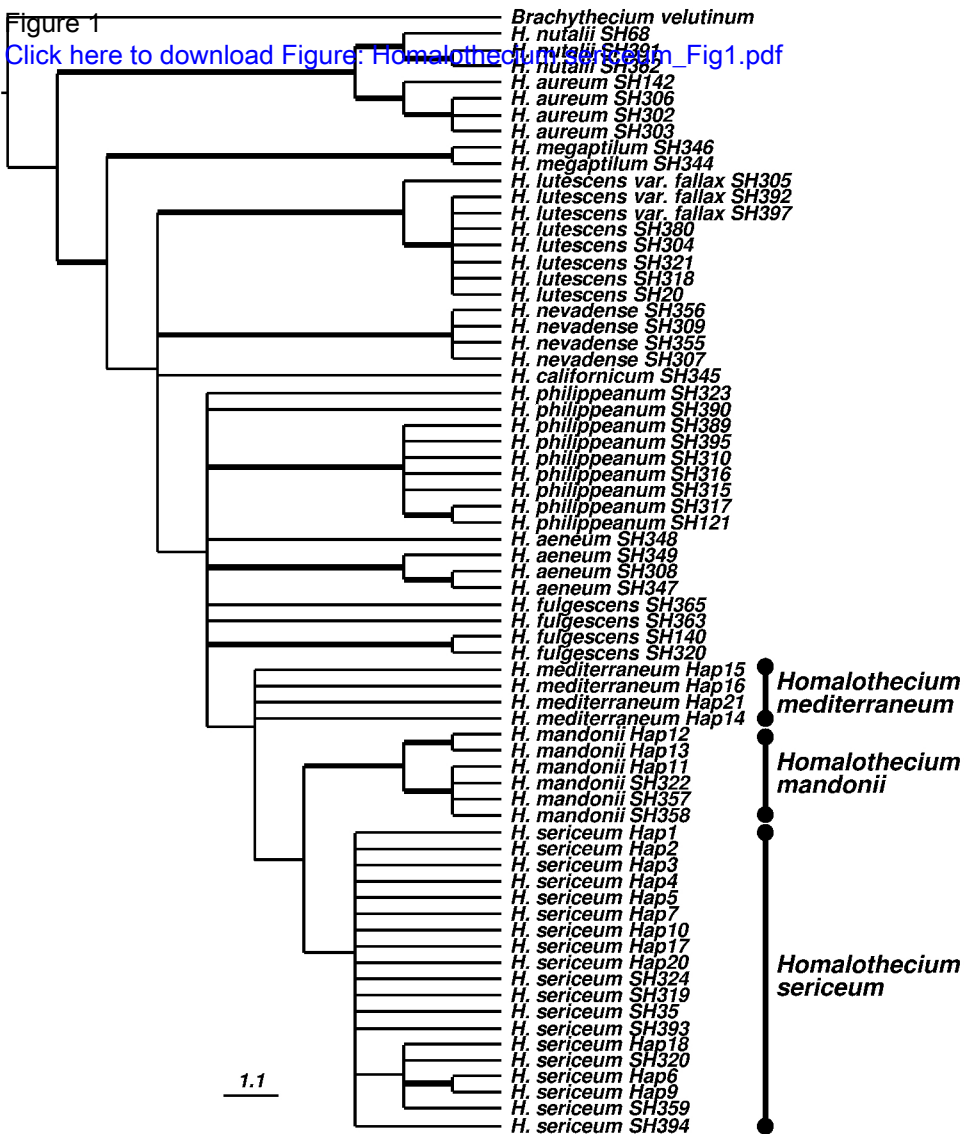


Figure 2

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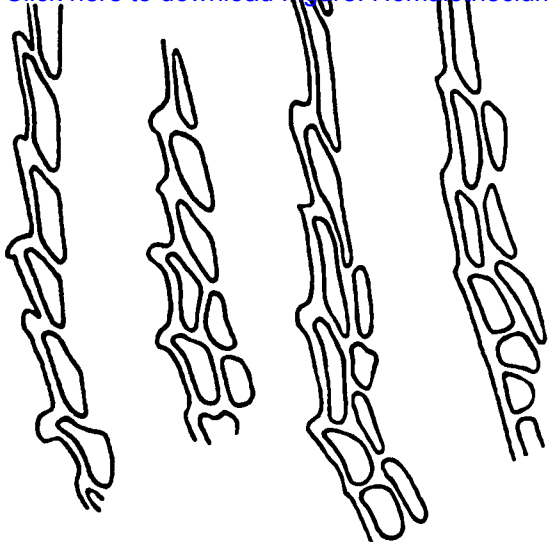


Figure 3

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