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

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

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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>

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

2

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20

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

26 of ‘forgotten’ taxa previously recognized within *H. sericeum* s.l. to one of those three species
27 based on their morphology. While a growing number of ‘cryptic species’ has been mentioned
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31 and *H. mediterraneum* Hedenäs stat. et nom. nov. clearly differ in sporophytic traits but the
32 identification of sterile specimens is challenged by the overlap in gametophytic characters.
33 As a consequence, 8-37% of the specimens were mis-classified in discriminant analyses in an
34 attempt to find the best combination of gametophytic traits to identify specimens that were
35 assigned to one of the three species on the basis of their genotype. This points to the
36 necessity of developing easy-to-use molecular identification tools in taxonomically
37 challenging plant groups, such as bryophytes. *Homalothecium mandonii* is the second case of
38 an endemic Macaronesian bryophyte species whose range encompasses the Cape Verde
39 Islands, the Canary Islands, Madeira, and the Azores. *Homalothecium mediterraneum* is
40 circum-Mediterranean and was reported from one locality in Lanzarote in the Canary Islands,
41 while *H. sericeum* occurs across Europe, eastern North America, and western Asia. The
42 distributions of the segregate species within *H. sericeum* s.l. reinforce the notion that many
43 disjunctions typically observed in moss distribution ranges are due to taxonomic
44 shortcomings and call for the necessity of substantial taxonomic revisions of previously
45 broadly defined bryophyte species.

46

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

49

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

51

52 INTRODUCTION

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

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

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

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

93

94 MATERIAL AND METHODS

95 Specimens representing each haplotype based on *rpl16* and *atpB-rbcL* sequences from all
96 130 accessions of *H. sericeum* s.l. included in Désamoré & al. (2012) were combined with
97 those generated for multiple accessions of each species of the genus by Huttunen & al.
98 (2008). The dataset thus created included 68 accessions in total (Appendix 1).
99 *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen was employed as outgroup.
100 Indels were scored using simple index coding (Simmons & Ochoterena, 2000) as
101 implemented in the plugin SeqState (Müller, 2004) of PhyDE v0.995 (Müller & al., 2006).

102 The data matrix was submitted to a MP analysis using DNAPars as implemented by Seaview
103 4.4.2 (Gouy & al., 2010) with 10 random starts, saving a maximum of 50000 most
104 parsimonious trees and using gaps as informative characters. Support for the branches was
105 assessed through a non-parametric bootstrap analysis with 100 replicates.

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

126 Seven gametophytic traits were scored: leaf length (mm); leaf width (mm); leaf length to
127 width ratio; median leaf lamina cell length (μm); median leaf lamina cell width (μm); median
128 leaf lamina cell length to leaf length ratio; and leaf margin denticulation (finely denticulate,
129 denticulate, strongly denticulate). Initial measurements were made in both stem and branch
130 leaves in three arbitrarily selected specimens of each lineage (*H. mediterraneum*: H69, H78,
131 H86; *H. mandonii*: H28, H29, H30; *H. sericeum* s.str.: H16, H19, H91; specimens cited
132 under Taxonomic treatment). Three stem and branch leaves that had reached their final size
133 were measured, for median lamina cells the total size range was noted, and for all
134 measurements the mid-point (median) values were used in the comparisons (cf. Hedenäs,
135 1996). These characters showed parallel patterns of variation in the two kinds of leaves, and
136 since it was substantially easier to obtain undamaged branch leaves than stem leaves (results
137 not shown), it was decided to use only branch leaves in order to potentially find
138 distinguishing characters among the three lineages. Leaf lamina cell width did not distinguish
139 the lineages based on the initial three specimens per entity due to too great overlap (branch
140 leaf lamina cell width 4.4-6.9 μm in *H. mediterraneum*, 4.2-8.4 in *H. mandonii*, and 4.6-8.4
141 in *H. sericeum* s.str.). This feature was therefore not measured in the remaining material, as it
142 seemed unlikely that it would be a useful character for taxon identification.

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

151 was then employed, using the same program, to identify which is the best combination of
152 morphological variables to identify *H. sericeum*, *H. mandonii*, and *H. mediterraneum*.
153 Variables were selected using backward selection with a probability to stay in the model of p
154 = 0.01. The discriminant functions were employed to assign the types of taxa previously
155 recognized within *H. sericeum* s.l. to one of the three species based on their morphological
156 features. To determine what is the actual error rate when attempting at identifying specimens
157 from morphological characters only, a cross-validation procedure, during which each
158 specimen was successively removed from the matrix, was employed.

159

160 **RESULTS**

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

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

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

182 Two variables, namely the leaf length to width ratio and the median lamina cell to leaf
183 length ratio, were selected in the LDA. On average, 79% of the specimens were assigned to
184 the correct taxa after cross-validation, which corresponds to a correct classification rate of
185 63%, 92%, and 80% in *H. mediterraneum*, *H. mandonii* and *H. sericeum* s.str., respectively.
186 The type specimens of *H. sericeum* var. *meridionale* and *Hypnum mandonii* were assigned to
187 *H. mediterraneum* and *H. mandonii*, respectively, while the types of *Camptothecium*
188 *aureolum* and *H. barbelloides* were assigned to *H. sericeum* s.str..

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

196 Among the three plastid loci (*atpB-rbcL*, *rpl16*, *trnG*) investigated by Désamoré & al.
197 (2012), *rpl16* exhibited three substitutions and one indel (Table 2) within the *H. sericeum*
198 complex, allowing for the unambiguous identification of any specimen that is recent enough
199 for DNA amplification. *TrnG* included one synapomorphic substitution for *H. sericeum* s.l.,

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

202

203 **DISCUSSION**

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

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

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

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

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

249 & al., 2011, 2012; but see Huttunen & al., 2012). Variation in gametophytic traits for
250 taxonomy and species identification might therefore be misleading (Zander & Vitt, 1979;
251 Olsson & al., 2011, 2012; Bell & Hyvönen, 2012; Câmara & Carvalho-Silva, 2013). In the *H.*
252 *sericeum* complex and other moss genera where species differentiation mostly relies on
253 continuous characters (e.g., *Leucobryum*, Vanderpoorten & al., 2003; *Rhynchostegium*,
254 Hutsemékers & al., 2012), specimen identification is challenged by the overlap in characters
255 among species. In the *H. sericeum* complex, this overlap results in a misidentification rate of
256 8-37% when only gametophytic characters are used. Sporophytic traits substantially assist
257 species identification but, as in many of the about 60% of moss species that are dioecious
258 (e.g., Wyatt, 1982; Hedenäs & Bisang, 2011), sporophytes are mostly lacking in the *H.*
259 *sericeum* complex. Although a combination of gametophytic and sporophytic characters
260 allows distinguishing the three species of the *H. sericeum* complex, as summarised in the
261 identification key given below, the present study points to the necessity of developing easy-
262 to-use molecular identification tools. Such molecular identification tools (DNA barcoding
263 markers) will improve biodiversity assessments and ecological research in taxonomically
264 challenging bryophyte groups (e.g., Stech & al., 2013; Lang & Stech, in press). Of the three
265 plastid markers (*atpB-rbcL*, *rpl16*, *trnG*) used in the phylogeographic study of Désamoré &
266 al. (2012), *rpl16* was the only locus that displayed sufficient levels of variation to on its own
267 allow for an unambiguous differentiation between the three species (Table 2). Although
268 *atpB-rbcL* and *trnG* were also partly informative, *rpl16* can best serve as an easy molecular
269 tool for identifying poorly developed and/or sterile *Homalothecium sericeum* s.l. specimens.
270 The locus was similarly shown to exhibit appropriate levels of inter-specific variation in
271 other genera, such as *Plagiomnium* (Wyatt & Odrzykoski, 2012), *Forsstroemia* (Olsson &
272 al., 2012), *Leptodon* (Sotiaux & al., 2009), and *Cratoneuron* (Hedenäs, 2011). *Rpl16* is not
273 among the regions that have been explored as DNA barcoding marker in mosses so far (see

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

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

297

298 **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 x 4.5-8.5 μm , many lamina cells distally and
331 dorsally prorate; median values (three leaves) for leaf width 0.28-0.54 μm , length to width
332 ratio 3.94-5.88, mid-leaf lamina cell length 49.35-82.95 μm , 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 x 15.5-27.5 μm , 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 synonym.* (\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 homomalous, 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 ,

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

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

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

444 Specimens studied (except types; 'D' with number = specimens included in Désamoré &
 445 al. (2012): **Cyprus**. Trodos Mts, at Pano Platres village, 18 September 2001, *B.Papp* (D
 446 H44), BP: 177881; Troodos Gebirge, Pano Platres, *Frahm 200691* (D H31), Herb. J.-
 447 P.Frahm BONN. **Greece**. Crete, Chania, *Frahm K-158* (D H34), Herb. J.-P.Frahm BONN;
 448 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

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

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

518 Known geographical distribution: *Homalothecium mandonii* is a Macaronesian endemic
519 distributed across Cape Verde, all of the Canary Islands, Madeira, and the Azorean islands
520 São Miguel and Santa Maria
521 (<http://www.azoresbiportal.angra.uac.pt/listagens.php?sstr=3&lang=en>; accessed 15 August
522 2013).

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

536

537 *Taxon with uncertain position*538 ***Homalothecium barbelloides* Dixon & Cardot**, J. Bot. 49: 6. 2. 1911.

539 Isotype: (Canary Islands). Teno Mts., Teneriffe, Evergreen woods, Dec. 1909, leg. Dr.

540 Salter; No. 52. Ex herb. H.N.Dixon. Orig. spec. (Herbarium G.Roth. 1842-1915, Herb.

541 H.Möller in S; reg. no. B107660) (Hofmann, 1998).

542

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

544 1. Branch leaves 3.9-5.9 times as long as wide, mostly widest 0-20% way up leaf; margin

545 denticulation at alar region well developed, with at least some teeth distinctly bent

546 outwards (Fig. 2). Exostome distinctly cross-striolate on lower outside.

547

H. sericeum s.str.

548 1. Branch leaves 3.0-4.3 times as long as wide, mostly widest 15-30% way up leaf; margin
 549 denticulation at alar region weak or absent, teeth rarely and only slightly bent outwards
 550 (Fig. 3C, G). Exostome smooth or weakly cross-striolate on lower outside. 2

551 2. Ratio between branch leaf lamina median cell length (μm)/median leaf length (mm)
 552 24.7-48.2. Seta frequently partly or entirely smooth; exostome border broad (Fig. 3A).

553 *H. mediterraneum*

554 2. Ratio between branch leaf lamina median cell length (μm)/median leaf length (mm)
 555 44.9-59.6. Seta rough throughout; exostome border narrow (Fig. 3E).

556 *H. mandonii*

557

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562

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

						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 Désamoré & 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*: Désamoré & al. (2012). *SH322*: EF531063, EF531009. *SH357*: EF531064, EF531010. *SH358*: EF531065, EF531011. ***Homalothecium mediterraneum*** Hedenäs - *Hap14*, *Hap15*, *Hap16*, *Hap21*: Désamoré & 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*: Désamoré & 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 μ m.

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 μ m (A, E); b: 1 mm (B, F); c: 50 μ m (C, D, G, H).

Figure 1

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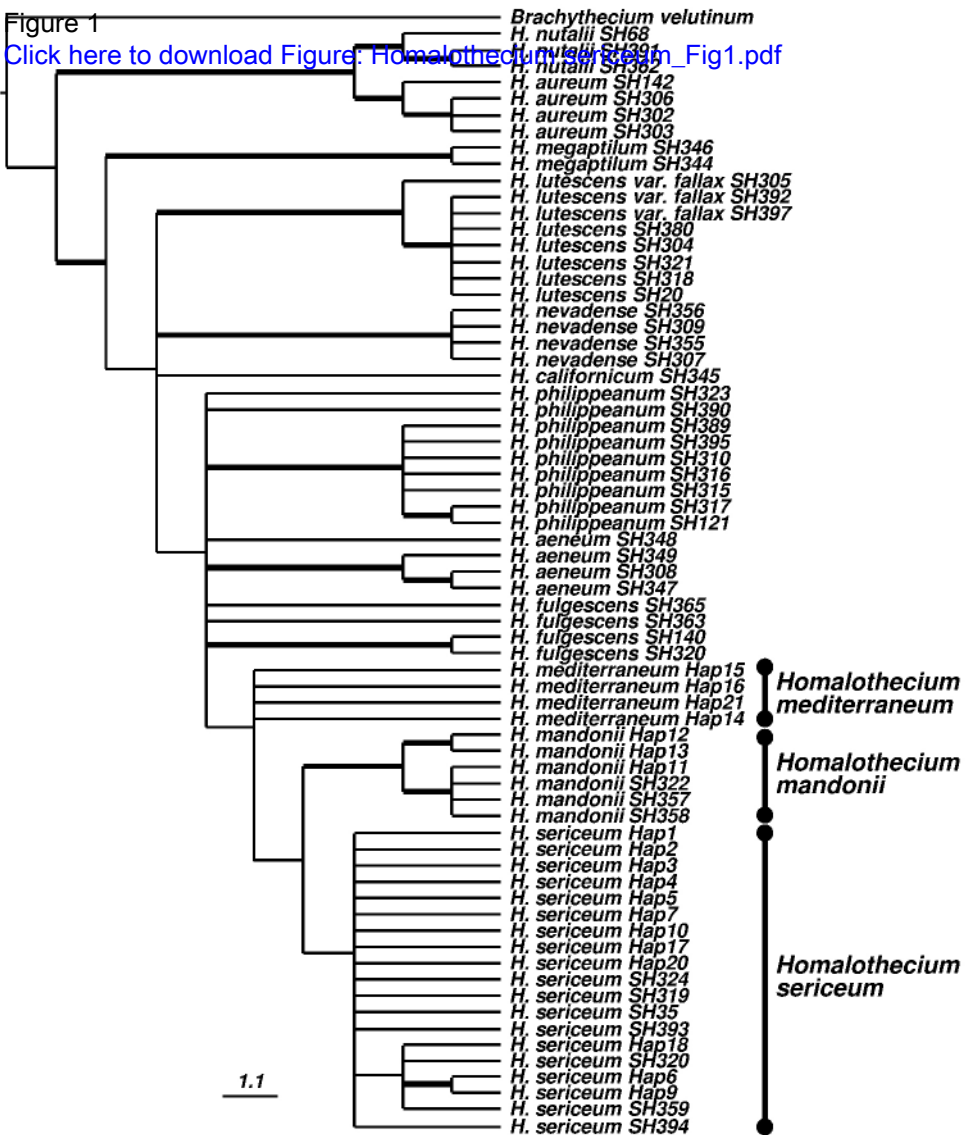


Figure 2

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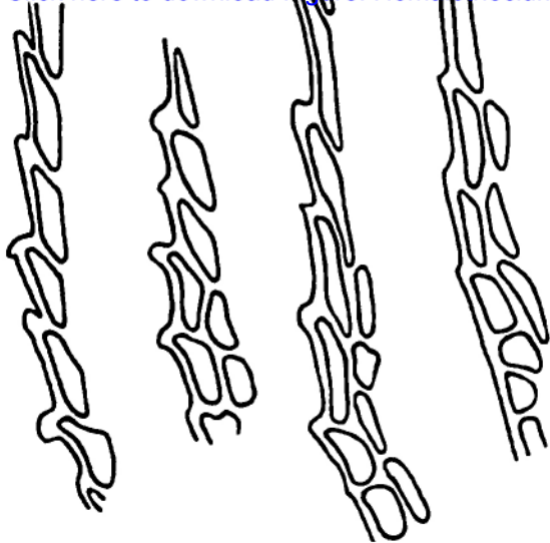


Figure 3

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