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

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Lars Hedenäs,[1] Aurélie Désamoré,[2] Benjamin Laenen,[2] Beata Papp,[3] Dietmar Quandt,[4] Juana Maria González-Mancebo,[5] Jairo Patiño,[2,5] Alain Vanderpoorten[2]* & Michael Stech[6]*

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

2 *Institute of Botany, University of Liège, B22 Sart Tilman, 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, P.O. 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 in a polytomy. Because the clades and the four haplotypes as one group 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 those three species based on their morphology. While a growing number of "cryptic species" has been reported 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. meridionale* (M.Fleisch. & Warnst) Hedenäs comb. & stat. 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. The three species differ in *rpl16*, a region that distinguishes species also in other moss genera and should be further explored as a candidate for DNA barcoding marker among mosses. *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 meridionale* 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 need of substantial taxonomic revisions of previously broadly defined bryophyte species.

Keywords bryophytes; cryptic species; discriminant analysis; DNA barcoding; Europe; Macaronesia; Mediterranean

Supplementary Material Electronic Supplement (Appendix S1: Full descriptions and lists of specimens studied morphologically for the three species of the *Homalothecium sericeum* complex) and alignment are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ 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 (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 reported 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 based only 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 reanalyze 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 at 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. meridionale*.

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.

■ MATERIALS 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 final dataset 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 v.0.995 (Müller & al., 2006). The data matrix was submitted to a MP analysis using DNApars as implemented by Seaview v.4.4.2 (Gouy & al., 2010) with 10 random starts, saving a maximum of 50,000 most parsimonious trees and using gaps as informative characters. Support for branches was assessed by Seaview v.4.4.2 (Gouy & al., 2010) through a non-parametric bootstrap analysis with 100 replicates.

Fourty-three out of the 130 specimens of *Homalothecium sericeum* s.l. included by Désamoré & al. (2012) were sampled to represent the morphological variation and distribution range of *H. meridionale* (11 accessions), *H. mandonii* (12 accessions), and *H. sericeum* s.str. (20 accessions) (Electr. Suppl.: Appendix S1). 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 *H. sericeum* s.str. occurs. As a dioicous species, *H. sericeum* s.l. is infrequently found with sporophytes and only three specimens included in Désamoré & 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. meridionale*, five *H. mandonii*, and one *H. sericeum* s.str. Sporophytes were only studied in one additional specimen of the last species since their character states were already largely studied in previous studies (Hedenäs, 2001, 2012). All morphologically studied specimens are cited in Appendix S1 (Electr. Suppl.).

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. meridionale*: H69, H78, H86; *H. mandonii*: H28, H29, H30; *H. sericeum* s.str.: H16, H19, H91; see Electr. Suppl.: Appendix S1). 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 (results not shown), and since it was substantially easier to obtain undamaged branch leaves than stem leaves, 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. meridionale*, 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 leaf 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. meridionale* 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 v.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. meridionale*. 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 the three species based on their morphological features. To determine the error rate when attempting to identify specimens from morphological characters only, a cross-validation procedure, during which each specimen was successively removed from the matrix, was employed.

■ RESULTS

The molecular data matrix included 1273 characters, of which 94 (22 indels) were parsimonyinformative. 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. meridionale* as well as a clade containing the accessions of reciprocally monophyletic *H. mandonii* and *H. sericeum* s.str. were recovered. Most branches did not receive bootstrap support ≥50%.

Among the three plastid loci (*atpB-rbcL*, *rpl16*, *trnG*) investigated by Désamoré & al. (2012), *rpl16* exhibited three substitutions and one indel (Table 1) 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*.
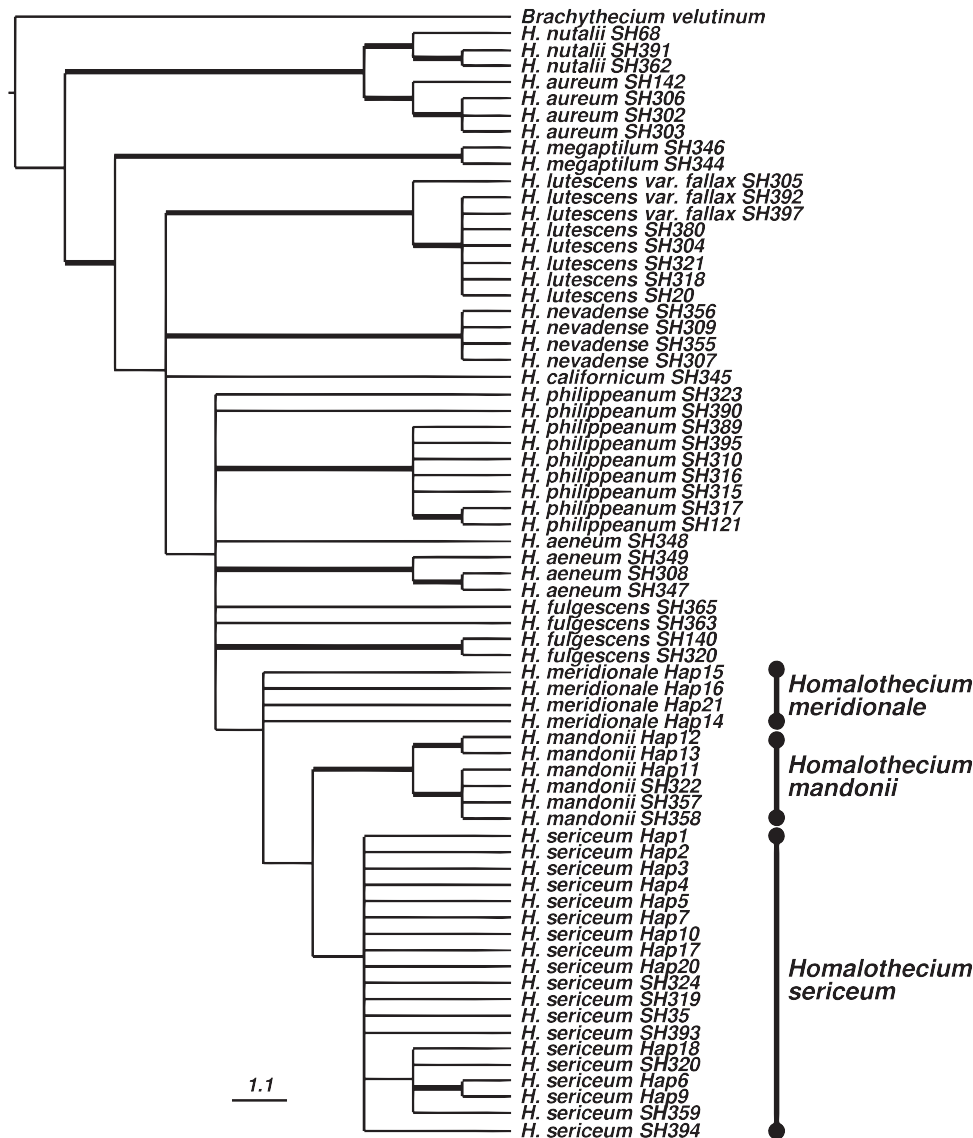

Fig. 1. Strict consensus of 887 equally parsimonious trees resulting from the MP analysis of *rpl16* and *atpB-rbcL* in *Homalothecium*. Thick branches indicate bootstrap support ≥50%.

Branch leaf length (*H. meridionale*, mean ± 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 2) 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 polytomy of *H. meridionale* according to Fisher's LSD test (Table 2). In *H. mandonii*, the lamina cells were significantly longer and the lamina cell length to leaf length ratio was significantly higher than in *H. meridionale* and *H. sericeum* s.str. (Table 2). 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

Table 1. Species-specific polymorphisms in the *rpl16* gene among *Homalothecium mandonii, H. sericeum,* and *H. meridionale.*

Position	594	703	619	832
H. mandonii	C	Poly-A (8 repeats)	T	A
H. sericeum	T	Poly-A (9 repeats)	C	G
H. meridionale	T	Poly-A (9 repeats)	T	A
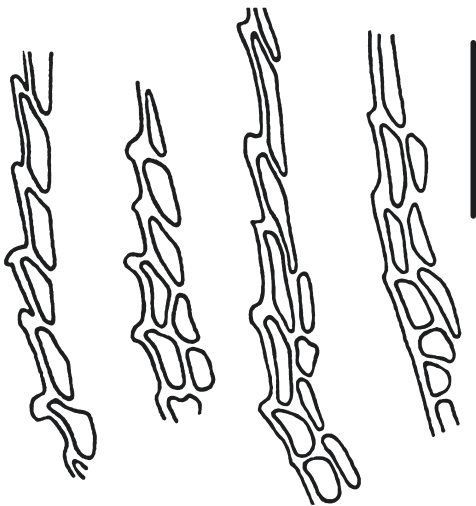
Fig. 2. Variation in leaf margin denticulation in the alar region of branch leaves in *Homalothecium sericeum* s.str. (Sweden. Södermanland, Utö, 15 May 2010, *L. Hedenäs,* S B175290). — Scale bar: 50 µm.

Table 2. Branch leaf and sporophyte characters that differentiate the three *Homalothecium sericeum* s.l. species.

	1. Leaf width [mm]	2. Leaf length to width ratio	3. Median lamina cell length [µm]	4. Median lamina cell length [µm] to leaf length [mm] ratio	5. Leaf widest at	6. Alar leaf margin denticulation	7. Seta ornamentation	8. Lower exostome outside	9. Exostome border
H. meridionale	(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 outwards	Rough, smooth in upper 1/4, or occasionally completely smooth	Smooth or weakly cross-striolate	Broad (Fig. 3A)
H. mandonii	(0.37) 0.49±0.01 (0.61)	(2.96) 3.29±0.06 (3.60)	**(65.10) 88.26±3.64** (103.95)	**(44.93) 55.05±1.27** (59.64)	15%–25% above leaf base	Weak, sometimes a few stronger teeth, rarely bent outwards	Rough throughout	Smooth or weakly cross-striolate	Narrow (Fig. 3E)
H. sericeum	**(0.28) 0.38±0.01** (0.54)	**(3.94) 4.61±0.10** (5.88)	(49.35) 65.31±2.12 (82.95)	(29.70) 37.92±1.02 (45.64)	0%–20% above leaf base	Mostly strong, occasionally dentate, often some teeth bent outwards	Rough throughout	Cross-striolate	Narrow
C. aureolum	0.22	4.62	52.50	51.55	–	–	–	–	–
H. sericeum var. *meridionale*	0.50	3.23	71.40	43.87	–	–	–	–	–
H. mandonii	0.48	3.06	95.55	64.54	–	–	–	–	–
H. barbelloides	0.20	5.63	79.80	69.09	–	–	–	–	–

Columns 1–4: Average and standard deviation of the median (mid-point) values of measured characters in *H. meridionale* (*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 differ in one species indicate a significant difference (*P* < 0.05) from those observed in the two other species according to Fisher's LSD test.
Columns 5–9: Other branch leaf and sporophyte characters that differentiate the three *Homalothecium* species.

width (Table 2). *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 leaf length to width ratio and median lamina cell length 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% for *H. meridionale*, *H. mandonii* and *H. sericeum* s.str., respectively. The type specimens of *H. sericeum* var. *meridionale* and *Hypnum mandonii* were assigned to *H. meridionale* 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. meridionale*. The outer exostome ornamentation was clearly cross-striolate in *H. sericeum* s.str., but smooth or only weakly cross-striolate in *H. meridionale* and *H. mandonii*. Finally, the exostome border in the lower portion of the teeth was broad in *H. meridionale* but narrow in the two clades (Fig. 3A, E).

■ 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.

Even if variation in *rpl16* and *atpB-rbcL* was sufficient to discriminate all *Homalothecium* species recognized to date, the four haplotypes labelled as *H. meridionale* 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. meridionale* and *H. mandonii*, respectively, which are therefore formally recognized below as *H. meridionale* (M.Fleisch & Warnst.) Hedenäs comb. & stat. nov. (see Taxonomic treatment) and *H. mandonii* (Mitt.) Geh.

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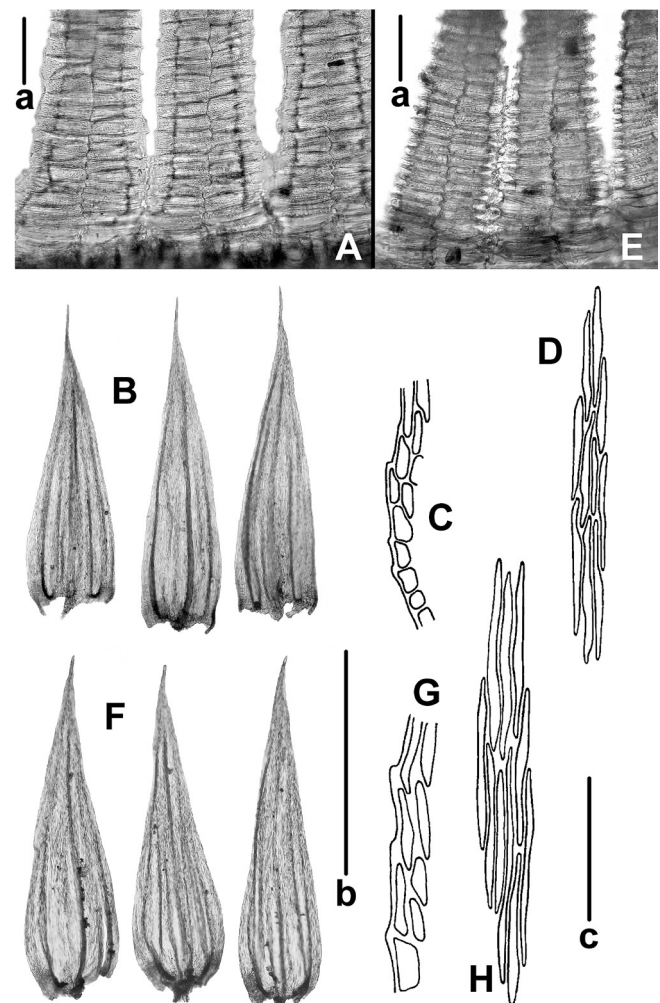
Fig. 3. A–D, *Homalothecium meridionale* (Greece. Crete, Chania, *Frahm K-158*, Herb. J.-P. Frahm BONN); **E–H,** *H. mandonii* (Canary Islands. El Hierro, Riscos de Sabinosa, March 1906, *C.J. Pitard*, S: B185186). **A, E,** lower exostome seen from the outside—note the exostome borders, visible as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

material is available, and the molecular identity could therefore not be determined.

Gametophytic traits significantly differ among *H. mandonii*, *H. meridionale* and *H. sericeum* s.str., but show substantial overlap (Table 2). 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* Hampe, Vanderpoorten & al., 2003; *Rhynchostegium* Bruch & Schimp., 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 had sufficient levels of variation to allow for an unambiguous differentiation among the three species (Table 1). 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 have appropriate levels of inter-specific variation in other genera, such as *Plagiomnium* T.J.Kop. (Wyatt & Odrzykoski, 2012), *Forsstroemia* Lindb. (Olsson & al., 2012), *Leptodon* D.Mohr (Sotiaux & al., 2009), and *Cratoneuron* (Sull.) Spruce (Hedenäs, 2011). *rpl16* is not among the regions that have been explored as DNA barcoding markers 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 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 have 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 & al., raising the question of why such vagile organisms failed to reach the North African and south-western European coasts. *Homalothecium meridionale* 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 north to 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

Homalothecium sericeum (Hedw.) Schimp. in Bruch & al., Bryol. Europ. 5: 93. 456 (fasc. 46–47 Mon. 3. 1). 1851 ≡ *Leskea sericea* Hedw., Sp. Musc. Frond.: 228. 1801 ≡ *Isothecium sericeum* (Hedw.) Spruce, Musci Pyrenaicae: 76. 1847 ≡ *Camptothecium sericeum* (Hedw.) Kindb. in Canad. Rec. Sci. 6(2): 73. 1894 ≡ *Pleuropus sericeus* (Hedw.) Dixon, Stud. Handb. Brit. Mosses: 395. 1896 ≡ *Burnettia sericea* (Hedw.) Grout in Bryologist 7: 31. 1904 – Lectotype (vide Hofmann in Lindbergia 23: 139. 1998): "*Leskea sericea* Hedw. St. Cr. V. 4 p. 43 t. 17. *Hypnum sericeum* Linn.*"* (G [Herb. Hedwig-Schwaegrichen]!).

= *Camptothecium aureolum* Kindb. in Rev. Bryol. 22: 85. 1895 – Lectotype (vide Hofmann in Lindbergia 23: 139. 1998): [NORWAY. Sör-Tröndelag] Norwegen, Opdal, 22 Feb 1880, *C. Kaurin* (S No. B17069 [Herb. N.C. Kindberg 19]!).

Plants with branches curved upwards-inwards when dry. *Stem leaves* from ovate-triangular, triangular or narrowly triangular base gradually narrowed to longly acuminate apex, not or slightly narrowed towards insertion; margin around upper alar region mostly distinctly denticulate to dentate, denticles or teeth often spreading or recurved; median leaf lamina cells 36.0–130.0 × 4.0–8.5 μm. *Branch leaves* widest 0%–20% way up, median leaf lamina cells 19.01–19.5 × 4.5–8.5 μm; median values (three adjacent leaves on well developed branch) for leaf width 0.28–0.54 μm, length to width ratio 3.94–5.88, mid-leaf lamina cell length 49.35–82.95 μm, lamina cell length (μm) to leaf length (mm) ratio 29.70–45.64. *Seta* 9–17 mm long, rough throughout. *Exostome* teeth red or pale reddish, lower outside cross-striolate, border in lower portion of teeth narrow.

Geographical distribution. – *Homalothecium sericeum* occurs across extra-Mediterranean Europe, eastern North America, western Asia eastwards to the Himalayas and in

Newfoundland (Hofmann, 1998). Earlier reports from China could not be substantiated (Wang & Hu, 2008).

Homalothecium meridionale (M.Fleisch & Warnst.) Hedenäs, **comb. & stat. nov.** ≡ *Homalothecium sericeum* var. *meridionale* M.Fleisch. & Warnst. in Bot. Centralbl. 72: 395. 1897 – Lectotype (vide Hofmann in Lindbergia 23: 139. 1998): [ITALY]. Sicilia: Mola bei Taormina an Kalkfelsen, 600 m, 6 Apr 1897, *M. Fleischer s.n.* (FH; isolectotype: S No. B185199!).
= *Homalothecium sericeum* var. *tunetanum* Besch. in Patouillard, Cat. Pl. Cell. Tunisie, Mousses: 11. 1897 – Lectotype (vide Hofmann in Lindbergia 23: 139. 1998): [TUNISIA]. Tunisie, Enfida–Zaktoun, 26 Jan [18]86, *A. Letournes s.n.* [?] (PC [Herb. Camus]).

Homalothecium meridionale Ravaud was published as a nomen nudum under *H. sericeum* var. *robustum* B.de Lesd. (Bouly de Lesdain, 1910). Since *H. meridionale* Ravaud is an invalid name it does not block the publication of the new combination *Homalothecium meridionale*, based on *H. sericeum* var. *meridionale* M.Fleisch. & Warnst.

Plants with branches curved upwards-inwards when dry. *Stem leaves* from cordate-triangular or rounded-triangular base gradually narrowed to longly acuminate apex, markedly narrowed towards insertion; margin denticles around upper alar region weak or absent, rarely bent slightly outwards; median leaf lamina cells 29.5–92.5 × 4.0–7.5 μm. *Branch leaves* widest 15%–30% way up, median leaf lamina cells 25.0–115.5 × 4.5–7.0 μm; median values (three adjacent leaves on well developed branch) for leaf width 0.34–0.56 μm, length to width ratio 3.03–4.26, mid-leaf lamina cell length 46.20–81.90 μm, lamina cell length (μm) to leaf length (mm) ratio 24.75–48.21. *Seta* 8–15 mm long, rough almost throughout or above weakly so or smooth, occasionally smooth almost throughout. *Exostome* teeth yellow-brown or pale yellow-brown, lower outside indistinctly cross-striolate to smooth, border in lower portion of teeth broad. (Fig. 3A–D)

According to Hofmann (1998), *H. sericeum* var. *meridionale* (*H. meridionale*) and *H. sericeum* var. *tunetanum* 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. meridionale* from the other two species recognized here (Table 2), *Homalothecium sericeum* var. *tunetanum* is considered as a synonym of *H. meridionale*.

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

Homalothecium mandonii (Mitt.) Geh. in Flora 69: 348. 1886 ≡ *Hypnum mandonii* Mitt. in Godman, Nat. Hist. Azores: 311. 1870 ≡ *Homalothecium sericeum* var. *mandonii* (Mitt.) Renauld & Cardot in Bull. Herb. Boissier, sér. 2, 2: 438. 1902 – Lectotype (vide Hofmann in Lindbergia 23: 139. 1998): [PORTUGAL. Madeira] Mandon: Mousses de Madère no. 36. *Homalothecium sericeum* Sch. Rib. das Cales, Marz, No. 36 (NY [Herb. Mitten]; isolectotypes: S Nos. B8823! & B88241!).

– "*Homalothecium sericeum* var. *meridionale*" Schimp. in Flora 69: 349. 1886, nom. nud. (Geheeb, 1886).

Plants with branches straight or curved upwards-inwards when dry. *Stem leaves* triangular or ovate-triangular, from shortly above insertion gradually narrowed to acuminate apex, distinctly constricted at insertion; margin around upper alar region finely denticulate or sometimes with a few stronger denticles, rarely bent slightly outwards; median leaf lamina cells 46.0–178.5 × 4.0–8.0 μm. *Branch leaves* widest 15%–25% way up, median leaf lamina cells 33.51–47.0 × 4.0–8.5 μm; median values (three adjacent leaves on well developed branch) for leaf width 0.37–0.61 μm, length to width ratio 2.96–3.60, mid-leaf lamina cell length 65.10–103.95 μm, lamina cell length (μm) to leaf length (mm) ratio 44.93–59.64. *Seta* 11–22 mm long, rough throughout. *Exostome* teeth light orange-brown, lower outside weakly cross-striolate to smooth, border absent, or present, narrow. (Fig. 3E–H)

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*.

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.azoresbioportal.angra.uac.pt/listagens.php?sstr=3&lang=en; accessed 15 Aug 2013).

Taxon with uncertain position

Homalothecium barbelloides Dixon & Cardot in J. Bot. 49: 6. 2. 1911 – Holotype: [SPAIN. Canary Islands], evergreen woods, Cumbre de Votico, Teno Mountains, Teneriffe, Dec 1909, *Dr. Salter s.n.* (BM [Herb. H.N. Dixon No. 52]; isotype: S No. B107660!).

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% above leaf base; 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% above leaf base; 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) 24.8–48.2. Seta frequently partly or entirely smooth; exostome border broad (Fig. 3A) …… ……………………………………………***H. meridionale***
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***

■ ACKNOWLEDGEMENTS

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Appendix 1. Haplotypes of Désamoré & al. (2012; *Hap* numbers) and voucher numbers (*SH*) and GenBank numbers (*rpl16*, *atpB-rbcL*) of Huttunen & al. (2008), respectively, for the phylogenetic analysis of *Homalothecium*.

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 meridionale* (M.Fleisch & Warnst.) 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.