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Disentangling Scandinavian species hidden within *Meesia uliginosa* Hedw. s.l. (Bryophyta, Meesiaceae)

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The molecular variation (*atpB-rbcL* spacer, *rpl16* G2 intron, *trnG_{UCC}* G2 intron) among 50 Scandinavian specimens of *Meesia uliginosa* s.l. was analysed in the context of three other *Meesia* species, with *Paludella squarrosa* as outgroup. The molecular variation within *M. uliginosa* correlates with morphology, and shows that three species exist: *M. uliginosa* Hedw., *M. minor* Brid. and *M. minutissima* Hedenäs sp. nov. Whereas *M. uliginosa* s.str. is widespread, in Scandinavia the other two species are restricted to the mountains. The three species differ in quantitative features, such as, plant size, leaf size, costa width, leaf apex shape, seta length and spore capsule size. Because the species overlap in several of these features, a combination of seta length and the ornamentation of the exostome outside are the safest characters for identification. Leaf apex shape, small spore capsules in *M. minutissima* and large spores in *M. minor* serve as additional identification help. *Meesia minutissima* is presently only known from Scandinavia. The other two species are more widespread, although further investigations are required to find out their exact distributions.

Keywords: integrative taxonomy, *Meesia minutissima* Hedenäs sp. nov., morphology, mountains, principal component analysis

Despite more than 200 years of investigations, scientists and gifted amateurs frequently discover bryophyte species new to Europe. Disregarding introductions by man, this includes species found for the first time in Europe and species new to science. Based on recent publications on new species, Mediterranean and oceanic regions (Gallego et al. 2000, Muñoz et al. 2009, Cezón et al. 2010, Bosanquet and Lara 2012, Hedenäs et al. 2014) and the European mountains and far north (Köckinger and Kučera 2007, 2016, Draper and Hedenäs 2009, Köckinger et al. 2012, Hedenäs 2018) are likely the areas that harbour most unrecognized species. During many years of fieldwork in northern and mountainous Scandinavia, I have come across several species which variation suggests that they may actually consist of more than one species. In connection with a study of northern and mountain intraspecific genetic variants within widespread species (Hedenäs 2019), it became evident that the genetic variation within *Meesia uliginosa* Hedw. correlates with morphological differentiation and deserves further study.

Within the Meesiaceae, seven of the thirteen recognized species belong to *Meesia*, and the remaining ones are distributed

among four small genera (Frey and Stech 2009). *Meesia* occurs predominantly in temperate to Arctic and Antarctic regions (Frey and Stech 2009), and four of the species are circum-Arctic (Frey et al. 2006, Ignatov et al. 2006, Favreau and Brassard 2011): *M. hexasticha* (Funck) Bruch, *M. longiseta* Hedw., *M. triquetra* (L. ex Jolycl.) Ångstr. and *M. uliginosa*. Some recognized species of *Meesia* are morphologically variable or intermediate between other species, which has been suggested to be a result of hybridisation, such as *M. hexasticha*, possibly a hybrid between *M. uliginosa* and *M. triquetra* (Nyholm 1998), and *M. longiseta* × *triquetra* Lindb. & Arnell (Lindberg and Arnell 1890). Variability of a different nature was found within *M. triquetra*, where Montagnes and Vitt (1991) showed that there exist latitudinal and ecoclimatic gradients in morphology in North America, and discussed if environmental or genetic variation could explain these differences. For European *M. uliginosa*, early authors thought that small phenotypes found in mountain areas represent distinct species (Bridel 1803, Bruch 1826, Bridel-Brideri 1827). Also in Scandinavia, such small mountain phenotypes of *M. uliginosa* were noted early, for example by Hartman (1832) and Ångström (1844), but although such phenotypes are still noted in modern Scandinavian floras, their taxonomic status has not yet been clarified (Nyholm 1958, 1998, Hallingbäck et al. 2008).

Meesia uliginosa s.l. occurs almost throughout Scandinavia (Sweden's Virtual Herbarium: <<http://herbarium.emg.umu.se/index.html>>; Norwegian Biodiversity Information

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Centre: <www.biodiversity.no/>, accessed 27 June 2019), but is rare or has vanished from many southern areas. The species, in its wide sense, is extremely variable in size as well as in some other characters. In the lowlands it typically grows in rich fens, the plants are large, up to ca 30 mm tall, the leaves have rounded apices, and the seta may be up to 70 mm tall. In exposed habitats in the mountains, it may in addition grow on base-rich, bare, peaty soil or often in rock crevices, and many plants are considerably smaller. Mountain plants vary in shoot length between 2 and 30 mm, in leaf apex shape from acuminate to rounded, and in seta length between 4 and 70 mm. In a recent study where Swedish *M. uliginosa* was included, three molecular lineages were revealed (Hedenäs 2019). Here, the wide morphological variation in *M. uliginosa* is evaluated in detail in the light of these molecular results, to understand whether it is primarily due to phenotypic plasticity or if more than one species could be involved.

Material and methods

Studied material

For the molecular evaluation, 50 Swedish specimens of *Meesia uliginosa* s.l., were studied. The sampling represents different areas and environments where it occurs in Sweden, and covers its known morphological variation. The sequences for *M. uliginosa* were available from Hedenäs (2019); new sequences were generated for two specimens of each of the species *M. hexasticha*, *M. longiseta* and *M. triquetra*, to assess the position of *M. uliginosa* s.l. within the genus, and for *Paludella squarrosa* (Hedw.) Brid., another member of the Meesiaceae, which was used as outgroup (cf. Goffinet et al. 2001, 2004). The molecularly studied specimens are listed in Table 1.

The morphological analysis was based on ten specimens representing each of the three molecular entities that were revealed within *M. uliginosa* s.l. (Table 1).

Molecular methods

The molecular part of this study is based on the plastid *atpB-rbcL* spacer (*atpB-rbcL*), *rpl16* G2 intron (*rpl16*) and *trnG_{UCC}* G2 intron (*trnG*). The methods used to generate the new sequences included here are described in Hedenäs (2019).

Sequence editing and analysis

Nucleotide sequence fragments were edited and assembled for each DNA region using PhyDE 0.9971 (<www.phyde.de/index.html>, accessed 22 November 2018). The assembled sequences were aligned manually in PhyDE. Regions of partially incomplete data in the beginning and end of the sequences were identified and were excluded from subsequent analyses. Gaps were coded in SeqStat (Müller 2005), using the simple indel coding method of Simmons and Ochoterena (2000), and since they provided additional evidence to distinguish haplotypes they were included in the analyses. The sequence alignments used in the analyses are

available on request. GenBank accession numbers are listed in Table 1.

Reticulation was revealed in a preliminary analysis using TCS (Clement et al. 2000; results not shown), and relationships were therefore evaluated in a network context using NeighborNet (NN) split networks produced in SplitsTree 4.12.6 (Huson and Bryant 2006). Potential support for lineages in a tree context was tested by Jackknife analyses (1000 replications) performed with the program TNT (Goloboff et al. 2003).

Morphological study and analysis of measurements

After the molecular relationships among the studied *M. uliginosa* s.l. specimens had been clarified, the morphology of ten selected specimens from each of the three distinguished entities was studied. For one of the entities, four specimens were included in the molecular sample, but since seta length in combination with exostome ornamentation unambiguously distinguish this entity, another six specimens could be added for the detailed morphological comparisons. Recent treatments based only on morphology (Nyholm 1958, 1998, Hallingbäck et al. 2008) had failed to distinguish well-circumscribed entities within *M. uliginosa* s.l. Therefore, both standard comparisons of qualitative and quantitative characters and detailed measurements of selected gametophyte and sporophyte features were performed, employing dissecting and compound microscopes.

Specimens for which selected gametophyte and sporophyte features were measured in detail are indicated with an asterisk (*) in Table 1. For each of these specimens, three vegetative leaves were sampled from two shoots (two leaves from one stem and one from the other, to avoid sampling all leaves from an untypical shoot for the specimen). In each leaf, the following features were measured or scored. (a) Length and maximal leaf width (mm), (b) costa width near base and 2/3 way up leaf (μm), (c) length (μm), width (μm) and length to width ratio of 20 cells in the middle portion of the upper lamina, and (d) leaf apex shape, scored as acuminate ($<45^\circ = 1$), acute ($45\text{--}90^\circ = 2$), obtuse ($> 90^\circ$ but still distinctly 'pointed' = 3) or rounded (4). When mature sporophytes were present, (a) length of the capsule neck (mm), (b) length and width of the urn (mm), (c) length (μm), width (μm) and length to width ratio of 20 exothecial cells in the dorsal portion of one arbitrarily selected urn and (d) spore diameters (μm) were measured. Other than for the numbers of exothecial cells in one capsule per specimen with mature sporophytes, the number of sporophyte measurements depended on the number of available sporophytes in good condition. Temporary images of leaves and cells were taken through a microscope using a digital camera and the Olympus cellSens Standard 1.13 software for automatic and continuous image stacking. Measurements were taken from these leaf and cell images, using the Olympus cellSens Standard 1.13 software.

Comparisons of the detailed measurements among the three entities within *M. uliginosa* s.l. are based on two approaches. First, measurements were compared between the entities. Potential influence of leaf size on lamina cell size was evaluated by adjusting cell sizes to a standard leaf length of 1.5 mm and a width of 0.3 mm, by dividing the actual

Table 1. (A) Specimen data and GenBank accession numbers for the sequences; accession numbers of newly generated sequences begin with MN. All specimens are in herbarium S, and except where noted their geographical origin is Sweden. (B) Swedish *Meesia minutissima* specimens identified by morphology and that were included in the detailed morphological study. * = leaf and selected sporophyte characters were measured in the detailed morphological study; LH=L.Hedenäs; NA=Sequence not available.

| Sample no.: Locality; Coll. year, Collector [collector's no.]; S herbarium registration no. | <i>atpB-rbcL</i> | <i>rpl16</i> | <i>trnG</i> |
|--|------------------|--------------|-------------|
| (A) | | | |
| <i>Meesia hexasticha</i> (Funck) Bruch | | | |
| D1499: Norway. Svalbard, Nordenskiöld land, Longyearbyen; 2007; T.Hallingbäck 44991; B123285 | MN419149 | MN419115 | MN419123 |
| D1500: Pite lappmark, Arjeplog, Mt Stuur-Jiervas; 2017, LH et al.; B259627 | NA | MN419116 | MN419124 |
| <i>Meesia longisetata</i> Hedw. | | | |
| D1501: Torne Lappmark, Jukkasjärvi, Lake Kaivosjärvi; 2002, LH; B74371 | MN419150 | MN419117 | MN419125 |
| D1502: Åsele lappmark, Vilhelmina, Lagmyran; 2016, N.Lönnell NL4079; B242755 | MN419151 | MN419118 | MN419126 |
| <i>Meesia minor</i> Brid. | | | |
| D1223*: Härjedalen, Storsjö, Mt Stor-Axhögen; 2007, LH; B122249 | MK467212 | MK466481 | MK466916 |
| D1227*: Lycksele lappmark, Tärna, Mt Raavriedenjuenie; 2016, LH; B237647 | MK467216 | MK466485 | MK466920 |
| D1231*: Pite Lappmark, Arjeplog, Mt Ribmotjåkkå; 2006, LH et al.; B114016 | MK467220 | MK466489 | MK466924 |
| D1335*: Jämtland, Frostviken, Mt Gervenåkkö; 1989, LH; B31485 | MK467230 | MK466499 | MK466934 |
| D1339*: Jämtland, Frostviken, Mt Brakkfjället; 2009, LH; B163273 | MK467234 | MK466503 | MK466938 |
| D1343*: Lule Lappmark, Jokkmokk, Sjnjerak; 1981, LH; B31481 | MK467238 | MK466507 | MK466942 |
| D1346*: Lule lappmark, Kåbrek; 2005, T.Hallingbäck 43235; B182781 | MK467241 | MK466510 | MK466945 |
| D1347: Lycksele Lappmark, Tärna, Gieravardo; 2012, LH et al.; B195151 | MK467242 | MK466511 | MK466946 |
| D1348*: Lycksele Lappmark, Tärna, Mt Atofjället; 2012, LH et al.; B195246 | MK467243 | MK466512 | MK466947 |
| D1356: Pite Lappmark, Arjeplog, Mt Ákháris; 2015, LH et al.; B223720 | MK467251 | MK466520 | MK466955 |
| D1359*: Torne Lappmark, Jukkasjärvi, Njulla; 1990, LH; B31472 | MK467254 | MK466523 | MK466958 |
| D1360*: Torne Lappmark, Jukkasjärvi, Njulla; 1990, LH; B31473 | MK467255 | MK466524 | MK466959 |
| D1441: Torne Lappmark, Jukkasjärvi, Viitátloapmi; 2017, LH; B254802 | MK467258 | MK466527 | MK466962 |
| <i>Meesia minutissima</i> Hedenäs | | | |
| D1331*: Härjedalen, Storsjö, Mt Stor-Axhögen; 2007, LH; B122912 | MK467226 | MK466495 | MK466930 |
| D1357*: Pite Lappmark, Arjeplog, Mt Lulep Guhkavárddo; 2015, LH et al.; B226808 | MK467252 | MK466521 | MK466956 |
| D1442*: Torne Lappmark, Jukkasjärvi, Vässečohka; 2017, LH; B254964 | MK467259 | MK466528 | MK466963 |
| D1443*: Torne Lappmark, Jukkasjärvi, E Kratersjön; 2017, LH; B256654 | MK467260 | MK466529 | MK466964 |
| <i>Meesia triquetra</i> (L. ex Jolycl.) Ångstr. | | | |
| D1497: Pite Lappmark, Arjeplog, N of Mávasjávrrre; 2015, LH et al.; B228147 | MN419147 | MN419113 | MN419121 |
| D1498: Lycksele Lappmark, Tärna, Mt Atofjället; 2012, LH et al.; B195295 | MN419148 | MN419114 | MN419122 |
| <i>Meesia uliginosa</i> Hedw. | | | |
| D1222*: Härjedalen, Hede, Västra Fröstsjöåsen; 2007, LH et al.; B121285 | MK467211 | MK466480 | MK466915 |
| D1224: Härjedalen, Tännäs, N Kvarnbäckstjärnen; 2014, LH; B207614 | MK467213 | MK466482 | MK466917 |
| D1225: Jämtland, Åre, W Silverfallet; 2010, LH; B177390 | MK467214 | MK466483 | MK466918 |
| D1226: Jämtland, Hæggenås, NNE Norderåsen; 2012, LH; B194024 | MK467215 | MK466484 | MK466919 |
| D1228*: Lycksele lappmark, Tärna, Tärnamo; 2016, LH; B237710 | MK467217 | MK466486 | MK466921 |
| D1229*: Lycksele lappmark, Tärna, NE Åldukejávrrre; 2016, LH; B237719 | MK467218 | MK466487 | MK466922 |
| D1230*: Norrbotten, Pajala, Jupukka; 1990, LH, M.Aronsson NT90-33; B31468 | MK467219 | MK466488 | MK466923 |
| D1232: Pite Lappmark, Arjeplog, Mt Ákháris; 2015, LH et al.; B227365 | MK467221 | MK466490 | MK466925 |
| D1233: Åsele Lappmark, Vilhelmina, Stuore Gämo; 2004, LH; B95122 | MK467222 | MK466491 | MK466926 |
| D1328: Härjedalen, Tännäs, WSW Mt Hem-Kröket; 2005, LH; B104166 | MK467223 | MK466492 | MK466927 |
| D1329: Härjedalen, Hede, Östra Fröstsjöåsen; 2007, LH et al.; B121306 | MK467224 | MK466493 | MK466928 |
| D1330: Härjedalen, Linsell, Glöte; 2007, LH et al.; B121454 | MK467225 | MK466494 | MK466929 |
| D1332*: Härjedalen, Storsjö, Svaalethahke; 2014, LH; B207575 | MK467227 | MK466496 | MK466931 |
| D1333*: Härjedalen, Sveg, S Rosstjärnarna; 1989, LH HD89-105; B234626 | MK467228 | MK466497 | MK466932 |
| D1334: Jämtland, Frostviken, Sipmekjeppe; 1988, LH J88-423; B31483 | MK467229 | MK466498 | MK466933 |
| D1336: Jämtland, Åre, Handölsforsen; 2005, LH et al.; B104947 | MK467231 | MK466500 | MK466935 |
| D1337: Jämtland, Kall, SSW Bratteggen; 2005, LH; B105487 | MK467232 | MK466501 | MK466936 |
| D1338: Jämtland, Kall, E Nyvallen; 2005, LH; B107631 | MK467233 | MK466502 | MK466937 |
| D1340: Jämtland, Frostviken, E Mt Brakkfjället; 2009, LH; B163736 | MK467235 | MK466504 | MK466939 |
| D1341*: Jämtland, Hæggenås, NNE Norderåsen; 2012, LH; B194031 | MK467236 | MK466505 | MK466940 |
| D1342: Medelpad, Borgsjö, Rankleven; 1987, LH; B242533 | MK467237 | MK466506 | MK466941 |
| D1344*: Lule Lappmark, Padjelanta, Kierkevare; 1998, T.-B.Engelmark; B63899 | MK467239 | MK466508 | MK466943 |
| D1345: Lule Lappmark, Jokkmokk, Haraudden; 1996, S.Westerberg; B125703 | MK467240 | MK466509 | MK466944 |
| D1349: Lycksele Lappmark, Lycksele, SSW Krániesuvvane; 2016, LH, G.Odelvik; B236851 | MK467244 | MK466513 | MK466948 |
| D1350: Lycksele lappmark, Tärna, Mt Raavriedenjuenie; 2016, LH; B237287 | MK467245 | MK466514 | MK466949 |
| D1351: Norrbotten, Tändö, Orjaskursu; 1990, LH, M.Aronsson NT90-797; B31469 | MK467246 | MK466515 | MK466950 |
| D1352*: Norrbotten, Pajala, Isonkivenmaa; 1990, LH, M.Aronsson NT90-104; B33187 | MK467247 | MK466516 | MK466951 |
| D1353: Norrbotten, Mäntyvaaranvuoma, E Tändö; 1998, O.Johansson; B125704 | MK467248 | MK466517 | MK466952 |
| D1354: Pite Lappmark, Arjeplog, Mt Ribmotjåkkå; 2006, LH et al.; B113742 | MK467249 | MK466518 | MK466953 |
| D1355*: Pite Lappmark, Björklidstormyrn, NE Björkliden; 2000, S.Westerberg; B125702 | MK467250 | MK466519 | MK466954 |

(Continued)

Table 1. Continued

| Sample no.: Locality; Coll. year, Collector [collector's no.]; S herbarium registration no. | <i>atpB-rbcL</i> | <i>rpl16</i> | <i>trnG</i> |
|--|------------------|--------------|-------------|
| D1358: Torne Lappmark, Karesuando, Håldimarrasat; 1990, LH, M.Aronsson NT90-517; B31463 | MK467253 | MK466522 | MK466957 |
| D1361: Torne lappmark, Jukkasjärvi, WSW Paddustieva; 1997, LH; B44150 | MK467256 | MK466525 | MK466960 |
| D1362: Åsele Lappmark, Dorotea, Kalvberget; 1991, LH; B74661 | MK467257 | MK466526 | MK466961 |
| <i>Paludella squarrosa</i> (Hedw.) Brid. | | | |
| D1495: Lycksele lappmark, Tärna, Tärnamo; 2016, LH; B237424 | MN419145 | MN419111 | MN419119 |
| D1496: Härjedalen, Storsjö, Mts Svaalejtjahkh-Veaketjahke; 2014, LH; B207583 | MN419146 | MN419112 | MN419120 |
| (B) | | | |
| <i>Meesia minutissima</i> Hedenäs | | | |
| MORF-1*: Pite lappmark, Arjeplog, Mt Stuur-Jiervas; 2017, LH et al.; B265765 (Holotype) | | | |
| MORF-2*: Pite lappmark, Arjeplog, Mt Stuur-Jiervas; 2017, LH et al.; B258266 | | | |
| MORF-3*: Torne Lappmark, Jukkasjärvi, Kaisepakte; 2017, LH; B254823 | | | |
| MORF-4*: Åsele Lappmark, Vilhelmina, Klimpfjäll area; 2004, LH; B93207 | | | |
| MORF-5*: Pite lappmark, Arjeplog, Mt Skärrim; 2017, LH et al.; B258087 | | | |
| MORF-6*: Jämtland, Åre, Snasahögarna, Getvalen; 1972, N.Hakelner; B33192 | | | |

leaf lengths or widths with these values and multiplying the resulting values with the cell lengths and widths, respectively. Shapiro Wilks W-test (normality) was mostly statistically significant, indicating that the data do not meet the criterion of normality. Thus, the nonparametric Kruskal–Wallis test for multiple comparisons was used to compare the measurements among or between the entities, respectively. Second, the gametophyte and sporophyte measurements were subjected to separate principal component analyses (PCA) to see whether the combined information within each data set corresponds with the molecularly identified entities. For the PCA the mean values for lamina and exothecial cell sizes were used to represent each leaf or capsule urn, and mean spore diameter to represent spore size in a specimen. For the gametophyte, leaf length, width, apex shape, costa width at the two positions, and the mean lamina cell length, width and cell length to width ratio, in total eight parameters, were included. For the sporophyte, mean capsule neck length, urn length and width, and the mean exothecial cell length, width and cell length to width ratio, and mean spore size, in total seven parameters, were included. All statistical calculations were made in STATISTICA 12 (StatSoft 2013).

Geographical distributions

The geographical distributions of the two species that are here segregated from *M. uliginosa* were evaluated based on a selection of specimens present in the Swedish Museum of Natural History (S) and the Museum of Evolution in Uppsala (UPS). Detailed information on these specimens is available at the Swedish Virtual Herbarium (<<http://herbarium.emg.umu.se/index.html>>, accessed 19 August 2019).

Results

Molecular relationships

The total number of aligned *atpB-rbcL* sites in the 56 studied *Meesia* specimens, and outgroup of two *Paludella squarrosa* specimens was 617. Of these, 26 sites were variable (nine in *Meesia uliginosa* s.l.), with 25 (8) of these parsimony-informative; 13 (5) indels were present, with 12 (4) informative. For *rpl16* the length was 671, 53 (28) sites were variable

and 49 (25) of these were parsimony-informative; 16 (10) indels with 14 (9) informative. For *trnG* the length was 617, 34 (18) sites were variable, and 27 (15) of these were parsimony-informative; 11 (2) indels with 9 (2) informative. The sequence lengths for the species were: *Meesia hexasticha* (n = 2; 1 for *atpB-rbcL*): 600 (*atpB-rbcL*), 653–660 (*rpl16*), 609–612 (*trnG*); *M. longiseta* (2): 600, 664, 612; *M. minor* (13): 600–604, 657–661, 612–613; a so far undescribed *Meesia* species (4): 602, 664, 614; *M. triquetra* (2): 601, 658, 611; *M. uliginosa* (25): 595–600, 661–664, 612; *Paludella squarrosa* (2): 600, 625, 612–613.

The NN split network and Jackknife analyses provide high support for the recognition of three lineages within *Meesia uliginosa* s.l. (Fig. 1). From now on, these are called *M. minor* Brid., *M. minutissima* Hedenäs sp. nov. and *M. uliginosa* s.str. *Meesia minor* and *M. minutissima* group most closely with *M. triquetra* and *M. hexasticha* specimen D1500 (only *rpl16* and *trnG*), whereas *M. uliginosa* s.str. groups with *M. longiseta* and *M. hexasticha* specimen D1499. Within *M. uliginosa*, three specimens from moderate elevations in middle Sweden (D1330 from Härjedalen; D1226, D1441 from Jämtland) form a well-supported lineage (Jackknife support 98). Within *M. minor*, three specimens from the middle third of the Swedish portion of the Scandinavian mountain range (D1339 from N-most Jämtland; D1227, D1347 from the mountains of Lycksele Lappmark) form a basal grade, distinguished from a well-supported lineage (95) with the remaining specimens of the species.

Morphological evaluation

When sporophytes are present, the three species within *Meesia uliginosa* s.l. can be distinguished from each other by a combination of seta length and the ornamentation of the exostome outside (Fig. 2). The seta in *M. uliginosa* s.str. is 17–70 mm and the exostome outside is smooth, or faintly reticulate to striolate. In *M. minor* the seta is 8–37(46) mm tall and the exostome outside has a well-developed reticulate or partly irregularly cross-striolate ornamentation, and in *M. minutissima* the seta is 4–17 mm tall and the exostome outside is almost smooth, or faintly cross-striolate to obliquely striolate. In addition, the apex of well-developed vegetative leaves is mostly rounded or obtuse in *M. uliginosa*

s.str., but mostly acuminate, acute or obtuse in the other two species.

The PCAs based on the detailed measurements of selected gametophyte and sporophyte features of *M. uliginosa* s.l., respectively, suggest three clusters corresponding with *M. minor*, *M. minutissima* and *M. uliginosa* s.str. (Fig. 3). *Meesia minor* overlaps to some degree with both the other species in the gametophyte features but hardly in the sporophyte features, whereas the two other species are distinct from each other in the PCAs. For the gametophyte, leaf cell length to width ratio and, to some degree, length contribute to the distribution along the second axis, whereas the other features correlate with the first axis (Fig. 3A, left). For the sporophyte, exothecial cell length to width ratio and, to some degree, cell length and spore size contribute to the distribution along the second axis, whereas all other measured features correlate with the first axis (Fig. 3B, left).

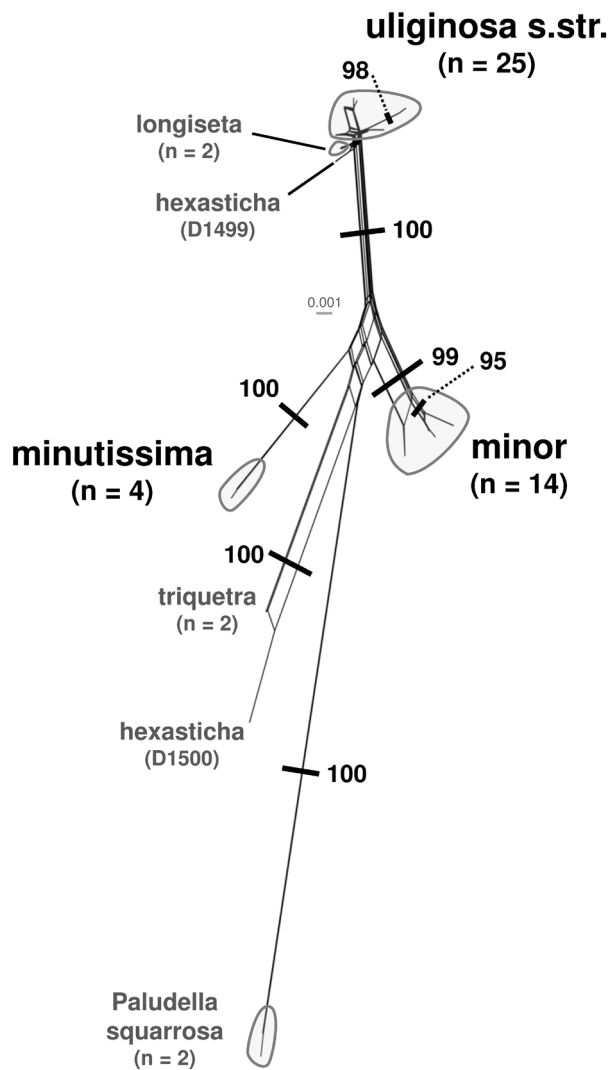


Figure 1. NeighborNet split network for the 56 studied *Meesia* (indicated by their species epithets) and two *Paludella squarrosa* (outgroup) specimens, based on *atpB-rbcL*, *rpl16* and *trnG*. Jack-knife support values of 95–100 are indicated by transverse black lines, with the corresponding support values indicated. The three species segregated from *M. uliginosa* s.l. are in black text and other species in grey; n: number of specimens.

All three species within *M. uliginosa* s.l. differ from each other in seven of the 18 individual quantitative characters measured in detail. *Meesia uliginosa* differs from the other two species in four additional characters, *M. minor* from the two other species in two additional ones, and *M. minutissima* from the other two in four (Table 2). When cell sizes were adjusted to a leaf length of 1.5 mm and a leaf width of 0.3 mm, the cells of *M. uliginosa* appear smaller than those of the other species, even if they are longer than those of *M. minutissima* and wider than those of both the other species in the actual measurement. For several characters, there is a wide overlap between the species despite statistically significant differences (Fig. 4). Additional observed differences are mentioned in the key and species descriptions.

Geographical distribution and habitat

The known Scandinavian distributions of *Meesia minor* and *M. minutissima* are mapped in Fig. 5, based on examined specimens in S and UPS. Whereas *M. uliginosa* s.str. occurs both in lowland and mountain environments, both the other species are typical mountain ones, with the somewhat more common *M. minor* collected between 460 and 1350 m a.s.l. and *M. minutissima* between 550 and 1400 m a.s.l. These two species can grow on exposed soil as well as in rock crevices and occur mainly in areas rich in calcareous or at least somewhat base-rich bedrock. *Meesia minutissima* appears to grow at on the average more exposed sites than *M. minor*, but otherwise there does not seem to be any clear distinction between the habitats of the two species. On two occasions, the two were even collected within the same square decimetre.

Discussion

The three entities of *Meesia uliginosa* s.l. belong to three separate and well-supported molecular lineages, with partly different affinities to other *Meesia* species. They differ in several morphological features, and therefore there can be no doubt that they represent three species despite their somewhat similar appearances. Any other treatment would be inconsistent as long as we recognize *M. triquetra* and *M. longiseta* as distinct species. Among the three entities segregated from *M. uliginosa* s.l. (Fig. 1), *M. uliginosa* s.str. clusters with *M. longiseta* and one of the *M. hexasticha* accessions, whereas the two well-supported lineages corresponding with *M. minor* and *M. minutissima*, respectively, are more closely related to *M. triquetra* and the second accession of *M. hexasticha*. *Meesia minor*, *M. minutissima* and *M. uliginosa* display statistically significant differences in several quantitative morphological characters, and can be efficiently distinguished by a combination of seta length and the ornamentation of the exostome outside. Additional important distinguishing characters are the shape of the leaf apex, the capsule size and spore size (Table 2, Fig. 4).

The situation for *M. hexasticha* is different. One of the markers for its accession D1500 could not be generated, but high support for the positions of this accession and D1499 in different portions of the NN split network suggest that this species is not homogeneous. This would agree with a

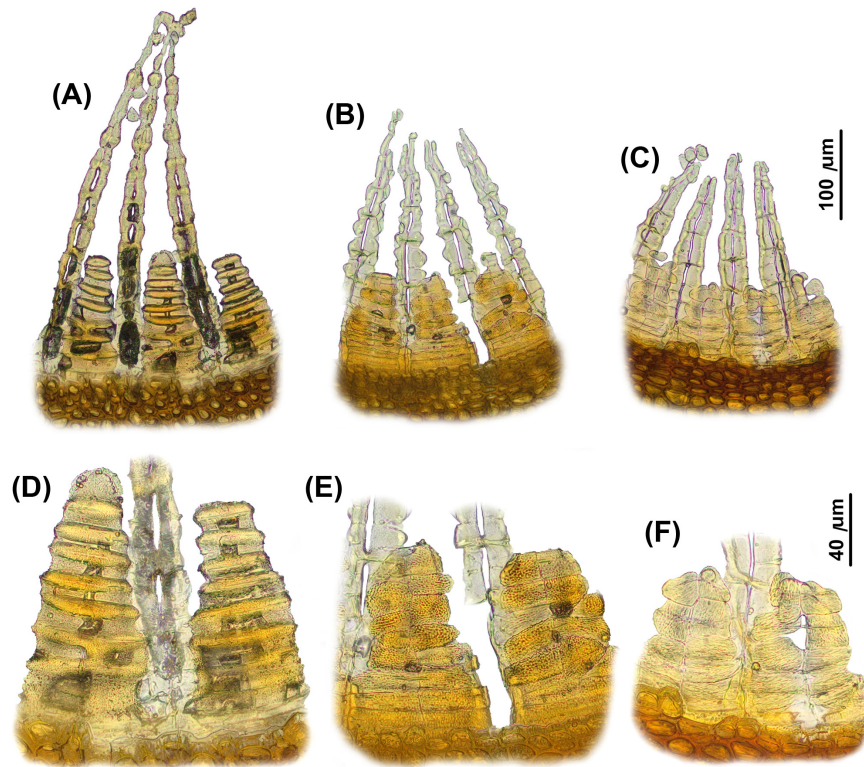


Figure 2. Peristome (A–C) and close-up on exostome outside (D–F) in *Meesia uliginosa* (A, D), *M. minor* (B, E) and *M. minutissima* (C, F). A, D: Sweden. Lycksele lappmark, Tärna, *L. Hedenäs*; S, B237287. B, C, E, F: Sweden. Pite lappmark, Arjeplog, *L. Hedenäs*; S, B258274 (both species growing close to each other).

hybrid origin (Nyholm 1998) and, if this hypothesis is correct, suggests that hybridisation has occurred at least twice. If, as suggested by Nyholm (1998), its parental species are *M. uliginosa* and *M. triquetra*, then *M. uliginosa* is the maternal parent for D1499 whereas *M. triquetra* is the maternal parent for D1500, since chloroplasts are maternally inherited in mosses (Duckett et al. 1983, McDaniel et al. 2007, Natcheva and Cronberg 2007). To clarify the origin of different *M. hexasticha* populations, additional material of *M. hexasticha* must be studied and a nuclear marker should be included in the evaluation. *Meesia hexasticha* is red-listed in several European countries (Ştefănuţ and Goia 2012, Henriksen and Hilmo 2015, Westling 2015, Hyvärinen et al. 2019). However, if the name *M. hexasticha* represents a plant phenotype that originated repeatedly due to hybridisation between other *Meesia* species, its inclusion in red-lists as an independently evolving lineage at the species level is questionable.

Investigations during the last couple of decades have added many moss species to the flora of the Scandinavian mountain range and far north. Besides *Meesia*, examples can be found in several genera, including *Oncophorus* (Hedenäs 2017), *Sanionia* (Hedenäs 1989) and *Schistidium* (Blom 1996) species new to science and species raised from lower taxonomic ranks in *Drepanocladus* (Hedenäs 1992) and *Schistidium* (Blom 1996). For other species, their status was earlier unclear, like in *Oncophorus* (Hedenäs 2017, 2018), *Orthothecium* (Hedenäs 1988), *Schistidium* (Blom 1996) and *Sciuro-hypnum* (Draper and Hedenäs 2008,

2009). Finally, in some cases finds were made outside previously known ranges, as in *Campylium* (Jacobson and Hedenäs 2015), *Encalypta* (Høitomt et al. 2016), *Funaria* (Rumsey 1990), *Schistidium* (Blom 1996), *Timmia* (Carlsson 2003) and *Tortella* (Hassel and Høitomt 2013). In addition to this recently discovered species diversity, so far unrecognized species still occur in these areas (Hedenäs unpubl.). In Europe, mountain regions and regions of the far north belong to those that will be most heavily affected by the future temperature increase (Berglöv et al. 2015a, b, Nylén et al. 2015), which underlines how urgent it is to explore northern and mountain diversity. As shown in the modelling study of Moen et al. (2004), most of the Swedish alpine region could potentially disappear until the year 2100. According to the models, such changes will be especially crucial for meadows, heaths and wetlands, where only a few per cent may remain. Kullman (2010) reviewed already visible changes in the Scandinavian mountain vegetation, but doubted that we will see very severe future negative effects of the changing climate. However, even if predictions are always uncertain, the magnitude of the changes suggested by the models of Moen et al. (2004) are too substantial to ignore.

Taxonomy

Meesia Hedw., nom. cons. (cf., Magill 1993), *Species Muscorum Frondosorum* 173–175, pl. 41, f. 6–9 (1801). – Type: *Meesia longiseta* Hedw.

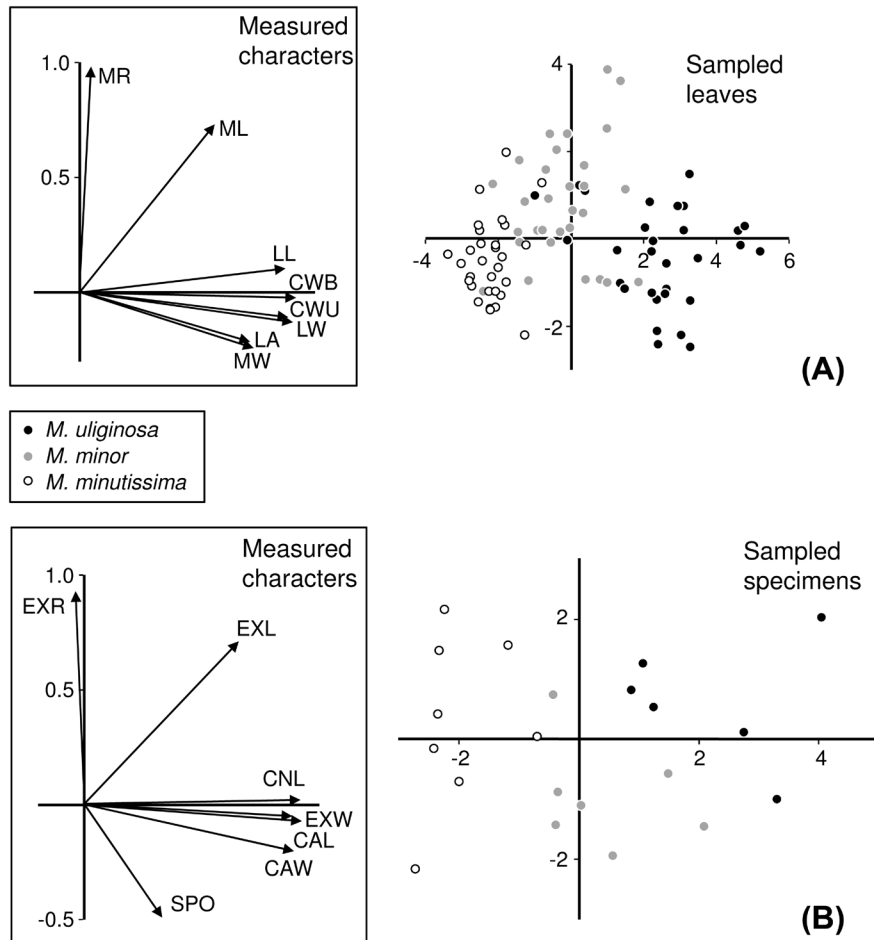


Figure 3. (A) The positions of three leaves from each of ten specimens of *M. minor*, ten of *M. minutissima* and ten of *M. uliginosa* s.str. (cf., Fig. 1), along the first two axes in a PCA. This PCA is based on each leaf's length (LL), width (LW), leaf apex shape (LA), mid-leaf lamina cell length, width and length/width ratio (ML, MW, MR), and costa width at base (CWB) and 2/3 way up leaf (CWU). Cell sizes length/width ratios are the mean values of 20 measured cells in each leaf. Factors 1 and 2 explain 60.4% and 20.5% of the variation. (B) The positions of seven specimens of *M. minor*, eight of *M. minutissima* and six of *M. uliginosa* s.str. (cf., Fig. 1), along the first two axes in a PCA. This PCA is based on the length of the capsule neck (CNL), urn length (CAL) and width (CAW), exothelial cell length, width and length/width ratio (EXL, EXW, EXR), and mean spore size (SPO). Capsule sizes based on 2–5 measured capsules per specimen, exothelial cell sizes and length/width ratios are the mean values of 20 measured cells in an urn, and spore sizes are the mean values of 13–32 measured spores in *M. minor*, 11–32 in *M. minutissima* and 10–26 in *M. uliginosa* s.str. Factors 1 and 2 explain 57.8% and 23.6% of the variation.

Key to the Scandinavian species of the *Meesia uliginosa* complex

Note. It is important to study numerous non-perichaetial leaves from the upper portions of shoots to judge the shape of the leaf apex.

1. Exostome yellow-brown, 2/5–2/3 of length of endostome; lower outside of exostome with well-developed reticulate or partly irregularly cross-striolate pattern; spores (46.0)48.0–66.0(69.5) μm ; seta 8–37(46) mm. Shoots medium-sized, mostly 2–12 mm tall.2. *M. minor*
- Exostome pale yellowish or when old yellowish to dark yellow, fragmentary, 1/5–1/2 of length of endostome; lower outside of exostome almost smooth or faintly striolate or reticulate; spores (37.0)38.5–58.0(62.5) μm ; seta 4–17 or 17–70 mm tall. Shoots short or tall.2
2. Seta 17–70 mm; dry capsule neck 0.8–1.2 mm long, dry urn 1.1–2.0 \times 0.6–1.1 mm. Shoots mostly 6–30 mm tall. Stem leaves 1.4–4.1 \times 0.2–0.6 mm; costa 105–311 μm

- wide at base, 39–126 μm at 2/3 up leaf; leaf apex mostly rounded or obtuse; median lamina cells (5.5)6.5–14.5(18.0) μm wide. Inner perichaetial leaves 1.9–5.4 mm long.1. *M. uliginosa*
- Seta 4–17 mm tall; dry capsule neck 0.3–1.0 mm long, dry urn 0.6–1.2 \times 0.4–0.8 mm. Shoots mostly 2–7 mm tall. Stem leaves 0.7–1.6 \times 0.2–0.3 mm; costa 63–134 μm wide at base, 26–61 μm at 2/3 up leaf; leaf apex mostly acuminate or acute, occasionally obtuse; median lamina cells (4.0)5.0–10.5(12.5) μm wide. Inner perichaetial leaves 1.2–2.1 mm long.3. *M. minutissima*

1. *Meesia uliginosa* Hedw. Fig. 2A, D
Species Muscorum Frondosorum 173–174. 1801. – Type: specimen 'a', '*Meesia uliginosa* Hedw., Cryptog. p. 1 t.1 f. 1–2 Bryum trichodes Linn.' on a sheet in herb Hedwig-Schwaegrichen [lecto-: G, s.n.!, (Ochyra et al. 2008)].
Meesia hymenostoma Cardot & Broth., *Kongliga Svenska Vetenskaps Akademiens Handlingar, Ny Följd* 63(10): 51. 1923. – Type: Patagonia: 'Herb. J. Cardot. Meesea

Table 2. Means plus standard errors for character measurements in *Meesia uliginosa* s.str., *M. minor* and *M. minutissima*. When mid-leaf cell length and width were adjusted, these were adjusted to leaves with a length of 1.5 mm and a width of 0.3 mm, respectively. The total number of measurements, n, are indicated for each species (*M. uliginosa*, *M. minor*, *M. minutissima*) under each character. Different letters (a, b, c) appended after the values for a character indicate statistically significant pair-wise differences between species, as revealed by the Kruskal–Wallis test, using the Bonferroni corrected p value corresponding with $p < 0.05$ (i.e. < 0.00092593).

| Measurement | <i>uliginosa</i> | <i>minor</i> | <i>minutissima</i> |
|---|------------------|---------------|--------------------|
| Leaf length, mm (LL) n=30, 30, 30 | 2.23 (0.11) a | 1.41 (0.06) b | 0.94 (0.03) c |
| Leaf width, mm (LW) n=30, 30, 30 | 0.42 (0.02) a | 0.29 (0.01) b | 0.23 (0.01) c |
| Leaf costa width 2/3 way up, μm (CWU) n=30, 30, 30 | 76.5 (3.6) a | 52.1 (2.3) b | 40.5 (1.5) c |
| Leaf costa width at base, μm (CWB) n=30, 30, 30 | 202.4 (8.6) a | 143.3 (6.1) b | 93.6 (3.2) c |
| Leaf apex shape, scored 1–4 (LA) n=30, 30, 30 | 3.4 (0.2) a | 2.2 (0.2) b | 1.5 (0.1) b |
| Mid-leaf cell length, μm (ML) n=600, 600, 600 | 31.5 (0.3) a | 31.5 (0.4) a | 22.6 (0.3) b |
| Mid-leaf adjusted cell length, μm (MAL) n=600, 600, 600 | 22.4 (0.3) a | 34.8 (0.5) b | 36.9 (0.5) b |
| Mid-leaf cell width, μm (MW) n=600, 600, 600 | 10.3 (0.1) a | 8.5 (0.1) b | 7.4 (0.1) c |
| Mid-leaf cell adjusted cell width, μm (MAW) n=600, 600, 600 | 7.6 (0.1) a | 8.9 (0.1) b | 9.8 (0.1) c |
| ML/MW ratio (MR) n=600, 600, 600 | 3.23 (0.05) a | 3.85 (0.06) b | 3.17 (0.05) a |
| MAL/MAW ratio (MAR) n=600, 600, 600 | 3.06 (0.05) a | 4.10 (0.06) b | 3.95 (0.06) b |
| Capsule neck length, mm (CNL) n=37, 30, 31 | 1.00 (0.02) a | 0.86 (0.03) a | 0.53 (0.03) b |
| Capsule urn length, mm (CAL) n=37, 30, 31 | 1.42 (0.04) a | 1.18 (0.03) a | 0.82 (0.03) b |
| Capsule urn width, mm (CAW) n=37, 30, 31 | 0.85 (0.02) a | 0.72 (0.03) a | 0.57 (0.02) b |
| Exothecial cell length, μm (EXL) n=200, 200, 180 | 52.3 (1.0) a | 41.0 (0.6) b | 40.0 (0.9) b |
| Exothecial cell width, μm (EXW) n=200, 200, 180 | 28.9 (0.4) a | 25.5 (0.4) b | 22.9 (0.4) c |
| EXL/EXW ratio (EXR) n=200, 200, 180 | 1.87 (0.04) – | 1.68 (0.04) – | 1.83 (0.05) – |
| Spore diameter, μm (SPO) n=121, 188, 187 | 48.9 (0.4) a | 56.4 (0.4) b | 48.6(0.4) a |

hymenostoma Card., sp. Nova. Chili, monte Baguales, T. Halle, 1909' in herb. Roth (lecto-: PC-CARD, n.v. (Matteri and Ochyra 1999); iso-: H-BROTH, n.v., PC-CARD, n.v., S, B166176!).

Plants mostly 6–30 mm tall, green or partly red (especially perichaetial leaves). Stem in transverse section round or rounded-triangular, with well-developed central strand and a cortex of 2–3 layers of small and slightly or moderately incrassate cells, outer cell wall thin. Rhizoids dark purplish, axillary, strongly branched and forming tomentum in lower stem, papillose. Axillary hairs with single or very rarely two, long, upper hyaline cell(s), 11–18 μm wide, basal 2–4 cells rectangular or longly so, red or pale red. Stem leaves 1.4–4.1 \times 0.2–0.6 mm; costa 105–311 and 39–126 μm wide at base and 2/3 up leaf, respectively, ending shortly below leaf apex; leaf apex mostly rounded or obtuse; median leaf lamina cells (13.0)18.0–50.5(63.5) \times (5.5)6.5–14.5(18.0) μm , (1.0)1.5–6.1(8.7) times as long as wide, short-rectangular to short-linear with square ends, incrassate, eporose; basal cells rectangular to linear, incrassate, decurrent, alar cells not differentiated. Autoicous, synoicous and female plants seen. Inner perichaetial leaves 1.9–5.4 \times 0.3–0.9 mm, apex

rounded, obtuse, rarely acute or even acuminate. *Calyptra* cucullate, fugacious. *Seta* 17–70 mm tall; when dry capsule neck 0.8–1.2 mm long, urn 1.1–2.0 \times 0.6–1.1 mm, operculum dome-shaped or conical, annulus separating; exothecial cells on upper side of capsule (26.5)30.5–85.5(106.0) \times (19.0)19.5–40.0(46.0) μm , (0.7)1.0–3.4(3.7) times as long as wide, stomata long-pored, abundant on capsule neck; exostome yellowish to dark yellow, fragmentary, 1/8–1/2 of length of endostome, smooth or faintly reticulate or faintly and often irregularly striolate, endostome strongly reduced, basal membrane low or indistinct, segments narrowly split along mid-line or partly so, cilia absent, short or fragmentary, 232–424 μm high, measured from capsule mouth. *Spores* (37.5)42.0–56.0(59.0) μm , finely papillose, often slightly elongate, often with irregular debris on surface.

This is the largest of the three species within *M. uliginosa* s.l. The seta length varies between 17 and 70 mm, the exostome outside is smooth or faintly ornamented, and the leaf apices are mostly rounded or obtuse. Specimens with a relatively short seta and obtuse leaf apices could easily be confused with *M. minor*, but the latter has a lower exostome outside with well-developed ornamentation and on

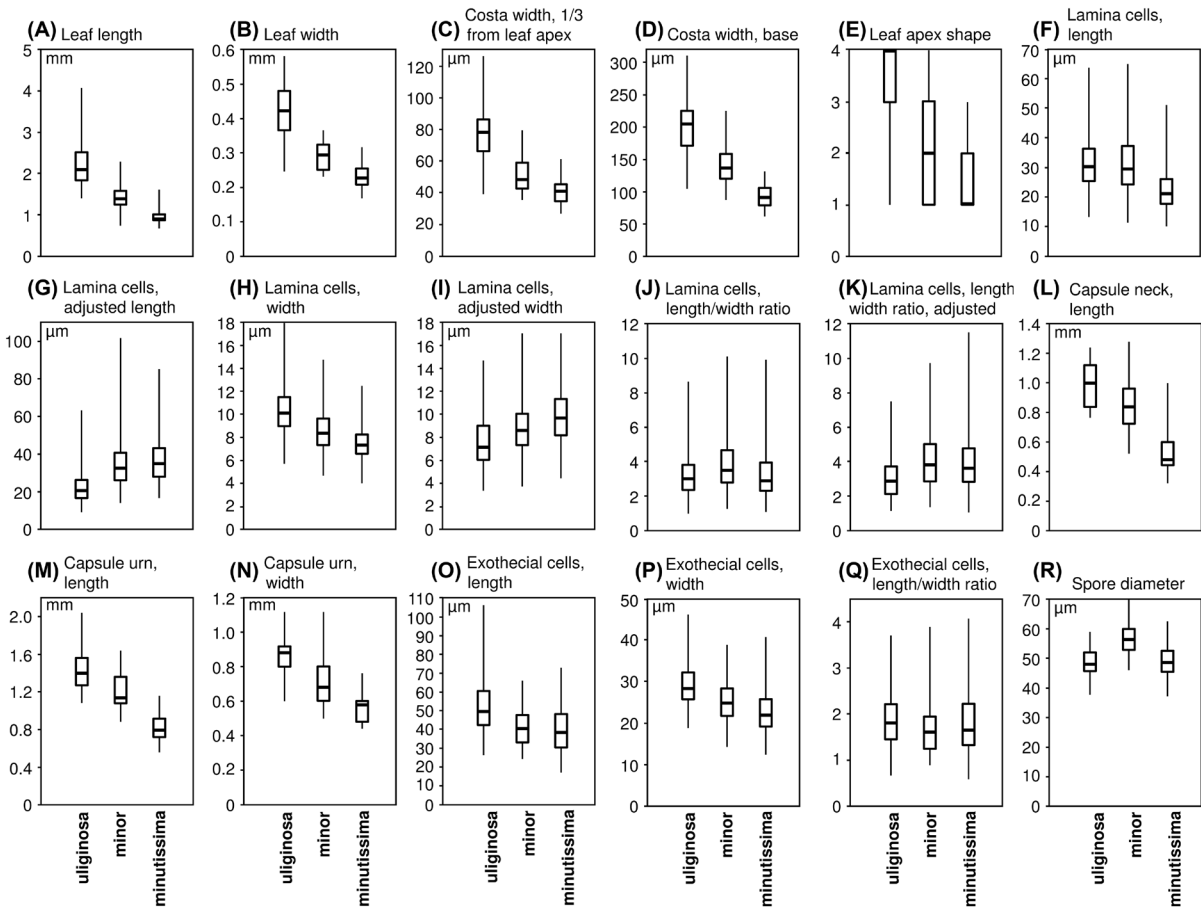


Figure 4. Boxplots with median values, quartiles and whiskers from maximum to minimum values, for measured characters in *Meesia uliginosa* s.str., *M. minor* and *M. minutissima* (cf. Fig. 1). For numbers of measurements, see Table 2.

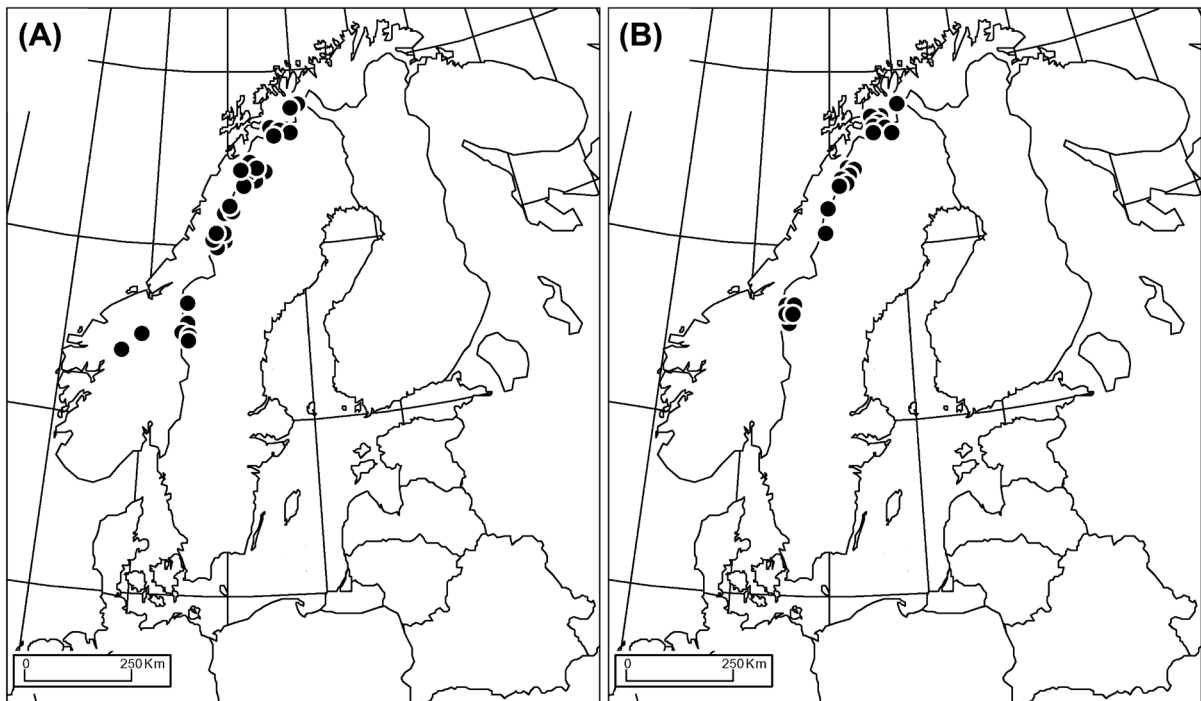


Figure 5. Geographical distributions of *Meesia minor* (A; n = 33) and *M. minutissima* (B; n = 25) in Scandinavia based on S and UPS material.

the average larger spores [(46.0)48.0–66.0(69.5) μm versus (37.5)42.0–56.0(59.0) μm].

Nomenclatural notes

The lectotype of *Meesia uliginosa* Hedw. (Ochyra et al. 2008) has a seta that is ca 46 mm long and the outer exostome ornamentation is weak. The vegetative as well as perichaetial leaves have a rounded apex. Thus, the name *M. uliginosa* Hedw. should be applied to the largest of the three species within *M. uliginosa* s.l.

The S isotype of *Meesia hymenostoma* Cardot & Broth. has a faintly ornamented exostome, and clearly belongs to *M. uliginosa* s.str.

Habitat and known distribution

This species is most frequent in mineral-rich fen or spring habitats, but it also grows on bare, peaty soil, occasionally in escarpments, in base-rich habitats. In Scandinavia, this is the most widespread of the three species within *M. uliginosa* s.l. (field observations; Hedenäs unpubl.). It occurs both in the mountains and in the lowlands, but is rare or has vanished from large portions of southern Scandinavia. The species is probably widespread in Europe and temperate to Arctic areas of Asia and North America (Nyholm 1998, Xing-jiang and He 2007, Vitt 2014, Ignatov and Ignatova 2018). It occurs in southern South America (type of *Meesia hymenostoma* Cardot & Broth. and Matteri and Ochyra 1999), whereas reports from the Antarctic area (Ochyra and Lewis-Smith 1999, Ochyra et al. 2008) likely refer to *M. minor*. Also for the Northern Hemisphere, some of the literature reports of *M. uliginosa* likely refer to *M. minor* and *M. minutissima*, especially from Arctic or mountainous regions.

2. *Meesia minor* Brid. Fig. 2B, E, 6

Muscologia Recentiorum 2(3): 168. 2 f. 13. 1803. – Type: ‘a’: ‘*Meesia uliginosa* v. *minor*. Bryol. Univ. Meesia minor. [Switzerland (Ct. Berne or Ct. Vaud)] In calcarius Alpius Sanensium’ on a sheet with *Meesia minor* in folder 620 in herb. Bridel (holo-: B, B31 0620 01!).

Meesia alpina Funck ex Bruch, *Flora* 9: 164. 1826. – Type: [Switzerland (Kt. Luzern)] ‘*Meesia uliginosa* Hedw. var. *alpina* (Funck) B. eur., In m. Pilato infra & supra Bründelalp, 7.8. Aug. 1821, Herb. Schaefer’, in herb Boissier (lecto-: G; s.n.!; designated here; syn-: M, M-0301567!, M-0301568!).

Meesia angustifolia Brid., *Bryologia Universa* 2: 62. 1827. – Type: [two labels for the same specimen; Switzerland (Ct. Berne or Ct. Vaud)] ‘*Meesia angustifolia* Br. Bryol. Univ. *Meesia uliginosa* var. *angustifolia*. Chateau d’Oex, Aout 1796!’ ‘*Meesia uliginosa*. In Alpi Sanensib, supra Chateau d’Oex, in sylvis uliginosis ad [...], Augustus [1]796’, on sheet 2 in folder 621 in herb. Bridel (lecto-: B, B31 0621 02!, designated here; syn-: on sheet 1 in folder 621 in herb. Bridel in B, B31 0621 01!, and on the sheet with the lectotype of *Meesia uliginosa* Hedw. in herb Hedwig-Schwaegrichen in G, s.n.!).

Meesia stricta Brid., *Bryologia Universa* 2: 61. 1827. – Type: [Austria] ‘*Meesia stricta*. Bryol. Univ. *Meesia minor*. Kärnten [...], Hornschuch misit, 1819’ on a sheet with *Meesia minor* in folder 619 in herb. Bridel (holo-: B, B31 0619 01!; iso-: on the sheet with the lectotype of *Meesia uliginosa* Hedw. in herb Hedwig-Schwaegrichen in G, s.n.!).

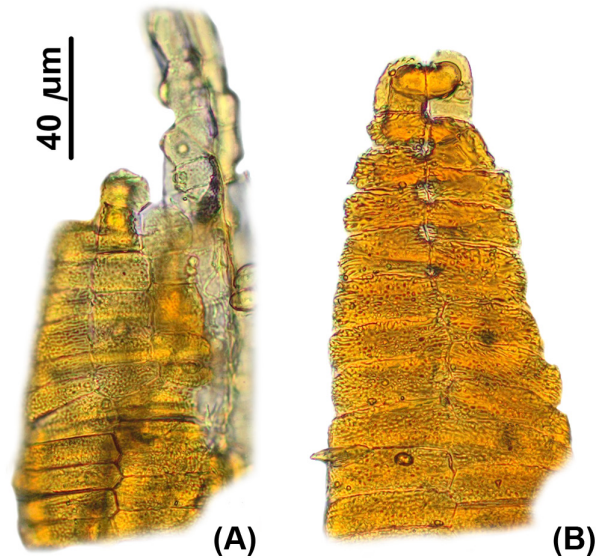


Figure 6. Exostome outside in the holotype of *Meesia minor* Brid. (A) and in the lectotype of *M. angustifolia* Brid. (B). (Both in B.)

Ceratodon kinggeorgicus Kanda, *Hikobia* 9: 324. f. 3. 1986. – Type: [Antarctica, South Shetland Islands] ‘King Georg Island, Potter Cove, 70 m alt., coll. H. Kanda 120’ [holo-: NIPR, n.v. – see Ochyra and Lewis-Smith (1999)].

Plants mostly 2–12 mm tall, green or partly red (especially perichaetial leaves). *Stem* in transverse section round or slightly rounded-triangular, with well-developed central strand and a cortex of 1–3 layers of small and slightly or moderately incrassate cells, outer cell wall thin. *Rhizoids* dark purplish, axillary, strongly branched and forming tomentum in lower stem, papillose. *Axillary hairs* with single, long, upper hyaline cell, 12–16 μm wide, basal 2–5 cells rectangular or longly so, reddish. *Stem leaves* 0.7–2.3 \times 0.2–0.4 mm; costa 88–226 and 35–79 μm wide at base and 2/3 up leaf, respectively, ending shortly below leaf apex; leaf apex mostly acute or obtuse or rarely acuminate or rounded; median leaf lamina cells (11.5)17.0–53.5(65.0) \times (4.5)5.5–12.0(14.5) μm , (1.3)1.8–7.4(10.1) times as long as wide, short-rectangular to short-linear with square ends, incrassate, eporose; basal cells rectangular to linear, incrassate,



Figure 7. Portion of holotype of *Meesia minutissima* Hedenäs (in S).

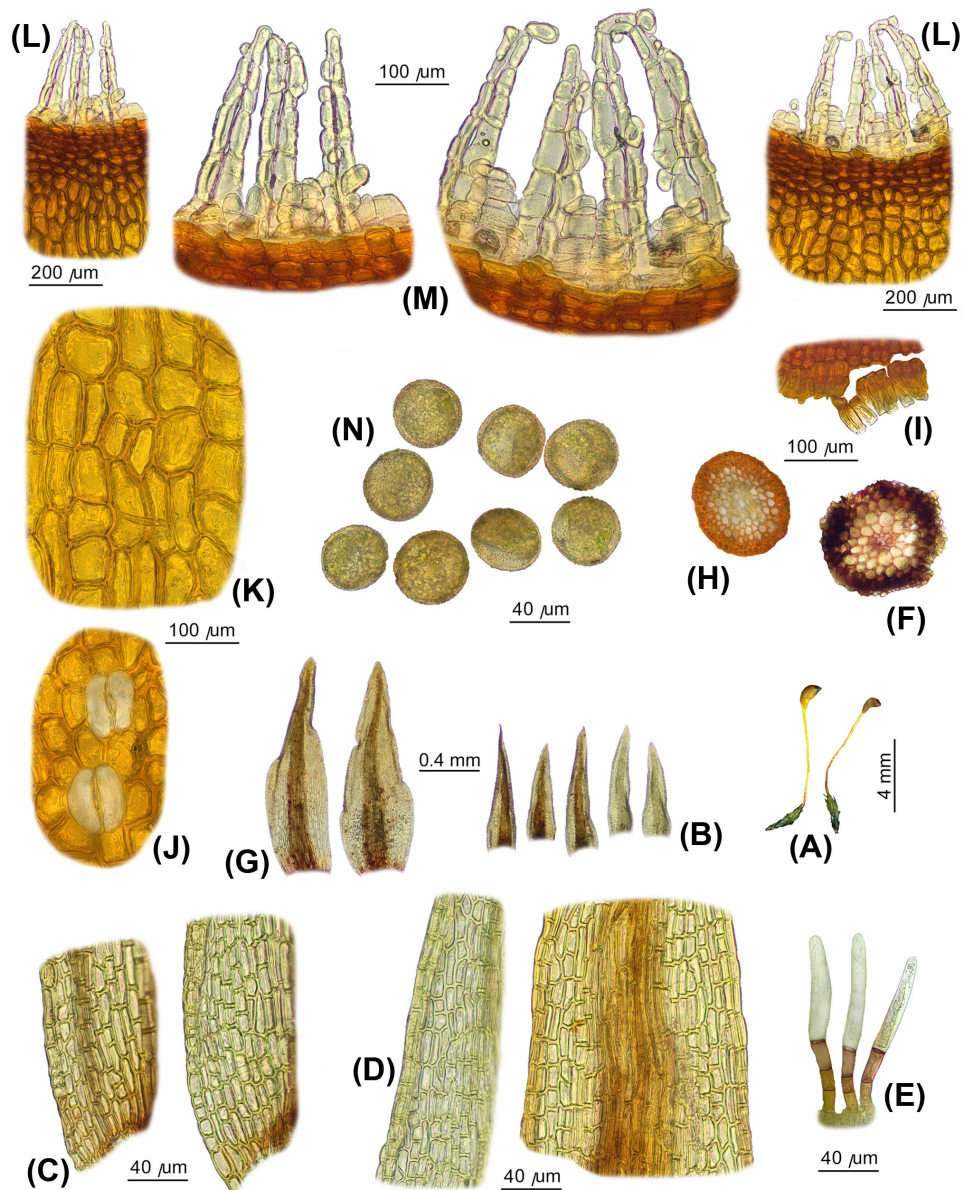


Figure 8. Holotype of *Meesia minutissima* Hedenäs (in S). (A) Habit, (B) stem leaves, (C) basal leaf lamina cells, (D) upper leaf lamina cells, (E) Axillary hairs, (F) Transverse section of stem, (G) Perichaetial leaves, (H) Transverse section of seta, (I) Annulus, (J) Stomata, (K) Exothelial cells on dorsal side of capsule, (L, M) Peristome, (N) Spores.

decurent, alar cells not differentiated. *Autoicous and female* plants seen. *Inner perichaetial leaves* (1.6)1.7–3.8 × 0.3–0.5 mm, apex rounded, obtuse or acute. *Calyptra* cucullate, fugacious. *Seta* 8–37(46) mm tall; when dry capsule neck 0.5–1.3 mm long, urn 0.9–1.6 × 0.5–1.1 mm, operculum lowly conical, annulus separating; exothelial cells on upper side of capsule (24.5)26.5–59.0(66.0) × (14.0)17.0–36.5(39.0) μm, 0.9–3.0(3.9) times as long as wide, stomata long-pored, abundant on capsule neck; exostome yellow-brown, 2/5–2/3 of length of endostome, with well developed reticulate or partly irregularly cross-striolate ornamentation on lower outside; endostome strongly reduced, basal membrane partial, low, segments narrowly split along mid-line, cilia absent or fragmentary, (149)167–257 μm high, measured from capsule mouth. *Spores* (46.0)48.0–66.0(69.5) μm, finely or sparsely papillose, often slightly elongate, often with irregular debris on surface.

Meesia minor is intermediate between *M. uliginosa* and *M. minutissima* in size and most other features. However, it can be distinguished from both the other species by its well-developed ornamentation on the exostome outside (at most faintly developed in the other two species) and by on the average larger spores [(46.0)48.0–66.0(69.5) μm versus (37.0)38.5–58.0(62.5) μm]. Other differences between *M. minor* and *M. uliginosa* or *M. minutissima* are provided under the latter two species.

Nomenclatural notes

There is only one specimen of *Meesia minor* Brid. in herbarium Bridel, with label information agreeing with information in the protologue, and this is therefore considered to be the holotype of the name. The stem leaves are gradually acuminate or narrowly obtuse, the seta is 16–18 mm tall, and the exostome outside ornamentation is distinct (Fig. 6A).

This is the oldest name for the intermediate-size species in the *M. uliginosa* complex.

In M, where herbarium Funck is located, three specimens fit the description in the protologue for *Meesia alpina* Funck ex Bruch, and could thus potentially be syntypes of this name: '*Meesia alpina* Funck, a. d. Schweiz', M-0301567; '*Meesia alpina* Funck, a. d. Schweiz com. Bruch', M-0301568; '*Meesia uliginosa* Hedw. v. *alpina*, *Meesia alpina* Funck, Alpen', M-0301565. Of these, the third could potentially come from portions of the Alps outside those mentioned by Bruch (1826: Tyroler-, Salzburger- und Schweizeralpen), and is therefore only considered to be a possible syntype. Two further specimens that could potentially be syntypes exist in G, where herbarium Bruch is located: '*Meesia uliginosa* Hedw. var. *alpina* (Funck) B. eur., In m. Pilato infra & supra Bründelalp, 7.8. Aug. 1821, Herb. Schaefer', in herb Boissier; '*Meesia alpina* Funck, August Müller, alpes Carinthiae, u.z. 1826', in herb. De Candolle in G. Considering that Bruch (1826) was published 21 March 1826, according to information just preceding the paper in the journal, it seems very unlikely that the second G specimen could have been collected and seen by Funck before the publication. The three remaining G and M samples all come from the Swiss Alps, and here the one in G is selected as lectotype since this is the only one that with certainty both agrees with the protologue and was collected before March 1826. Its leaves are acuminate or narrowly obtuse, and the seta is 8–15 mm. Unfortunately, its exostome is in a too poor condition for evaluation.

Two syntypes of *Meesia angustifolia* Brid. are present in herbarium Bridel in B ['c' 'Nr. 177. Si la mousse [...] Mr Thomas que Vous a vez determine...etc.'], on sheet 1 in folder 621, reg. no. B 31 0621 01; '*Meesia angustifolia* Br. Bryol. Univ. *Meesia uliginosa* var. *angustifolia*. Chateau d'Oex, Aout 1796' / '*Meesia uliginosa*. In Alpib Sanensib, supra Chateau d'Oex, in sylvis uliginosis ad [...], Augustus [1]796' (two labels for one specimen), on sheet 2 in folder 621, reg. no. B 31 0621 02], and one in herbarium Hedwig-Schwaegrichen in G ('b'), 'angustifolia, alp Helvet.' s.n., on the sheet with the lectotype of *Meesia uliginosa* Hedw.). Because all specimens fit the protologue, the well-developed one that is richest in material is selected as lectotype of the name (Fig. 6B).

Ceratodon kinggeorgicus Kanda was synonymised with *M. uliginosa* by Ochyra and Lewis-Smith (1999). Based on their illustration and since their remark that the Antarctic material is uniform and agrees with the concept of 'var. *minor*', *M. minor* is probably the species occurring in the Antarctic.

Habitat and known distribution

This species grows on bare, peaty soil or rocks, or often in rock crevices, mostly in base-rich habitats. In King George Island it was reported from acidic habitats (Ochyra and Lewis-Smith 1999). In Scandinavia, it is widespread in the mountains (Fig. 5A), where field observations (Hedenäs, unpubl.) suggest that it is significantly more common than *M. minutissima*. As shown by the origin of the type of the name and the types of its listed synonyms, it occurs also in the European Alps. The discussion under *M. uliginosa* by Favreau and Brassard (2011) suggests that *M. minor* may be widespread in the Arctic of North America.

Additional specimens seen (not in Table 1)

Norway. Oppland, Dovre, Blåhøe, 1858, *J.E. Zetterstedt*; UPS, B-839683. Sör-Trøndelag, Kongsvold, 1858, *J.E. Zetterstedt*; UPS, B-839619. Sör-Trøndelag, Kongsvold, Drifelfven, 1854, *J.E. Zetterstedt*; UPS, B-839613. Nord-Trøndelag, Røyrvik, Mt Guelehtstjähke, 2014, *L. Hedenäs*; S, B205419. Nord-Trøndelag, Røyrvik, Storøya, 2014, *L. Hedenäs*; S, B205293. Salten, Skaiti, 1931, *I. Söderberg*; UPS, B-839633. Troms, Målselv, Gaiseluokka, 1980, *L. Hedenäs*; S, B269537. **Sweden.** Härjedalen, Tännäs, Funäsdalen, Ösjöån, 1920, *G.R. Cedergren*; UPS, B-839457. Härjedalen, Storsjö, Nedalen, Grävålen, 1950, *O. Mårtensson*; UPS, B-839444. Härjedalen, Storsjö, Nedalen, Predikstolen, 1948, *O. Mårtensson*; UPS, B-839448. Härjedalen, Storsjö, Mt Stor-Axhögen, 2007, *L. Hedenäs*; S, B122918 (together with *M. minutissima*). Jämtland, Snasahögen, Getvalen, 1850, *R. Hartman*; UPS, B-839500. Åsele Lappmark, Vilhelmina, Mt Stikken, 2004, *L. Hedenäs*; S, B100336. Lycksele Lappmark, Tärna, Mt. Atofjället, 2012, *L. Hedenäs et al.*; S, B195278. Pite lappmark, Arjeplog, Mt Stuur-Jiervas, 2017, *L. Hedenäs et al.*; S, B258274 (together with *M. minutissima*). Pite lappmark, Arjeplog, Mt Tjåpkåvárddo, 2017, *L. Hedenäs et al.*; S, B258444. Lule lappmark, Jokkmokk, Tseggok, 1914, *T.Å. Tengwall*; UPS, B-839527. Torne lappmark, Jukkasjärvi socken, Gardertjåkko, 1946, *O. Mårtensson*; UPS, B-839536. Torne Lappmark, Jukkasjärvi, Vässečohka, 2017, *L. Hedenäs*; S, B254968. Torne lappmark, Karesuando, Pältsa, 1948, *O. Mårtensson*; UPS, B-839550.

3. *Meesia minutissima* Hedenäs, sp. nov. Fig. 2C, F, 7, 8

Type: 'Sweden. Pite lappmark, Arjeplog, Mt Stuur-Jiervas, Juosakläpptå, 1000 m a.s.l., 66°85'65.32"N, 16°04'51.76"E, large boulder, 24 Aug 2017, Lars Hedenäs, Göran Odelvik, Martin Westberg' (holo-: S; reg. no. B265765; iso-: B!, BM!)

Diagnosis

Meesia minutissima differs from *Meesia uliginosa* Hedw and *M. minor* Brid. in its smaller size and shorter seta. From *M. uliginosa* it also differs by its acuminate or acute leaves and from *M. minor* in its faintly ornamented exostome outside.

Etymology

The species epithet '*minutissima*' refers to the minute stature of the species.

Plants mostly 2–7 mm tall, green or partly red (especially perichaetial leaves). *Stem* in transverse section round, with well-developed central strand and a cortex of 1–2(3) layers of small and slightly or moderately incrassate cells, outer cell wall mostly thin. *Rhizoids* dark purplish, axillary, strongly branched and forming tomentum in lower stem, papillose. *Axillary hairs* with single, long, upper hyaline cell, 8–14 µm wide, basal 2–3 cells rectangular or longly so, pale red or reddish brown. *Stem leaves* 0.7–1.6 × 0.2–0.3 mm; costa 63–134 and 26–61 µm wide at base and 2/3 up leaf, respectively, ending shortly below or up to 10 cells below leaf apex; leaf apex mostly acuminate or acute, occasionally obtuse; median leaf lamina cells (10.0)12.5–39.5(51.0) × (4.0)5.0–10.5(12.5) µm, (1.1)1.5–6.1(9.9) times as long as wide, short-rectangular to short-linear with square ends, incrassate, eporse; basal cells rectangular to linear, incrassate,

decurrent, alar cells not differentiated. *Synicous and female* plants seen; inner perichaetial leaves 1.2–2.1 × 0.3–0.5 mm, apex pointed acute or obtuse. *Calyptra* cucullate, fugacious. *Seta* 4–17 mm tall; when dry capsule neck 0.3–1.0 mm long, urn 0.6–1.2 × 0.4–0.8 mm, operculum almost dome-shaped or lowly conical, annulus separating; exothelial cells on upper side of capsule (17.0)21.0–67.0(73.0) × (12.5)14.5–34.0(42.0) μm, (0.6)0.8–3.7(4.1) times as long as wide, stomata long-pored, abundant on capsule neck; exostome pale yellowish (when old sometimes brownish yellow), fragmentary, 1/5–1/3 of length of endostome, almost smooth to faintly cross-striolate or obliquely striolate; endostome strongly reduced, basal membrane low or absent, segments split along mid-line, cilia absent or fragmentary, 122–240 μm high, measured from capsule mouth. *Spores* (37.0)38.5–58.0(62.5) μm, finely and densely papillose, often slightly elongate, often with irregular debris on surface.

When well-developed sporophytes are present, this species has a very short seta (4–17 mm) and small capsules (neck 0.3–1.0 mm long, urn 0.6–1.2 × 0.4–0.8 mm) with an almost smooth to faintly striolate exostome outside. The leaf apices are mostly acuminate or acute, which makes it similar to some phenotypes of *M. minor*. However, when the latter has sporophytes the seta is taller [8–37(46) mm], the capsules larger (neck 0.5–1.3 mm long, urn 0.9–1.6 × 0.5–1.1 mm), the exostome outside ornamentation is well developed, and the spores are on the average larger [(46.0)48.0–66.0(69.5) μm versus (37.0)38.5–58.0(62.5) μm].

Habitat and known distribution

This species grows on bare, peaty soil or rocks, or often in rock crevices, in base-rich habitats. It seems to grow in, on the average, somewhat more exposed habitats than *M. minor*. In Scandinavia, it is widespread in the mountains (Fig. 5B), where field observations (Hedenäs unpubl.) suggest that it is much less common than *M. minor*. *Meesia minutissima* is presently only known from Scandinavia, but in view of its widespread habitat it likely occurs also in other mountain regions and in the far north. Because the description of *M. uliginosa* from Arctic North America by Favreau and Brassard (2011) mentions seta lengths from 6 mm it seems likely that their *M. uliginosa* includes *M. minutissima*.

Additional specimens seen (not in Table 1)

Norway. Troms, Bardu, Lake Steinelvatnet, 2008, *L. Hedenäs*; S, B138427. Troms, Bardu, Rubben, 1891, *H.W. Arnell*; UPS, B-839644. **Sweden.** Härjedalen, Storsjö, Helagsfjället, 1913, *H. Smith*; UPS, B-839463. Härjedalen, Storsjö, Jelgatsäive, 1914, *H. Smith*; UPS, B-839441. Härjedalen, Storsjö, Mt Stor-Axhögen, 2007, *L. Hedenäs*; S, B122918 (together with *M. minor*). Jämtland, Åre, Handölsforsen, 1989, *L. Hedenäs*; S, B31486. Pite lappmark, Arjeplog, Mt Stuur-Jiervas, 2017, *L. Hedenäs et al.*; S, B258274 (together with *M. minor*). Lycksele lappmark, Tärna, Långfjället, 1963, *O. Mårtensson*; UPS, B-839516. Lule lappmark, Jokkmokk, Kerkevare, 1946, *O. Mårtensson*; UPS, B-839532. Lule lappmark, Jokkmokk, Sarek, Store Rissbak, 1902, *C. Jensen*; UPS, B-839526. Torne lappmark, Jukkasjärvi, Lake Kratersjön, 2017, *L. Hedenäs*; S, B256566.

Torne lappmark, Jukkasjärvi, Nuolja, 1911, *E. Jäderholm*; UPS, B-839553. Torne lappmark, Jukkasjärvi, Vässečohka, 2017, *L. Hedenäs*; S, B254946. Torne lappmark, Jukkasjärvi, Vässečohka, 2017, *L. Hedenäs*; S, B254947. Torne lappmark, Karesuando, Mt. Pältsa, 1980, *L. Hedenäs*; S, B269527.

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