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Incipient speciation in Scandinavian *Distichium capillaceum* (Distichiaceae, Bryophyta)

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The intraspecific variation of the morphologically variable moss *Distichium capillaceum* is studied based on the nuclear marker ITS (1 and 2) and the plastid markers *rpl*16 and *trn*L-*trn*F for 86 specimens collected mainly in Scandinavia, using *D. inclinatum* as outgroup. A wider specimen set, including GenBank sequences of eight *D. capillaceum* and two *D. hagenii*, was analysed based on ITS only. Since potential reticulation was revealed and significant evidence for recombination was found, network analyses were performed. The ITS analysis revealed *D. hagenii* as more closely related to *D. capillaceum* than to *D. inclinatum*. The analysis based on all molecular markers identified one grade and four lineages in *D. capillaceum*. No lineage received strong molecular support, and morphology could not effectively distinguish the five entities. The grade and four lineages occur in different geographical areas, which were suggested to be a result either of different glacial and postglacial histories or different habitat requirements. The lack of high jacknife support for the lineages in combination with strongly overlapping morphological variation and the geographic differentiation between the entities is interpreted as indicating incipient speciation.

Keywords: *Distichium capillaceum* var. *compactum*, *Distichium capillaceum* var. *curvatum*, NeighborNet split network, sampling effect

Distichium capillaceum (Hedw.) Bruch & Schimp. is a common acrocarpous moss in base-rich to calcareous habitats. The strongly flattened shoots with distichous leaves and the usually present straight and orthotropous capsules make this species easily recognizable. The species is strongly variable in size, how compact its tufts are, leaf length, and in spore capsule length. Tufts growing in humid and shaded or otherwise protected habitats are relatively loose, with leaves up to 4 mm long, whereas tufts in dry and strongly exposed habitats are compact, with leaves sometimes less than 2 mm (Hallingbäck et al. 2006, Flora of North America Editorial Committee 2007, Hedenäs unpubl.). Short-leaved plants forming compact tufts are sometimes recognized as var. *compactum* (Huebener) Dalla Torre & Sarnth. or var. *brevifolium* Bruch & Schimp. (Limpricht 1885–1890, Nyholm 1987). Capsule length varies from around 1 mm to around 2 mm, and this variation is independent of that in the mentioned vegetative features. Tufts with different capsule lengths sometimes grow close to each other, seemingly without intermediate capsule lengths. The capsules are usually straight, but curved or predominantly curved capsules occur in occasional tufts (Limpricht 1885–1890). Such plants can be confused with *D. inclinatum* (Hedw.) Bruch & Schimp. and Flowers (1973) described such plants as var. *curvatum* Flowers. He believed these could have resulted from hybridisation between *D. capillaceum* and *D. inclinatum*.

The occurrence of *D. capillaceum* in widely disparate habitats in combination with its wide morphological variation suggest either 1) strong habitat-related morphological plasticity or 2) so far unrecognized intraspecific diversity or even the presence of morphologically recognizable species. The latter was found in several traditionally circumscribed European moss species that displayed significant morphological variation (Köckinger et al. 2010, Hedenäs 2017, 2020c, Hassel et al. 2018, Hedenäs et al. 2020). Here, I use molecular information in combination with morphological evaluation of revealed molecular entities to find out whether additional species are hidden within *D. capillaceum*. I also discuss implications of the geographical distributions of the found molecular entities.

Material and methods

Study species

The core portion of this study includes 86 samples of *Distichium capillaceum* (Appendix 1). Sixty-nine come from

Sweden, 16 from mainland Norway and one from Svalbard. The samples cover its phenotypic variation in Scandinavia. To explore *Distichium* relationships in a wider context I downloaded internal transcribed spacers 1 and 2 (ITS) sequences from GenBank for eight additional *D. capillaceum* specimens, from mainland Norway (3 samples), Jan Mayen (1), Svalbard (1), Greenland (2) and Antarctica (1), and two sequences of *D. hagenii* Ryan ex H. Philib. The beginnings of the downloaded ITS sequences were less complete than the newly generated ones and they were therefore not included for the sequence length information in the Results. Two specimens of *D. inclinatum* were used as outgroup based on its position as sister to the other two species of the genus in the study by Fedosov et al. (2016).

Molecular methods

Total DNA was extracted using the Mag-Bind Plant DNA Plus 96 Kit (Omega Biotek) with the KingFisher Flex and Duo magnetic particle processors. Double stranded DNA templates were prepared by polymerase chain reaction (PCR). PCR was performed using IllustraTM Hot Start Mix RTG (GE Healthcare) in a 25 µl reaction volume according to the manufacturer's instructions.

In all cases, the specified PCR programs were initiated by a denaturation step of 5 min at 95°C and followed by a final extension period of 8 min at 72°C. The PCR programs were, for ITS and for the plastid *trn*LUAA intron plus *trn*LUAA-*trn*FGAA spacer (*trn*L-*trn*F), 4 cycles of 30 s at 95°C, 40 s at 57°C and 1 min at 72°C, 4 cycles of 30 s at 95°C, 30 s at 55°C and 1 min at 72°C, 35 cycles of 30 s at 95°C, 30 s at 52°C and 1 min at 72°C. The primers 'ITSbryoR' (Hedenäs 2014) and 'ITS4bryo' (Stech 1999) were used to amplify ITS and the primers 'trnC' and 'trnF' (Taberlet et al. 1991) to amplify *trn*L-*trn*F. For the plastid *rpl*16 G2 intron (*rpl*16) the PCR program was 43 cycles of 30 s at 95°C, 40 s at 58°C and 1 min 15 s at 72°C, with the primers 'F71' (Jordan et al. 1996) and 'rpl16-antR2' (Hedenäs 2008).

The amplified PCR products were purified from excess primers and nucleotides by adding 1 µl of Exonuclease I (20 U μl^{-1}) and 4 µl of FastAP Thermosensitive Alkaline Phosphatase (1 U μl^{-1}) (Thermo Scientific) and incubating at 37°C for 30 min followed by an enzyme inactivation step at 80°C for 15 min. The purified PCR products, together with the same primers used for PCR amplification, were subsequently sent to Macrogen Europe B.V for single-stranded sequencing on an Applied Biosystems 3730XL sequencer.

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 16 March 2021). 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 using the simple indel coding of Simmons and Ochoterena (2000) in SeqState (Müller 2005). Gaps provided additional information, and this was included in the analyses. The sequence alignments used in the analyses are available in the Dryad Digital Repository (Hedenäs 2021). GenBank accession numbers are listed in Appendix 1.

ITS paralogues are occasionally encountered in bryophytes (Košnar et al. 2012, Hedenäs et al. 2019). The ITS chromatograms included in this study did not show 'messy' patterns or noise that could suggest paralogy, and the 5.8S gene was invariable among the samples (cf. Shaw et al. 2002, Feliner and Rosselló 2007). Therefore, the revealed ITS variation was interpreted as being among homologous haplotypes.

Potential reticulation was revealed using TCS (Clement et al. 2000) and the phi-test in SplitsTree ver. 4.12.6 (Huson and Bryant 2006) provided statistically significant evidence for recombination ($p = 0.01885$). Relationships among specimens were therefore evaluated in a network context. The relationships were evaluated in NeighborNet (NN) split networks, produced in SplitsTree and in TCS networks, and potential support for lineages in a tree context was tested by jacknife analyses (1000 replications) performed with the program TNT (Goloboff et al. 2003). Two analyses were performed. The first included all specimens for which ITS was available, incorporating the sequences downloaded from GenBank. The second analysis included all three molecular markers and thus only the Scandinavian specimens for which new sequences were generated. Because visual inspection of jacknife results and NN split networks revealed no conflicts between well-supported structures in the nuclear and plastid NN split networks, all sequence data were combined in the second analysis.

The possible existence of molecularly defined groups was also tested for the specimen set with all three markers in the online assemble species by automatic partitioning (ASAP) tool (Puillandre et al. 2021; <https://bioinfo.mnhn.fr/abi/public/asap/>; accessed 17 September 2021), using the default settings. For this analysis, the two samples lacking ITS information (P739, P751) were excluded.

Morphological study and analysis of measurements

After the molecular relationships among the studied *D. capillaceum* specimens had been clarified, the morphology of 3–10 selected specimens from each lineage or grade (from here onwards informally called 'groups') were studied in detail, in total 39 specimens that are indicated with an asterisk (*) in Appendix 1. Both standard comparisons of qualitative and quantitative characters and detailed measurements of selected gametophyte and sporophyte features were performed, employing dissecting and compound microscopes.

For each specimen, detailed gametophyte characters were measured in two stems (to avoid sampling all leaves from an untypical stem). The lengths (mm) and maximal widths (mm) of the basal sheathing and the apical lamina were measured in five leaves from each stem. For three of these leaves (two leaves from one stem and one from the other), length (µm), width (µm) and length to width ratio of 20 cells was measured in the lower portion of the apical lamina and in the basal sheathing lamina. When available, the length (mm) of 20 capsules, length (µm), width (µm) and length to width ratio of 20 exothecial cells from an arbitrarily selected capsule, and the diameter of 20 spores (µm)

were measured. An Olympus SC50 digital camera and the Olympus cellSens Standard ver. 1.13 software for automatic and continuous image stacking were used to produce temporary images of leaves and cells. Measurements were taken from such leaf and cell images, using the Olympus cellSens Standard 1.13 software.

To compare the detailed measurements between the groups within *D. capillaceum* the measurements were first compared in two principal component analyses (PCA) based on 1) the leaf sizes and mean values of the 20 measured cells from the three leaves which cells were measured, in total 117 leaves, and 2) the mean values of the remaining measurements. These analyses show whether the combined information in the sets of ten and ten characters, respectively, correspond with the molecularly identified groups. Corresponding PCA results with the cell length/width ratios excluded were compared with the mentioned ones to explore if these ratios may have put additional weight to the cell size characters. Secondly, the individual characters were compared between the molecularly identified groups. Both the Levene and Brown-Forsythe tests of homogeneity of variance were significant for most characters and plots of residuals in preliminary Anovas showed many deviations from normality. Thus, the nonparametric Kruskal–Wallis Anova by Ranks for multiple comparisons was used to compare the measurements among or between the groups, respectively. All statistical calculations were made in STATISTICA 13.3 (TIBCO-Software-Inc. 2017). Bonferroni corrections were applied in cases of multiple statistical comparisons.

Distribution maps for the identified molecular groups were produced in QGIS ver. 3.16 (<https://qgis.org/en/site/>; accessed 16 March 2021).

Results

Molecular relationships

The total number of aligned ITS sites in the 92 studied *Distichium capillaceum*, two *D. hagenii* and two *D. inclinatum* specimens for which ITS sequences could be generated, after deletion of regions at the beginnings and ends that were incomplete for some specimens, was 762. Of these, 59 sites were variable (32 in *D. capillaceum*), with 35 (14) parsimony-informative; 47 indels were present (22), with 32 (15) informative. For the 86 *D. capillaceum* and two *D. inclinatum* specimens for which *rpl*16 sequences were generated, the length was 647, 37 (11) sites were variable, and 34 (7) were parsimony-informative; 8 (3) indels with 8 (3) informative. For the 86+2 specimens for which *trn*L-*trn*F sequences were generated, the length was 549, 32 (17) sites were variable, and 28 (12) of these were parsimony-informative; 8 (3) indels with 7 (2) informative. Sequence lengths for newly generated sequences of *D. capillaceum* were, for ITS 655–664 (n = 84), for *rpl*16 644–645 (86), and for *trn*L-*trn*F 496–512 (86) and of *D. inclinatum*, for ITS 727–744 (n = 2), for *rpl*16 640 (2) and for *trn*L-*trn*F 516 (2).

In the NN split network based on ITS, a high jacknife support (90–100) was provided for *D. capillaceum* plus *D. hagenii*, and for a branch within group (grade) E (Fig. 1a). The same branches got a high support in the analysis based on all three molecular markers (Fig. 1b), and in addition four other branches within *D. capillaceum* got a moderate support, groups (lineages) C, D, and less inclusive branches within groups B and E. The latter network corresponds with the configuration of the TCS network (Fig. 2). From

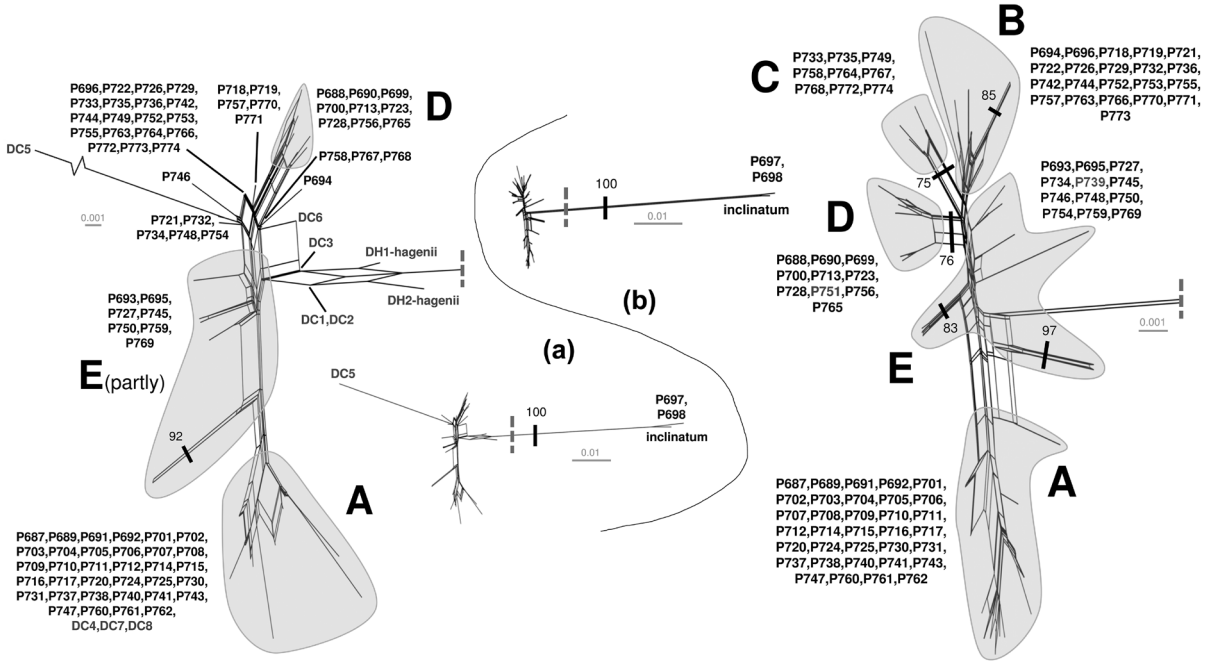

Figure 1. (a) NN split networks based on ITS for *Distichium capillaceum*, using *D. hagenii* and *D. inclinatum* as outgroups. DC and DH numbers in grey represent sequences downloaded from GenBank, see Appendix 1. (b) NN split networks based on ITS, *rpl*16 and *trn*L-*trn*F for *D. capillaceum*, using *D. inclinatum* as outgroup. Grey numbers indicate specimens for which ITS could not be generated. The letters A–E indicate lineages or grades of the network that are discussed in the text (cf. Fig. 2).

the TCS network, it is also evident that within group E and especially groups A and D reticulation seems to occur.

The ASAP analysis based on all three markers suggested that only two statistically supported groups of specimens exist, one including the two *D. inclinatum* samples and one including all *D. capillaceum* samples.

Morphological evaluation

The PCAs based on the detailed measurements of 1) the three selected leaves per specimen and 2) other measured features of *D. capillaceum* suggest considerable morphological overlap between the different groups identified in the NN split networks (Fig. 3a–b). In the first PCA, cell length and cell length/width in the leaf acumen mainly explain the variation along the y-axis, whereas the other characters explain the variation along the x-axis (Fig. 3c). In the second PCA, spore size and exothecial cell width mainly explain the variation along the y-axis, whereas the other characters explain the variation along the x-axis (Fig. 3d). In the corresponding PCAs with the ratios between cell lengths and widths excluded similarly large overlaps

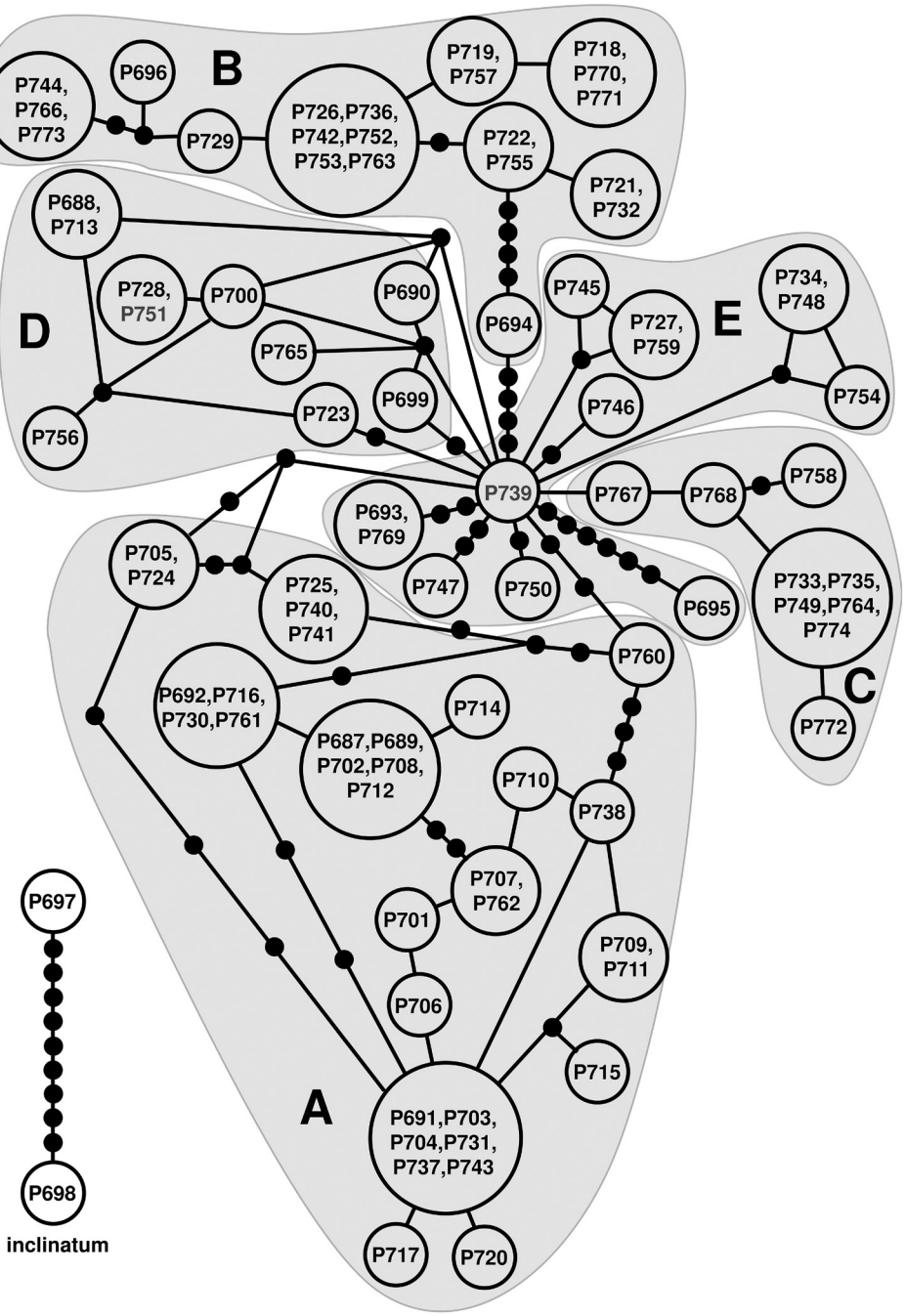

Figure 2. TCS haplotype network on ITS, *rpl*16 and *trn*L-*trn*F for *D. capillaceum*, using *D. inclinatum* as outgroup. Grey numbers indicate specimens for which ITS could not be generated. The letters A–E indicate lineages or grades of the network that are discussed in the text (cf. Fig. 1).

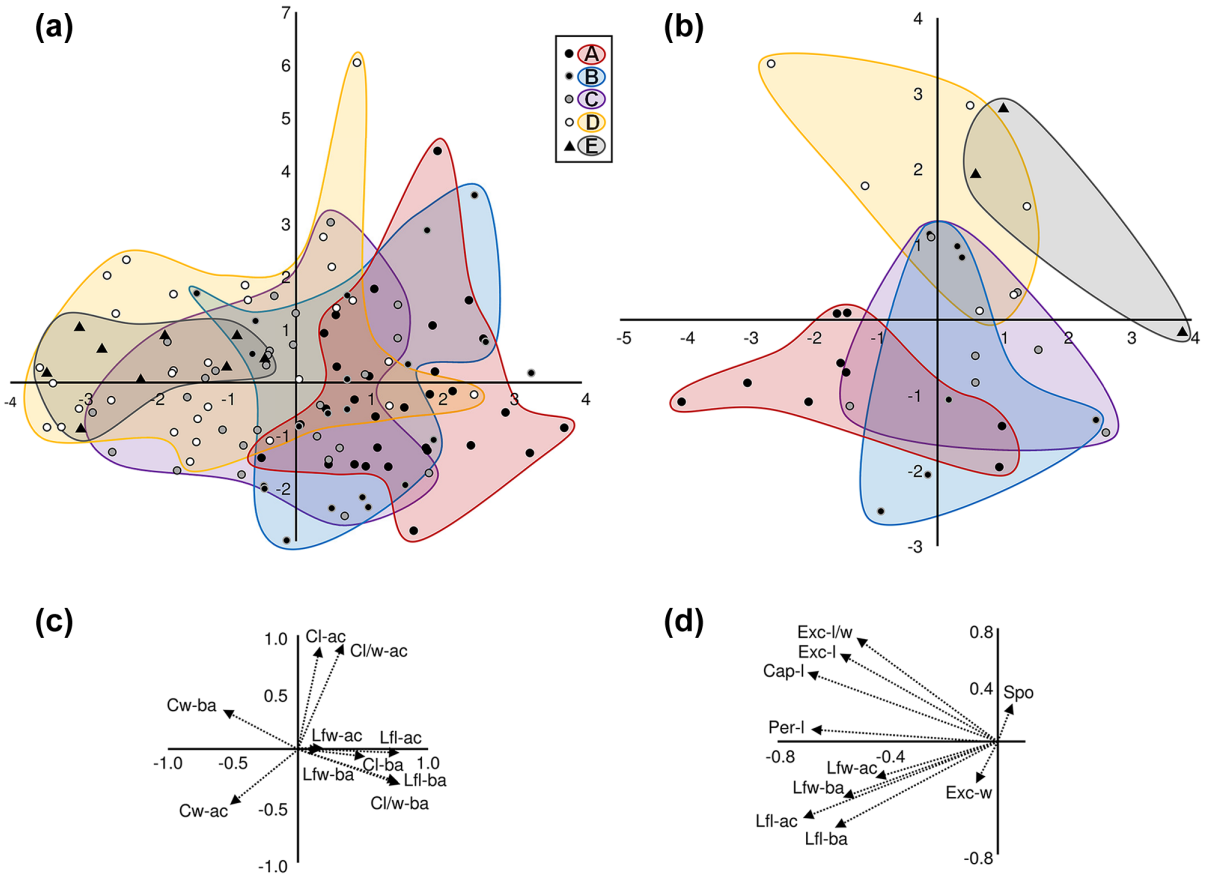

Figure 3. PCAs based on ten specimens (9 in c) of group A, seven (7) of group B, nine (7) of C, ten (6) of D and three of group E (cf. Fig. 1). (a) The positions of three leaves from each specimen based on leaf and leaf lamina cell sizes, along the first two axes in a PCA. Factors 1 and 2 explain 29.25% and 22.11% of the variation, respectively. (c) Explanatory factors in the plane of factors 1 and 2 in (a). This PCA is based on the following, for each leaf: length and width of the leaf acumen (Lfl-ac, Lfw-ac), length and width of the leaf base (Lfl-ba, Lfw-ba), mean cell length, width and length/width ratio for 20 cells in the leaf acumen (Cl-ac, Cw-ac, Cl/w-ac), and mean cell length, width and length/width ratio for 20 cells in the leaf base (Cl-ba, Cw-ba, Cl/w-ba). (c) The positions of specimens based on leaf and sporophyte features, along the first two axes in a PCA. Factors 1 and 2 explain 29.01% and 22.21% of the variation, respectively. (d) Explanatory factors in the plane of factors 1 and 2 in (b). This PCA is based on the following, for each specimen: mean length and width of acumen and base of ten leaves from two shoots (Lfl-ac, Lfw-ac, Lfl-ba, Lfw-ba), mean capsule length based on 20 capsules (Cap-l), and mean exothecial cell length, width and length/width ratio from one arbitrarily selected capsule (Exc-l, Exc-w, Exc-l/w), median length of peristome teeth in two capsules (Per-l) and mean spore size based on 20 spores (Spo).

between the different groups as in Fig. 3a and b were found (not shown).

When individual measured characters are compared between the species, the means differ between some groups in most cases (Table 1, Fig. 4), but again the overlap is great and no pattern that consistently distinguishes one or several groups from the other ones exist. No other characters were found that distinguished either of the groups. Instead, also characters like costa excurrency and roughness, how strongly the ends of meeting leaf lamina cells project, and exostome teeth splits and ornamentation varied strongly within the groups.

Habitat and geographical distribution

No habitat differentiation between the molecular groups of Scandinavian *D. capillaceum* was evident from the label information of the specimens, whereas different geographical distributions were observed (Fig. 5). The mostly southern group A is absent from the northern third of Scandinavia and is rare at higher elevations, except for one GenBank specimen (DC7) collected in northern Norway, whereas the northern group B is absent in the southern third. Groups C and E are primarily found in the mountain range or close to the mountains and group D, finally, was found in the mountains and far north plus the Baltic Sea region.

Discussion

Distichium capillaceum includes five groups, A–E, that were distinguished when all three markers were evaluated together. Based on ITS only, groups A, D, and to some degree E were distinguished, and this marker also suggested that *D. hagenii* is more closely related to *D. capillaceum* than to *D. inclinatum*. A closer relationship between *D. hagenii* and *D. capillaceum* than between *D. hagenii* and *D. inclinatum* was suggested also by *rps*4 and *nad*5, or these markers in combination with *rbc*L (Fedosov et al. 2016). GenBank

Table 1. Means plus standard errors for measurements of *Distichium capillaceum* lineages/grades. Measurements of length and width of leaf acumen and leaf base were from 5+5 leaves from two different shoots per specimen, of 20 lamina cells in leaf acumen and 20 in the sheathing base from 2+1 leaves from two different shoots, lengths of 20 capsules per specimen (if available), of 20 exothecial cells from upper side of one arbitrarily selected capsule per specimen (if available), and of 20 spores per specimen (if available). The number of measurements, n, is indicated in the column to the left of the mean values. Overall significant differences among lineages/grades revealed by the Kruskal–Wallis test are indicated (*), for the Bonferroni corrected p values corresponding with $p < 0.05$. For characters with found overall differences, pair-wise differences are indicated in Fig. 4.

	Lineage/grade										
	A		B		C		D		E		
	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n	Mean (SD)	p
Length of leaf acumen, mm	100	2.6 (0.0)	70	1.8 (0.0)	90	1.4 (0.0)	100	1.2 (0.0)	30	1.0 (0.0)	*
Width of leaf acumen, mm	100	0.2 (0.0)	70	0.1 (0.0)	90	0.2 (0.0)	100	0.2 (0.0)	30	0.1 (0.0)	*
Length of leaf base, mm	100	1.1 (0.0)	70	1.1 (0.0)	90	0.9 (0.0)	100	0.8 (0.0)	30	0.8 (0.0)	*
Width of leaf base, mm	100	0.4 (0.0)	70	0.3 (0.0)	90	0.4 (0.0)	100	0.3 (0.0)	30	0.3 (0.0)	*
Cell length in acumen, µm	600	10.8 (0.1)	420	10.2 (0.2)	540	10.2 (0.1)	600	11.8 (0.1)	180	10.1 (0.2)	*
Cell width in acumen, µm	600	6.1 (0.0)	420	5.9 (0.1)	540	6.2 (0.0)	600	6.7 (0.1)	180	6.1 (0.1)	*
Cell length/width ratio in acumen	600	1.9 (0.0)	420	1.8 (0.0)	540	1.7 (0.0)	600	1.9 (0.0)	180	1.7 (0.0)	n.s.
Cell length in leaf base, µm	600	44.5 (0.5)	420	44.7 (0.1)	540	45.0 (0.4)	600	46.9 (0.5)	180	38.0 (0.8)	*
Cell width in leaf base, µm	600	5.8 (0.0)	420	6.1 (0.1)	540	6.7 (0.1)	600	7.6 (0.1)	180	7.3 (0.1)	*
Cell length/width ratio in leaf base	600	7.9 (0.1)	420	7.6 (2.5)	540	7.0 (0.1)	600	6.4 (0.1)	180	5.4 (0.1)	*
Capsule length, mm	200	1.3 (0.0)	140	1.3 (0.0)	180	1.2 (0.0)	150	1.6 (0.0)	60	1.2 (0.0)	*
Exothecial cell length, µm	200	68.1 (0.8)	140	59.5 (1.1)	180	62.3 (1.0)	160	76.6 (1.4)	60	65.8 (2.5)	*
Exothecial cell width, µm	200	22.5 (0.3)	140	21.7 (0.4)	180	21.8 (0.2)	160	22.7 (0.3)	60	21.2 (0.4)	n.s.
Exothecial cell l/w	200	3.2 (0.1)	140	2.9 (0.1)	180	2.9 (0.1)	160	3.5 (0.1)	60	3.1 (0.1)	*
Spore diameter, µm	180	19.8 (0.2)	140	20.0 (0.2)	140	18.6 (0.2)	120	20.8 (0.2)	60	22.1 (0.3)	*

specimen DC7, from northernmost Norway was labelled as *D. inclinatum*, but clearly belongs in *D. capillaceum* group A. Morphologically, the five groups overlap strongly, but the geographical distributions in Scandinavia differ between several groups.

Molecular and morphological patterns

The ITS-based NN split network included *Distichium* specimens from Scandinavia as well as a few from areas outside this region (Fig. 1a). It shows that even if *D. hagenii* is morphologically most similar to *D. inclinatum* (Hagen 1899–1904, Mönkemeyer 1927, Nyholm 1987, Hallingbäck et al. 2006, Hassel et al. 2013), it is more closely related to *D. capillaceum*. The available molecular information, including that of Fedosov et al. (2016), therefore suggests that *D. inclinatum* is molecularly strongly differentiated from both the other species. Interestingly, four out of eight GenBank specimens of *D. capillaceum*, from Svalbard, Jan Mayen and southern Norway, were situated closest to *D. hagenii* in the network. It seems possible that when every second GenBank specimen of *D. capillaceum* was found in this position, and GenBank specimen DC5 sits on a long branch, this could possibly be due to an artefact. Finally, the northern Norwegian *D. inclinatum* specimen included by Hassel et al. (2013), i.e. DC7 in the present investigation, actually belongs to *D. capillaceum* group A. Thus, the Maximum likelihood tree based on *atp*F-*atp*H in the study by Hassel et al. (2013) includes only *D. capillaceum* and *D. hagenii* and does not provide information regarding the relationships between the three species of the genus.

The five *D. capillaceum* groups identified in the network based on all three markers included lineages A–D that apparently evolved from the grade E (Fig. 1b). Neither lineage received strong jacknife support. Together with the revealed recombination, the suggested reticulation in the TCS network (Fig. 2), and the ASAP results this suggests that the lineages are best understood as within a single species. This was borne out also by the morphological data, which suggested that groups A–E differ only slightly and with strong overlaps between most groups. The PCAs suggested that groups A and D could be distinguished from each other when sporophytes are present, but only sometimes based on the measured leaf characters. The weakly supported molecular lineages and the weak and mostly overlapping morphological differentiation between the five groups suggest early stages in the speciation process, that is, incipient speciation (cf. de Queiroz 2007).

Unlike the situation in other recently investigated and morphologically variable Scandinavian mosses, such as *Meesia uliginosa* Hedw., *Oncophorus wahlenbergii* Brid., *Plagiopus oederi* (Brid.) Limpr., *Racomitrium lanuginosum* (Hedw.) Brid. and *Tomentypnum nitens* (Hedw.) Loeske (Hedenäs 2018, 2020a, b, c, Hedenäs et al. 2020), neither additional cryptic nor morphologically recognizable species are present. Further evidence supporting this is that plants corresponding with the morphological concepts of *D. capillaceum* var. *compactum* and var. *curvatum* were found in more than one of the five groups.

Habitat and geographical distribution

All groups of *D. capillaceum* occur in a variety of base-rich to calcareous habitats in Scandinavia. The plants are highly modifiable, depending on habitat exposure and humidity, and especially small plants in compact tufts from the most exposed sites are striking.

The samples for which new sequences were generated suggest that group A is absent from the northern third of

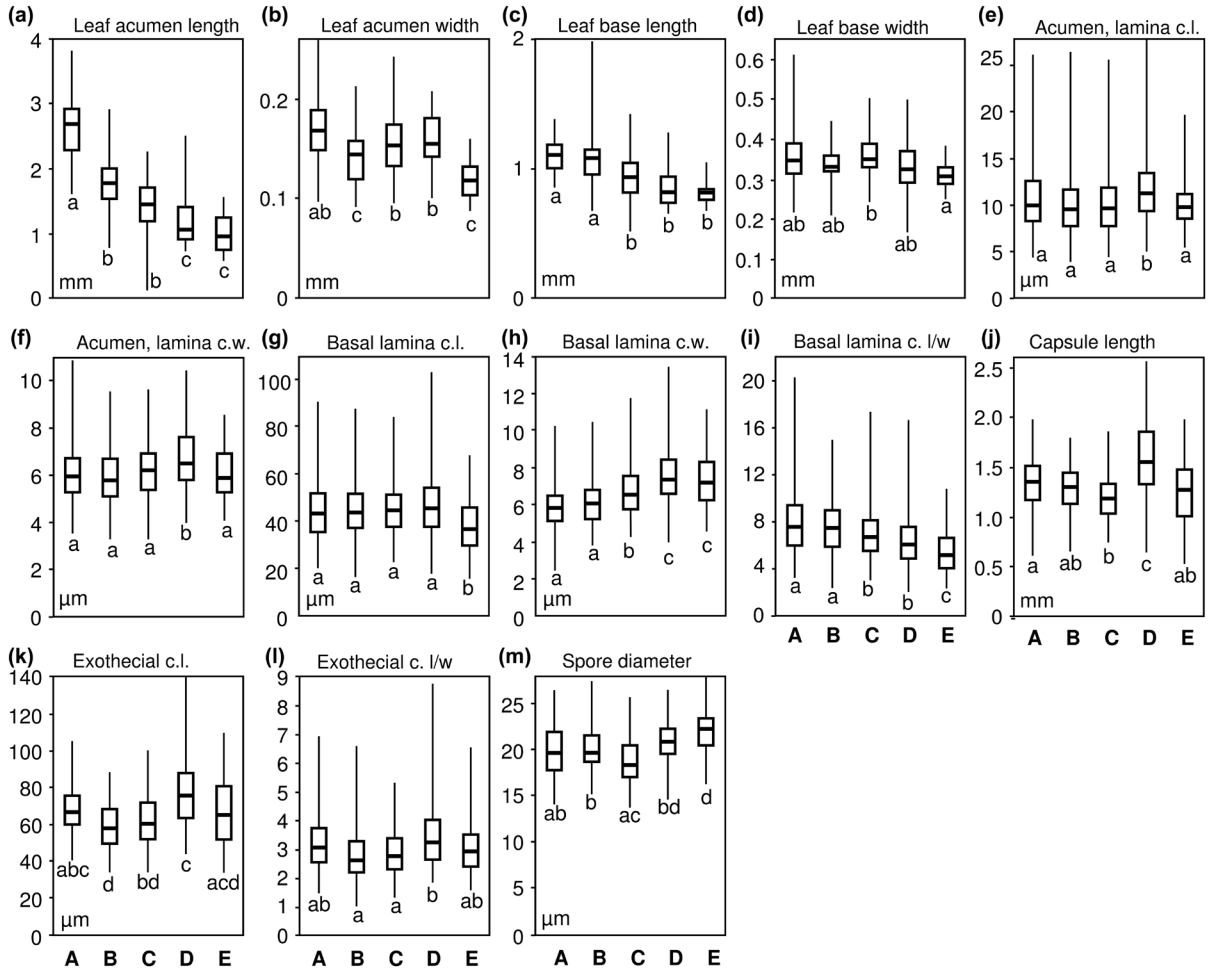

Figure 4. Boxplots with median values, quartiles and whiskers from maximum to minimum values, for measured characters in *Distichium capillaceum* groups A–E (cf. Fig. 1). Only characters where overall significant differences were found among the groups are included (Table 1). Groups with different letters under the lower whiskers differ significantly from each other in pairwise comparisons (Kruskal–Wallis Anova by Ranks). For n, see Table 1.

Scandinavia. However, one GenBank specimen (DC7) collected in northern Norway and included in the ITS network showed that group A occurs at least rarely also further north and underlines that ample sampling is required to correctly interpret geographical ranges. This lends further support to the results of Collart et al. (2021), emphasizing that small samples can be problematic when interpreting and modelling distributions. Among Scandinavian bryophytes this is illustrated also by *Scorpidium cossonii* (Schimp.) Hedenäs. Hedenäs (2009) found its basal haplotypes only in the farthest north of Scandinavia, in the study by Hedenäs (2019) such haplotypes were shown to occur south to southern Lapland in Sweden, and further sampling (Hedenäs, unpubl.) revealed a few occurrences in the Scandinavian mountain range south to Oppland in Norway. Based on GenBank samples, *D. capillaceum* group A occurs also in Antarctica (DC8), thus displaying a bipolar distribution pattern. Whether this group is the only one occurring in the relatively wide Southern Hemisphere distribution area (see map in Ochyra et al. 2008) remains to be investigated. Presently, it seems like groups C and E occur primarily in or near the mountain range and group D, finally, occurs in the mountains and far north plus the Baltic Sea region. The distribution of group D reminds of that found for one plastid lineage of *Syntrichia norvegica* F. Weber (Hedenäs et al. 2019) and for species like *Buckia vaucheri* (Lesq.) D. Ríos, M.T. Gallego & J. Guerra and *Campylium bambergeri* (Schimp.) Hedenäs, Schlesak & D. Quandt (Hedenäs et al. 2014).

The different geographical distributions of the *D. capillaceum* grade and lineages suggest that they survived the last glacial period in different refugia and entered Scandinavia along different post-glacial routes, or that groups C and E are restricted to the mountains and the far north due to lack of adaptations to thrive under milder climates. The distribution seen for group D and genotypes or species with similar distribution patterns could also be due to poor competitive abilities combined with relaxed competition from larger plants both in the mountains and the limestone habitats of the Baltic region (Hedenäs 2014, 2015). As discussed above for GenBank specimen DC7, considering that relatively few specimens were sampled these interpretations are necessarily preliminary.

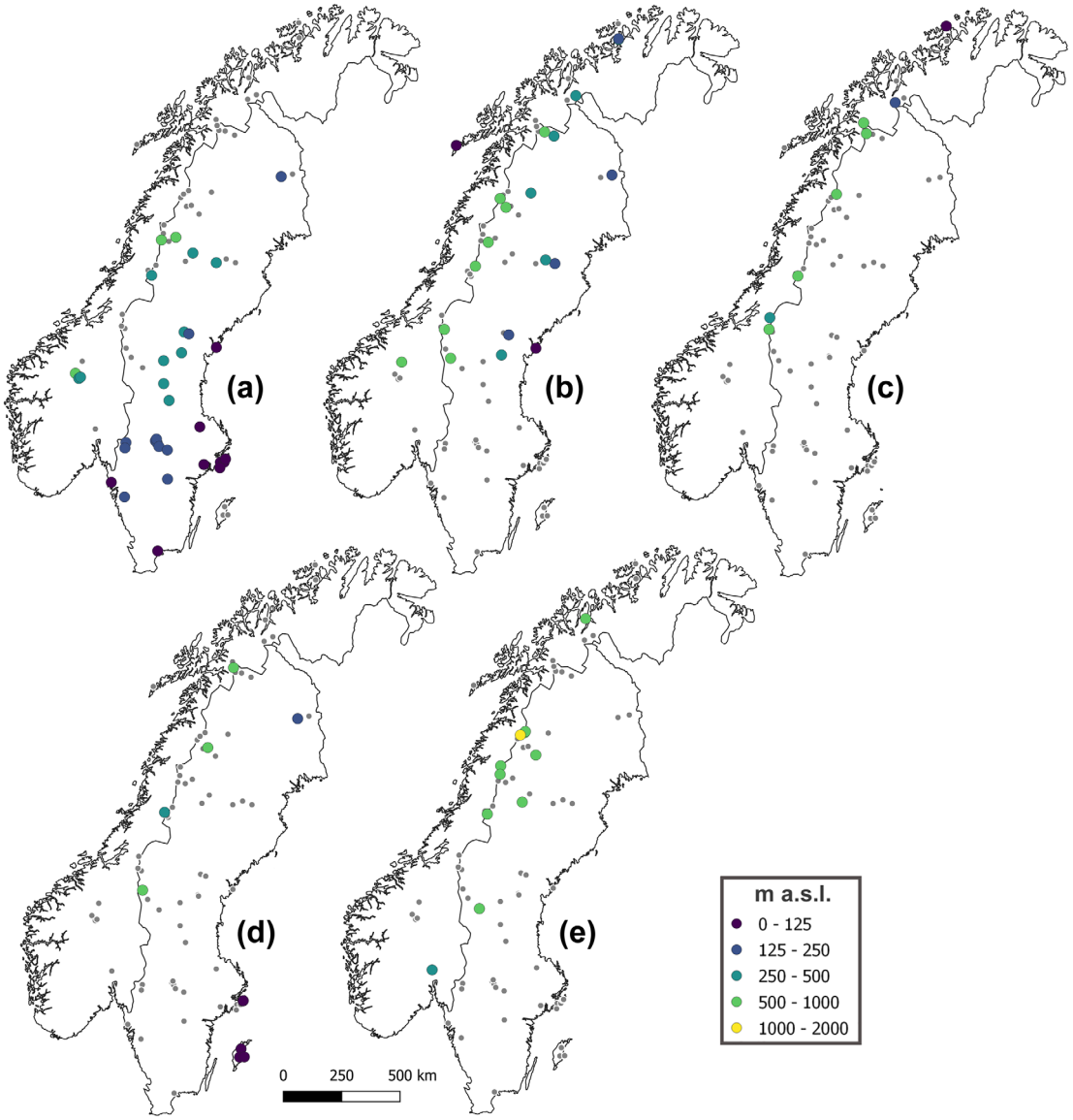

Figure 5. The Scandinavian distributions of specimens belonging to groups A–E (a–e), based on all three molecular markers (Fig. 1). Grey dots indicate the sampling locations, and the larger coloured dots superimposed on these indicate the geographical and elevational distributions of the respective group.

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Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.nvx0k6dtg> (Hedenäs 2021).

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Appendix 1. GenBank accession numbers for the studied ***Distichium capillaceum*** and outgroup specimens. Data format: **Sample No.**: Locality; Collection date, Collector [collector's no.]; Herbarium [Herbarium no.] [only B number = in S]; GenBank accession numbers for ITS, ***rpl***16, and ***trn***L-***trn***F. [NA = not available]. In two samples, two tufts with markedly differing capsule lengths were sampled separately. These are annotated with L (long capsule) and S (short capsule), respectively. Specimens for which selected gametophyte and sporophyte features were measured in detail are indicated with an asterisk (*).

Distichium capillaceum (Hedw.) Bruch & Schimp.:			
P687 (A): Sweden. Skåne. Ivö, Blaksudden; 1990, L.Hedenäs; B144626;	MW969810	MW964202	MW964290
P688 (D*): Sweden. Gotland, Hejnum, Hejnum hällar; 2015, L. Hedenäs; B220561;	MW969811	MW964203	MW964291
P689 (A): Sweden. Södermanland, Dalarö, Vinåkersviken; 2013, L.Hedenäs; B200761;	MW969812	MW964204	MW964292
P690 (D*): Sweden. Uppland, Djurö, Runmarö, Noreträsk; 1996, L.Hedenäs; B281188;	MW969813	MW964205	MW964293
P691 (A*): Sweden. Jämtland, Ragunda, Mt Degerberget; 2014, L. Hedenäs; B205113;	MW969814	MW964206	MW964294
P692 (A): Sweden. Lycksele lappmark, Tärna, L. Åldukejávrrie; 2016, L.Hedenäs; B237890;	MW969815	MW964207	MW964295
P693 (E): Sweden. Pite lappmark, Arjeplog, N of Mávasjávrre; 2015, L.Hedenäs et al.; B223570;	MW969816	MW964208	MW964296
P694 (B): Sweden. Torne lappmark, Jukkasjärvi, SW of Kaisepakte; 2017, L.Hedenäs; B254757;	MW969817	MW964209	MW964297
P695 (E*): Svalbard. Billefjorden, Adolfbukta, River Thomsonelva; 2019, L.Hedenäs & I.Bisang; B290587;	MW969818	MW964210	MW964298
P696 (B): Sweden. Pite lappmark, Arjeplog, Mt Skärrim; 2017, L. Hedenäs et al.; B258077;	MW969819	MW964211	MW964299
P699 (D*): Sweden. Gotland, Buttle, SE of Hägsarve; 2016, L. Hedenäs; B235983;	MW969820	MW964212	MW964300
P700 (D*): Sweden. Gotland, Östergarn, S of Falhammars; 2016, L.Hedenäs; B235937;	MW969821	MW964213	MW964301
P701 (A): Sweden. Västergötland, Skepplanda, Bergsjön; 2017, A. Stansvik AS769; B266108;	MW969822	MW964214	MW964302
P702 (A): Sweden. Bohuslän, Bärfendal, Ilsbacka; 2016, A.Stansvik AS265; B266109;	MW969823	MW964215	MW964303
P703 (A*): Sweden. Östergötland, Motala, Hålberget; 1986, N. Hakelier; B281190;	MW969824	MW964216	MW964304
P704 (A): Sweden. Värmland, Filipstad, Långban; 2010, L.Hedenäs & G.Odelvik; B178583;	MW969825	MW964217	MW964305
P705 (A): Sweden. Värmland, Filipstad, Saxån; 2010, L.Hedenäs & G.Odelvik; B179331;	MW969826	MW964218	MW964306
P706 (A*): Sweden. Värmland, Gåsborn, Mt Hundhallberget; 2010, L.Hedenäs & G.Odelvik; B178597;	MW969827	MW964219	MW964307
P707 (A): Sweden. Västmanland, Grythyttan, Gruvudden; 2010, L. Hedenäs & G.Odelvik; B178562;	MW969828	MW964220	MW964308
P708 (A*): Sweden. Västmanland, Nora, Nedre Bondborn; 2015, L.Hedenäs; B226663;	MW969829	MW964221	MW964309
P709 (A): Sweden. Södermanland, Nämdö, Mörtö; 2012, L.Hedenäs; B193365;	MW969830	MW964222	MW964310
P710 (A): Sweden. Södermanland, Vårdinge, L. Sjundasjön; 1993, L. Hedenäs; B49212;	MW969831	MW964223	MW964311
P711 (A*): Sweden. Södermanland, Utö, Kroka; 2015, L.Hedenäs; B211904;	MW969832	MW964224	MW964312
P712 (A): Sweden. Uppland, Djurö, Storön; 2014, L.Hedenäs; B208345;	MW969833	MW964225	MW964313
P713 (D*): Sweden. Uppland, Djurö, Runmarö, Nore; 2009, L. Hedenäs; B158457;	MW969834	MW964226	MW964314
P714 (A*): Sweden. Dalarna, Ore, Fjäckan; 2018, L.Hedenäs; B288107;	MW969835	MW964227	MW964315
P715 (A): Sweden. Gästrikland, Hedesunda, Gundbo; 2003, G. Odelvik & B.Hellström; B93408;	MW969836	MW964228	MW964316
P716 (A): Sweden. Dalarna, Hamra, Lillhamra, Jordalsberget; 2000, L.Hedenäs; B37587;	MW969837	MW964229	MW964317
P717 (A): Sweden. Medelpad, Borgsjö, Mt. Bergåsen; 2019, L. Hedenäs; B292125;	MW969838	MW964230	MW964318
P718 (B): Sweden. Medelpad, Borgsjö, Rankleven; 1987, L.Hedenäs; B281186;	MW969839	MW964231	MW964319
P719 (B*): Sweden. Ångermanland, Hemsö, Prästhushamn; 2013, L.Hedenäs et al.; B200829;	MW969840	MW964232	MW964320
P720 (A*): Sweden. Ångermanland, Hemsö, Prästhushamn; 2013, L.Hedenäs et al.; B200821;	MW969841	MW964233	MW964321

P721 (B): Sweden. Västerbotten, Norsjö, Mensträsk; 2016, L. Hedenäs & G.Odelvik; B240977;	MW969842	MW964234	MW964322
P722 (B*): Sweden. Norrbotten, Pajala, Isonkivenmaa; 1990, L. Hedenäs & M.Aronsson NT90-121; B7658;	MW969843	MW964235	MW964323
P723 (D*)^{L}: Sweden. Norrbotten, Tärendö, Orjaskursu; 1990, L. Hedenäs & M.Aronsson NT90-733; B281184;	MW969844	MW964236	MW964324
P724 (A*)^{S}: Sweden. Norrbotten, Tärendö, Orjaskursu; 1990, L. Hedenäs & M.Aronsson NT90-733; B281184;	MW969845	MW964237	MW964325
P725 (A): Sweden. Härjedalen, Överhogdal, Frägnhällorna; 2016, L. Hedenäs; B238785;	MW969846	MW964238	MW964326
P726 (B): Sweden. Härjedalen, Tännäs, Mt. Hem-Kröket; 2005, L. Hedenäs; B107832;	MW969847	MW964239	MW964327
P727 (E): Sweden. Härjedalen, Linsell, Glöte; 2007, L.Hedenäs et al.; B121282;	MW969848	MW964240	MW964328
P728 (D*): Sweden. Härjedalen, Tännäs, Mt Ramundberget; 2007, L.Hedenäs; B122838;	MW969849	MW964241	MW964329
P729 (B*): Sweden. Jämtland, Ragunda, Mt Kaststenberget; 2014, L. Hedenäs; B205129;	MW969850	MW964242	MW964330
P730 (A): Sweden. Jämtland, Ragunda, Mt Prästberget; 2014, L. Hedenäs; B205127;	MW969851	MW964243	MW964331
P731 (A*): Sweden. Jämtland, Frostviken, Jormvattnet; 2009, L. Hedenäs; B164643;	MW969852	MW964244	MW964332
P732 (B*): Sweden. Jämtland, Åre, Snasahögarna; 2010, L.Hedenäs; B177239;	MW969853	MW964245	MW964333
P733 (C*): Sweden. Jämtland, Åre, Storlien; 2007, L.Hedenäs; B122292;	MW969854	MW964246	MW964334
P734 (E*): Sweden. Jämtland, Frostviken, Mt Brakkfjället; 2009, L. Hedenäs; B163744;	MW969855	MW964247	MW964335
P735 (C*): Sweden. Jämtland, Frostviken, Mt Brakkfjället; 2009, L. Hedenäs; B163776;	MW969856	MW964248	MW964336
P736 (B): Sweden. Jämtland, Frostviken, Raure; 1988, L.Hedenäs J88-571; B7653;	MW969857	MW964249	MW964337
P737 (A): Sweden. Värmland, Eda, Vittensten; 1983, S.Fransson 1983/532; B106141;	MW969858	MW964250	MW964338
P738 (A): Sweden. Värmland, Älgå, Fallåsen; 1989, S.Fransson 1989/195; B281191;	MW969859	MW964251	MW964339
P739 (E): Sweden. Åsele lappmark, Dorotea, Kalvberget; 1991, L. Hedenäs; B53408;	NA	MW964252	MW964340
P740 (A): Sweden. Lycksele lappmark, Björksele, Bjurbäckliden; 1986, L.Hedenäs; B281181;	MW969860	MW964253	MW964341
P741 (A): Sweden. Lycksele lappmark, Stensele, Strömsundsavan; 2018, L.Hedenäs; B279990;	MW969861	MW964254	MW964342
P742 (B): Sweden. Lycksele lappmark, Malå, Máláge; 2016, L. Hedenäs & G.Odelvik; B239290;	MW969862	MW964255	MW964343
P743 (A): Sweden. Lycksele lappmark, Tärna, L. Åldukejávrrie; 2016, L.Hedenäs; B237716;	MW969863	MW964256	MW964344
P744 (B): Sweden. Lycksele lappmark, Tärna, Tärnamo; 2016, L. Hedenäs; B237699;	MW969864	MW964257	MW964345
P745 (E): Sweden. Lycksele lappmark, Tärna, Mt. Guhkiesvaerie; 2016, L.Hedenäs; B237847;	MW969865	MW964258	MW964346
P746 (E*): Sweden. Lycksele lappmark, Tärna, Mt. Raavriedenjuenie; 2016, L.Hedenäs; B237279;	MW969866	MW964259	MW964347
P747 (E): Sweden. Lycksele lappmark, Tärna, Mt Atofjället; 2012, L. Hedenäs et al.; B195236;	MW969867	MW964260	MW964348
P748 (E): Sweden. Pite lappmark, Arjeplog, Mávasjávrre; 2015, L. Hedenäs et al.; B227366;	MW969868	MW964261	MW964349
P749 (C*): Sweden. Pite lappmark, Arjeplog, Mávasjávrre; 2015, L.Hedenäs et al.; B227587;	MW969869	MW964262	MW964350
P750 (E): Sweden. Pite lappmark, Arjeplog, Jäkkvik; 2006, L. Hedenäs et al.; B113650;	MW969870	MW964263	MW964351
P751 (D*): Sweden. Pite lappmark, Arjeplog, Mt Tjidtják; 2017, L. Hedenäs et al.; B266473;	NA	MW964264	MW964352
P752 (B*): Sweden. Pite lappmark, Arjeplog, Vuoggatjålme; 2017, L. Hedenäs et al.; B258427;	MW969871	MW964265	MW964353
P753 (B): Sweden. Pite lappmark, Arjeplog, Mt. Skärrim; 2017, L. Hedenäs et al.; B264242;	MW969872	MW964266	MW964354
P754 (E): Sweden. Pite lappmark, Arjeplog, Mt Stuor-Jiervas; 2017, L.Hedenäs et al.; B259633;	MW969873	MW964267	MW964355
P755 (B): Sweden. Lule lappmark, Jokkmokk, Kvikkjokk; 1981, L. Hedenäs; B281179;	MW969874	MW964268	MW964356
P756 (D*): Sweden. Torne lappmark, Jukkasjärvi, Ståktjekvarasj; 1983, L.Hedenäs; B269433;	MW969875	MW964269	MW964357

P757 (B*): Sweden. Torne lappmark, Jukkasjärvi, Njulla; 1990, L. Hedenäs; B281174;	MW969876	MW964270	MW964358
P758 (C*): Sweden. Torne lappmark, Jukkasjärvi, Vassijaure; 2017, L.Hedenäs; B254967;	MW969877	MW964271	MW964359
P759 (E): Norway. Oppland, Jevnaker, Svenåa; 1980, L.Hedenäs; B281194;	MW969878	MW964272	MW964360
P760 (A): Norway. Oppland, Dovre, Öyadalen; 2012, L.Hedenäs; B193275;	MW969879	MW964273	MW964361
P761 (A*): Norway. Oppland, Sel, Slettmolykkja; 2012, L.Hedenäs; B193252;	MW969880	MW964274	MW964362
P762 (A): Norway. Oppland, Sel, Formofetten; 2012, L.Hedenäs; B193234;	MW969881	MW964275	MW964363
P763 (B): Norway. Sör-Tröndelag, Mt Dovrefjell, Kongsvold; 2015, B.Axelius 1502; B222025;	MW969882	MW964276	MW964364
P764 (C*): Norway. Nord-Tröndelag, St Olavs Bru; 2000, G.Een & P.Een; B39252;	MW969883	MW964277	MW964365
P765 (D*): Norway. Nord-Trøndelag, Røyrvik, Storøya; 2014, L. Hedenäs; B205280;	MW969884	MW964278	MW964366
P766 (B): Norway. Nordland, Flakstad, Krystad, L. Kvalvikvatnet; 2015, L.Hedenäs; B221801;	MW969885	MW964279	MW964367
P767 (C*)^{L}: Norway. Troms, Bardu, Salangsdalen; 2008, L.Hedenäs; B138734;	MW969886	MW964280	MW964368
P768 (C*)^{S}: Norway. Troms, Bardu, Salangsdalen; 2008, L.Hedenäs; B138734;	MW969887	MW964281	MW964369
P769 (E): Norway. Troms, Lyngen, Mts Kjostindane; 1992, L. Hedenäs; B84942;	MW969888	MW964282	MW964370
P770 (B*): Norway. Finnmark, Söröysund, Seiland; 2001, L.Hedenäs; B63183;	MW969889	MW964283	MW964371
P771 (B): Norway. Finnmark, Söröysund, Seiland; 2001, L.Hedenäs; B63180;	MW969890	MW964284	MW964372
P772 (C*): Norway. Finnmark, Hammerfest, Sørøya; 2010, L. Hedenäs; B176648;	MW969891	MW964285	MW964373
P773 (B): Norway. Troms, Storfjord, Helligskogen; 1992, L.Hedenäs; B281168;	MW969892	MW964286	MW964374
P774 (C*): Norway. Troms, Storfjord, Signaldalen; 1992, L.Hedenäs; B281166;	MW969893	MW964287	MW964375
DC1. Svalbard. Albert I Land, Mitrahalvøya, Willeberget; 1974, A.A.Frisvoll; TRH;	KC333194	NA	NA
DC2. Norway. Sør-Trøndelag, Oppdal, Kongsvold; 1970, A.A.Frisvoll; TRH;	KC333195	NA	NA
DC3. Norway. Sør-Trøndelag, Oppdal, Kongsvold; 1970, A.A.Frisvoll; TRH;	KC333196	NA	NA
DC4. Greenland. Wollaston Foreland, Zackenberg; 2009, K.Hassel & T. Prestø; TRH;	KC333197	NA	NA
DC5. Greenland. Wollaston Foreland, Zackenberg; 2009, K.Hassel & T. Prestø; TRH;	KC333198	NA	NA
DC6. Norway. Jan Mayen, Mohnberget N, Berg; 1972, A.A.Frisvoll; TRH;	KC333199	NA	NA
DC7. Norway. Finnmark, Kautokeino, Virdneguoika; 1983, A.A.Frisvoll; (as D. inclinatum) TRH;	KC333202	NA	NA
DC8. Antarctica. Kerguelen Islands; KRAM B1198/06;	MN179599	NA	NA
Distichium hagenii Ryan ex H. Philib.:			
DH1. Svalbard. Haakon VII Land, Liefdefjorden; 1960, O.Rønning; TRH;	KC333200	NA	NA
DH2. Svalbard. Oscar II Land, Kongsfjorden, Haavimbfjell; 1974, A.A.Frisvoll; TRH;	KC333201	NA	NA
Distichium inclinatum (Hedw.) Bruch & Schimp.:			
P697: Norway. Nord-Trøndelag, Røyrvik, Storøya; 2014, L.Hedenäs; B205291;	MW969894	MW964288	MW964376
P698: Sweden. Södermanland, Utö, Norra Skogen; 2015, L.Hedenäs; B211889;	MW969895	MW964289	MW964377